Production and decay of mangrove (*Avicennia marina* subsp. *australasica*) detritus and its effects on coastal benthic communities

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ABSTRACT

Temperate mangrove forests have been poorly studied compared to their tropical counterparts, because they constitute just 1.4% of the global mangrove forest area. Research from tropical mangrove forests suggests they are open systems that provide a large array of ecosystem goods and services. For example, tropical mangrove forests frequently support invertebrate communities in adjacent habitats through the production, export, decomposition and uptake of organic matter. However, ecological differences between temperate and tropical mangrove forests means that information collected in tropical regions cannot be readily extrapolated to temperate systems. Therefore, it is unclear how, or if, temperate mangrove forests supply an organic subsidy to estuarine ecosystems. Here I investigate the linkages between mangrove organic matter production and the role that decomposing mangrove detritus (dead, broken down organic matter) plays in structuring estuarine benthic communities. Research was conducted at two sites (encompassing small-scale differences in sediment properties and macrofaunal communities) in Whangamata Harbour, New Zealand. The production of mangrove detritus was quantified by measuring litter production and its decomposition into detritus. A manipulative detritus addition experiment explored the role of exported mangrove detritus in structuring benthic communities of unvegetated intertidal flats.

The temperate Whangamata Harbour mangrove forest produced the equivalent of 3.24 - 5.38 t DW ha^{-1} yr^{-1} of litter, which is comparable to forests at similar latitudes and overlaps with the lower range of tropical mangrove productivity. The decomposition rates of litter following summer litterfall were dependent upon the type of litter, as well as the burial state. However, hypotheses that tidal position and site would affect litter degradation rates were not supported. Leaf and wood litter that was buried in the sediment decomposed significantly slower (1.3 - 1.4 times slower) than litter on the sediment surface. Leaf litter decomposition was faster (63 days to decay by 50%) than wood and root material (460 and 316 days, respectively). Decay models predicted that wood and root material will take years to breakdown, which has implications for New Zealand

mangrove removal plans, where wood and roots often remain *in situ* (following clearances). Finally, a manipulative detrital addition experiment found that mangrove detritus created subtle changes in the relative abundances of a few dominant taxa, rather than shifts in whole community species composition. Communities responded similarly to the addition of mangrove detritus, with the same dominant taxa responding at both experimental sites. The subtle benthic community responses to the large amount of detritus added suggests that mangrove detritus plays a relatively minor role in shaping communities on temperate intertidal flats. The studies that comprise this thesis have together shown that as a result of different input and decomposition rates of mangrove litter, temperate estuarine benthic communities are probably less reliant on mangrove productivity than tropical communities.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 Introduction

Mangroves are terrestrial angiosperms that have adapted to grow along the terrestrial-marine boundary in sheltered, low flow environments such as estuaries and coastal lagoons (Kathiresan 2005). Mangrove trees have adaptations that enable them to grow under the variable conditions of coastal intertidal environments, with fluctuations in salinity, temperature and tidal inundation period (Saenger 2002; Tomlinson 1986). Mangrove forests can often dominate the intertidal zone (between high and low tide) in estuaries and lagoons; however in some regions they are found to grow subtidally (Lugo & Snedaker 1974). Globally, mangrove forests are distributed between the equator and latitudes of 32º north and 38º south (de Lange & de Lange 1994; reviewed by Morrisey et al. 2010). Their global distribution is thought to be limited by a number of factors including climate, temperature (frost tolerance) and dispersal capabilities (de Lange & de Lange 1994; Saenger 2002). Mangrove forests in tropical and sub-tropical regions (< 30º N and S) are often comprised of up to six tree species (in a single forest) and can grow up to 30 – 40 m in height (Hutchings & Recher 1983; Tomlinson 1986). However, temperate forests (> 30º N and S) often contain only one tree species (max. 3 species), and at higher latitudes are commonly less than 2 m in height (reviewed by Morrisey et al. 2010).

In the tropical regions, important ecosystem services are provided by mangroves both within the forest and to the wider coastal environment (Alongi 1990; Alongi et al. 1989; Jennerjahn & Ittekkot 2002; Lugo & Snedaker 1974; Odum & Heald 1975; Sheaves & Molony 2000). For instance, tropical mangroves provide important habitat services, where a rich diversity of fauna (both terrestrial and aquatic) reside in the complex habitat structures of the forests (Hutchings & Recher 1983; Nagelkerken et al. 2008; Snedaker 1978). Mangrove habitats are also an essential spawning and rearing ground for fish, resulting in connectivity between mangrove forests and other coastal habitats (Beck et al. 2001; Collette

1983; Laegdsgaard & Johnson 2001; Snedaker 1978). Mangroves can provide physical services, which protect coastlines by trapping terrestrial sediments and contaminants, as well as preventing coastal erosion (Kathiresan & Rajendran 2005; Mazda et al. 1997; Othman 1994; Victor et al. 2004). Tropical mangrove forests are also important in supplying dissolved nutrients to coastal waters, which can sustain and enhance microbial productivity (Alongi 1996; Dittmar & Lara 2001; Wafar et al. 1997). The contribution of mangrove litter to coastal primary productivity and its subsequent uptake by organisms represents another important ecological service of tropical mangrove forests (e.g. Demopoulos et al. 2007; Granek et al. 2009; Guest et al. 2006; Nordhaus & Wolff 2007; Sheaves & Molony 2000; Werry & Lee 2005).

Early research stated that mangrove forests are highly productive ecosystems that provide a valuable spatial subsidy to surrounding coastal habitats, and four points of evidence were put forward in support of this (Odum & Heald 1975). First, mangrove forests produce large amounts of organic material. Second, mangroves are highly valuable to surrounding ecosystems due to the export of organic matter from the forest to neighbouring coastal waters. Third, organic material decomposes into detritus (dead, broken down organic matter), via a microbial pathway, which is available to consumers. Fourth, exported mangrove detritus is assimilated into estuarine food webs (concepts are depicted in Figure 1.1; Odum & Heald 1975). Numerous examples found in the recent literature have confirmed that tropical mangrove forests often act as important spatial subsidies to adjacent marine habitats, where organic matter is exported across habitat boundaries and utilised by marine organisms (e.g. Guest et al. 2006; Granek et al. 2009; Werry & Lee 2005). In the tropical regions, mangrove organic matter can support invertebrates located as far as 10 km away from the forest (Granek et al. 2009). While the export and uptake of mangrove organic matter often applies in tropical regions, it remains unknown if mangrove forests at temperate latitudes adhere to the above criteria.

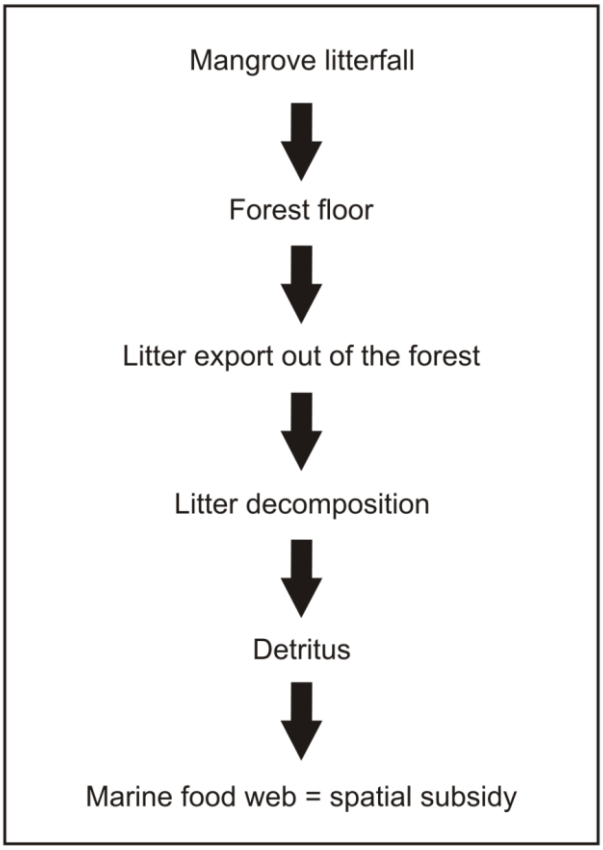

Figure 1.1. Schematic diagram showing the potential linkages between mangrove organic matter production and adjacent coastal ecosystems, based on concepts in the reviewed literature of tropical mangrove forests (e.g. Odum & Heald 1975).

Temperate mangrove forests constitute only 1.4% of the global mangrove area and literature surrounding their ecological functions is lacking (Twilley et al. 1992). While tropical mangroves can produce up to 18 t ha^{-1} yr^{-1} (dry weight) of litter, temperate forests are generally less productive and the tree species diversity of temperate forests is often limited to a single species (Ellison 2002; Saenger & Snedaker 1993). While tropical forests can be productive throughout the year, the organic matter production of temperate forests is commonly limited to the summer months (Duke 1990; Goulter & Allaway 1979; May 1999; Twilley et al. 1986; Woodroffe 1985). When compared to tropical regions, temperate mangroves house a lower diversity of fauna and this could be due to the lower habitat complexity of temperate forests (Alfaro 2006). Ecological differences between regions mean that temperate mangrove forests are likely to function differently to their tropical counterparts with regard to the ecosystem services that they provide. The presumption that temperate mangrove systems may lack the

ecological integrity of tropical systems has influenced the conservation management of temperate coastal regions (Harty 2009; Morrisey et al. 2007; Park 2004).

Differences in the seasonality and quantity of organic matter production between tropical and temperate forests mean that the linkages depicted in Figure 1.1 are likely to be different between the regions. Tropical forests can produce large quantities of litter throughout the year (Duke 1990; Saenger & Snedaker 1993). This large litter contribution to coastal regions in the tropics drives communities that are adapted and reliant on mangrove litter as a food source (e.g. Granek et al. 2009; Sheaves & Molony 2000). In addition, many tropical habitats such as coral reefs are often nutrient limited, and mangrove detritus provides an important food source that supports coastal food webs (Granek et al. 2009; Lapointe et al. 1987; Sheaves & Molony 2000; Werry & Lee 2005). However, the lower productivity and strong seasonality measured in temperate regions (Duke 1990; Morrisey et al. 2010; Saenger & Snedaker 1993) could suggest that these linkages (Figure 1.1) will be weaker, because communities may be adapted to utilising other primary production sources. This presumption is currently unknown and research on temperate systems is required to determine the ecological role of mangroves.

In order to determine if there are linkages (Figure 1.1) between mangrove productivity and nearby faunal communities in temperate regions, it is necessary to examine a number of site-specific aspects of temperate forest dynamics. The first step to identifying such linkages is to quantify the supply of organic matter produced by the mangrove forest (Mangrove litterfall → Forest floor → Litter export out of the forest; Figure 1.1). The amount of litter produced by the forest is an accepted measure of forest productivity, as it is an important component in determining the contribution of organic matter from a forest to an estuary (Snedaker 1978). Secondly, the decomposition of mangrove litter into detritus is an important step that links forests and adjacent marine habitats (Litter export out of the forest → Decomposition → Detritus; Figure 1.1; Odum & Heald 1975). Fresh mangrove litter is a poor quality food resource and the decomposition process turns litter into a palatable biologically available form (detritus) (Fell et al. 1984; Odum & Heald 1972; Nordhaus et al. 2011; Robertson 1988). Therefore, it

is important to determine the factors that affect decomposition rates of litter to establish the flow of energy between mangrove forests and nearby coastal habitats. Thirdly, in order to determine the ecological services that temperate mangroves provide to coastal systems, it is essential to explore whether exported detritus represents a subsidy of organic matter to nearby coastal habitats (Detritus → Marine food web = spatial subsidy; Figure 1.1). One way of doing this is to identify the role that mangrove detrital deposition plays in structuring communities in habitats outside of the forest (Bishop & Kelaher 2008; Bishop et al. 2010; Kelaher & Levinton 2003). Such investigations are limited in a temperate setting and therefore the ecological roles of temperate mangrove forests in coastal ecosystem functioning remain unknown.

Mangroves (*Avicennia marina* (Forsk.) Vierh subsp. *australasica* (Walp.) J. Everett) have inhabited New Zealand for around 19 million years, preceding human arrival (Morrisey et al. 2007; Sutherland 2003). Consequently, *Avicennia marina* subsp. *australasica* is classified as an indigenous species of New Zealand and is protected under the New Zealand Coastal Policy (Harty 2009; Morrisey et al. 2007). *A. marina* is abundant in estuaries of the northern North Island and has a southern limit of Ohiwa Harbour on the east coast and Kawhia Harbour on the west coast. Ohiwa Harbour represents the second southern-most natural population of mangroves in the world (de Lange & de Lange 1994). New Zealand has seen a significant expansion of *A. marina* forests since urbanisation, deforestation and agriculture intensified in the 1940s. Such changes in catchment land-use have led to increased sedimentation and nutrient runoff, and as a result mangrove forests have expanded (Basheer 2007; Harty 2009; Morrisey et al. 2007; Park 2004; Singleton 2007).

Local communities that surround estuaries often consider mangroves a nuisance because they block estuarine views and access ways (Basheer 2007). Mangroves have been termed "invasive pest plants" (personal communication with a member of the public) and "troublesome mangroves" (Cousins 2010, Bay of Plenty Times), that are thought to be aesthetically displeasing. Some communities are anxious that mangrove trees will eventually encroach harbours and invade other important estuarine habitats (Basheer 2007; Harty 2007). As a result of the rapid expansions and the opinions expressed by local community

groups, decisions to remove and control mangroves now prevail. Control of mangrove expansion has included plans to remove seedling colonists and/or adult trees (Harty 2009). However, the ecological impact of the disturbance involved during clearances has recently been debated in the media (Morton 2011, Bay of Plenty Times). The impact of mangrove clearances remains largely unknown due to a lack of knowledge of the ecological services that temperate mangrove systems provide.

1.2 Thesis outline

This thesis addresses a gap in temperate mangrove ecological research and attempts to determine the linkages between mangrove organic matter and the ecosystem functioning of benthic estuarine communities. The thesis aimed to determine if the linkages depicted in Figure 1.1 apply in temperate mangrove ecosystems. Chapter 2 examines the supply of organic matter (in the form of litter) from a temperate mangrove forest to the estuary, to determine seasonal variability of organic matter inputs. This chapter also explores the decomposition rates of different litter types into detritus, which is then potentially available for the incorporation into the marine food web. In addition, measuring the decomposition of mangrove wood and root litter allows an estimation of the recovery time following a mangrove clearance (where wood and roots are left *in situ* following clearances). Chapter 3 attempts to investigate the role that mangrove detrital inputs play in shaping estuarine benthic communities on unvegetated intertidal flats; where the deposition of exported litter from the forest could drive community variability in soft-sediment habitats. Chapter 4 summarises the experimental results that inform and provide recommendations for future ecological research of temperate mangrove habitats. Overall, this research follows mangrove litter from when it falls from the tree, through the decomposition process into detritus, and finally explores the role of detritus in structuring benthic communities on unvegetated intertidal flats; where mangrove detrital material potentially provides an important source of primary production and thus a spatial subsidy.

Chapters 2 and 3 are structured as stand-alone papers that can be read on their own or as part of this thesis.

CHAPTER TWO

THE PRODUCTION OF MANGROVE DETRITUS: THROUGH LITTERFALL AND DECOMPOSITION IN A TEMPERATE NEW ZEALAND ESTUARY

2.1 Introduction

Tropical mangrove forests have been well represented in the literature, which has shown that these systems are both ecologically important and highly productive (e.g. Granek et al. 2009; Lugo & Snedaker 1974; Odum & Heald 1975; Saenger & Snedaker 1993). In tropical regions, mangrove forests act as spatial subsidies that support widespread coastal systems, through the production, export and decomposition of organic matter that can be incorporated by marine food webs (Granek et al. 2009; Lugo & Snedaker 1974; Odum & Heald 1975; Sheaves & Molony 2000). However, temperate mangrove forests (latitudes greater than 30º N and S), constitute only 1.4% of the world's mangrove areas and have received less attention in the literature (reviewed by Morrisey et al. 2010; Twilley et al. 1992). Temperate mangroves differ from their tropical counterparts given that they are generally less productive (lower litter production) and tree species diversity is low (often monoculture forests) (Ellison 2002; reviewed by Morrisey et al. 2010; Saenger & Snedaker 1993). Such differences mean that any ecological information gathered in tropical regions cannot be applied to temperate mangrove systems. Therefore, there is little understanding of the role that temperate mangroves play in supporting nearby coastal habitats through the supply of organic matter. It is presumed that the importance of mangrove organic matter as a source of primary production in temperate coastal systems could be less than in tropical regions because production in temperate forests is often relatively low.

The flow of energy between mangrove forests and surrounding coastal habitats requires two stages. First, the production of organic matter from litterfall and second the degradation of this organic matter into detritus (dead, broken down organic matter; a form biologically available to benthic consumers) (Odum & Heald 1975; Rice & Tenore 1981; Robertson 1988; Snedaker 1978; Wafar et al.

1997). International research has quantified primary production of mangrove forests by measuring organic matter input into estuaries (reviewed by Morrisey et al. 2010). The amount of organic matter produced by a mangrove forest in the form of litter fall is a widely accepted measure of its productivity (Snedaker 1978). While litter fall measurements do not measure the increase in plant biomass, they are regarded as an important component of primary productivity in determining organic matter contribution to the estuary (Snedaker 1978; Woodroffe 1982). A clear global trend has been established and shows that net primary production and tree height, decrease with increasing latitude (Harty 2009; Twilley et al. 1992; Saenger & Snedaker 1993). In order to understand the role that mangroves play in ecosystem functioning and estuarine energy dynamics, it is essential to determine the site-specific input of mangrove organic matter into the estuarine system.

The decomposition of mangrove leaf litter into detritus, via microbial breakdown, is an important pathway for organic matter entering the marine food web, both within the forest and in surrounding habitats (Odum & Heald 1975; Moran et al. 1991; Robertson 1988; Snedaker 1978; Steinke et al. 1990; Steinke & Charles 1986; Werry & Lee 2005). Fresh mangrove leaf litter contains high concentrations of tannins that are unpalatable to most benthic marine invertebrates. Litter decay turns unpalatable litter into detritus that is available for consumption by benthic consumers (Fell et al. 1984; Odum & Heald 1972; Nordhaus et al. 2011; Robertson 1988). Therefore, the decomposition rate of leaf material into detritus potentially governs the rate that mangrove primary production can be utilized by benthic consumers (Fell et al. 1984; Fourqurean & Schrlau 2003; Nordhaus et al. 2011).

Latitudinal patterns in mangrove leaf degradation have found that rates of litter weight loss decrease with increasing latitude (Mackey & Smail 1996). Rates are influenced by meteorological variables such as rainfall, humidity, temperature, salinity and solar radiation; therefore decomposition rates are likely to be highly site-specific (Dick & Osunkoya 2000; Imgraben & Dittmann 2008; Sánchéz-Andres et al. 2010; Steinke & Charles 1986). In addition, small-scale local environmental variability, such as tidal submergence times, sediment properties and macrofaunal community (i.e. grazing and shredding fauna), often play a key role in litter decomposition (Dick & Osunkoya 2000; Holmer & Olsen 2002;

Oñate-Pacalioga 2005; Proffitt & Devlin 2005; Robertson 1988; Werry & Lee 2005). Therefore, decomposition rates are expected to be dependent on the destination of the fallen litter, which will determine the conditions that the litter might be exposed to during decomposition. Degradation rates can be faster in areas of greater tidal submergence (e.g. Dick & Osunkoya 2000; Robertson 1988). Consequently, mangrove litter that is exported from the forest may decompose relatively quickly. Conversely, litter that is retained within the forest is often buried due to sedimentation (per. obs.). In a tropical forest, buried litter showed different elemental dynamics during decomposition (compared to surface degradation), which reflected differences in the decay process (Fourqurean & Schrlau 2003). Although it is expected that anoxic decomposition will be slow, it is unclear how the anoxic conditions of burial will affect the rate of litter decay within the forest. Currently, research of anoxic mangrove litter decomposition has been limited to root material in a temperate setting (van der Valk & Attiwill 1984; Albright 1976).

The temperate mangroves of New Zealand have received little attention in relation to ecological research. The quantification of mangrove productivity in temperate New Zealand has been limited (May 1999; Oñate-Pacalioga 2005; Woodroffe 1985; Woodroffe 1982), and litter decomposition experiments have been restricted to the Auckland region (Albright 1976; Oñate-Pacalioga 2005; Woodroffe 1982). New Zealand studies have focused on leaf decay, with only one study exploring root degradation (Albright 1976). In order to determine the rate of organic matter incorporation into the estuarine detrital pool (and potentially the food web), it is necessary to estimate the site-specific production of litterfall and rates of mangrove litter decomposition. Recent expansion in the distribution of New Zealand mangroves has resulted in decisions to remove them from many North Island estuaries (Basheer 2007; Singleton 2007; Harty 2009; Park 2004). The decay rate of root and wood material will govern the rate of recovery after mangrove clearances (where wood and root matter is left *in situ*), and therefore this research is important for New Zealand coastal management.

This study makes a contribution to the relatively limited information available on the production of mangrove detritus (through both litterfall and decomposition) in a temperate situation. The study firstly quantifies forest

productivity in both mature and newly established regions of a forest. Secondly, decomposition rates of mangrove leaf, wood and root material at different tidal positions and burial states are determined. Although previous temperate experiments have quantified litterfall and decomposition, this study is the first to incorporate, in one study, the decomposition of all three litter types (leaf, wood and root) as well as the effect of tidal position and burial state. In addition, the study tested whether small-scale environmental variability of a site (observed differences in sediment characteristics and benthic community structure) affect litter decomposition rates. Leaf carbon and nitrogen dynamics were measured in order to determine differences in the decomposition process between different sites, burial states and tidal positions. Carbon and nitrogen dynamics are also useful to determine changes in the nutritional value of leaf litter to consumers. My study tests the hypothesis that litter decomposition rates will vary with tidal position, burial state and local small-scale site conditions. Therefore, it is expected that the rate of litter decay will be dependent upon the destination of the litter once it has fallen from the forest. The fall of litter and its decomposition into detritus is an important step that potentially links mangrove forests with adjacent habitats, where mangrove litter may provide a spatial subsidy.

2.2 Methodology

2.2.1 Study site

The study was conducted in the northern region of Whangamata Harbour, located in the North Island of New Zealand (Figure 2.1). The New Zealand endemic mangrove *Avicennia marina* subsp. *australasica* is abundant throughout the harbour and covers an area of 101 ha (approximately 25% of the harbour area; Singleton 2007). Since the 1940s mangroves in the harbour have increased in extent from 31 ha to 101 ha, largely as a result of human urban development (Singleton 2007). The northern harbour exhibits a gradient between sand and mud sediments and therefore two study sites were chosen to encompass differences in small-scale variability (i.e. changes in the observable sediment properties and macrofaunal communities). Site 1 (sand; S 37º 10’ 43.4”, E 175º 51’ 37.4”) was located approximately 40 - 50 m from the adjacent Site 2 (muddy sand; S 37º 10’ 39.9”, E 175º 51’ 36.8”) (Figure 2.1).

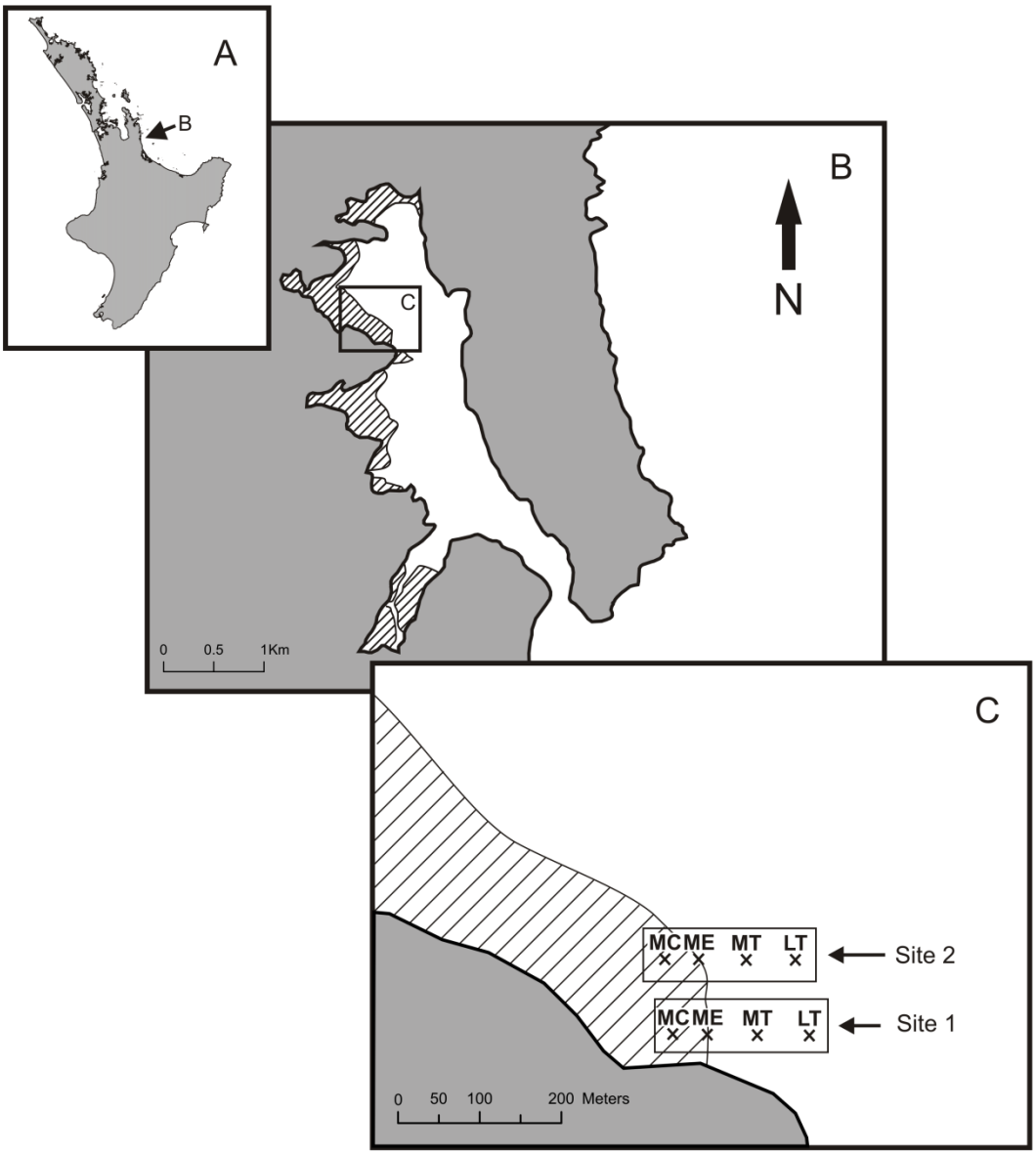

Figure 2.1. (A) North Island of New Zealand and (B) Whangamata Harbour, with (C) study sites and positions of decomposition bag deployments marked. Site descriptors: mangrove canopy (MC), mangrove edge (ME), mid-tide (MT), low-tide (LT). Hatched areas indicate areas of mangrove forest.

Sediment properties and macrofaunal community were measured at the mid-tide level at each site, but not throughout the whole site. At the mid-tidal position, macrofaunal community structure was significantly different between the two sites, driven primarily by differences in the relative abundances of some species. Sediment properties also varied; Site 1 had a mean mud content (silt/clay fraction, particles < 63 µm) of 14.4% and a median grain size of 197.6 µm, whereas Site 2 had a mean mud content of 29.9% and a median grain size of 130.8 µm (see Chapter 3 results). The mean monthly air temperature in Whangamata Harbour ranged from 10 - 23 ºC throughout the experimental period. Tree heights 40 m within the mangrove forest ranged from 1.5 - 3 m, and on the edge of the forest trees were 1.2 - 1.9 m in height. Mean tree density (>1 m height) within the mangrove forest was 14 (± 3; SE) trees per 100 m² and 7 (± 1; SE) trees per 100 m² on the edge of the mangrove forest.

2.2.2 Mangrove litterfall

Measurements of litter fall were made by using litter traps placed under the mangrove canopy. Litter traps were constructed using nylon shade cloth with 2 mm mesh, consistent with previous studies (e.g. May 1999; Woodroffe 1985; Woodroffe 1982). Traps were conical (0.5 m depth), with a 0.25 m² opening that tapered to a 0.06 m² base and were designed to minimise litter loss (Brown 1984). Twelve replicate traps (3 m² sample area) were randomly positioned under the mangrove trees at the edge of the mangrove forest (herein referred to as 'edge'), as well as 40 m within the mangrove forest (herein referred to as 'within'). Traps were randomly distributed across the mangrove forest to encompass both Sites 1 and 2 (Figure 2.1). Trap openings were placed above the high tide water level to minimise litter loss during tidal inundation. Litter traps were sampled at monthly intervals beginning in February 2011 and ending in January 2012. Monthly collection intervals aimed to minimise litter decomposition between sampling dates. Mangrove litter samples were rinsed with freshwater over a 500 µm sieve to remove any sediment and salt from the surface and then dried to constant weight at 60 ºC. The litter was separated into leaf, wood, fruit/seed and infloresences (reproductive flower parts). Dry weight (DW) of litter was used to estimate annual litterfall of the mangrove forest in Whangamata Harbour, as this is comparable to litterfall estimates in the literature.

2.2.3 Mangrove litter decomposition into detritus

The decomposition rates of mangrove wood, root (pneumatophores) and leaf litter were measured at each site in Whangamata Harbour (Sites 1 and 2; Figure 2.1). Decomposition rates were measured using litter bags (16 cm x 16 cm) made from 2 mm mesh nylon shade cloth (as in Woodroffe 1982). The 2 mm mesh size allowed small invertebrates access to the decomposing litter, although excluded larger macrofauna. The litter bag method has been criticised for excluding macro-invertebrates, which may aid in the breakdown of litter into detritus (Fell et al. 1984). However, in a temperate intertidal study, no significant difference in litter decay rate was found when using both litter bags that allowed entry of macro-invertebrates and bags that excluded them (Goulter & Allaway 1979).

The litter decomposition experiment began in summer (January 2011), to coincide with the time period when the majority of mangrove litter is produced (May 1999; Woodroffe 1982). Yellow senescent leaves were collected from mangrove trees at Whangamata Harbour, by selecting and picking leaves that detached easily (i.e. leaves that were ready to abscise) (Robertson 1988). Yellow senescent leaves were chosen as opposed to green leaves, in an attempt to simulate natural leaf fall and subsequent decomposition. Wood material with a branch diameter of 5 to 10 mm was collected from trees. Root matter was collected and fibrous root mass was removed from pneumatophores (only pneumatophores were used in this study). The leaf, wood and root material were rinsed under freshwater to remove sediment and salt, and then allowed to air dry for 48 hours, at constant temperature and humidity, in an air conditioned laboratory. The air dried leaves, root and wood material were then weighed into subsamples (5 g leaves, 4 g roots, 7 g wood) and placed into the decomposition bags. To determine initial dry weight, twenty sub-samples of each litter type were dried at 60 ºC to constant weight.

At each site the decomposition bags were placed at four tidal positions (Figure 2.1): low-tide (LT), mid-tide (MT), mangrove edge (pneumatophore zone with no canopy cover; ME) and under the mangrove canopy (MC). Additionally, at the ME and MC positions, some of the bags were buried in order to test the

effect of burial on decomposition rates (b = buried, s = sediment surface). At Site 1, tidal submergence periods of LT bags were approximately 2 - 2.5 hours longer than submergence of bags at the MC position. At Site 2, the difference in submergence times between LT and MC was approximately 1 - 1.5 hours. The effect of tidal position on root (pneumatophore) decomposition was not tested and root bags were only placed at the MC and ME positions. At each tidal position, decomposition bags were tied to a central stake and then pegged down (13-18 bags on each stake; four replicate stakes at each tidal position and site). The bags were allowed to float a few centimetres off the sediment surface with tidal inundation, which would naturally occur when the tide comes in. Buried decomposition bags were tied to coloured pegs and then buried to a depth of approximately 10 - 15 cm, to test rates of anoxic decomposition (Van der Valk & Attiwill 1984).

Four replicate bags (1 bag of each litter type from each stake) were collected from each position at 11, 24, 38, 51, 81, 169 and 357 days following initial deployment set up (only leaf samples were collected at 11 and 38 days; wood samples were also collected at 262 days). Following each collection, samples were carefully rinsed with freshwater over a 500 µm sieve, placed in foil dishes and oven dried to constant weight at 60 ºC. Decomposition was characterised by DW loss over time. Dried leaf samples for MC-s, MC-b, ME-s, ME-b and LT-s were analysed for total carbon (C) and total nitrogen (N) by grinding to a fine powder using a ball mill and then analysed using an Elementar Vario EL cub C and N analyser. C and N content were analysed in leaf samples up to 169 days of decomposition because sample sizes were too small after 357 days.

2.2.4 Data analysis

Litterfall data (raw) were analysed using a single t-test to determine a significant difference in total annual litterfall between mangroves on the edge of the forest (i.e. newly established trees) and mangroves 40 m within the mangrove forest (i.e. established trees).

Decomposition data were analysed using three different multi-way analyses of variance (ANOVA):

1) to test the effect of tidal position on decomposition rates of mangrove wood and leaves, with litter type (wood, leaf), site (1, 2) and tidal position (MC-s, ME-s, MT-s, LT-s) as fixed factors to compare means of weight loss after 357 days of decomposition;
2) to test the effect of burial state on decomposition with litter type (wood, root, leaf), site (1, 2), position (MC, ME) and burial state (b, s) as fixed factors to compare means of weight loss after 357 days;
3) to test the effect of burial state and tidal position on C and N dynamics of leaf litter after 169 days of decomposition, with site (1, 2) and decomposition bag positions (MC-s, MC-b, ME-s, ME-b, LT-s) as fixed factors.

Percentage data were arcsine transformed and C and N raw data were used, and assumptions of normality and homogeneity of variances met. Newman-Keuls post-hoc tests determined where significant differences occurred.

Decay rates of leaf litter were calculated using exponential decay models (to describe weight loss through time), which have been suggested as most suitable (Wieder & Lang 1982). A single exponential decay model of $X_{(t)} = e^{-kt}$, where $X_{(t)}$ is the proportion of mangrove material remaining after time t (days) and k (day $^{-1}$) is the decay constant, was used to describe the decay of mangrove leaf litter that was left on the sediment surface. The decomposition of buried leaves was more suitably described by the asymptotic model (single $r^2 < 0.3$; asymptotic $r^2 > 0.8$), $X_{(t)} = C + (1-C)e^{-kt}$, which assumes there is a fast initial decay of easily broken down labile material (k), followed by a completely decay-resistant recalcitrant fraction (C) (Wieder & Lang 1982). This asymptotic model assumes that litter will never decay completely, and therefore is unrealistic in nature. However, the asymptotic model can be useful to describe litter decomposition rates during the period of the study (Wieder & Lang 1982). The wood and root weight loss data were highly variable and exponential decay models did not provide a good fit (r^2 = 0.3-0.6). Due to the highly variable nature of the data, a linear decay rate (a) from t = 0 to t = 357 days was assumed (only data from t = 0 and t = 357 was used in the analysis). In order to compare with previous studies, t_{50} (time taken for litter to decay to 50% of its initial weight) was estimated using decay models and constants (e.g. Mackay & Smail 1996; Oñate-Pacalioga 2005; Robertson 1988).

Multi-way ANOVAs found no significant differences in weight loss (after 357 days) among tidal positions and sites (see results), therefore decay constants and t_{50} values presented are a mean value of means pooled across sites and tidal positions for each litter type and burial state (surface and buried). All statistical analyses were performed using the STATISTICA software program.

2.3 Results

2.3.1 Mangrove litterfall

Mean annual litterfall 40 m within the forest (538 ± 74 g DW m^{-2} yr^{-1}; ±SE) was significantly higher (t-test, $p = 0.015$, $n = 12$) than that of the younger trees on the edge of the forest (324 ± 43 g DW m^{-2} yr^{-1}; ±SE). Annual litterfall consisted of 60 - 65% leaf, 9 - 11% wood, 25 - 26% fruit and 1 - 3% infloresences both on the edge and within the mangrove forest. At both locations the majority of the litterfall (77%) occurred during the warmer months of November to February (Figure 2.2). Leaf and wood fall occurred all year round but was minimal in the colder months (March - October). Fruit fall was largest in the summer months, where it contributed 28 - 32% of the summer litterfall, but was low for the rest of the year (2%). Infloresences were collected all year round although they represented a very small proportion of the annual litterfall (1 - 3%).

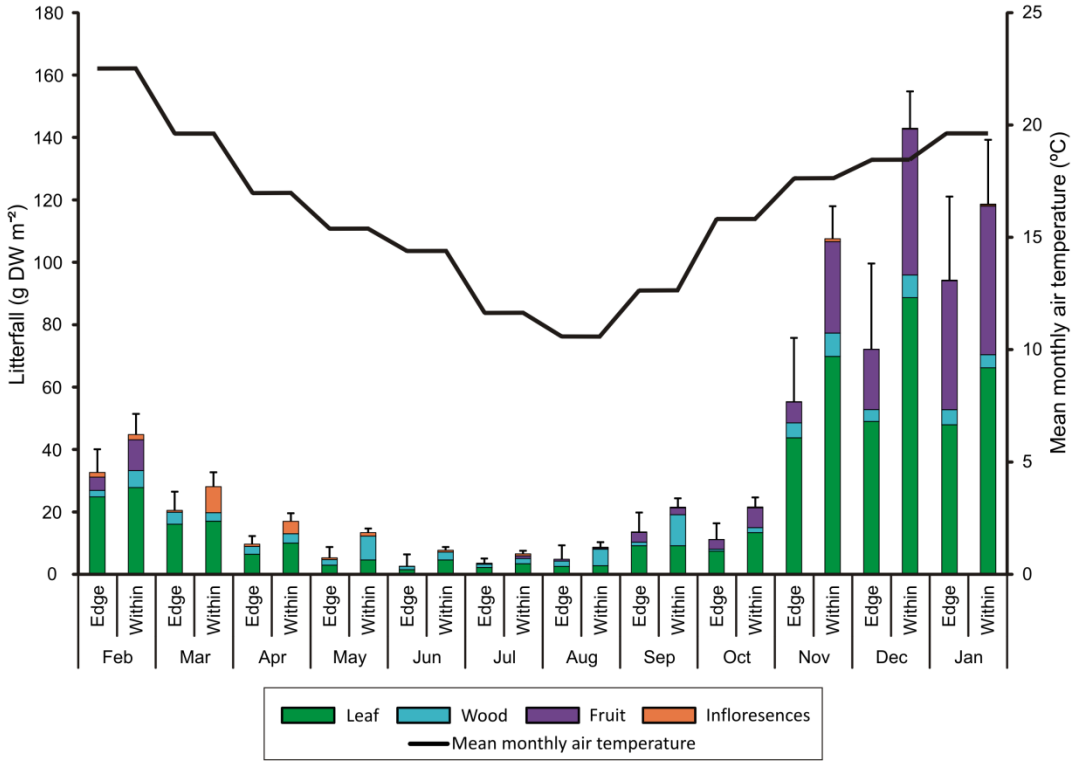

Figure 2.2. Mean (+1 SE; n = 12) mangrove monthly litterfall (February 2011 - January 2012), on the edge and 40 m within the forest. Secondary y-axis shows mean monthly air temperature.

2.3.2 Mangrove litter decomposition into detritus

ANOVA tested the effect of tidal position on the decay of wood and leaf litter. It was found that tidal position had no significant effect on weight loss for both wood and leaf litter (Table 2.1; Figure 2.3). However, the weight of wood litter remaining after 357 days of decomposition was significantly higher than that of leaf litter (Table 2.1).

A second ANOVA tested the effect of burial state, site and litter type on the decomposition of leaf, wood and root material. ANOVA showed that the percentage of initial litter weight remaining after 357 days of decomposition (all three litter types) was not significantly different between the two sites (Figure 2.3; Table 2.2). However, there was a significant interaction between litter type and burial state, indicating that litter weight loss was significantly different between litter types and burial states (Table 2.2). Of the litter that was left to decompose on the sediment surface, leaf material showed the greatest weight loss after 357 days (94.7%), followed by root material (59.4%) and wood (39.6%) lost the least weight (Figure 2.3, Table 2.2). Buried leaf and root material lost the same weight over 357 days (61.0 and 58.3%, respectively), but lost 2 times more weight than buried wood litter (29.6%) (Table 2.2). Surface leaves lost significantly more weight (94.7%) than buried leaves (61.0%) and the same occurred for wood litter (39.6% surface, 29.6% buried) (Table 2.2). Root weight loss over the year did not significantly differ between buried roots (58.3%) and roots on the sediment surface (59.4%) (Table 2.2).

Table 2.1. Summary of multi-way ANOVA comparing mean percentage weight remaining after 357 days (arcsine transformed), between sites (1, 2), litter types (Wood, Leaf), and tidal positions (MC, ME, MT, LT). Significant results ($p < 0.05$) are indicated in bold. Table includes results of Newman-Keuls post-hoc test.

Source of variation	df	Mean-square	F-ratio	*p*	Post-hoc
Site	1	0.01	0.62	0.436	
Litter type	1	7.49	420.31	**<0.001**	**Wood > Leaf**
Tidal position	3	0.03	1.66	0.189	
Site*Litter type	1	0.01	0.69	0.411	
Site*Tidal position	3	0.01	0.30	0.824	
Litter type*Tidal position	3	0.05	2.71	0.056	
Site*Litter type*Tidal position	3	0.01	0.29	0.829	
Error	47	0.02			

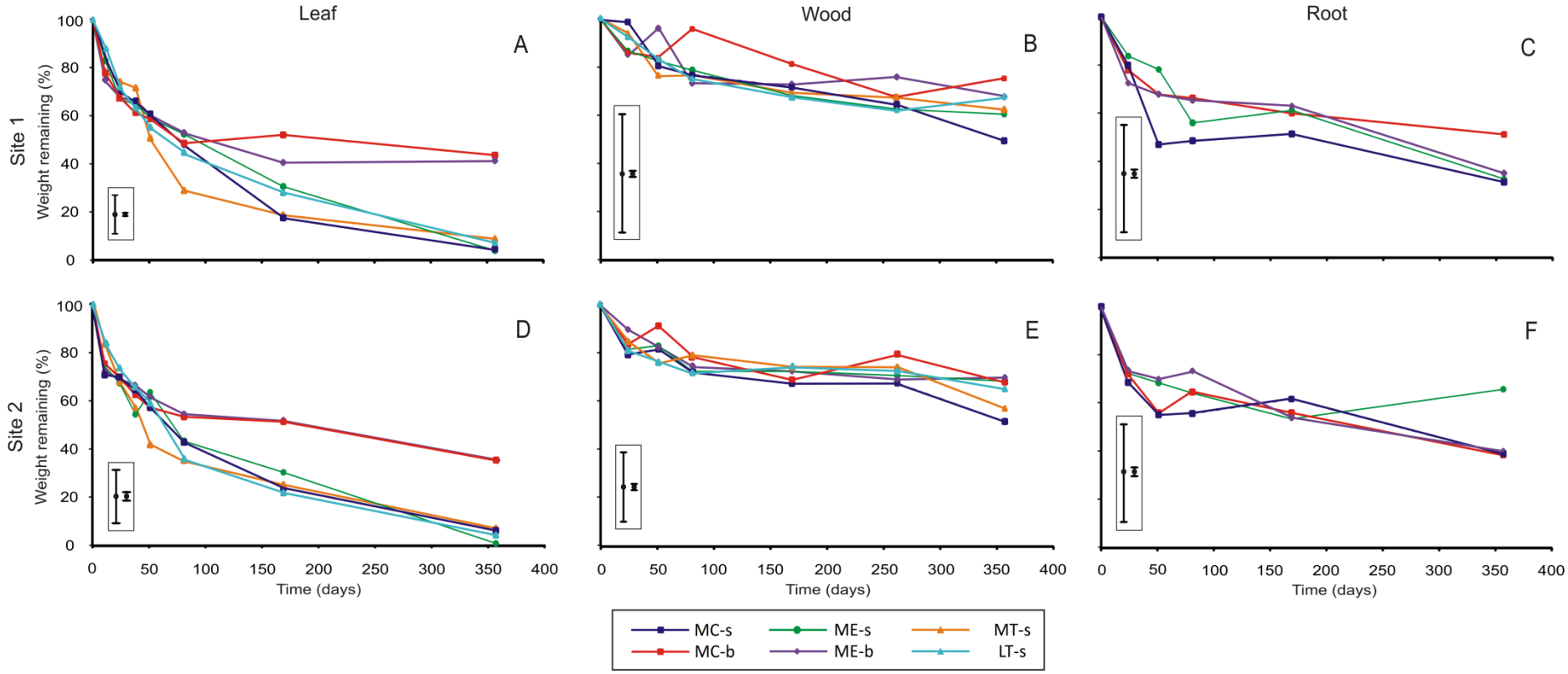

Figure 2.3. Mangrove litter decomposition (expressed as the percentage of original weight remaining through time) at varying tidal positions and burial states. A) Leaves - Site 1; B) Wood - Site 1; C) Roots (pneumatophores) - Site 1; D) Leaves – Site 2; E) Wood – Site 2; F) Roots (pneumatophores) – Site 2. Figure shows the maximum and minimum standard error of each graph (see Tables A1.1 – A1.3 in Appendix 1 for means and standard errors of all data points).

Table 2.2. Summary of multi-way ANOVA comparing mean percentage weight remaining after 357 days (arcsine transformed), between sites (1, 2), litter types (wood, leaf, root), positions (MC or ME) and burial states (buried or surface). Significant results ($p < 0.05$) are indicated in bold. Table includes results of Newman-Keuls post-hoc tests.

Source of variation	df	Mean-square	F-ratio	*p*	Post-hoc
Site	1	0.01	0.24	0.626	
Litter type	2	1.86	88.21	**<0.001**	
Position	1	0.01	0.31	0.580	
Burial state	1	0.91	42.93	**<0.001**	
Site*litter type	2	0.04	1.68	0.195	
Site*Position	1	0.04	1.98	0.165	
Litter type* Position	2	0.02	1.18	0.316	
Site*Burial state	1	0.07	3.32	0.073	
Litter type*Burial state	2	0.48	22.94	**<0.001**	**Buried: Wood > Root = Leaf**
Position *Burial state	1	0.06	2.78	0.101	**Surface: Wood > Root > Leaf**
Site*Litter type* Position	2	0.03	1.48	0.235	**Leaf: Buried > Surface**
Site*Litter type*Burial state	2	0.02	1.04	0.359	**Wood: Buried > Surface**
Site* Position * Burial state	1	0.00	0.07	0.794	**Root: Buried = Surface**
Litter type* Position * Burial state	2	0.04	2.10	0.131	
Site*Litter type* Position * Burial state	2	0.01	0.26	0.774	
Error	60	0.02			

Differences in decay models show that litter decomposes in different ways and explains the disparity in weight loss between litter types and burial treatments (Table 2.3). The decay of leaves on the sediment surface was best explained by a single exponential decay model ($r^2 > 0.83$), illustrating a constant exponential decay rate (*k*) (Table 2.3). Buried leaves decayed in a different way, where initial decomposition was rapid, but slowed after 169 days. Therefore, the decay of buried leaves was best described by an asymptotic decay model (asymptotic $r^2 > 0.8$, single $r^2 < 0.3$) (Table 2.3). Wood and root material decomposed slower than leaf material and did not show the same exponential decay as leaf decomposition (exponential models $r^2 = 0.3\text{-}0.6$) (Table 2.3). The time it took for litter to lose 50% of its original weight is indicated by t_{50} and differed between litter types and litter burial state. The mean t_{50} of buried leaves was approximately 1.4 times greater (an additional 25 days) than for surface leaves (Table 2.3). The decay models predicted that buried wood will take approximately 1.3 times longer (an additional 153 days) to decay to 50% of its original weight compared to wood left to decompose on the surface (Table 2.3). The t_{50} of wood was about 7 times that for leaves. The t_{50} of root material was 3 - 5 times greater than for leaf decomposition but between 1.5 - 2 times less than for wood decomposition (Table 2.3).

Table 2.3. Mean decomposition rates of litter expressed by different decay constants (*k, C, a*) depending on the decay model that best described the decay of litter. The t_{50} value represents the time (days) it takes for litter to decay to 50% of its initial weight (calculated from decay model equations and rate constants). Table includes mean decay constants, r^2 values and t_{50} values as well as their associated SE and 95% confidence intervals (CI). Means are calculated from means pooled across sites and tidal positions (where ANOVA found no significant difference).

	Model	***k* ± SE**	**95% CI**	***C* ± SE**	**95% CI**	***a* ± SE**	**95% CI**	**r^2 ± SE**	**t_{50}± SE**	**95% CI**
Leaves-surface	Single[a]	0.0111±0.0005	0.0102-0.0120	-	-	-	-	0.90±0.01	63±3	58-68
Leaves-buried	Asymptotic[b]	0.0327±0.0042	0.0256-0.0399	0.4632±0.0134	0.4405-0.4860	-	-	0.83±0.06	88±6	78-97
Wood-surface	Linear[c]	-	-	-	-	0.0011±0.0001	0.001-0.0012	0.86±0.04	460±28	409-511
Wood-buried	Linear[c]	-	-	-	-	0.0008±0.0001	0.0007-0.0009	0.82±0.09	613±43	539-686
Roots	Linear[c]	-	-	-	-	0.0016±0.0001	0.0014-0.0018	0.91±0.05	317±30	263-373

[a] $X_{(t)} = e^{-kt}$, [b] $X_{(t)} = C + (1-C)e^{-kt}$, [c] $Y = a X + 1$

2.3.3 Carbon and nitrogen content of decomposing mangrove leaves

C and N dynamics of mangrove leaves changed during the decomposition process. In the first 169 days of decomposition, average total N increased in all leaf litter from an average of 0.96% to 1.31% (Figure 2.4A & B). ANOVA found no significant differences in N content between leaves decomposing at different sites, tidal positions and burial states (after 169 days; Table 2.4).

Total C content of leaves (after 169 days of decomposition) was dependent on site and burial state, but was unaffected by tidal position. Total C content (%) of leaf litter decreased in leaves decomposing on the sediment surface from 45.11% (initial) to 42.71% and 38.95% (at Sites 1 and 2 respectively) (Figure 2.4C & D). However, C content of buried leaves remained the same, or increased slightly, during the decomposition process (Figure 2.4C & D). Consequently, the C content of buried leaves after 169 days of decomposition (47.58% Site 1, 45.83% Site 2) was found to be significantly higher than for leaves on the surface (42.71% Site 1, 38.95 Site 2) (Table 2.4). In addition, ANOVA revealed that leaves decomposed at Site 2 had a significantly lower total C content (45.83% buried, 38.95 % surface) than leaves at Site 1 (47.58% buried, 42.71% surface) (Table 2.4).

As a result of N enrichment, the ratio between C and N decreased in all leaves from a mean of 47 on day 0 to 31 (surface) and 37 (buried) after 169 days (Figure 2.4E & F). Buried leaves had a significantly higher C:N ratio (mean of 37) after 169 days compared to leaves on the sediment surface (mean of 31). No significant site effect was detected in leaf C:N ratios after 169 days.

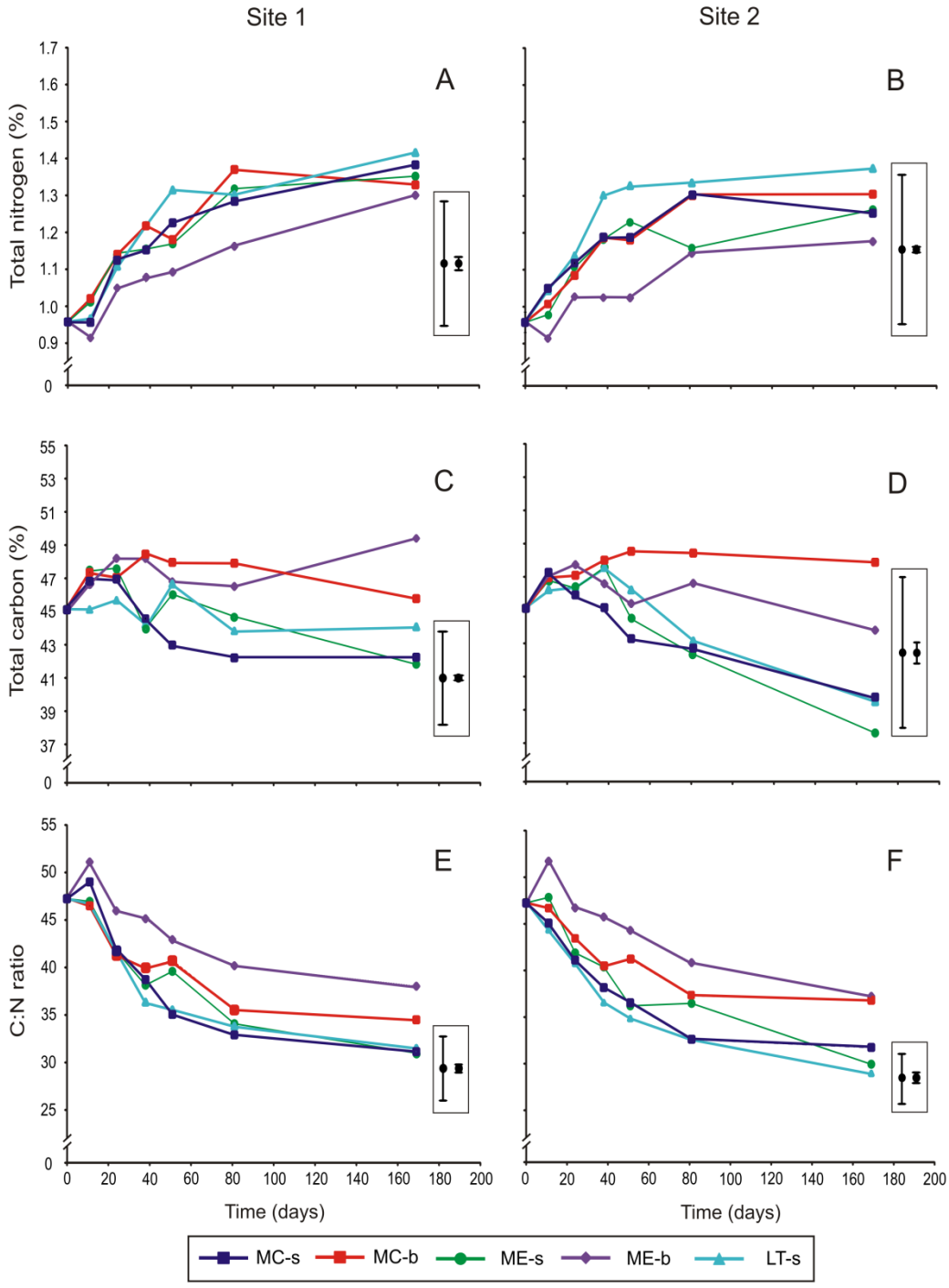

Figure 2.4. Carbon and Nitrogen dynamics of leaf litter during 169 days of decomposition. A) Total nitrogen content of leaves at Site 1; B) Total nitrogen content of leaves at Site 2; C) Total carbon content of leaves at Site 1; D) Total carbon content of leaves at Site 2; E) C:N ratio of leaves at Site 1; F) C:N ratio of leaves at Site 2. Figures show maximum and minimum standard error of each graph (see Tables A1.4 – A1.6 in Appendix 1 for means and standard errors of all data points).

Table 2.4. Summary of ANOVA for %C, %N and C:N ratios in leaves after 169 days of decomposition, comparing differences between sites (1,2) and decomposition bag positions (MC-s, MC-b, ME-s, ME-b, LT-s). Significant results ($p < 0.05$) are indicated in bold. Results of Newman-Keuls post-hoc tests are shown as footnotes.

	% N				% C				C:N ratio			
Source of variation	**df**	**Mean-square**	**F-ratio**	***p***	**df**	**Mean-square**	**F-ratio**	***p***	**df**	**Mean-square**	**F-ratio**	***p***
Bag position	4	0.02	0.74	0.571	4	78.12	5.70	**0.002**[a]	4	78.97	12.30	**<0.001**[c]
Site	1	0.06	2.08	0.161	1	77.27	5.64	**0.025**[b]	1	0.75	0.12	0.735
Bag position*Site	4	0.00	0.14	0.967	4	16.03	1.17	0.347	4	5.78	0.90	0.478
Error	26	0.03			26	13.70			26	6.42		

[a] ME-b = MC-b > MC-s = ME-s = LT-s [b] Site1 > Site 2 [c] MC-b = ME-b > MC-s = ME-s = LT-s

2.4 Discussion

2.4.1 Mangrove litterfall

During 2011, annual litterfall estimates in Whangamata Harbour were 324-538 g DW m^{-2} (equivalent to 3.24 - 5.38 t DW ha^{-1} yr^{-1}), which are within the range of estimates reported in the literature of mangroves at similar latitudes (Table 2.5; May 1999; Woodroffe 1985). However, some variability across regions in New Zealand can be noted (1.3-8.1 t DW ha^{-1} yr^{-1}; Table 2.5), which could be a result of temporal variation in climatic variables between study years (Clarke 1994). Litter composition was shown to be similar to other studies, where leaf litter makes up the largest proportion of the litter (60-65%) (e.g. Imgraben & Dittmann 2008; May 1999; Steinke & Ward 1990; Woodroffe 1985). Litterfall estimates of this study are consistent with the lower range of tropical mangrove forests, where tropical trees of similar height produce litter weights comparable to this study (Table 2.5; Cunha et al. 2006; de Boer 2000; reviewed by Morrisey et al. 2010). However, some tropical mangrove forests can produce up to 18 t DW ha^{-1} annually (Saenger & Snedaker 1993). Litter production of younger trees on the edge of the Whangamata mangrove forest was almost half that of the taller trees within the forest. Tree heights and the corresponding litter production reported here are comparable to other sites in New Zealand, but are generally less than tropical mangrove forests (Table 2.5; May 1999; Morrisey et al. 2010; Saenger & Snedaker 1993; Twilley et al. 1997; Woodroffe 1985).

The seasonal variation in litterfall was shown to be consistent with the literature of temperate regions and has been attributed to seasonal changes in temperature, rainfall and evapotranspiration (Clarke 1994; May 1999; Oñate-Pacalioga 2005; Sanchez-Andres et al. 2010; Woodroffe 1985). It has been found, both here and in previous studies, that temperate mangrove forests release a pulse of litter in the summer months, with minimal production during the rest of the year (Duke 1990; Goulter & Allaway 1979; May 1999; Oñate-Pacalioga 2005; Woodroffe 1985). Conversely, in some tropical regions seasonality in litter production is absent (Duke 1990; Twilley et al. 1986). The seasonality and relatively low productivity of temperate mangrove forests, means that these systems are likely to function differently compared to tropical systems with regard to consumer response and nutrient cycling.

Table 2.5. Summary of the literature on litterfall of mangroves in different regions (table modified from Morrisey et al. 2010).

Location	Latitude	Species	Tree height (m)	Litter production (t DW $ha^{-1}yr^{-1}$)	Reference
Whangamata Habour, New Zealand	37°10'S	*A. marina*	1.2 - 1.9	3.24	This study
			1.5 - 3	5.38	
Tuff Crater, Auckland, New Zealand	36°48'S	*A. marina*	<1	2.90 - 3.65	Woodroffe 1985
			4	7.12 - 8.10	
Rangaunu Harbour, New Zealand	34°57'S	*A. marina*	1.68	1.77	May 1999
			3.06	3.89	
			5.12	4.83	
			6.23	6.24	
Whangateau Estuary, Auckland, New Zealand	36°19'S	*A. marina*	<1 - 1.5	1.68	Oñate-Pacalioga 2005
			2 - 4	1.56	
Tramcar Bay, Auckland, New Zealand	36°19'S	*A. marina*	2 - 4	1.3	
Temperate range	> 30° S and N	various species	<0.5 - 10	0.11 - 11.68	Reviewed by Morrisey et al. 2010
Sub-tropical range	23° - 30° S and N	Various species	1 - 12.5	1.3 - 16.31	Reviewed by Morrisey et al. 2010
Tropical range	23° N - 23°S	Various species	3.9 - 35	3.74 - 18.7	Reviewed by Morrisey et al. 2010

2.4.2 Mangrove litter decomposition into detritus

This study is the first to measure, in one study, the decomposition rates of three mangrove litter types, at different tidal positions, burial states and experimental sites. The rate of litter weight loss was significantly affected by burial state and was different between litter types. However, small-scale variability among sites and tidal positions did not significantly affect litter weight loss. The decomposition rate (expressed as t_{50}) of leaf litter reported here is within the range reported for leaf decomposition in previous New Zealand studies; though such studies are limited to the Auckland region (Table 2.6; Albright 1976; Oñate-Pacalioga 2005; Woodroffe 1985). Decomposition of both wood and root material were significantly slower than leaf litter; however, comparisons are limited because previous investigations are lacking (Table 2.6; Albright 1979; Mackay & Smail 1996; Van der Valk & Attiwill 1984).

Surface leaf degradation measured in this study was slow (t_{50} = 63 days) when compared with tropical forests where degradation is rapid and t_{50} is often reached within one week (Table 2.6; e.g. Bosire et al. 2005; Sánchéz-Andres et al. 2010). Consequently, it is expected that organic matter cycling and detrital production is faster in tropical forests in comparison to those of temperate New Zealand. It has been suggested that the decomposition rate could influence the extent of litter export or retention within a forest. Rapid decomposition rates may be associated with a lower incidence of litter export and a greater chance of nutrient recycling within the mangrove forest, with slow decomposition rates exhibiting the reverse (Adame & Lovelock 2011; Imgraben & Dittmann 2008). A leaf marking study in New Zealand found that the extent of leaf litter retention within the forest (and therefore assumed export from the forest) was site dependent, and retention was greatest in mature forests compared with newly established ones (Oñate-Pacalioga 2005). However, other temperate and sub-tropical studies have found that the assimilation of mangrove material can be restricted to within the forest and export is therefore probably minimal at these sites (Alfaro et al. 2006; Guest & Connolly 2004). The fate of fallen mangrove litter in temperate forests is likely to be different to tropical regions, due to the dissimilarity in decay rates and could be highly site dependent. To determine if temperate mangroves provide the same organic matter subsidy to coastal regions

as their tropical counterparts, further quantification of the extent of litter export in temperate regions is required.

Buried leaves were found to follow a different pattern of decomposition, where the recalcitrant fraction of the leaf decomposed at a slower rate compared with leaves left to decompose on the surface (shown by the different decay models). The asymptotic decay model (used to describe buried litter decay) has been associated with litter decomposition that excludes faunal activity (Wieder & Lang 1982). It has been suggested that some macrofauna (e.g. shredding species) may aid in the breakdown of litter (Oñate-Pacalioga 2005; Proffitt & Devlin 2005; Slim et al. 1997; Werry & Lee 2005). Anoxic decomposition of buried leaves is likely to be primarily through bacterial breakdown, because decomposing macrofaunal abundance would be minimal at 10 - 15 cm depth (Rodrigues et al. 2007). Previous studies have also suggested that physical properties, such as climatic variables and tidal inundation, aid in the breakdown of the decay resistant fraction of the leaf (Davis III et al. 2003; Mackay & Smail 1996; Robertson 1988; Woitchik et al. 1997). The absence of such physical properties and the minimal macrofaunal abundance at 10 - 15 cm depth may contribute to the slow decay compared to surficial leaf decomposition. The results reported here differ to results from subtropical Florida, where weight loss during surficial leaf decay was the same as for buried leaf decay, possibly as a result of the site sediment characteristics (Fourqurean & Schrlau 2003).

The differences in mass loss between buried and surficial leaves were reflected in the carbon dynamics of the leaf (after 169 days of decomposition). Buried leaves had a significantly higher C:N ratio after 169 days associated with the low carbon loss compared with leaves on the surface. It has been proposed that a large proportion of leaf carbon is locked up in the recalcitrant decay resistant fraction (Davis III et al. 2003), which in this study was shown to resist decay to a greater extent in buried leaves (asymptotic decay model) compared to surficial leaves (single decay model). Leaf litter that is retained within the mangrove forest and buried due to sedimentation could result in nutrient recycling within the forest. However, the recycling of buried litter is likely to be slow in New Zealand forests due to the slow rate of weight loss and carbon decay under anoxic conditions.

The C:N ratio in leaves decreased in the first 81 days of decomposition as a result of nitrogen enrichment and carbon loss, but then stabilised. Initial nitrogen enrichment is expected to be a result of bacterial nitrogen fixation and is consistent with previous research in sub-tropical and tropical regions (Davis III et al. 2003; Fell et al. 1984; Fourqurean & Schrlau 2003; Mfilinge et al. 2002; Steinke & Charles 1986; Rice & Tenore 1981; Robertson 1988; Woitchik et al. 1997). Fresh mangrove leaves are a relatively low quality food resource to marine consumers (high tannins and C:N ratios). The decomposition process turns unpalatable leaf litter into detritus via a microbial pathway, which is then available to primary consumers (Alongi 1990; Alongi et al. 1989; Jennerjahn & Ittekkot 2002; Nordhaus et al. 2011; Robertson 1988; Skov & Hartnoll 2002). Lower C:N ratios and bacterial colonisation of mangrove leaf litter have been associated with increased palatability to consumers, such as detritus feeding crabs (Fell et al. 1984; Nordhaus et al. 2011). Previous sub-tropical and tropical studies show that C:N ratios initially decrease by approximately 10, then stabilise after 3 months (Dick & Osunkoya 2000; Rice & Tenore 1981). The results reported here show a similar decrease in C:N ratios during decomposition. However, in some tropical mangrove species C:N ratios can decrease from 75 to 37.5 in 160 days (Robertson 1988). Results presented from this study propose that mangrove litter in Whangamata Harbour may only be available for the incorporation into marine food webs after at least 3 months of decomposition (following the initial decrease in C:N ratio).

Although wood comprises 9 - 18% of annual mangrove litterfall (this study; May 1999), wood decomposition studies are lacking in New Zealand, as well as in other temperate regions. Mangrove wood and root material is often left *in situ* following mangrove removals in New Zealand estuaries (Stokes 2009; Lundquist et al. 2012); therefore it is essential to describe the decay of such material. Model predictions (linear decay) suggest that wood decomposing on the sediment surface will take on average 460 days to lose 50% of its initial weight, but will take 613 days when buried. This result is consistent with a study conducted in a tropical estuary in Florida, where buried mangrove wood was found to decay much slower than surficial mangrove wood (Romero et al. 2005). Wood degradation rates reported by this study are slower than those found in sub-tropical Australia during

the summer months (Table 2.6; Mackay & Smail 1996). This difference could be associated with the lower temperatures of temperate regions. Conversely, in South Africa (sub-tropical) wood decay rates were found to be comparable to rates presented here, but no similar studies have been conducted in a temperate setting to provide comparison (Table 2.6; Steinke et al. 1983). From the results reported here and in sub-tropical and tropical estuaries it is expected that wood litter will take years to decompose into detritus (Table 2.6; Mackay & Smail 1996; Robertson & Daniel 1989; Romero et al. 2005; Steinke et al. 1983). Therefore, wood litter is likely to represent a minor proportion of the detrital pool in New Zealand estuaries. In addition, such results have implications for mangrove removal projects because wood material left *in situ* following a mangrove clearance is expected to take years to decay and disappear, extending site recovery times. Some wood material will be buried due to sedimentation and algal colonisation (pers. obs.), and will take up to a third longer than surface wood to decompose.

Root degradation was found to take on average 317 days to reach 50% of its initial weight, indicating pneumatophores could take at least two years to decompose. However, it has been observed that mangrove root matter can persist for at least 3 - 6 years following a mangrove removal in New Zealand (Stokes 2009; pers. obs.). The burial of pneumatophores had no significant effect on weight loss, which could be because pneumatophores have adapted to withstand both anaerobic (buried) and aerobic (surface) conditions (Albright 1976). This study measured decomposition of pneumatophores and excluded the fibrous root material. A previous study in New Zealand found that pneumatophores and fibrous root mass exhibited similar weight loss over 5 months (Albright 1976). Conversely, in temperate Australia, pneumatophores decomposed significantly faster than fibrous roots, which only lost 20% of their original weight in 272 days (Van der Valk & Attiwill 1984). Decomposition rates estimated here could therefore provide an underestimate of complete root degradation.

Tidal elevation has previously been found to play a key role in the decomposition of mangrove litter, where greater inundation times associated with low tidal elevations have been linked with relatively fast decomposition rates (Dick & Osunkoya 2000; Mackay & Smail 1996; Robertson 1988; Woitchik et al.

1997). However, this study found no significant effect of tidal position on litter decomposition, both in weight loss and carbon and nitrogen dynamics. In previous investigations where tidal inundation was found to control litter degradation rates, differences in the inundation periods among treatments were greater than measured in this study. Some studies compared decomposition in litter that was continually submerged in tidal creeks with litter that was in the intertidal zone (Robertson 1988; Woitchik et al. 1997). In other studies, litter at the high tidal positions was inundated infrequently and litter at the low tidal positions was inundated during every high tide (Dick & Osunkoya 2000; Mackay & Smail 1996). The absence of an effect of tidal position on litter decay rate in this study could be attributed to the relatively flat nature of experimental sites, where differences in the inundation times between high and low tidal positions were only 1 - 2.5 hours (less than previous investigations).

This study found no significant site effect on decomposition rates of weight loss. Local variation in sediment characteristics and benthic community structure between sites (measured at the mid-tide position; Chapter 3) did not affect the decomposition rate of mangrove litter. In Kenya, differences between nearby sites with distinct macrofaunal communities were reflected in decomposition rates (Bosire et al. 2005). The current study employed a litter bag method, which has been criticised for the exclusion of large macrofauna that may aid in leaf decay (Fell et al. 1984). While these litter bags permitted entry of small invertebrates (pers. obs.), exclusion of larger fauna could explain why no site differences were detected in weight loss of litter; where differences in macrofauna community structure were expected to influence litter decay rates. However, macrofaunal community differences measured between the two sites of this study were a result of differences in the relative abundances of species rather than differences in species composition (Chapter 3 results).

Although no site effect was detected in weight loss, the two sites exhibited differences in leaf carbon content. The muddy Site 2 exhibited a significantly higher loss of carbon from leaf litter, which could indicate a slightly greater rate of degradation (large quantity of carbon in the decay resistant fraction of the leaf; Davis III et al. 2003). The breakdown of refractory components of the leaf is often dependent on site characteristics such as sediment organic content, temperature,

benthic community and tidal energy dynamics (Davis III et al. 2003; Holmer & Olsen 2002; Robertson 1986; Robertson 1988). Therefore, the muddier sediments at Site 2 may have caused a slight increase in the decay of recalcitrant components of leaf litter (and therefore carbon content). However, this increase was not significantly detected in mass loss through time.

2.5 Conclusions

Results reported here confirm that litterfall dynamics in temperate mangrove forests are different from their tropical counterparts in both seasonality and productivity. This study is the first to report the decomposition rates of three different mangrove litter types at varying tidal locations, burial states and sites in a single study. It was found that litter decomposition rates are dependent on the type of litter (e.g. wood, root or leaf) and the burial state of litter (buried or surficial). However, the hypotheses that decay rates would be affected by tidal position and local small-scale site variability (i.e. benthic community and sediment properties) were not supported by this investigation. Leaf litter decayed much faster than wood and root matter and therefore leaf litter is more likely to be incorporated into the estuarine detrital pool (and potentially the marine food web). The slow decay of mangrove wood and root material has considerable implications for mangrove removal projects, by identifying removal methods that may delay ecosystem/habitat recovery. Burial state had a significant influence on litter breakdown. Therefore, the destination of litter (following tree abscission) will influence the rate of decay, where litter that is retained within the forest and buried, will breakdown slower than exported litter that remains on the surface. The slow litter decomposition measured here compared to tropical systems, could mean that litter has a greater chance of being exported out of the forest following tree abscission. However, further research is required to determine whether temperate mangrove forests export or retain leaf litter. Future studies that determine the fate and role of mangrove litter in temperate estuaries would be beneficial to establish whether mangrove detritus provides an important spatial subsidy to temperate coastal habitats.

Table 2.6. Summary of litter decomposition studies in different regions (table modified from Morrisey et al. 2010)

Location	Latitude	Species	Season	t_{50} (days)			Reference
				Leaf	Wood	Root (pneumatophore)	
New Zealand studies							
Whangamata Habour, New Zealand	37°10'S	*A. marina*	Summer	63 88 (buried)	460 613 (buried)	317 (surface and buried)	This study
Tuff Crater, Auckland, New Zealand	36°48'S	*A. marina*	Summer Winter	42 (creek bank) 56 (tidal flat) 35 - 70 (creek bank) 39 - 42 (tidal flat)			Woodroffe 1982
Whangateau Harbour, Auckland, New Zealand	36°19'S	*A. marina*	Autumn Spring	56 >84			Oñate-Pacalioga 2005
Whangateau Harbour, Auckland, New Zealand	36°19'S	*A. marina*	Summer	53		>154 (surface and buried)	Albright 1976
Other temperate studies:							
Western Port Bay, Australia	38°20'S	*A. marina*	Summer	70		~ 250 (buried)	Van der Valk & Attiwill 1984
Port Gawler, South Australia	34°38'S	*A. marina*	Summer	42 (low-shore)			Imgraben & Dittmann 2008
Middle Beach, South Australia	34°36'S	*A. marina*	Summer	11 (low and high shore) 14 (mid-shore)			
Newcastle, Australia	33°52'S	*A. marina*	Summer	<30 (tidal side of floodgate) >180 (behind floodgate)			Dick & Osunkoya 2000
Sydney, Australia	33°46'S	*A. marina*	Winter	56			Goulter & Allaway 1979

Table 2.6 (Continued). Summary of litter decomposition studies in different regions (table modified from Morrisey et al. 2010)

Location	Latitude	Species	Season	t_{50} (days)			Reference
				Leaf	Wood	Root (pneumatophore)	
Subtropical examples:							
Mgeni Estuary, South Africa	29°48'S	*A. marina*	Spring	21	421		Steinke et al. 1983
		Bruguiera gymnorrhiza		42			
Mgeni Estuary, South Africa	29°48'S	*A. marina*	Summer	14			Steinke et al. 1990
		Bruguiera gymnorrhiza		63			
Brisbane, Australia	27°24'S	*A. marina*	Summer	44 (low-tide)	179 (low-tide)		Mackay & Smail 1996
				59 (high-tide)	383 (high-tide)		
			Winter	78 (low-tide)	1207 (low-tide)		
				98 (high-tide)	1327 (high-tide)		
Oura Bay, Okinawa Island, Japan	26°N	*Bruguiera gymnorrhiza*		32			Mfilinge et al. 2002
		Kandelia candel		11			
Florida Bay, USA	25°N	*Rhizophora mangle*		98 (buried and surface)			Fourqurean & Schrlau 2003
Tropical examples:							
North Queensland, Australia	19°17'S	*A. marina*		90 (forest)			Robertson 1988
				11 (submerged)			
		Rhizophora stylosa		226 (forest)			
				39 (submerged)			
		Ceriops tagal		228 (forest)			
				27 (submerged)			
Gazi Bay, Kenya	4° S	*Sonneratia alba*	Dry	5			Bosire et al. 2005
			Wet	3			
		Rhizophora mucronata	Dry	27			
			Wet	12			

CHAPTER THREE

THE RESPONSE OF INTERTIDAL BENTHIC ASSEMBLAGES TO MANGROVE DETRITAL INPUTS AT TWO CONTRASTING SITES

3.1 Introduction

Recent research has emphasised that spatially distinct habitats are often connected by the transfer of organisms, nutrients and/or organic matter. Numerous examples exist in marine ecosystems where one spatially distinct habitat is dependent on another for energy, a concept known as a 'spatial subsidy' (Polis et al. 1997). The marine environment offers suitable conditions for the movement of organisms, nutrients and/or organic matter across habitat boundaries. For example, sources of primary production can be carried either directly in tidal currents, or assimilated by organisms and then dispersed through the food web (Palumbi 2003). Moreover, a recent investigation has shown that terrestrially derived organic matter can cross the terrestrial-marine boundary and is important in supporting marine coastal benthic communities (McLeod & Wing 2009). Similarly, exported macroalgae, seagrass and mangrove organic matter can support marine food webs, not only at their growing sites, but also in nearby coastal regions (e.g. Connolly et al. 2005; Doi et al. 2009; Granek et al. 2009; Orr et al. 2005; Werry & Lee 2005). Macrophyte and macroalgae litter is decomposed, via microbial breakdown, and is typically exported across habitat boundaries as detritus (dead, broken down organic matter; Rice & Tenore 1981; Robertson 1988).

Detritus is a key source of carbon and therefore energy into many estuarine systems (Findlay & Tenore 1982a; Moore et al. 2004; Odum & Heald 1975), and can be utilised directly by benthic detritivores (Demopoulos et al. 2007; Findlay & Tenore 1982b; Oakes et al. 2010). Moreover, the decomposition of detritus can fuel the growth of microorganisms that are important sources of primary production (Rublee 1982). The deposition of detritus and wrack (whole pieces of dead, washed up seaweed and seagrass) has been found to enhance

microphytobenthos (benthic microalgae) growth on intertidal flats, which is likely to be due to the nutrient release during decomposition (e.g. Bishop & Kelaher 2007; Bishop et al. 2007; Levinton 1985; Rossi & Underwood 2002). Detrital deposition and distribution is a key factor in controlling small-scale benthic community variability of soft-sediment marine habitats (Kelaher & Levinton 2003). Seasonal and spatial variability in the deposition of detritus can determine the distribution of some deposit-feeding macrofauna that require such inputs in their diets (Lopez & Levinton 1987). Therefore, detritus can play a key role in ecosystem functioning through structuring soft-sediment benthic communities. Catchment land-use is modifying sources of primary productivity, including detritus (Vitousek et al. 1997). Consequently, it is important to determine the role that different detrital sources play in structuring coastal benthic communities. Conservation of detrital sources may be important in order to maintain coastal ecosystem functioning.

Studies investigating the effects of macrophyte and macroalgae detritus or wrack on benthic fauna in estuaries have found that community assemblages are often modified in response to the organic enrichment of the sediment (e.g. Bishop et al. 2010; Bishop & Kelaher 2008; Kelaher & Levinton 2003; Rossi & Underwood 2002; Taylor et al. 2010; Webb 1996; Zhou 2001). In many cases, additions of detritus or wrack support increased abundances of invertebrates (e.g. Bishop et al. 2010; Kelaher & Levinton 2003; Kelaher et al. 2003; Rossi & Underwood 2002). For example, a New York study showed that annelid populations on an intertidal sand flat peaked after one month in response to the addition of macroalgal detritus (Kelaher & Levinton 2003). It has also been found that benthic recolonisation of sediments can be enhanced in sediments containing macrophyte detritus (Ford et al. 1999; Zhou 2001). In other similar studies, the abundance and species richness of benthic fauna were unaffected, or decreased, as a result of a detrital enrichment (e.g. Bishop & Kelaher 2008; Bishop et al. 2007; Olabarria et al. 2010; Taylor et al. 2010). Responses are often dependent on the amount, type and mixtures of detritus added to the sediment (Bishop & Kelaher 2008).

The majority of studies that have examined benthic community responses to detrital deposition have incorporated sampling over one or two time periods (e.g.

Bishop et al. 2010; Bishop et al. 2007; Bishop & Kelaher 2007, 2008; Kelaher et al. 2003; Levinton 1985; Olabarria et al. 2010; Rossi 2006; Rossi & Underwood 2002; Taylor et al. 2010). Few studies have included temporal scale while exploring macrofaunal community response to detrital additions (Bishop & Kelaher 2007; Kelaher & Levinton 2003). These studies have shown variable response times of different communities to detrital deposition. An Australian study of intertidal benthic species showed that species abundances took 24 weeks to show increases after the addition of seagrass detritus (Bishop & Kelaher 2007). In contrast, a New York investigation showed that some annelid species responded to an *Ulva* detrital addition after 4 weeks (Kelaher & Levinton 2003). These examples suggest that community responses may be variable through time as a result of detrital type, and that different components of the communities may respond to detrital deposition over different time scales.

Intertidal soft-sediment communities are dynamic and vary in space and time (Morrisey et al. 1992; Thrush 1991; Thrush et al. 1994). Therefore, community responses to organic subsidies are likely to be dependent on a number of biotic and abiotic variables. There are few studies that have investigated the site-specific impacts of wrack or detrital deposition on intertidal estuarine benthic community structure (Olabarria et al. 2010; Rossi 2006; Rossi & Underwood 2002), and only one study has incorporated differences in community and sediment properties among sites (Rossi & Underwood 2002). The burial of algal wrack in Australia resulted in different benthic community responses on mud flats compared with sand flats, where different species responded to the enrichment across sites. Such responses to the deposition of wrack were found to be dependent on initial species abundances, where species responded in some sites but not in others (Rossi & Underwood 2002). Site-specific responses to detrital deposition may be driven by food availability, where communities that are resource limited could exhibit different responses compared to sites that are resource rich. Alternatively, different species may have the ability to utilise detrital material as a food source (Lopez & Levinton 1987). Therefore, it is probable that distinct communities associated with varying sediment characteristics will respond differently to inputs of broken down detritus.

Globally, mangrove forests contribute considerable amounts of organic matter (in the form of detritus) to coastal regions. Mangroves in tropical regions can produce up to 18 t DW ha^{-1} of litter annually (Saenger & Snedaker 1993). In many tropical mangrove ecosystems, exported litter plays a critical role in supporting coastal food webs, such as coral reefs (e.g. Demopoulos et al. 2007; Granek et al. 2009; Meziane & Tsuchiya 2000; Odum & Heald 1975; Werry & Lee 2005). This connectivity between habitats means that tropical mangroves are often vital to maintain the ecosystem functioning of adjacent coastal habitats, by supplying an organic matter subsidy (e.g. Lugo & Snedaker 1974; Odum & Heald 1975; Sheaves & Molony 2000). However, temperate mangrove forests have low productivity and tree species diversity compared to their tropical equivalents, which means that these two systems may differ in the ecological services that they provide (Ellison 2002; Saenger & Snedaker 1993; Chapter 2). It remains largely unknown if mangrove forests in temperate regions provide the same spatial subsidy as tropical forests. The low inputs of organic matter into temperate estuarine systems (compared with those in the tropics) could mean that marine communities are less dependent on mangrove production, because they may be adapted to utilise other more readily available sources of primary production. The limited knowledge of the ecosystem services provided by temperate mangroves to the wider coastal systems, highlights the need to determine the ecological value of these forests.

Here I investigate one ecosystem service that is potentially provided by temperate mangroves; the role of exported mangrove detrital inputs in structuring adjacent intertidal benthic communities. Mangrove detrital additions were manipulated in order to test if mangrove detritus contributes to the community variability of temperate intertidal flats. Mangrove detritus was added to plots on two unvegetated intertidal flats (with distinct sediment properties and macrofaunal communities) and changes in the benthic community were monitored through time following the enrichment. Previous studies have added different types of detrital material to intertidal flats and monitored benthic communities; however few of these have incorporated community specific responses into experimental designs. In addition, studies that determine temporal variability in community responses to detrital deposition are lacking and few studies have used mangrove

detritus in experimental manipulations. First, it was predicted that mangrove detrital deposition would alter macrofaunal community structure of unvegetated intertidal flats, by changing species abundances/composition. Second, it was expected that different communities (inhabiting sites with distinct sedimentary properties) would behave differently following the addition of detritus to the sediment, because responses are likely to be taxa-specific. Third, it was hypothesised that responses would vary through time as a result of decomposition and that different communities would respond over different temporal scales.

3.2 Methodology

3.2.1 Study site

The study was carried out in the northern region of Whangamata Harbour (North Island, New Zealand). The New Zealand endemic mangrove *Avicennia marina* subsp. *australasica* inhabits 101 ha of the harbour (approximately 25% of the 409.5 ha harbour area), which has expanded from 31 ha since urbanisation, deforestation and agriculture increased in the 1940s (Singleton 2007). The study sites occupy areas of the harbour that represent different habitat types in terms of sediment type and macrofaunal community. Site 1 (S 37º 10’ 43.0”, E 175º 51’ 36.9”) is characterised by fine organic-poor sands and the adjacent Site 2 (S 37º 10’ 38.6”, E 175º 51’ 36.5”) has a higher mud content and relatively organic-rich sediments. Both Sites 1 and 2 are unvegetated intertidal flats, located 20-40 m from the mangrove forest edge. There was approximately 50 m between the two sites and both were located at a similar mid-tidal elevation.

3.2.2 Field methods

In early February 2011 (late summer), 18 circular plots with a 1.15 m diameter (1.04 m^2) were established at each field site (32 m × 14 m). Plots were assigned one of three treatments (detrital addition, procedural control, control), and each treatment was replicated 6 times. Detrital addition (DA) plots were enriched with mangrove detritus by finger churning 270 g of detritus into the top 3 cm of sediment (e.g. Bishop et al. 2010; Bishop & Kelaher 2008; Kelaher & Levinton 2003). In procedural control (PC) plots, the sediment was also finger churned, identical to DA plots, but no detritus was added. Procedural controls

were designed to delineate any effect on the benthic community caused by the one off disturbance of the addition. Control (C) plots were left untouched. The amount of detritus added represents the amount of leaf litter that enters the system over the summer months, which was based on the average of past litterfall measurements in New Zealand (e.g. May 1999; Oñate-Pacalioga 2005; Woodroffe 1982), and is similar to measurements reported in Whangamata Harbour during 2011 (Chapter 2). The detritus addition took place at the end of summer (February) because it has been found that the majority of litter falls in the summer months from November - February (May 1999; Oñate-Pacalioga 2005; Woodroffe 1982, 1985; Chapter 2). The positioning and distribution of plots was achieved by a randomised block design, where three rows of six plots were established at each site, separated by 5 m between each plot. Each row of six plots had two plots that were randomly assigned to each treatment.

Benthic community response to the detrital addition was monitored for 12 weeks following the manipulation, because this time scale is equal to, or longer than, that used by similar studies (e.g. Bishop et al. 2010; Bishop et al. 2007; Bishop & Kelaher 2007, 2008; Kelaher et al. 2003; Kelaher & Levinton 2003; Levinton 1985; Olabarria et al. 2010; Rossi 2006; Rossi & Underwood 2002; Taylor et al. 2010). On day 0, sites were sampled for macrofauna (13 cm diameter core, 15 cm depth), and surface sediment properties (chlorophyll *a*, organic content and grain size), at six randomly chosen locations outside of the experimental plots. Sediment samples consisted of 3 pooled syringe core samples (3 cm diameter, 2 cm depth), and were taken within a few centimetres of each macrofaunal core. Subsequent macrofauna and surface sediment properties were sampled from the experimental plots at 2, 4, 8 and 12 weeks following the detrital addition. This monitoring encompassed a range of sampling dates to determine temporal variability in macrofaunal responses to detrital inputs. Macrofaunal cores were taken from different positions within the plots and the resulting core holes were filled with defaunated sand; to minimise the effect of repeated sampling on the benthic community (Lohrer et al. 2010). Macrofaunal cores were sieved over a 500 µm mesh sieve and preserved in 70% Isopropyl alcohol (IPA). Sediment core samples were kept in dark, cold conditions immediately after collection, and then stored frozen awaiting later analysis.

The mangrove detritus used in the manipulation was prepared by firstly collecting yellow senescent (ready to abscise) mangrove leaves from trees in Whangamata Harbour (January 2011). To simulate natural mangrove detritus, the leaves were oven dried at 60 ºC to constant weight and ground into 2 mm pieces, using a 2 mm mesh sieve (Bishop & Kelaher 2007, 2008; Lee 1999; Zhou 2001). Drying the leaf material is thought to be comparable to the drying out a fallen leaf would experience if it fell on a sunny day at low tide (Bishop & Kelaher 2008). The dried mangrove detritus was weighed into 270 g portions and frozen until field additions took place.

3.2.3 Sample analysis

Sediment samples were homogenised and subsamples taken to analyse the sediment properties. Chlorophyll *a* (chl *a*) analysis was performed within 6 weeks of sample collection, by extraction of freeze-dried samples (~ 0.1 g) in 90% buffered acetone for 24 hours. Extracted samples were centrifuged and a Turner 10-AU fluorometer was used to determine chl *a* and phaeophytin (phaeo; after acidification) concentrations of the extract (Arar & Collins 1997). Grain size (GS) analysis was undertaken using a Malvern Mastersizer 2000 instrument (particle size range 0.05 – 2000 µm), with sediment that was digested in 10% hydrogen peroxide (until bubbling ceased; Singer et al. 1988). Sediment for organic matter content (OM) analysis was dried in pre-weighed foil dishes at 60 ºC to constant weight and then combusted at 550 ºC for 4 hours. Sediment OM was measured as the percentage weight loss of dried sediments after furnace combustion. Macrofaunal samples were stained with Rose Bengal solution and fauna separated then identified to the lowest possible taxonomic level under a stereo microscope. Additionally, detritus (> 500 µm) was elutriated from the DA and initial (day 0) macrofauna cores using a sugar solution (approx. 500 g sugar dissolved in 2 litres of water) to separate light material from heavier sediment and shell hash (similar to methods used in Anderson 1959). Samples were elutriated at least three times (until no more material was observed to be floating off) and the elutriate material was retained in a 500 µm sieve. It was assumed that the majority of the elutriated material was made of organic detritus because macrofauna had previously been removed from samples. Elutriate material was dried to constant weight at 60 ºC and weighed. The amount of detritus remaining throughout the experiment was

quantified to determine if there were elevated levels of detritus in DA plots. Detritus in initial samples (day 0) was relatively low compared to DA samples, therefore only DA cores were elutriated after day 0 (see results).

3.2.4 Data analysis

One-way analyses of variance (ANOVA) were used to test for significant changes in macrofauna taxonomic richness and abundance, as well as sediment properties among treatments (fixed factor); with each sampling time and site analysed separately (STATISTICA). Sampling times were analysed separately in these analyses to explore differences among treatments, while excluding any effects of natural temporal variability. Newman-Keuls post-hoc tests were performed when necessary to determine where significant differences occurred. Raw data conformed to assumptions of homogeneity of variances and normality, therefore no transformations were necessary.

All multivariate analyses were performed using the PRIMER statistical software program (Plymouth Routines In Multivariate Ecological Research; Clarke & Gorley 2006). Non-metric multi-dimensional scaling (MDS) analysis, using Bray-Curtis dissimilarity matrices, was used on macrofauna abundance data (raw) to plot and compare benthic community structure among treatments (sites were analysed separately). Community data was compared through time and between treatments using permutational multivariate analysis of variance (PERMANOVA, Bray-Curtis dissimilarity), with time, treatment and site as fixed factors. Significant interactions between time and site meant that separate pair-wise tests (sites and times analysed separately) were used to determine significant treatment effects (see results). Although this study was a repeated measures design, PRIMER does not have a specific repeated measures version of the PERMANOVA test. SIMPER analysis was used to determine the taxa that contributed to the dissimilarity/similarity in community between treatments at each sampling time (sites analysed separately). Raw data were used for multivariate analyses as transformations did not alter the results. Statistical analyses found that initial communities and sediment properties were different between sites, and in addition PERMANOVA found a significant site-time interaction when comparing community assemblages (see results). Therefore,

statistical tests compared differences among treatments at each sampling time and site separately.

3.3 Results

3.3.1 Sediment properties

Sediment properties were significantly different between sites (Table 3.1). For instance, sediment OM at Site 2 was double the amount measured at Site 1 (day 0, Newman-Keuls, p = 0.0002). In addition, both chl *a* and phaeo pigments were higher at Site 2 than at Site 1 (day 0, Newman-Keuls, chl *a* p = 0.0002 and phaeo p = 0.0517, marginally significant). Site 2 had a high mud content (% of particles < 63 µm), that was two times that found at Site 1 and the median grain size was significantly lower at Site 2 (day 0, Newman-Keuls, p = 0.0002 for both mud and median GS). Sediment properties were mostly unaffected by the addition of detritus and although there was some temporal variability, this was minimal as shown by the narrow range of means through time (Table 3.1). ANOVA revealed the only significant result of treatment on sediment properties to be at 2 weeks, Site 1, where organic content of the sediment was 0.3% greater in DA plots compared to PC and C plots, however this did not persist throughout the remainder of the experiment.

Elutriated material (assumed to be organic detrital material) was low in the initial core samples (before the addition) and therefore only DA samples were analysed for detritus after day 0. A small amount of elutriated material was found in the initial samples, which indicates there was a small amount of naturally occurring detritus present at the study sites. However, an elevated level of detritus in DA plots (0.9-2.3 g DW core^{-1}) compared with initial samples (0.3 g DW core^{-1}; where no detritus was added) suggests that the detrital addition successfully raised sediment detritus above ambient levels (Figure 3.1). Detrital material remained in DA plots for at least 12 weeks, but decreased throughout the experiment, probably as a result of breakdown or dispersion outside the plot.

Table 3.1. Temporally averaged sediment properties (range through time in brackets), as a function of site and treatment (control – C, procedural control – PC, detritus addition – DA).

	OM (%)		Chl a (µ mg^{-1})		Phaeo (µ mg^{-1})		Median GS (µm)		Mud content (%)	
Site 1										
Initial	1.90		10.50		2.79		197.6		14.4	
C	2.18	(2.09-2.23)	9.34	(8.33-10.76)	2.80	(2.55-3.00)	227.7	(194.5-252.5)	12.4	(9.2-17.7)
PC	2.18	(2.02-2.49)	9.64	(8.51-11.79)	3.04	(2.50-4.11)	225.6	(197.8-241.7)	12.5	(9.5-15.6)
DA	2.28	(2.12-2.44)	8.34	(7.14-10.55)	3.30	(2.80-4.18)	231.2	(201.9-245.2)	11.2	(9.1-13.4)
Site 2										
Initial	4.05		23.80		4.52		130.8		29.9	
C	4.20	(4.06-4.35)	19.90	(18.16-20.90)	4.90	(4.08-5.62)	162.0	(123.2-183.5)	25.1	(21.7-33.1)
PC	4.06	(3.90-4.24)	19.72	(18.15-21.89)	5.54	(4.65-6.01)	149.5	(116.7-180.0)	27.4	(21.5-33.4)
DA	4.39	(4.14-4.63)	18.74	(16.28-21.06)	5.78	(4.83-6.52)	155.9	(128.6-184.2)	27.1	(21.4-31.2)

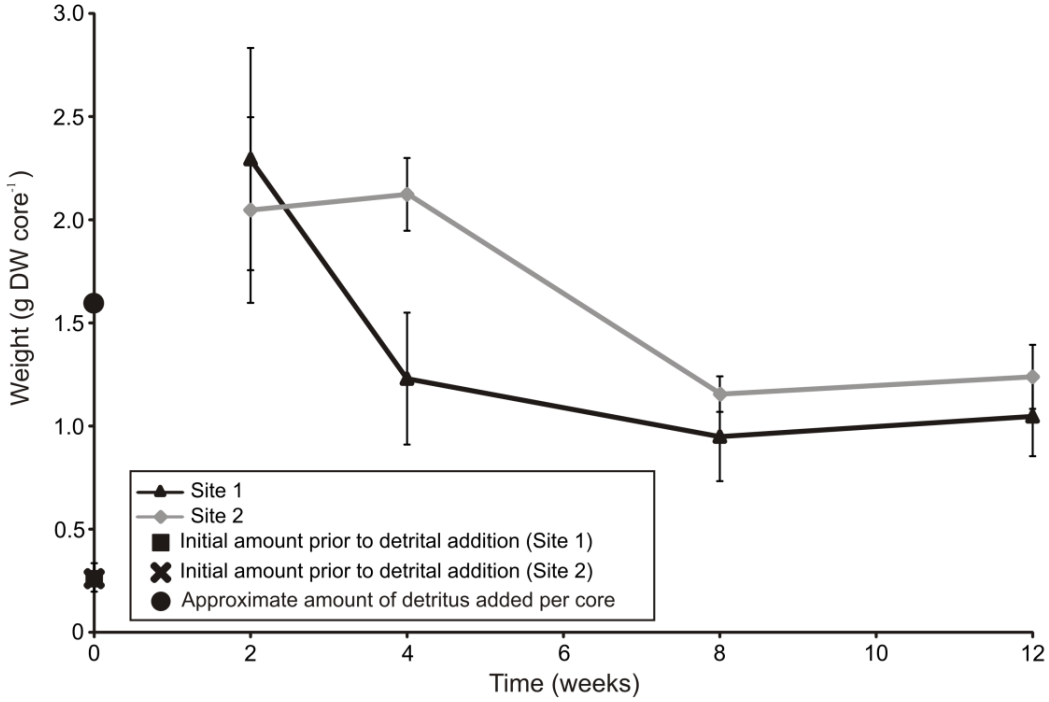

Figure 3.1. Mean weight of detritus (> 500 µm; ± 1 SE) remaining in detrital addition (DA) cores (13 cm diameter, 15 cm depth) throughout the 12 week experiment at the two sites. Figure also shows the amount of detritus present in initial (day 0) core samples prior to the detrital addition (i.e. the amount of detritus that naturally occurs), as well as the estimated amount added per core.

3.3.2 Macrofauna community

3.3.2.1 Initial community composition of sites

The two experimental sites had distinct community compositions, with key differences in overall abundance and dominant species. The sandy Site 1 comprised a significantly lower total macrofaunal abundance than the muddy Site 2 (day 0, Newman-Keuls, $p = 0.005$), where on day 0 Site 2 had almost double the number of individuals (175 core^{-1}) found at Site 1 (101 core^{-1}). Species richness was similar at the two sites (day 0, ANOVA, $p > 0.05$), and on average 14 - 15 taxa per core were counted before the detrital addition. Moreover, the two experimental sites had different initial macrofaunal community structure (Figure 3.2; PERMANOVA, pseudo-F = 22.78, $p = 0.001$). Dissimilarity between sites was 58.75% and the taxa that contributed the greatest to this dissimilarity were the polychaetes *Prionospio aucklandica, Aonides trifida* and *Heteromastus filiformis*

(Table 3.2). Significant differences between sites were driven by differences in the relative abundances of some species, but not by differences in species composition. *P. aucklandica* was almost 5 times more abundant at Site 2 compared with Site 1, and contributed the largest amount to the dissimilarity between sites (46.65%). *A. trifida* was abundant at Site 1 (23 individuals core^{-1}) but relatively rare at Site 2 (< 1 core^{-1}), and contributed 14.48% to the dissimilarity of the two sites. *H. filiformis* was 15 times more abundant at Site 2 than at Site 1 and contributed 12.05% to inter-site dissimilarity. Bivalve species (*Austrovenus stutchburyi* and *Arthritica bifurca)* were slightly more abundant at Site 1, however contributed little to the dissimilarity of sites (< 4% each; Table 3.2).

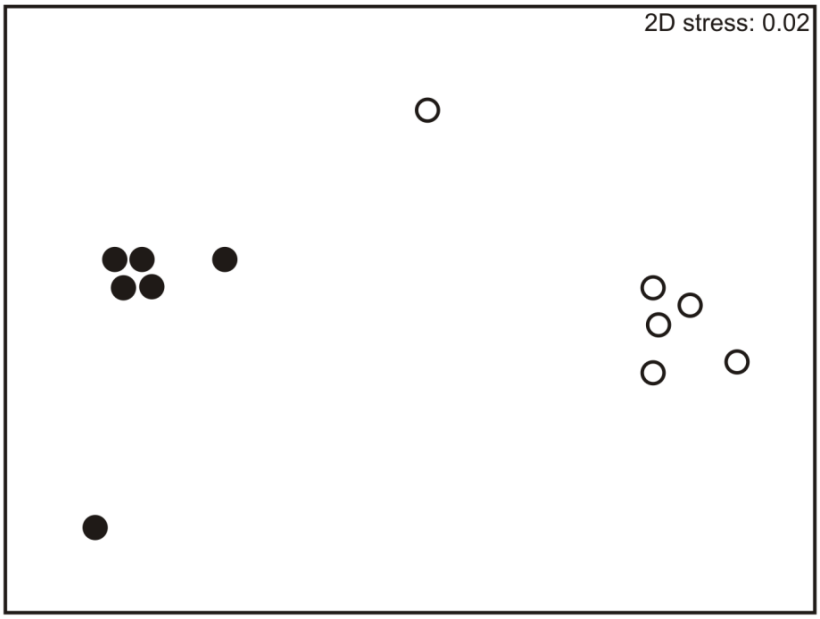

Figure 3.2. Non-metric MDS ordination (Bray-Curtis dissimilarity) showing the dissimilarity in benthic community structure between Sites 1 (black circles) and 2 (white circles) at day 0. Each point represents one replicate macrofauna core sample.

Table 3.2. Results of SIMPER analysis, using Bray-Curtis dissimilarity, showing the main taxa that contributed >80% to the cumulative dissimilarity between sites.

Taxon	Site 1 Mean abundance (# individuals core^{-1})	Site 2 Mean abundance (# individuals core^{-1})	Contribution (%)
Prionospio aucklandica	23.17	101.00	46.65
Aonides trifida	23.33	0.50	14.48
Heteromastus filiformis	1.33	20.67	12.05
Oligochaeta	4.17	9.67	3.62
Austrovenus stutchburyi	11.50	8.33	3.17
Arthritica bifurca	7.00	5.83	3.12
Average dissimilarity between sites (%) = 58.75			

3.3.2.2 Benthic community response to detrital addition

Community abundance showed some trends associated with the detrital addition at both sites. At Site 1, DA plots had lower total macrofaunal abundances than C and PC, though some of these were not statistically significant and PC plots were sometimes intermediate between DA and C plots (Figure 3.3A). At Site 1, 2 weeks after the detrital addition, overall abundance was significantly lower (ANOVA 2 weeks, $p = 0.024$) in DA plots compared with PC and C plots, but this pattern did not persist through time (Figure 3.3A). The number of taxa at Site 1 was unaffected by the addition of mangrove detritus throughout the experiment (Figure 3.3C).

Temporal patterns in total abundance were different at Site 2. Abundance was reduced in DA and PC plots compared to C plots in week 4, indicating that the effect could be caused by the procedure of disturbing the sediment, rather than the detrital enrichment (Figure 3.3B; ANOVA, $p = 0.037$). However, at 8 weeks, Site 2, DA plots exhibited a significantly lower total abundance than both PC and C plots (ANOVA, $p = 0.004$). This indicates that the decreased total abundance in DA plots was a result of the detrital addition (rather than the procedural disturbance), but this did not continue at 12 weeks (Figure 3.3B). The mean number of taxa at Site 2 declined in DA plots 2 weeks after the addition (ANOVA, $p = 0.023$), but this did not persist throughout the remainder of the experiment (Figure 3.3D).

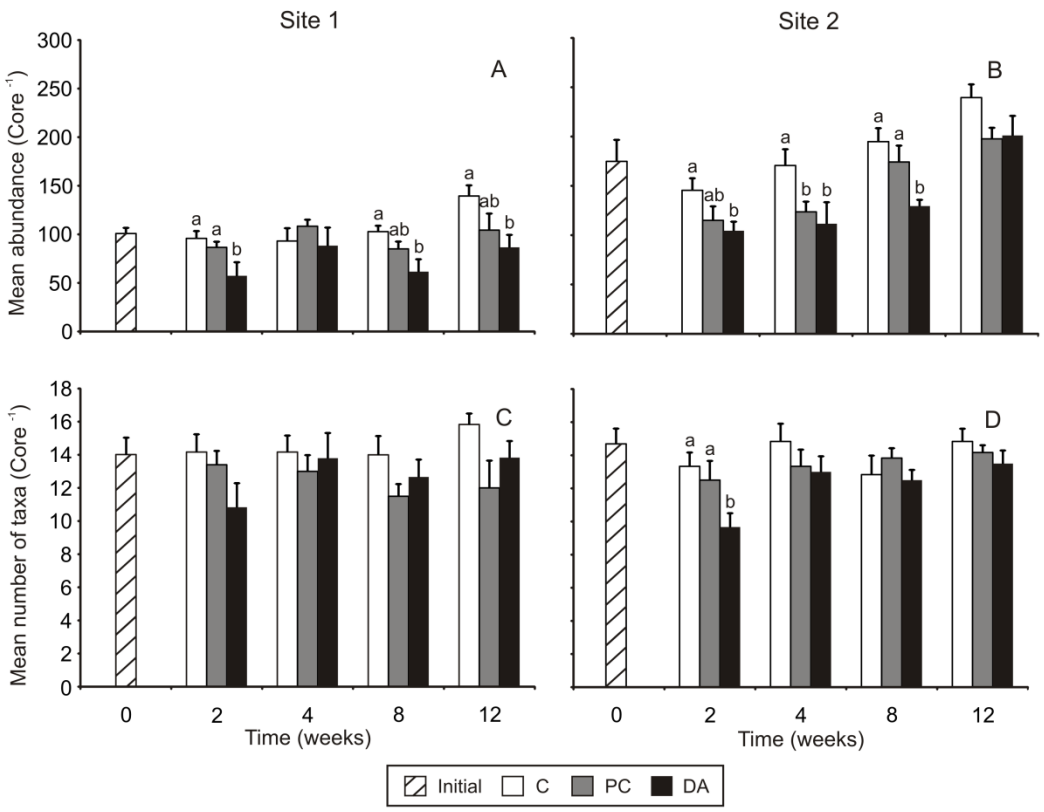

Figure 3.3. Mean abundance and species richness at Site 1 and 2 on day 0 (initial), and 2, 4, 8, and 12 weeks following the detrital manipulation in detrital addition (DA), procedural control (PC) and control (C) plots. Letters above bars indicate significant differences between treatments at each sampling date (Newman-Keuls; $p < 0.05$), where bars sharing the same letter are not significantly different from each other. Data are the mean (+SE) of 6 replicate cores.

Patterns presented by MDS ordinations (averaged data) suggest that benthic community responses to the mangrove detrital input differed between sites (Figure 3.4A & B). At Site 1, the DA community assemblages cluster away from PC and C plot communities throughout the 12 week experiment. PC and C plots clustered together indicating no effect from the procedure of mixing the sediment at Site 1 (Figure 3.4A). The clustering of DA plots away from PC and C suggests an effect of the detrital treatment at Site 1, where benthic community structure is altered following the addition of mangrove detritus.

Benthic assemblages at Site 2 showed a different response to the treatments, where at 2 and 4 weeks the PC and DA plots follow a very different trajectory to the C communities (Figure 3.4B). The clustering of DA and PC communities together suggests that the response is likely to be caused by the sediment mixing

rather than the detrital enrichment (i.e. detrital addition effects cannot be delineated from the effect of the procedure). Conversely, at 8 and 12 weeks (Site 2) the community in PC plots returns toward C plots, and the DA community follows a different path, suggesting a response to the detrital treatment from 8 weeks onwards (Figure 3.4B).

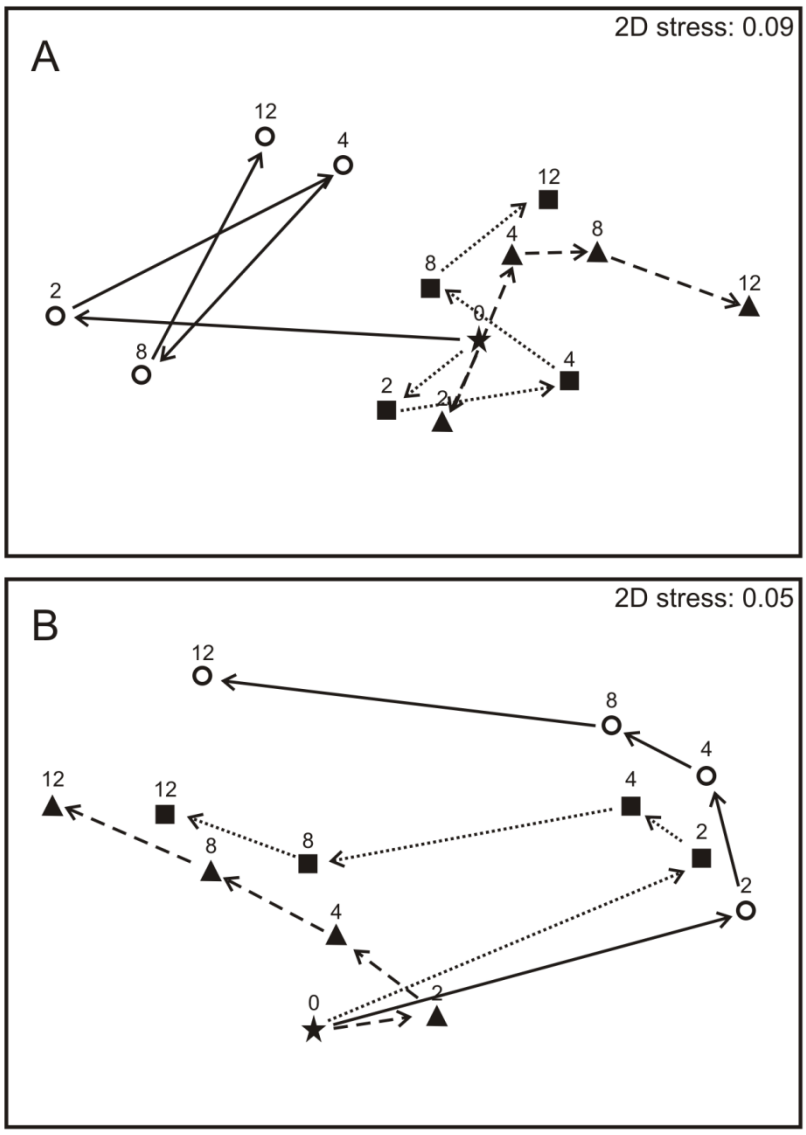

Figure 3.4. Non-metric MDS ordinations (Bray-Curtis dissimilarity) showing changes in benthic community from the initial (★) samples to detrital addition (O), control (▲) and procedural control (■) plots through time following the mangrove detrital manipulation at Site 1 (A) and Site 2 (B). Numbers above points indicate the number of weeks after detrital enrichment. Data points are the average of 6 replicate plots.

The trends observed from MDS analyses were not always consistent with the PERMANOVA results due to the highly variable nature of the data. Significant interactions between site and time, as well as site and treatment, meant pairwise tests were needed to compare treatments at each site and time separately. The benthic community response at Site 1 showed marginally significant (90% significance level) detritus addition effects at 2 and 8 weeks following the detrital addition (Table 3.3; a significant detritus addition effect is where C = PC ≠ DA). Although, several significant differences were found in pairwise tests, detritus effects on community structure were inconsistent through time (Table 3.3). Site 2 demonstrated procedural effects of the sediment mixing at 4 weeks after the addition, followed by a significant detrital addition effect at 8 weeks (Table 3.3; a significant procedural effect is where PC = DA ≠ C).

In most cases the dissimilarity between DA and control (both PC and C) communities was greater than the dissimilarity between PC and C communities (SIMPER; Table 3.4). SIMPER analysis revealed the taxa that contributed the greatest percentage to dissimilarities between DA and control plots. The dominant polychaetes *P. aucklandica* and *A. trifida* contributed the greatest percentages (> 40% cumulative) to the dissimilarities between treatments at Site 1 (Table 3.4). At Site 2, dominant polychaetes *P. aucklandica* and *H. filiformis* were responsible for the greatest proportion (> 40% cumulative) of the dissimilarity seen between treatments (Table 3.4). Dissimilarity between treatments was driven by a change in the relative abundances of some taxa, rather than a change in species composition of the community, and was similar at both sites.

Table 3.3. Summary of multi-way PERMANOVA (Bray-Curtis dissimilarity) comparing benthic communities in detrital addition (DA), control (C) and procedural control (P) plots through time (90% significance level, $p < 0.1$ are indicated in bold).

Source	**df**	**MS**	**Pseudo-F**	**P**
Time	3	3623.4	6.41	**0.001**
Site	1	91436	161.74	**0.001**
Treatment	2	3756.5	6.64	**0.001**
Time x Site	3	1124.7	1.99	**0.003**
Time x Treatment	6	586.48	1.04	0.434
Site x Treatment	2	2876.2	5.09	**0.001**
Time x Site x Treatment	6	607.99	1.08	0.36
Res	118	565.32		
Pair-wise tests	**P**	**Pair-wise tests**		**P**
Site 1 week 2		**Site 2 week 2**		
C = PC	0.778	C = PC		0.222
C ≠ DA	**0.028**	C = DA		0.158
PC ≠ DA	**0.085**	PC = DA		0.541
Site 1 week 4		**Site 2 week 4**		
C = PC	0.113	**C ≠ PC**		**0.033**
C = DA	0.155	**C ≠ DA**		**0.052**
PC ≠ DA	**0.014**	PC = DA		0.395
Site 1 week 8		**Site 2 week 8**		
C = PC	0.438	C = PC		0.734
C ≠ DA	**0.002**	**C ≠ DA**		**0.003**
PC ≠ DA	**0.059**	**PC ≠ DA**		**0.002**
Site 1 week 12		**Site 2 week 12**		
C ≠ PC	**0.070**	C = PC		0.149
C ≠ DA	**0.003**	**C ≠ DA**		**0.051**
PC ≠ DA	**0.065**	PC = DA		0.332

Table 3.4. Results of SIMPER analysis (Bray-Curtis dissimilarity), showing the taxa that contributed > 50% to the cumulative dissimilarity between treatments: detrital addition (DA), procedural control (PC) and control (C) (* denotes significant differences between treatments from PERMANOVA pair-wise tests in Table 3.2).

Taxon	**Week 2**		**Week 4**		**Week 8**		**Week 12**	
	Contribution	Dissimilarity	Contribution	Dissimilarity	Contribution	Dissimilarity	Contribution	Dissimilarity
SITE 1	%	%	%	%	%	%	%	%
C vs. PC		**31.89**		**30.30**		**31.88**		**31.26***
Prionospio aucklandica	15.24		18.82		23.41		20.18	
Austrovenus stutchburyi	14.32		10.14		15.83		14.76	
Aonides trifida	20.19		23.63		14.64		13.50	
Arthritica bifurca	9.27							
Oligochaeta							11.52	
C vs. DA		**48.87***		**39.69**		**47.67***		**39.05***
Prionospio aucklandica	20.52		22.25		31.18		27.04	
Aonides trifida	26.93		18.64		18.99		18.92	
Austrovenus stutchburyi			10.88		14.16		12.90	
Nereidae	8.13							
DA vs. PC		**46.93***		**40.05***		**45.37***		**39.48***
Prionospio aucklandica	18.01		18.27		23.81		18.49	
Aonides trifida	28.80		25.54		22.21		19.10	
Austrovenus stutchburyi	11.30		10.40		11.54		10.94	
Arthritica bifurca							10.54	

Table 3.4 (Continued). Results of SIMPER analysis (Bray-Curtis dissimilarity), showing the taxa that contributed > 50% to the cumulative dissimilarity between treatments: detrital addition (DA), procedural control (PC) and control (C) (* denotes significant differences between treatments from PERMANOVA pair-wise tests in Table 3.2).

Taxon	**Week 2**		**Week 4**		**Week 8**		**Week 12**	
	Contribution	Dissimilarity	Contribution	Dissimilarity	Contribution	Dissimilarity	Contribution	Dissimilarity
SITE 2	%	%	%	%	%	%	%	%
C vs. PC		**34.57**		**29.80***		**22.84**		**21.35**
Prionospio aucklandica	45.89		40.71		28.15		23.81	
Macomona liliana					10.46			
Nereidae					10.08		8.24	
Heteromastus filiformis	11.38		8.33					
Oligochaeta			9.67				20.69	
C vs. DA		**32.13**		**37.78***		**31.62***		**24.31***
Prionospio aucklandica	48.71		47.43		37.51		25.28	
Heteromastus filiformis	10.20		9.51		11.18			
Macomona liliana					7.90			
Oligochaeta							25.06	
DA vs. PC		**33.24**		**35.46**		**29.21***		**21.12**
Prionospio aucklandica	40.48		40.76		37.90		27.78	
Heteromastus filiformis	14.62		12.68		13.48		9.61	
Oligochaeta							13.89	
Austrovenus stutchburyi					7.71			

The significant differences between treatments at both sites were driven mainly by the numerically dominant polychaete species *P. aucklandica*. Trends in the abundance of *P. aucklandica* are similar to those found in overall abundance. Therefore, it is likely that decreases in overall abundance (Figure 3.3A & B) are mostly due to the decrease in *P. aucklandica* (Figure 3.5A & B). Decreases in *P. aucklandica* were associated with the addition of detritus (at both sites), as well as the short-term disturbance of mixing the sediment (at Site 2). Hence, *P. aucklandica* decreased significantly in DA plots compared with controls at Site 1, after 8 weeks (Figure 3.5A). However, at Site 2 *P. aucklandica* decreased significantly in DA and PC plots at 4 weeks (procedural effect) and only in DA plots after 8 weeks (detrital addition effect) (Figure 3.5B).

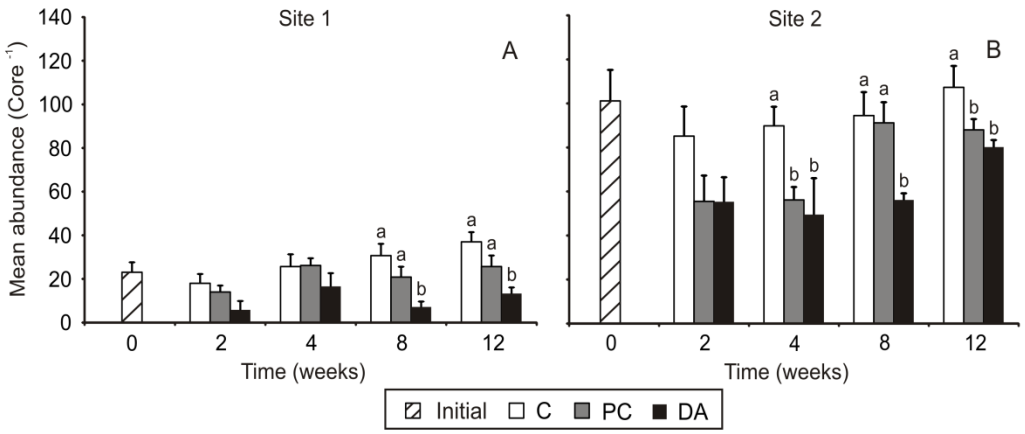

Figure 3.5. Mean abundance of *Prionospio aucklandica* at Site 1 and 2 on day 0 (initial), and 2, 4, 8, and 12 weeks following the detrital manipulation in detrital addition (DA), procedural control (PC) and control (C) plots. Letters above bars indicate significant differences between treatments at each sampling date (Newman-Keuls, $p < 0.05$), where bars sharing the same letter are not significantly different from each other. Data are the mean (+SE) of 6 replicate cores.

3.4 Discussion

Mangrove detritus was successfully added to the sediment on two unvegetated intertidal flats, where it remained for at least 12 weeks. Several studies have manipulated detrital additions to determine the role of different detrital sources in creating small-scale variability of soft-sediment benthic communities (e.g. Bishop et al. 2010; Bishop & Kelaher 2008; Kelaher & Levinton 2003; Taylor et al. 2010).

However, the use of mangrove detritus has been limited to only a few studies (Bishop & Kelaher 2008; Zhou 2001), and comparisons between sites with varying sedimentary properties and communities are lacking. My study explored whether exported mangrove detritus is an important factor in controlling benthic community structure on intertidal flats. The study discovered that community responses to the experimental manipulations were site-specific. However, responses of benthic macrofauna to mangrove detrital deposition were subtle and involved changes in the relative abundances of some species rather than shifts in whole community composition.

The two sites in Whangamata Harbour exhibited variation in benthic community responses to the manipulative experiment. The procedure of mixing the sediment had significant short-term effects (at least 4 weeks) on macrofaunal assemblages, in muddy sediments (Site 2). Therefore, detrital addition effects could not be delineated from this disturbance. In contrast, sediment mixing did not elicit a disturbance response of the macrofaunal community in sandy sediments (Site 1). Previous experiments (on mud and sand flats) that have manipulated sediments and added detrital material have concluded that the procedure of the one-off mixing/burial of detrital material does not cause variation in macrofaunal assemblages away from an ambient state (Kelaher & Levinton 2003; Olabarria et al. 2010). However, results reported here suggest that short-term disturbance effects of small-scale surficial sediment mixing occur in finer sediments with high mud content, but not in sandy areas. Although this result does not agree with previous detrital addition experiments (Kelaher & Levinton 2003; Olabarria et al. 2010), it fits with the literature of mechanical disturbances on soft-sediment communities. Physical disturbances have been found to cause a greater response in muddy sediments compared to sandy sediments (e.g. Ferns et al. 2000; Schratzberger & Warwick 1999).

Macrofaunal assemblages responded to the deposition of detritus within 2 weeks at the sandy site (Site 1). However, in muddier sediments (Site 2), the effects of the detrital treatment could only be delineated from procedural effects after 8 weeks. Detrital addition (at both sites) and procedural (at Site 2) effects resulted in the decrease of overall macrofaunal abundance, which was largely driven by the reduction in the numerically dominant polychaete species *P.*

aucklandica and to a lesser extent other dominant polychaete species (*A. trifida* at Site 1 and *H. filiformis* at Site 2). Previous studies examining the effects of macroalgae on intertidal communities show similar results to this study, and detected only subtle decreases in a few fauna following detrital additions. These studies hypothesized that the intertidal communities examined are accustomed to detrital depositions, and that these systems may be effective at recycling nutrients to buffer the effects of organic enrichment (Olabarria et al. 2010; Rossi 2006).

Mangrove detritus has been found to decrease macrofaunal abundance and diversity at high levels of addition, which was attributed to the effects of tannins leaching from leaf litter (Bishop & Kelaher 2008; Lee 1999). However, at lower levels of deposition, mangrove detritus (and other sources) had small positive effects on macrofauna abundance and species richness (Bishop & Kelaher 2008). Additionally, meiofaunal colonisation is enhanced in sediments containing mangrove detritus (Zhou 2001). This study only investigated responses of macrofauna and therefore meiofaunal response in this system is unknown. Future research ventures could determine responses of lower trophic levels to mangrove detrital deposition.

The distribution and composition of soft-sediment communities exhibit both temporal and spatial heterogeneity as a result of abiotic and biotic factors (Morrisey et al. 1992; Thrush 1991; Thrush et al. 1994). Consequently, responses to the burial of algal wrack have been found to differ among sites with different sediment and benthic community properties (Rossi & Underwood 2002). Although sites of the current study had significantly different communities and physical properties, the subtle responses in the relative abundances of dominant polychaetes were the same for both sites. In contrast, the burial of *Ulva* sp. wrack, in Australia, resulted in species responses that were dependent on initial abundances of species prior to burial, where different species responded at sandy sites compared with muddy sites (Rossi & Underwood 2002). Here, both sites responded similarly to the enrichment of mangrove detritus, which could indicate that only a few particular species (e.g. *P. aucklandica*) are sensitive to organic enrichment and these responses are not dependent on initial species abundances.

Both mangrove detrital enrichment and the disturbance of sediment mixing created subtle changes in the relative abundances of a few species, but species diversity was unaffected and community shifts did not occur. Temperate intertidal estuarine flats are highly productive systems that are driven by large concentrations of microphytobenthos (benthic microalgae; MacIntyre et al. 1996; Miller et al. 1996). Microphytobenthos represents a highly nutritive and preferred food source to many primary consumers, whereas mangrove detritus is a relatively refractory poor-quality food resource (Miller et al. 1996; Nordhaus et al. 2011). Mangrove litter has a high C:N (carbon:nitrogen) ratio compared with other food sources, which has been associated with low nutritional quality to benthic consumers (Enríquez et al. 1993; Nordhaus et al. 2011; Skov & Hartnoll 2002). During leaf decomposition, carbon is lost and nitrogen is enriched, resulting in a reduction of leaf C:N ratios (Chapter 2). In temperate mangroves, decomposition is slow (63 - 88 days to decay by 50%) compared to tropical regions (Chapter 2), therefore reductions in C:N ratio will be slower. In addition, C:N ratios of mangrove litter (47; Chapter 2) are higher than those of microphytobenthos (5 - 15; Cook et al. 2004; Cook et al. 2009; Fell et al. 1984). Exported mangrove organic matter can support food webs in tropical systems such as coral reefs; however these habitats are often nutrient limited and litter decomposition is rapid compared with temperate systems (Bosire et al. 2005; Granek et al. 2009; Lapointe et al. 1987). In temperate estuarine sediments that contain a highly productive and abundant microphytobenthic biomass (MacIntyre et al. 1996; Miller et al. 1996), mangrove detrital material may not offer the same importance in directly supporting macrofaunal communities.

The amount of detritus (dry weight) used in this manipulation is similar to the upper end of the range added in previous studies (e.g. Bishop et al. 2010; Bishop & Kelaher 2007; Kelaher et al. 2003; Levinton 1985; Olabarria e al. 2010; Taylor et al. 2010). In some of these earlier studies, a similar amount of detritus addition has resulted in initially negative responses of some macrofauna, as a result of sediment anoxia from detrital breakdown (Bishop & Kelaher 2008; Kelaher & Levinton 2003). However, the large amount of detritus added during this experiment (amount fallen from the trees during November – February) did not create anoxic conditions or produce films of sulphide reducing bacteria (pers. obs.)

that have been observed in previous studies. Moreover, the detrital addition of this study instigated only subtle responses, even though the level of addition was relatively large. This result further suggests that mangrove detrital deposition in this intertidal system plays an insignificant role in shaping benthic macrofaunal communities.

Mangrove leaf litter is highly refractory and decomposes relatively slowly in temperate regions (e.g. t_{50} = 63 - 88 days; Chapter 2). Conversely, in some tropical regions mangrove litter can lose 50% of its weight within one week (e.g. Bosire et al. 2005; Sánchéz-Andres et al. 2010). The relatively slow decomposition of temperate mangrove leaf litter (Chapter 2) could provide one explanation for the lack of macrofaunal response to the mangrove detrital additions found by this investigation. Some previous studies have found strong community responses to detrital deposition, but they have added macroalgae and/or seagrass detritus (e.g. Bishop et al. 2010; Kelaher & Levinton 2003; Kelaher et al. 2003; Rossi & Underwood 2002), which could represent a more nutritive source of food to benthic consumers (lower C:N ratios than mangrove leaf litter; Enríquez et al. 1993; Kristensen 1994). Additionally, decay rates of macroalgae and seagrass are in some cases faster than mangrove litter (de Boer 2000; Enríquez et al. 1993; Holmer & Olsen 2002). A review of the available literature on plant decomposition rates in both tropical and temperate regions, found that the decay rate (k, day $^{-1}$) of seagrass and macroalgae was often greater than for mangrove litter, although there was some overlap in the range of decay rates (seagrass k = 0.0007-0.0357 day $^{-1}$, macroalgae k = 0.0038-0.0321 day $^{-1}$, mangrove k = 0.0002-0.0189; Enríquez et al. 1993). A subtropical experiment found seagrass decay to be almost twice that of mangrove litter (mangrove t_{50} = 69 days, seagrass t_{50} = 41 days; de Boer 2000). Slow decay could be associated with minimal changes to sediment biogeochemistry during decomposition. Therefore, perhaps in temperate regions mangrove litter is not biologically available to macrofaunal consumers, due to the relatively slow rates of decomposition.

Although mangrove detritus did not represent an important factor in controlling macrofaunal community variability in this study, previous research has found that detrital inputs can increase the chlorophyll *a* concentration of the

sediment (indicator of microphytobenthos biomass; Bishop & Kelaher 2007, 2008; Bishop et al. 2007; Levinton 1985; Rossi & Underwood 2002). The decomposition of plant material can release nutrients that could potentially accelerate and fuel the growth of micro-organisms such as benthic microalgae, a key source of primary production on intertidal flats (Miller et al. 1996; Rublee 1982). The current study found no impact of mangrove detrital input on chlorophyll *a* concentrations (and therefore microphytobenthos). However, it has been previously noted that increases in microphytobenthos can be concealed when an effective grazing community is present (Bishop et al. 2007; Levinton 1985). Therefore, in the current study positive effects of mangrove detritus on microphytobenthos could have been suppressed by benthic grazing species. Previous research has recorded an increase in microphytobenthic biomass associated with detrital deposition, but none have yet measured whether this increase in biomass relates to increased productivity of the system (Bishop & Kelaher 2007, 2008; Bishop et al. 2007; Levinton 1985; Rossi & Underwood 2002). Future research could endeavour to determine if mangrove detrital depositions enhance primary productivity of microphytobenthos by releasing nutrients during the decomposition process.

My study found that mangrove detrital deposition is likely to represent a minor role in controlling benthic community variability. However, data was highly variable and hypotheses were tested at small spatial scales (1 m^2 plots). Soft-sediment community distributions are patchy in space and time and it is often difficult to obtain statistical power in field designs (Thrush 1991). Although the current field experiment incorporated plot sizes (0.25 - 1 m^2) and replication levels (3 - 7 replicates) comparable to other studies (e.g. Bishop & Kelaher 2007, 2008; Kelaher et al. 2003; Levinton 1985; Rossi & Underwood 2002), statistically stronger results may have been obtained if the experiment encompassed a larger scale with greater replication. A potential limitation of the study design is that recruitment effects may have been overlooked, where small juveniles could be excluded by the sampling techniques utilised (sieve size of 500 µm). Furthermore, the temporal scale of the experiment (12 weeks) may have been too short to encompass any recruitment effects of the detrital addition. Studies of a similar nature have often sampled benthic assemblages on just one or two occasions

following a detrital enrichment (e.g. Bishop et al. 2010; Bishop et al. 2007; Bishop & Kelaher 2008; Levinton 1985; Olabarria et al. 2010; Rossi & Underwood 2002; Rossi 2006; Taylor et al. 2010). However, results presented here demonstrate that one off sampling can fail to detect temporal effects such as the short-term disturbance effect found in muddy sediments. For instance, limiting the current study to sampling once at 8 weeks (as in similar studies) would have yielded very different conclusions and discussions. Temporally restricted sampling would have concluded that both sites responded similarly to the manipulations and the experimental design would have missed short-term procedural effects.

3.5 Conclusions

It is suggested that mangrove detrital deposition plays a minor role in shaping benthic community variability on temperate intertidal flats at the small scale analysed. Site-specific responses included disturbance effects in muddier sediments, but later both sandy and muddy communities responded similarly to detrital deposition. The addition of mangrove detritus did not create shifts in benthic community composition or diversity, but rather caused subtle changes in the relative abundances of a few taxa. The slow decomposition and low nutritional value of temperate mangrove detritus compared with other detrital sources could provide explanation for why a relatively large mangrove detrital deposition was found to represent a minor factor in shaping community variability of temperate intertidal flats. It is proposed that in these temperate intertidal systems, the highly productive and nutritive microphytobenthos may be a dominant factor in controlling spatio-temporal variability of benthic macrofaunal communities. Therefore, effects of mangrove detrital deposition may not be an important factor affecting macrofaunal communities directly, but could influence them indirectly via lower trophic levels. Future studies could endeavour to determine if mangrove detritus affects macrofaunal communities indirectly by fuelling benthic microbial primary productivity, or by influencing the distribution of meiofaunal communities.

CHAPTER FOUR

THESIS SUMMARY AND RECOMMENDATIONS

4.1 Thesis summary

Mangroves in tropical regions are highly productive habitats that provide an essential subsidy of organic matter to nearby spatially distinct coastal habitats (Granek et al. 2009; Guest et al. 2006; Nordhaus & Wolff 2007; Odum & Heald 1975; Sheaves & Molony 2000; Werry & Lee 2005). Temperate mangrove forests are different to those in the tropical regions in several ways. Mangrove forests in temperate regions are less productive (smaller tree heights) and contain less tree species than those of tropical regions (reviewed by Morrissey et al. 2010). These dissimilarities suggest that the information collected from tropical mangrove systems cannot be readily extrapolated to temperate regions. For example, the limited ecological knowledge of temperate mangrove forests provides little understanding of whether these systems will offer the same organic matter subsidy as found in the tropics. This thesis aimed to increase the current knowledge deficit of the ecological services that temperate mangroves provide to estuarine ecosystems. The two research chapters followed mangrove organic matter from tree fall, through decomposition, to unvegetated intertidal flats where it potentially supports benthic communities. The aim of the investigations was to determine if the linkages between tropical mangrove production and estuarine ecosystem function (as depicted in Figure 1.1) apply in a temperate setting.

The first section of this thesis (Chapter 2) focused on the production of mangrove detritus in Whangamata Harbour, through the fall of litter and the subsequent decomposition into a detrital form. In order to establish the role mangroves play in estuarine ecosystem function it is important to ascertain the extent of organic matter production. To determine the magnitude of organic matter contribution to the estuary, mangrove annual productivity was estimated in Whangamata Harbour by measuring litterfall. Productivity (litterfall) estimates in Whangamata Harbour were equivalent to 3.24 - 5.38 t DW ha^{-1} yr^{-1}, which fell within the range reported from other sites in New Zealand (May 1999; Oñate-

Pacalioga 2005; Woodroffe 1985). However, the result confirmed the existence of regional variability in mangrove productivity. Productivity estimations in the Whangamata Harbour mangrove forest are less than that typically measured at tropical latitudes. However, a review of the literature found some overlap with the lower range of tropical productivity (Cunha et al. 2006; de Boer 2000; reviewed by Morrisey et al. 2010).

Decomposition of mangrove litter into detritus is an important process that governs the length of time mangrove organic matter will take to enter the estuarine detrital pool, and therefore potentially the marine food web (Fell et al. 1984; Snedaker 1978; Wafar et al. 1997). Degradation rates of litter were found to be dependent on litter type and burial state. However, the local conditions of different sites (such as sediment and benthic community characteristics) and tidal position did not represent important factors in controlling degradation rates. The investigation found that the decay of leaf litter was determined in part by burial state (i.e. whether the leaf was left on the surface or buried). The burial of leaf litter resulted in decay rates that were significantly slower than surficial litter, in both weight and carbon loss. Therefore, the frequent burial of litter that is retained on the forest floor (pers. obs.) is likely to result in slow nutrient recycling within the forest in this temperate system. Exported litter on the other hand will probably decay relatively fast, because it is likely to remain on the sediment surface. Previous research has suggested that tidal elevation has an influence on litter degradation (e.g. Dick & Osunkoya 2000; Mackay & Smail 1996; Robertson 1988; Woitchik et al. 1997). However, this study found no differences in decomposition as a result of the position of the litter in the intertidal zone. Differences in submergence periods between positions at the field sites were perhaps not large enough to drive a significant response.

Mangrove clearance projects in New Zealand have frequently allowed mulched wood and root material to remain *in situ* (pers. obs.; Lundquist et al. 2012). The decomposition rates of wood and root material are therefore an important issue, as they will influence the recovery times of clearance sites. This thesis has found that anoxic decay of wood takes a third longer than surficial decay, which is significant given the large amount of wood matter that is buried following mangrove clearances (pers. obs.). The results reported in Chapter 2

have confirmed observations that wood and root material will take years to decay. Therefore, mangrove removal schemes, with the intention of leaving roots and wood matter *in situ,* will potentially delay site recovery times.

The second part of this thesis (Chapter 3) concentrated on the functional role of exported mangrove detritus, as a factor in controlling benthic community variability on intertidal flats. Mangrove detritus was used to enrich the sediment at two intertidal flats (sand and muddy sand) in Whangamata Harbour. It was expected that the benthic communities inhabiting the two sites would respond differently to the deposition of detritus (Rossi & Underwood 2002). However, this manipulative experiment found that the two different communities responded to the detrital additions similarly, where the same taxa at both sites were responsible for community changes. The procedure of the experiment (mixing the sediment) elicited a significant short-term response in the muddy sediments, which was not shown in the sandy sediments. While the experiment found a benthic community response to depositions of mangrove detritus, it was a relatively subtle one. The large volume of mangrove detrital material added (equivalent to summer litterfall) created only slight changes in the relative abundances of a few species, rather than shifts in whole community composition and diversity. These subtle changes suggest that mangrove detrital depositions play a relatively minor role in structuring benthic communities of estuarine intertidal soft-sediments. This could be attributed to the slow decay of mangrove litter, compared to other detrital sources (Enríquez et al. 1993). It is suggested that the abundant microphytobenthic biomass that inhabits such intertidal flats may be of greater importance in supporting macrofaunal communities of the benthos. However, my study did not test other aspects of ecosystem function, such as the potential role mangrove detritus could have in faunal colonisation, fuelling primary productivity, and structuring lower trophic communities (e.g. meiofauna).

The studies that comprise this thesis have together addressed an omission in temperate mangrove ecological research, by determining the role of mangrove detrital production in supporting estuarine communities as a spatial subsidy. The importance of mangrove litter as a spatial subsidy depends firstly upon the input of organic matter into the system, and secondly the biological availability of the organic matter to marine organisms (Odum & Heald 1975). In tropical regions,

the large mangrove litter production and fast decomposition into detritus means that many coastal invertebrate communities are reliant on this primary food source (Granek et al. 2009; Sánchéz-Andres et al. 2010; Sheaves & Molony 2000; Snedaker 1978; Werry & Lee 2005). However, my study has demonstrated that temperate estuarine communities may be less reliant on mangrove organic matter as a subsidy, possibly as a result of lower production and decomposition rates.

4.2 Conclusions and recommendations for future research

This thesis has shown that temperate mangrove forests function differently to those of tropical regions. Temperate mangrove productivity is frequently less than in tropical regions; however there is some overlap with the lower tropical production range. Decomposition rates of mangrove material in temperate New Zealand are less than in tropical regions and therefore the fate of leaf litter in temperate estuaries is likely to be different. Initially slow decomposition rates could be associated with a greater chance of export from the forest. However, the role of exported mangrove detritus in shaping communities of unvegetated intertidal flats was found to be minimal, and only a few species responded to sediment enrichment with detritus. Perhaps the rich microphytobenthic biomass in temperate intertidal systems is a dominant factor in controlling variability in soft-sediment macrofaunal communities.

Further research is required to establish the fate of mangrove litter, as this remains essentially unknown in a temperate setting. Some food web studies have suggested that the movement of organic matter from temperate and sub-tropical forests is limited (e.g. Alfaro et al. 2006; Guest & Connolly 2004). Conversely, a New Zealand study found that retention of litter within various Auckland forests was 8-50%, suggesting some litter export out of the forest (Oñate-Pacalioga 2005). The litter export from, or retention within, forests will influence the rate of further decomposition, and consequently the energy dynamics of the estuary. Litter that is retained and buried within the forest (pers. obs.) will probably result in relatively slow nutrient recycling within the forest. If litter is exported, decay into detritus could be faster, as surficial decomposition is likely to be aided by macrofaunal activity as well as climatic conditions. Various tropical studies report the frequent export of mangrove litter across habitat boundaries, as well as the subsequent

uptake by marine organisms (e.g. Granek et al. 2009; Sheaves & Molony 2000; Werry & Lee 2005). Therefore, studies that investigate the movement of litter across the mangrove forest boundary are essential in order to quantify the ecological services provided by temperate mangrove forests to coastal habitats.

Mangrove litterfall and litter decomposition rates have been associated with many biotic and abiotic factors. Decomposition rates and litterfall production are influenced by physical variables such as temperature, evapotranspiration, rainfall, solar radiation and tidal regime (Dick & Osunkoya 2000; Imgraben & Dittmann 2008; Sánchéz-Andres et al. 2010; Steinke & Charles 1986). In addition, decomposition has been found to be influenced by animals that aid in the breakdown through litter shredding (Oñate-Pacalioga 2005; Werry & Lee 2005). Therefore, it is expected that mangrove forest production and litter decomposition rates will be highly site-specific. Further studies similar to those presented here that encompass a larger range of sites, will potentially show clearer regional trends of the variability in mangrove litter dynamics between sites.

My study (Chapter 3) found that mangrove detritus is likely to play a relatively minor role in shaping estuarine macrofaunal assemblages in temperate New Zealand. However, the study did not incorporate lower trophic groups (e.g. meiofauna). A previous tropical field experiment found that meiofaunal colonisation of sediments was enhanced by the presence of mangrove detritus (Zhou 2001). Future studies could aspire to determine the role that temperate mangrove organic matter deposition plays in shaping meiofaunal communities and controlling faunal colonisation. Detrital deposition and decomposition releases nutrients into the sediment and has been associated with an increase in the production of microalgae (an important source of primary productivity in estuarine systems; Bishop & Kelaher 2007; Bishop et al. 2007; Levinton 1985; Miller et al. 1996; Rossi & Underwood 2002; Rublee 1982). Mangrove detrital deposition in temperate estuaries could play a significant role in fuelling primary production of the sediments, by increasing microphytobenthic biomass. Examination of how mangrove detritus affects primary production in estuarine sediments would advance the current state of mangrove ecological knowledge in New Zealand and in temperate latitudes in general.

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APPENDICES

Appendix 1:

Table A1.1. Mean (±SE) percentage weight remaining for roots (pneumatophores) during decomposition at different decomposition bag positions, at Site 1 and 2.

Time (Days)	MC-s	MC-b	ME-s	ME-b
Site 1				
0	100.0	100.0	100.0	100.0
24	79.7 ± 6.5	77.9 ± 4.1	83.7 ± 7.1	72.4 ± 3.6
51	47.0 ± 16.4	67.9 ± 2.4	78.1 ± 6.0	67.8 ± 5.8
81	48.5 ± 3.5	66.2 ± 10.4	55.9 ± 8.0	65.3 ± 1.7
169	51.3 ± 3.5	59.9 ± 6.5	61.2 ± 4.1	62.9 ± 12.2
357	31.3 ± 4.3	51.2 ± 4.2	32.7 ± 7.0	35.0 ± 22.2
Site 2				
0	100.0	100.0	100.0	100.0
24	68.7 ± 9.7	72.3 ± 4.0	72.4 ± 4.5	73.7 ± 3.3
51	55.3 ± 3.7	56.2 ± 4.8	68.6 ± 8.6	70.1 ± 5.1
81	55.8 ± 3.9	64.7 ± 5.7	64.3 ± 6.1	73.5 ± 2.7
169	61.8 ± 10.0	56.1 ± 3.7	53.6 ± 16.0	54.2 ± 5.5
357	38.8 ± 9.2	38.6 ± 1.9	65.9 ± 20.3	40.2 ± 4.3

Table A1.2. Mean (±SE) percentage weight remaining for leaves during decomposition at different decomposition bag positions, at Site 1 and 2.

Time (days)	MC-s	MC-b	ME-s	ME-b	MT-s	LT-s
Site 1						
0	100.0	100.0	100.0	100.0	100.0	100.0
11	83.2 ± 1.7	77.6 ± 4.5	82.8 ± 2.2	74.9 ± 0.7	78.3 ± 4.0	87.9 ± 2.2
24	69.9 ± 4.5	67.8 ± 3.7	67.0 ± 4.2	67.7 ± 2.8	74.1 ± 3.9	71.9 ± 5.3
38	65.5 ± 3.4	61.3 ± 3.6	64.6 ± 3.3	66.4 ± 4.0	71.5 ± 5.0	63.5 ± 2.1
51	60.9 ± 6.2	58.6 ± 2.8	59.1 ± 5.6	59.9 ± 2.3	50.7 ± 4.3	55.2 ± 4.2
81	47.5 ± 3.6	48.5 ± 6.0	52.3 ± 8.0	52.8 ± 2.9	28.9 ± 4.8	44.7 ± 2.5
169	17.7 ± 5.2	52.0 ± 3.5	30.6 ± 1.3	40.5 ± 4.5	18.7 ± 7.0	28.0 ± 5.6
357	4.6 ± 2.6	43.6 ± 4.8	4.0 ± 2.4	41.3 ± 2.4	8.8 ± 1.5	7.2 ± 1.3
Site 2						
0	100.0	100.0	100.0	100.0	100.0	100.0
11	70.9 ± 3.7	75.7 ± 2.1	74.5 ± 3.3	72.7 ± 4.6	83.9 ± 4.5	84.7 ± 6.6
24	70.2 ± 6.8	69.6 ± 3.4	67.7 ± 2.6	68.9 ± 1.8	68.3 ± 3.3	74.0 ± 1.4
38	64.7 ± 4.5	62.7 ± 6.1	54.6 ± 4.4	66.7 ± 9.6	57.4 ± 5.2	65.3 ± 2.4
51	57.1 ± 5.4	57.5 ± 1.0	63.9 ± 6.4	61.9 ± 0.9	42.0 ± 5.9	59.3 ± 5.8
81	44.0 ± 2.7	53.6 ± 4.5	43.5 ± 6.1	54.8 ± 4.3	35.5 ± 1.4	36.2 ± 4.5
169	24.0 ± 6.2	51.6 ± 1.3	30.5 ± 7.7	52.1 ± 2.6	25.4 ± 11.1	22.0 ± 6.0
357	6.2 ± 3.5	35.5 ± 7.6	1.0 ± 0.7	35.7 ± 6.1	7.3 ± 4.8	4.4 ± 1.7

Table A1.3. Mean (±SE) percentage weight remaining for wood during decomposition at different decomposition bag positions, at Site 1 and 2.

Time (days)	MC-s	MC-b	ME-s	ME-b	MT-s	LT-s
Site 1						
0	100.0	100.0	100.0	100.0	100.0	100.0
24	98.8 ± 13.9	85.9 ± 3.1	86.9 ± 1.3	85.0 ± 1.4	94.0 ± 11.9	92.6 ± 6.9
51	80.6 ± 3.6	84.2 ± 10.3	82.7 ± 5.8	96.2 ± 13.5	76.7 ± 5.9	83.4 ± 6.8
81	77.1 ± 6.3	95.9 ± 24.6	78.9 ± 4.6	73.5 ± 2.5	76.5 ± 2.0	75.2 ± 2.9
169	71.8 ± 3.4	81.4 ± 4.8	68.3 ± 2.0	73.1 ± 2.5	69.5 ± 7.2	67.9 ± 4.2
262	64.6 ± 5.0	67.6 ± 3.3	62.7 ± 4.3	76.1 ± 4.7	67.5 ± 6.1	62.2 ± 6.4
357	49.6 ± 6.7	75.4 ± 4.7	60.6 ± 13.5	67.8 ± 14.9	62.5 ± 8.7	67.4 ± 8.1
Site 2						
0	100.0	100.0	100.0	100.0	100.0	100.0
24	79.6 ± 5.1	83.9 ± 4.9	81.9 ± 3.3	90.1 ± 4.9	85.0 ± 3.1	81.3 ± 2.6
51	81.9 ± 2.1	91.6 ± 9.0	83.4 ± 4.4	82.6 ± 9.5	76.0 ± 2.9	76.5 ± 13.1
81	72.3 ± 6.9	79.0 ± 6.6	72.7 ± 1.6	75.0 ± 7.3	79.4 ± 4.7	72.1 ± 4.3
169	67.7 ± 7.7	69.2 ± 1.8	72.7 ± 8.4	72.8 ± 1.1	74.7 ± 3.6	74.3 ± 13.6
262	67.8 ± 6.2	79.9 ± 5.6	71.0 ± 2.6	69.4 ± 4.5	74.4 ± 5.5	72.9 ± 9.2
357	51.9 ± 14.5	68.3 ± 2.1	68.6 ± 5.0	70.2 ± 8.7	57.3 ± 4.0	65.4 ± 1.2

Table A1.4. Mean (±SE) total carbon (%) in leaves during decomposition at different decomposition bag positions, at Site 1 and 2.

Time (Days)	MC-s	MC-b	ME-s	ME-b	LT-s
Site 1					
0	45.11 ± 0.28	45.11 ± 0.28	45.11 ± 0.28	45.11 ± 0.28	45.11 ± 0.28
11	46.82 ± 0.36	47.35 ± 0.34	47.44 ± 0.68	46.67 ± 0.80	45.12 ± 0.50
24	46.95 ± 1.29	47.05 ± 0.45	47.61 ± 0.80	48.19 ± 0.65	45.67 ± 0.90
38	44.57 ± 1.40	48.46 ± 1.04	43.98 ± 2.27	48.18 ± 0.46	44.21 ± 1.56
51	42.98 ± 1.04	47.96 ± 0.37	46.04 ± 1.15	46.80 ± 1.34	46.65 ± 0.95
81	42.20 ± 2.80	47.91 ± 1.09	44.69 ± 1.25	46.50 ± 0.47	43.83 ± 1.70
169	42.24 ± 2.21	45.77 ± 1.27	41.82 ± 2.45	49.40 ± 0.14	44.08 ± 2.62
Site 2					
0	45.11 ± 0.28	45.11 ± 0.28	45.11 ± 0.28	45.11 ± 0.28	45.11 ± 0.28
11	47.27 ± 0.17	46.95 ± 0.99	46.78 ± 0.27	47.02 ± 0.98	46.23 ± 0.64
24	45.91 ± 1.97	47.09 ± 0.76	46.31 ± 1.20	47.73 ± 0.87	46.36 ± 0.35
38	45.15 ± 0.91	48.00 ± 0.34	47.57 ± 0.81	46.58 ± 1.36	47.56 ± 0.76
51	43.28 ± 1.66	48.54 ± 0.49	44.47 ± 2.47	45.39 ± 2.89	46.21 ± 0.54
81	42.72 ± 3.58	48.43 ± 1.40	42.35 ± 2.83	46.61 ± 1.06	43.14 ± 3.85
169	39.77 ± 2.81	47.87 ± 0.28	37.61 ± 1.78	43.79 ± 2.13	39.48 ± 4.48

Table A1.5. Mean (±SE) total nitrogen (%) in leaves during decomposition at different decomposition bag positions, at Site 1 and 2.

Time (Days)	MC-s	MC-b	ME-s	ME-b	LT-s
Site 1					
0	0.96 ± 0.03	0.96 ± 0.03	0.96 ± 0.03	0.96 ± 0.03	0.96 ± 0.03
11	0.96 ± 0.02	1.02 ± 0.04	1.01 ± 0.02	0.91 ± 0.02	0.97 ± 0.02
24	1.12 ± 0.03	1.14 ± 0.02	1.14 ± 0.04	1.05 ± 0.02	1.11 ± 0.07
38	1.15 ± 0.03	1.22 ± 0.05	1.15 ± 0.04	1.07 ± 0.04	1.22 ± 0.05
51	1.23 ± 0.03	1.18 ± 0.04	1.17 ± 0.05	1.09 ± 0.04	1.31 ± 0.03
81	1.28 ± 0.07	1.37 ± 0.17	1.32 ± 0.08	1.16 ± 0.06	1.30 ± 0.08
169	1.38 ± 0.16	1.33 ± 0.05	1.35 ± 0.05	1.30 ± 0.03	1.42 ± 0.15
Site 2					
0	0.96 ± 0.03	0.96 ± 0.03	0.96 ± 0.03	0.96 ± 0.03	0.96 ± 0.03
11	1.05 ± 0.02	1.01 ± 0.04	0.98 ± 0.01	0.91 ± 0.06	1.04 ± 0.02
24	1.12 ± 0.05	1.08 ± 0.02	1.11 ± 0.01	1.03 ± 0.05	1.14 ± 0.01
38	1.18 ± 0.02	1.19 ± 0.03	1.18 ± 0.04	1.02 ± 0.08	1.30 ± 0.01
51	1.19 ± 0.04	1.18 ± 0.04	1.23 ± 0.05	1.02 ± 0.05	1.33 ± 0.03
81	1.31 ± 0.06	1.30 ± 0.07	1.16 ± 0.05	1.14 ± 0.05	1.34 ± 0.15
169	1.25 ± 0.06	1.30 ± 0.06	1.26 ± 0.09	1.18 ± 0.04	1.37 ± 0.20

Table A1.6. Mean (±SE) carbon to nitrogen ratio (C:N) in leaves during decomposition at different decomposition bag positions, at Site 1 and 2.

Time (Days)	MC-s	MC-b	ME-s	ME-b	LT-s
Site 1					
0	47.25 ± 1.20	47.25 ± 1.20	47.25 ± 1.20	47.25 ± 1.20	47.25 ± 1.20
11	49.00 ± 1.16	46.49 ± 1.80	46.96 ± 1.49	51.10 ± 0.77	46.71 ± 0.44
24	41.75 ± 0.74	41.26 ± 0.44	41.69 ± 0.88	45.96 ± 0.97	41.49 ± 2.00
38	38.72 ± 1.05	39.90 ± 1.22	38.14 ± 2.36	45.13 ± 1.83	36.35 ± 1.22
51	35.07 ± 0.17	40.72 ± 1.32	39.59 ± 2.27	42.93 ± 1.51	35.54 ± 1.16
81	32.90 ± 1.49	35.52 ± 3.36	34.08 ± 1.38	40.18 ± 1.54	33.81 ± 1.52
169	31.14 ± 2.37	34.49 ± 0.73	30.99 ± 1.99	38.02 ± 0.97	31.48 ± 1.51
Site 2					
0	47.25 ± 1.20	47.25 ± 1.20	47.25 ± 1.20	47.25 ± 1.20	47.25 ± 1.20
11	45.08 ± 0.91	46.69 ± 1.06	47.84 ± 0.83	51.71 ± 2.68	44.36 ± 1.28
24	41.11 ± 1.32	43.44 ± 0.66	41.88 ± 1.33	46.71 ± 2.22	40.75 ± 0.59
38	38.16 ± 1.19	40.42 ± 0.80	40.38 ± 1.96	45.73 ± 2.59	36.54 ± 0.57
51	36.53 ± 1.76	41.26 ± 1.75	36.20 ± 1.90	44.29 ± 1.03	34.84 ± 0.65
81	32.62 ± 1.47	37.30 ± 1.09	36.47 ± 1.14	40.83 ± 1.34	32.58 ± 1.86
169	31.74 ± 1.60	36.80 ± 1.71	29.94 ± 1.12	37.22 ± 1.17	28.95 ± 1.26