Implications of sea-level rise on estuarine benthic biodiversity and ecosystem functioning

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Abstract

Estuarine habitats are among the most productive ecosystems around the globe. The macroinvertebrate communities within these habitats underpin ecosystem functioning and therefore the provision of ecosystem services valued by society. Due to their geographic positioning, coastal areas represent a human-ocean interface and are consequently at the forefront of anthropogenic pressure. Sea-level rise (SLR) is one major consequence of anthropogenic climate change that poses a great threat to coastal environments and will result in extensive intertidal area loss. There is an evident bias within coastal SLR research towards the implications for the abiotic environment such as impacts on geomorphology but the ecological implications however, have been largely overlooked despite their likely significance. In this thesis, I aim to address this knowledge gap by investigating how benthic macroinvertebrate communities and their contributions to ecosystem function will respond to SLR within a large temperate estuary.

To explore how benthic macroinvertebrate community structure will respond to future SLR, I employed a space-for-time approach. In this study, I considered site depth as a proxy for SLR to gauge how macroinvertebrate communities may shift with increasing depth as sea level is elevated. This study was based on data obtained from 119 unvegetated soft-sediment sampling locations throughout Tauranga Harbour.

An initial hierarchical cluster analysis was performed on the macroinvertebrate abundance data to reveal groups of sites that shared significantly similar community structure. Three clusters of sites were identified at a > 34% similarity level with significantly different macroinvertebrate community structure. Clustered groups were generally characterised by different depth ranges that we could consider representative of intertidal, shallow subtidal and deep subtidal habitats. Similarly, depth was identified as the most important environmental variable for predicting variation in macroinvertebrate community structure using distance-based linear modelling (explaining 12%) and gradient forest analysis indicated it is important in explaining rates of compositional turnover (6%). Chl-*a*, mud content and average current speed were among the next most important predictors explaining variation in community structure (5%, 4% and 2%, respectively) and compositional turnover (6%, 3%, 4%, respectively). Functional trait analysis indicated low functional redundancy for a key intertidal suspension-feeding bivalve (*Austrovenus stutchburyi*) and the lack of a shallow subtidal functional replacement should intertidal habitats become inundated by SLR.

The findings of this thesis strongly suggest SLR and the associated environmental changes will significantly alter estuarine macroinvertebrate communities, indicating implications for ecosystem function and resilience. Key findings of this thesis will complement management strategies of coastal areas and encourage they are not treated as static systems as ecological shifts are predicted to occur with SLR over time. Well-informed management of important estuarine habitats that recognises their spatial and temporal dynamicity will be critical for ensuring ecosystem functions and services they deliver will be conserved for future generations.

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I wish to dedicate this thesis to my cousin Anatea, whom passed away in recent months. All that you had achieved in your 26 years truly amazes me. You have inspired me to use each precious day as another opportunity to keep fighting for the changes I desire to see in the world.

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Chapter 1

Introduction

Coastal environments comprise some of the world's most productive and widespread ecosystems and deliver vital ecosystem services used by humans around the globe (Costanza et al. 1997; McLusky & Elliot 2004). New Zealand's coastline is estimated to extend around 15,000 kilometres (LINZ 2020) and possesses a highly heterogeneous mosaic of habitat types ranging from exposed rocky reefs to sheltered soft-sediment estuaries. There are over 400 estuaries dominating New Zealand's coast and many with extensive intertidal areas (Hume et al. 2016). These dynamic and complex environments provide valuable habitat for benthic organisms that underpin many ecosystem services humans value such as food provision, nutrient and carbon processing, coastal protection and recreational activities (Barbier et al. 2011; Shepard et al. 2011; Duarte et al. 2013). This highlights the importance of understanding how benthic community structure and ecosystem functioning will respond to changing environmental conditions.

The significance of intertidal macro-benthic communities (i.e. organisms > 500 μm) in sustaining valued ecosystem services is well recognised. These organisms foster ecosystem functionality by contributing to important processes such as primary production, secondary production, nutrient cycling/processing, sediment stabilisation, habitat formation and carbon sequestration when undertaking activities such as bioturbation, burrowing and feeding/grazing (Snelgrove 1998; Welsh 2003; Lohrer et al. 2004; Lohrer et al. 2010; Lohrer et al. 2016; Schenone & Thrush 2020). In shallow coastal ecosystems, processes occurring in the overlying water column and upper trophic levels are also highly dependent on those taking place within sediments and the benthic macroinvertebrates act as a fundamental connection between these habitats (Duffy 2003). This connection is often referred to as benthic-pelagic coupling in which sedimentary processes facilitate exchange of nutrients, energy and mass between the seafloor and water column (Griffiths et al. 2017), thus supporting pelagic food webs and foraging seabird populations (Nilsson 1980; Bonsdorff et al. 1990). This tight coupling means that anthropogenic stressors that impact benthic communities will have cascading consequences for other interconnected ecosystems, their contributing species and overall functionality.

Not all species are equal with their contributions to ecosystem functioning and some contribute disproportionately to the services utilised by humans. There is evidence indicating larger organisms within intertidal estuarine sediments play a greater role in facilitating solute fluxes (e.g. nitrogen and oxygen) and maintaining community structure than smaller ones. In particular, large bivalves such as the suspension-feeding cockle (*Austrovenus stutchburyi*) and deposit-feeding wedge shell (*Macomona liliana*) are recognised as key contributors, often regulating community structure and functioning (e.g. Thrush et al. 2006). Furthermore, the response of ecosystem processes to reductions of large organisms can also be habitat-dependent (Hillman et al. 2020). This highlights the importance of understanding how functionally important taxa will respond to changing environmental conditions. Through their activities (e.g. feeding and bioturbating), other large macroinvertebrates also influence benthic-pelagic coupling by destabilising and oxygenating sediment (de Deckere et al. 2001; Lohrer et al. 2004; Li et al. 2017). In soft-sediments this is critical as sediment pore water oxygen concentration is important for regulating benthic processes such as denitrification, organic carbon sequestration and organic matter recycling (Canfield 1994; Kristensen & Holmer 2001; Glud 2008; Serpetti et al. 2016; Kitidis et al. 2017). This illustrates that taxa groups distinguished by functional traits (e.g. bioturbating bivalves) often hold unique roles in ecosystem functionality, suggesting that the functional group diversity response to altered environmental conditions should also be considered when assessing community structure in addition to species diversity.

Measures of biodiversity are not limited to traditional methods comparing individual species diversity indices (i.e. species richness and evenness). As all species should not be presumed as equivalent in their functional capabilities (Walker 1992; Bengtsson 1998), the idea of grouping species based on their functional traits versus focusing on the roles held by individual species has become more widespread in community ecology (Cadotte et al. 2011). Functional redundancy is usually determined by the number and abundance of species sharing similar traits and therefore carrying out similar functions (Rosenfield 2002). Exploring functional trait diversity allows us to gauge the resilience (determined by the degree of functional redundancy) associated with functional groups and therefore the functions regulating important processes such as primary production and nutrient cycling (O'Gormann et al. 2011). For example, functional groups that possess a high level of resilience include those with a greater number of species that can persist under varying stressors, such that a loss of an individual species will not necessarily mean loss of the key functions and respective ecosystem services they contribute to (Rosenfield 2002; Ellingsen et al. 2007; Naeem 2008). In marine sediments, loss of functional diversity can impact important biogeochemical processes including oxygen and phosphate fluxes (Waldbusser et al. 2004), thus having flow-on effects on overall ecosystem function (Foster & Fulweiler 2019). Furthermore, findings of Waldbusser et al. (2004) also indicated that alterations in benthic community structure (using both species and functional groups) can disturb the balance between sediment oxygen supply-demand dynamics in response to large shifts in sediment oxygen consumption rates. Thus, reinforcing the importance of exploring how both species and functional group diversity may shift with rising anthropogenic stressors.

1.1 Anthropogenic stressors

Despite high levels of ecological, economic and cultural importance, coastal ecosystems are continually threatened by anthropogenic activities (Gillanders et al. 2011; Lü et al. 2016; Seitz et al. 2018). As coastal environments exist at the interface between the land and sea, estuarine habitats act as a link between terrestrial, freshwater and marine ecosystems. This means they are positioned at the forefront of localised anthropogenic stressors such as sedimentation, eutrophication and pollution, often resulting from excess inputs of terrestrial sediment, nutrients and contaminants (Smith 2003; Jaffe et al. 2007). Human-related stressors can extend beyond a local scale to a global scale, for example climate change associated stressors including warming ocean temperatures, ocean acidification and sea-level rise (Laffoley & Baxter 2016). Furthermore, local and global stressors can interact with natural sources of environmental variability including El Niño Southern Oscillation (Jones 1988; Trenberth et al. 2002; Hewitt et al. 2016; Clark et al. 2021) and natural disasters such as volcanic eruptions (Mass & Portman 1989; Church et al. 2005). In general, the impacts of anthropogenic activity on the oceans is well recognised, however long-term implications of climate change in benthic estuarine communities is largely unknown.

The implications of local anthropogenic stressors have received considerable attention in estuarine environments. Change in land-use practices by humans (e.g. urbanisation, agriculture) is one central threat to estuarine habitats and many of the implications are well researched (Arthington 2012; Lü et al. 2016; Bernardino et al. 2020; Booth 2020;

Gladstone-Gallagher et al. 2020; Torres et al. 2022). These practices can drive increases of terrestrial sediment suspended in the water column, elevating turbidity. Elevated turbidity levels in estuaries have been linked to widespread consequences including constrained microphytobenthic productivity due to reduced light levels (Mangan et al. 2020) and impairment of juvenile fish development (Lowe et al. 2015). This suggests the potential for local (e.g. sedimentation, increased turbidity) and global anthropogenic stressors (e.g. climate change induced sea-level rise) to interact, creating a diminished light climate within estuarine habitats, with implications for biodiversity and ecosystem function. As terrestrial sediment inputs have increased due to rising erosion rates (Addo 2018), more fine sediments in the water column not only heighten turbidity, but also smother estuarine benthic communities (Norkko et al. 2002). In turn, this smothering can have implications for benthic macroinvertebrates including disruption of larval settlement and recruitment (Rhoads & Young 1971; Marinelli & Woodin 2002) and obstructing the structures of suspension feeders (Ellis et al. 2002).

Eutrophication is another consequence of anthropogenic land-use change and is caused by excess nutrient loading into estuaries (Howarth & Marino 2006), often originating from sewage outlets and intensive agriculture. To some extent, increased nutrient input is considered favourable as it stimulates estuarine primary productivity (Woodland et al. 2015). However, excessive nutrient concentrations lead to eutrophication where decomposition of surplus organic matter consumes more oxygen, reducing oxygen availability in estuarine habitats. This is the result of excess algal growth and contributes to declines in water quality, altering biodiversity and ecosystem functioning via altered light climate and species mortality (Smith 2003; Bricker et al. 2008). Direct stressors on estuarine benthic communities such as overharvesting also pose a threat to biodiversity and functioning. For example, removal of valued shellfish species such as *Austrovenus stutchburyi* can undesirably alter soft-sediment habitats through reduced filtration capacity that is fundamental for offsetting water quality degradation (Jones et al. 2017). Yet, despite extensive research on the implications of localised anthropogenic pressures, gaps remain regarding diffuse global stressors such as climate change and the associated repercussions for estuarine communities.

1.2 Climate change

It is well known that climate change strongly influences patterns of biodiversity in ecosystems around the globe (e.g. Peterson et al. 2002; Rosenzweig et al. 2008; Cheung et al. 2009). Following the industrial revolution, the earth's atmospheric CO_2 concentration has increased around 47% (280 ppm to 412 ppm), in which an increase of 11% (370 ppm to 412 ppm) since 2000 has been recorded (Buis 2019). Heat trapping properties of CO_2 and other greenhouse gases (e.g. methane) has caused average global temperature to rise 1°C above pre-industrial levels (IPCC 2018). Around 90% of this excess anthropogenic heat has been absorbed by the ocean since 1971 and research has since indicated that average sea temperature for the upper 700 m has increased around 0.8ºC since 1901 (Johnson & Lyman 2020; Dahlman & Lindsay 2021). Some consequences of warming sea temperatures have already been explored, including mass coral bleaching events (Baker et al. 2008), declines in marine phytoplankton production (Bestion et al. 2020) and accelerated rate of sea ice melt (Liu & Curry 2010). Shifts in spatial distribution of species and communities have also been suggested as marine species will likely alter their depth and latitudinal range in response to warming (Parmesan 2006; Dulvy et al. 2008), with the potential to cause local extinctions in more extreme environments (e.g. sub-polar regions and tropics; Cheung et al. 2009).

In marine ecosystems, in addition to rising atmospheric and sea temperatures, the chemistry of the oceans has also been altered due to the absorption of around 30% of CO_2 emissions from the atmosphere (Sabine et al. 2004), increasing hydrogen (H^+) ions and decreasing carbonate (CO_3^{2-}) ions concentrations. As a result, the ocean's acidity has increased around 30% more than pre-industrial levels, and is projected to increase up to 120% more by 2100 (Caldeira & Wickett 2005; IPCC 2013). The implications of ocean acidification on marine ecosystems has received considerable attention and links have been established between lower seawater pH and impaired growth of calcifying organisms (e.g. molluscs, echinoderms, corals, calcifying plankton; Kurihara et al. 2004; Kurihara et al. 2007; Clark et al. 2009; Kroeker et al. 2013), compromised olfactory senses and homing ability of fishes (Munday et al. 2009) and altered inter-specific relationships (Ferrari et al. 2011; Amaral et al. 2012). Generally, the impacts of climate change (i.e. ocean warming and acidification) on marine organisms are well reviewed in the literature, however little is known about how sea-level rise and the concomitant loss of critical intertidal areas will influence patterns of benthic biodiversity and functioning in estuarine environments.

1.3 Sea-level rise

Sea-level rise (SLR) is a recognised symptom of human-induced climate change and poses various direct and indirect threats to coastal environments around the globe. SLR is primarily a result of glacial melt and thermal expansion of seawater caused by our warming climate (Gomez 2015). The ensuing impacts of SLR vary by both nature and magnitude including alteration of coastal geomorphology, biological communities and water column and sediment characteristics. SLR induced changes to coastal geomorphology are relatively well documented, with mounting evidence linking coastal erosion, increased depths and amplified wave energy to landwards migration of coastal landforms (e.g. mudflats, sandflats) (Roman & Pethick 1996; Pethick & Crooks 2000; Crooks 2004; Alpar 2009; Olsen et al. 2018). There is also evidence that biological communities within the sediments will experience shifts in composition with rising sea level that can be attributed to an altered water column and sedimentary environment (Fujii & Raffaelli 2008). Increasing depth in coastal habitats is likely to drive greater salt intrusion into these areas, consequently increasing relative salinity levels (Jones 1994). Additionally, there is evidence that the intertidal sedimentary environment will shift with greater wave energy towards coarser sediment with steeper slopes (Brown & McLachlan 1990). It is well recognised that salinity and sedimentary characteristics are important environmental factors influencing benthic macroinvertebrate communities and their contributing species (Beukema 2002; Ysebaert et al. 2003; Liao et al. 2016; Amorim et al. 2020), thus reinforcing the need for further exploration of how SLR and the associated changes in the water column and sedimentary environment will impact benthic communities and their respective contributions to ecosystem functionality.

Estuarine intertidal flats are particularly threatened by SLR where the spatial coverage of these areas will be reduced. This reduction is often referred to as ‘coastal squeeze’ in which intertidal habitats (e.g. mudflats, sandflats, saltmarshes) will lose area as sea-level rises relative to land (Jones 1994; Galbraith et al. 2002). The degree of habitat loss may be particularly heightened in areas where sea defences exist (e.g. coastal towns, valued land, storm barriers, cliffs/mountains) as natural migration inland of intertidal areas will be constrained by claimed land or natural topographical features. Coastal squeeze has many established ecological and cultural consequences of its own, including loss of foraging habitat for sea birds (Galbraith et al. 2002), loss of nesting sites of marine fauna

(Mazaris et al. 2009) and loss of cultural ecosystem services (Smart et al. 2021). Furthermore, reductions in intertidal area will result in decreases in benthic primary production in turbid estuaries due to the resilience tidal emergence provides (Drylie et al. 2018) and consequently impact coastal-marine food webs (Christianen et al. 2017). As demonstrated above, the literature indicates there is no doubt that intertidal habitats play a critical role in supporting a wide range of species and associated ecological processes. Therefore, investigating in what way dominant benthic species spatial distribution and density will be impacted by loss of intertidal will be vital to gauge both positive and negative outcomes driven by expected shifts in community structure and function.

Due to the large spatial extent and high environmental variability (e.g. sediment composition, wind-wave exposure) of the intertidal zone in New Zealand (Hume et al. 1992), these coastlines provide an ideal setting for studying the consequences of increased depth and reduced intertidal areas. The expected loss of intertidal area as a function of multiple SLR scenarios up to 1.4 m has been calculated for 12 New Zealand estuaries (Fig. 1.1; Mangan et al. 2020). Under current predictions, sea-level is estimated to rise between 0.3 m and 2.5 m by 2100 following lowest and highest global greenhouse gas emission pathways, respectively (NOAA 2021). As an example, using a one-metre SLR scenario, intertidal areas of New Zealand estuaries will experience reductions of 5-80% (Fig. 1.1; Mangan et al. 2020). Therefore, this high potential for extensive intertidal habitat loss raises concerns regarding biodiversity and functional responses.

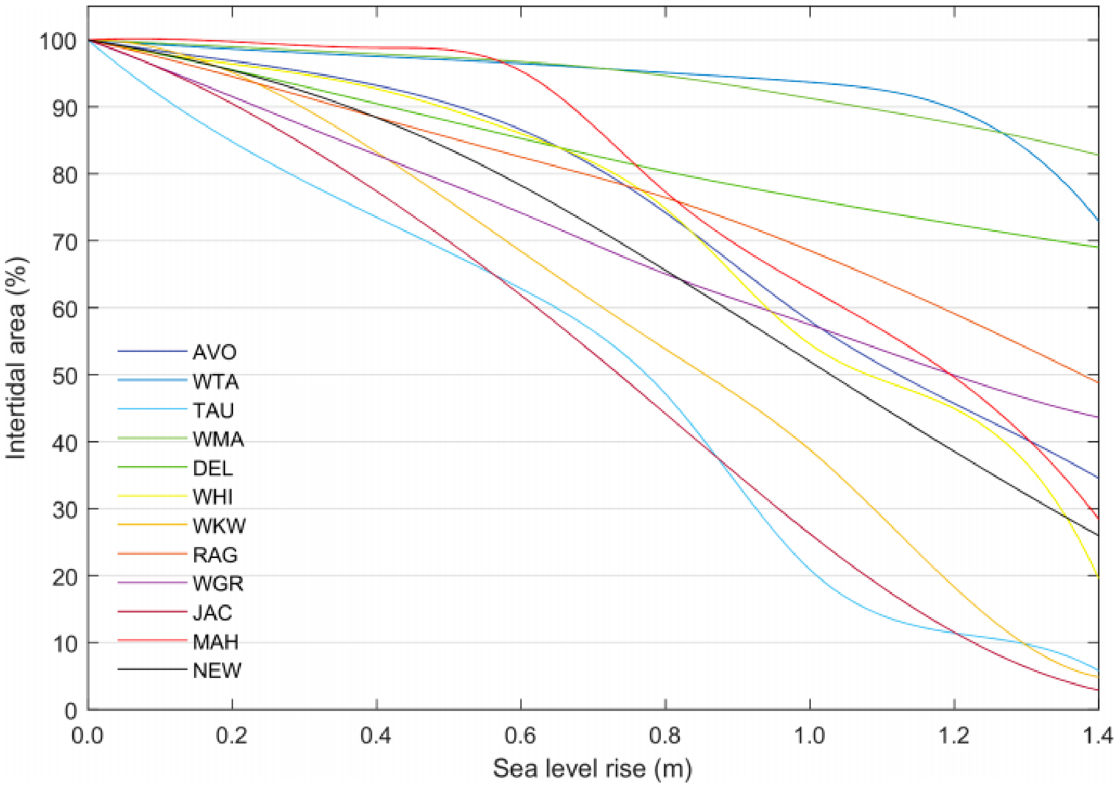

Figure 1.1 The calculated change in intertidal area as a function of sea-level rise up to 1.4 m for 12 New Zealand estuaries. Avon-Heathcote; AVO, Whangateau; WTA, Tauranga; TAU, Waimea; WMA, Delaware; DEL, Whitianga; WHI, Waikawa; WKW, Raglan; RAG, Whangarei; WGR, Jacobs River; JAC, Mahurangi; MAH, New River; NEW. From Mangan et al. (2020).

1.4 Methods for modelling relationships between communities and their environment

When aiming to address ecological impacts linked to climate change, it is important to identify critical points along environmental gradients (or thresholds) where significant changes in species abundance and/or overall community structure occurs. The vulnerability of a species to changing climatic conditions is often evaluated using species distribution models (SDMs; Guisan & Thuiller 2005) which are a tool to forecast the likelihood of species occurrence based on established relationships with environmental gradients. Despite the effectiveness of SDMs for predicting species occurrences, they do not capture environmental thresholds where significant changes occur. However, another approach known as Threshold Indicator Taxa Analysis (TITAN; Baker & King 2010) was developed as a statistical method for detecting changes in abundance/density of a set of species along a single environmental gradient. For example, this approach has been effective in identifying a dissolved oxygen threshold where a disproportionately large shift in bacterial community structure occurred relative to other positions along the environmental gradient within an estuarine setting (Spietz et al. 2018). However, being restricted to only one environmental variable can be problematic as single-stressor analysis does not account for high correlations with other environmental stressors, nor stressors acting in multiplicative or interactive ways (Wagenhoff et al. 2017).

An alternative statistical approach to community threshold identification, Gradient Forest (GF), was developed as an extension to Random Forest (RF) modelling to assess rates of community compositional turnover across multiple environmental gradients (Ellis et al. 2012). GF analysis employs an assemblage of RF models, where each RF model describes the relationship between the abundance of an individual species and multiple environmental gradients (Breiman 2001). The GF method has been successful for exploring community responses to anthropogenic and natural environmental stressors in pelagic fishes and marine benthos (Compton et al. 2013; Couce et al. 2020; Clark et al. 2021). The use of GF has also proven to be effective for exploring climate change related stressors ranging from global warming on tree species (Vanhove et al. 2021), sea surface salinity on coastal invertebrates (Durack et al. 2012; Neilsen et al. 2021) and sea surface temperature on coastal fish, macroinvertebrate and macroalgal communities (Thomson et al. 2014). After considering these examples of GF modelling, it has become clear that this approach would be favourable for identifying potential thresholds where disproportionately greater shifts in benthic macroinvertebrate community structure occur along multiple important environmental gradients such as depth.

1.5 Knowledge gap

As discussed above, the response of benthic community structure and function to a range of environmental conditions (including anthropogenic stressors) in estuarine habitats have been assessed on numerous occasions (e.g. Smith & Knapp 2003; Lü et al. 2016; Seitz et al. 2018; Foster & Fulweiler 2019; Clark et al. 2021; Neilson et al. 2021). However, despite the global significance of climate-change related stressors, and the overall importance of healthy estuarine habitats and the communities they support, there is an evident gap within the scientific literature. Specifically, there is a seeming lack of research addressing the ecological impacts of SLR within coastal environments. Generally, climate change research has traditionally focussed on implications associated with warming and tended to overlook the future impacts of diffuse stressors that will arise from warming. Within the realm of coastal research that has been SLR focussed, the literature is largely dominated by exploration of physical impacts such as changes to coastal geomorphology (e.g. Pethick & Crooks 2000; Crooks 2004; Alpar 2009), including coverage of consequences of reduced intertidal areas (e.g. Galbraith et al. 2002; Fujii & Raffaelli 2008; Mazaris et al. 2009). However, the ecological impacts (i.e. biodiversity and ecosystem function shifts) likely to arise in response to an altered coastal environment (i.e. deeper water column, steeper slopes, changed sedimentary environment) are not well documented (but see Beukema 2002; Fujii & Raffaeli 2008; Yamanaka et al. 2013; Mangan et al. 2020).

1.6 Study objectives

The central objective of this study is to address a component of this gap in the scientific literature by exploring the potential implications of SLR on macroinvertebrate community structure and ecosystem functioning within an estuarine setting. Like most temporal matters, predicting how climate change related stressors will impact ecosystems is challenging, particularly when we aim to determine cause and effect relationships due to the large time scale associated with climate change. A common approach to work around this issue is by using space as a proxy for time (Pickett 1989) and has been used globally to predict future ecological impacts of climate change (e.g. Frauendorf et al. 2020; Horrocks et al. 2020; Thyrring et al. 2021). Therefore, I will employ a space-for-time approach using increasing depth as a proxy for SLR.

Throughout this thesis, I aim to reveal the response of community structure to shifts in water column depth and the influence of additional environmental factors that are also expected to shift with SLR. Additionally, using GF analysis, I will investigate if there is evidence of environmental thresholds indicated by points along an environmental gradient where disproportionately greater shifts in community structure occur. To further understand the ecosystem-level consequences of changes in community structure, I will also assess the response of functional group community structure to shifts in water column depth (and the respective environmental characteristics). Analysis will be based on a comprehensive dataset entailing both biological and environmental data (including water column depth) spanning 119 sites across Tauranga Harbour.

Chapter 2

Methodology

2.1 Study area

Data used for this research was collected within Tauranga Harbour (37°40’S, 176°10’E; Figure 2.1) on the north-eastern coast of New Zealand’s North Island. Tauranga Harbour is characterised as a large (~200 km^2), shallow (< 10 m depth, mean depth = ~3m), barrier-enclosed estuarine lagoon (Inglis et al. 2008; Tay et al. 2012). It is sheltered from the Pacific Ocean by two Holocene barrier tombolos, Mount Maunganui at the Southern entrance, and Bowentown at the Northern entrance, with a 24 km island (Matakana) barrier (Davies-Colley & Healy 1978). The Harbour has an extensive intertidal area constituting approximately 66% of the estuary (Inglis et al. 2008), and experiences a semi diurnal tidal cycle with a tidal range up to 1.96 m (LINZ 2020). Average water residence time in the central channels ranges from 1.7 to 3.1 days, indicating the harbour is well flushed although sub-estuaries with narrow entrances in upper reaches of the harbour have greater residence times (averaging 3.1 to 8.2 days) (Tay et al. 2013). There are broad intertidal flats in the harbour’s centre that limit connectivity and water flow between the northern and southern basin. New Zealand’s fifth most populous city Tauranga (~140,000 residents; Statistics New Zealand) is adjacent to the southern limit of the Harbour. The area is also a hotspot for industrial development where the country’s largest shipping port (Port of Tauranga) is located at Sulphur Point. The harbour catchment is extensive (~1,300 km^2) and includes horticultural, agricultural and urban land where water runs from these landscapes into the large estuary.

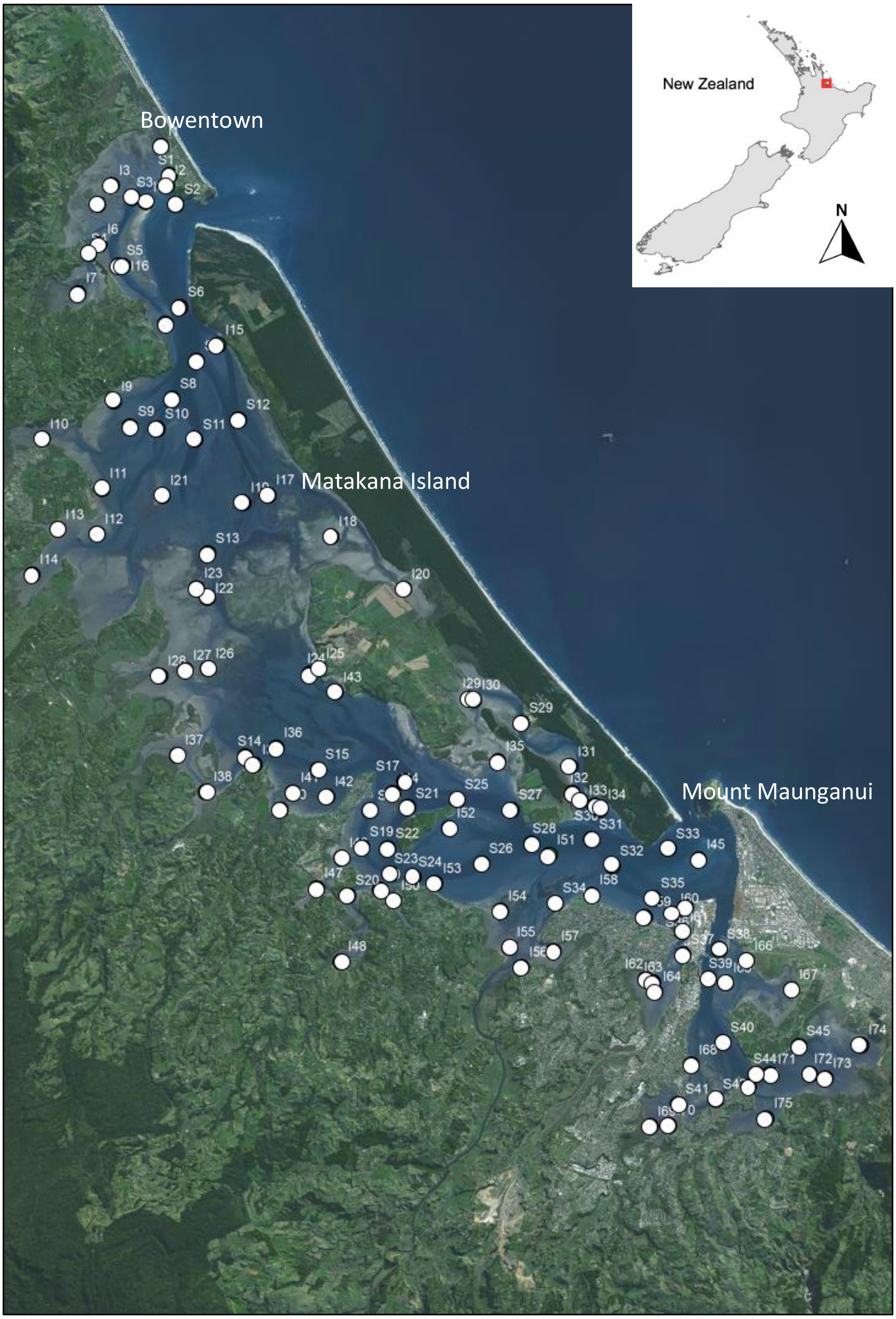

Figure 2.1 Location of Tauranga Harbour on the east coast of the North Island of New Zealand (insert) and the locations of all 119 sampling sites collated from the MTM and OTOT research programmes used in analyses. Site ID is given for each sampling location. Sampling site details are provided in Appendix 1.

2.2 Data acquisition and sampling methodologies

Data were acquired from two ecological surveys undertaken in Tauranga Harbour. An intertidal survey was conducted for the Manaaki Taha Moana (MTM) research programme from December 2011 to February 2012 (austral summer) and spanned 75 sites throughout the Harbour. A subtidal survey was carried out for the Oranga Taiao Oranga Tangata (OTOT) research programme between March and May 2016 (late austral summer/autumn) and included 44 sites. Biological data (i.e. benthic macroinvertebrate abundance data) and environmental variables were documented at each site (total n = 119) (Fig. 2.1). Sampling locations were selected to ensure a broad range of environmental gradients were represented, aiming to cover the full spatial extent and depth range (up to 9 m corrected to chart datum) of the harbour. The sampling design and methods were consistent with the standardised Estuary Monitoring Protocol (Robertson et al. 2002). A summary of field sampling and lab methodologies is provided in the sections below; for a detailed account of these methodologies see Ellis et al. (2013) (intertidal survey) and Clark et al. (2018) (subtidal survey). In addition to these reports, several papers have been published based on these datasets to develop benthic health models (Ellis et al. 2015; Clark et al. 2020) and assess stressor impacts within Tauranga Harbour (Clark et al. 2016; Ellis et al. 2017; Tremblay et al. 2017). Clark et al. (2018) noted significant differences in macroinvertebrate community structure between intertidal and subtidal survey sites, however sites were assigned to a priori groups based on which survey they were sampled. The community differences observed by Clark et al. (2018) does suggest further analysis is warranted, yet overlap in site depths between surveys (i.e. some intertidal survey sites were deeper than some subtidal survey sites) indicates tidal zones may not have been truly represented. Therefore, to explore changes in community structure with depth, I integrated the survey datasets so no a priori groups were established, eliminating bias of assigning tidal zones arbitrarily.

2.2.1 Environmental variables

An array of water column and sedimentary parameters were obtained at each site (Table 2.1). Only parameters that were included in both surveys were considered in this study. In the intertidal survey, 10 small sediment core samples (20 mm diameter, 20 mm deep) were collected at each site and combined into a single sample. Similarly, in the latter subtidal survey, six sediment cores (20 mm diameter, 20 mm deep) were taken and composited into a single sample. For both surveys, samples were processed to quantify sediment characteristics including grain size, Chlorophyll-*a* (Chl-*a*), nutrient content (total phosphorus, TP; total nitrogen, TN), organic content (measured as ash-free dry weight, AFDW) and heavy metals (lead, Pb; zinc, Zn; copper, Cu) (see Table 2.1 for extraction methods). Current speeds were estimated for the coordinates of each site from the Estuary Transport Module (Knight 2019), where average and maximum values were obtained for this study. Two current speed measurements were used to discern if average current speed or maximum current speed had a greater influence on macroinvertebrate diversity. Chart datum (CD) depths for each site were determined by subtracting 1.08 m from mean sea-level (MSL) values (MSL to CD conversion published by LINZ) obtained from a hydrodynamic model grid developed by de Ruiter et al. (2019), that incorporates LiDAR data, multibeam survey measurements and LINZ bathymetric data.

Table 2.1 Summary of measured environmental parameters, analysis methods and unit measurements.

Variable	Measurement extraction method	Unit
TN	Catalytic combustion, separation, thermal conductivity detector.	mg/kg (dry weight)
TP	Hydrochloric/nitric acid digestion, ICP-MS.	mg/kg (dry weight)
Chl-*a*	Extraction with 95% ethanol, spectroscopy. (NIWA Periphyton Monitoring Manual).	µg/kg
Metals (Cu, Pb, Zn)	Hydrochloric/nitric acid digestion, ICP-MS.	mg/kg (dry weight)
AFDW	Dry sediment weight loss after combustion at 550°C.	g/100 g
Mud	Grain size < 63 µm	g/100 g
Sand	Grain size ≥ 63 µm, < 2 mm.	g/100 g
Gravel	Grain size ≥ 2mm	g/100 g
Average current speed	Estimated from Estuary Transport Module (Knight, 2019)	m/s
Maximum current speed	Estimated from Estuary Transport Module (Knight, 2019)	m/s
Depth	Elevation model grid corrected to chart datum (CD) (de Ruiter 2019).	m

TN; total nitrogen, TP; total phosphorous, Chl-*a*; Chlorophyll-*a*, Cu; copper, Pb; lead, Zn; zinc, AFDW; organic content.

2.2.2 Macroinvertebrate data

Three replicate core (13 cm diameter, 15 cm deep) samples were taken at each site and sieved over a 0.5 mm mesh to obtain macroinvertebrate abundance count data. Macroinvertebrates were preserved in a diluted ethanol solution (~70% with seawater) and identified to the lowest attainable taxonomic resolution by experts. Individual organisms were counted and recorded with taxonomic classification consistent with the World Register of Marine Species (WoRMS) database. The intertidal and subtidal benthic macroinvertebrate survey datasets were combined and taxonomic resolution was standardised to be consistent across surveys. Where individual taxa counts were low (< 10 across the combined data set) and taxonomic resolution was poor, I chose to remove these taxa groups from analysis (e.g. removed Bivalvia as individual count = 8). This ensured taxonomic resolution of important species was maintained (e.g. *Austrovenus stutchburyi*), while preventing taxon to be represented by more than one taxa group. Counts of larval/juvenile taxa were also removed from the dataset to reduce any influence of recruitment events on the statistical models. Site averages (n=3) for macroinvertebrate abundance data (i.e. average abundance per core) were calculated and used for all analyses.

2.3 Functional group assignment

The use of functional trait diversity has become a common tool to assess how organisms contribute to ecosystem function. Understanding the functional roles of species (e.g. promoting nutrient cycling, sediment stabilisation) within benthic ecosystems often better reflects ecosystem stability compared to traditional biodiversity measures (i.e. using taxonomic diversity) (Bengtsson et al. 1998; Bremner et al. 2003; Luck et al. 2009). To assess prospective implications of environmental change on ecosystem function, each taxa group was assigned to one of the 26 functional groups developed by Greenfield et al. (2016). This functional group index considers a range of functional traits representing life history, physical morphology and behavioural characteristics that influence stability in estuarine ecosystems (Table 2.2). In this study, as taxonomic resolution was not always to species level, in the case where a taxa group (hereafter referred to as ‘species’) exhibits more than one ‘version’ of a trait (e.g. different Spionidae species qualified for different functional groups), the most dominant functional group was assigned.

Table 2.2 Summary of defining traits for each functional group (1 – 26) as described by Greenfield et al (2016). Most abundant species from each functional group are given as examples.

Functional Group #	Description of traits	Example species (most abundant)
1	Calcified, Suspension feeding, Attached	*Austrominius modestus*
2	Calcified, Suspension feeding, Top 2 cm, Freely mobile	*Austrovenus stutchburyi*
3	Calcified, Suspension feeding, Top 2 cm, Limited mobility	*Arthritica bifurca*
4	Calcified, Suspension feeding, Top 2 cm, Sedentary	*Musculista senhousia*
5	Calcified, Deposit/Pred.Scav/Grazer, Above surface, Freely mobile	*Zeacumantus lutulentus*
6	Calcified, Deposit feeding, Top 2 cm, Limited mobility	*Linucula hartvigiana*
7	Calcified, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile	*Amalda australis*
8	Calcified, Deposit feeding, Deep, Limited mobility, No habitat structure, Large	*Macomona liliana*
9	Soft-bodied, Suspension feeding, Attached	*Anthopleura aureoradiata*
10	Soft-bodied, Suspension feeding, Tube structure	*Euchone sp*
11	Soft-bodied, Deposit feeding, Top 2 cm, Freely mobile	Nematoda
12	Soft-bodied, Deposit feeding, Below surface, Freely mobile	*Scoloplos sp*
13	Soft-bodied, Deposit feeding, Below surface, Limited mobility	*Heteromastus filiformis*
14	Soft-bodied, Deposit feeding, Deep	*Hyboscolex longiseta*
15	Soft-bodied, Below surface, Tube structure	Spionidae
16	Soft-bodied, Predator/Scavenger, Top 2 cm, Freely mobile	Ptychoderidae
17	Soft-bodied, Predator/Scavenger, Top 2 cm, Limited mobility	Oligochaeta
18	Soft-bodied, Predator/Scavenger, Below surface + Deep, Freely mobile, No habitat structure	Nemertea
19	Soft-bodied, Predator/Scavenger, Below surface, Limited mobility	Hesionidae
20	Soft-bodied, Above surface, Top 2 cm, Below surface, Deep, Sedentary, Tube structure	*Owenia petersenae*
21	Rigid, Suspension feeding, Top 2 cm	Tanaidacea

Functional Group #	Description of traits	Example species (most abundant)
22	Rigid, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile, No habitat structure	Amphipoda
23	Rigid, Above surface, Freely mobile	Cumacea Ostracoda
24	Rigid, Above surface, Freely mobile, Large	*Patirella regularis*
25	Rigid, Predator/Scavenger, Attached	No individuals identified.
26	Rigid, Predator/Scavenger, Below surface, Freely mobile, Large burrow former	*Austrohelice crassa*

2.4 Statistical analyses

2.4.1 Benthic macrofauna

To compare environmental parameters associated with SLR between potential distinct macroinvertebrate communities, I first had to explore if there were unidentified assemblages of sites that could be grouped together based on significantly similar community structure (α = 0.05). Here, a hierarchical cluster (CLUSTER) analysis (see Clarke et al. 2014) was performed on square-root transformed macroinvertebrate abundance data. This clustering approach forms groups based on samples (in this case; sites) that share the highest mutual community similarity determined by a permuted (9999 permutations) similarity profiling analysis using Bray-Curtis similarity. Sites that shared significantly similar macroinvertebrate community structure at a > 34% similarity level were grouped together. Standard community structure analyses were performed on each clustered group independently to assess sampling effort adequacy. These analyses are important for ensuring community structure observed is representative of each cluster. Species accumulation curves (SAC) were produced by plotting the number of species against the number of sites surveyed. To best account for the heterogeneous nature of estuarine communities, SAC were produced using the Ugland, Gray and Ellingsen (UGE) distribution (Ugland et al. 2003).

A range of univariate analyses were conducted to explore overall similarities and differences in community structure between cluster groups. These analyses were performed on raw macroinvertebrate data where average abundance per core, species richness, Shannon-Wiener diversity and the overall 5 most abundant species were determined.

To explore how community structure varied between clustered groups, non-metric multidimensional scaling (nMDS) was employed (Clarke et al. 2014). To achieve this, Bray-Curtis dissimilarities were determined based on the macroinvertebrate abundance data after square-root transformation to reduce the influence of high-abundance species on any result outputs. Dissimilarities in community structure between clustered groups were visualised in ordination space using nMDS with these groups specified as the grouping factor. The centroids of each site were placed in multidimensional space (2-D or 3-D) based on their dissimilarities, where distances between each site in ordination space represents the magnitude of dissimilarity between macroinvertebrate communities. To assess overall similarity in community structure between clustered groups, and establish the proportion each species contributes to observed similarities and dissimilarities (in terms of abundance and occurrence), a similarity percentage (SIMPER) analysis was performed using the square-root transformed macroinvertebrate abundance data. SIMPER analysis uses the Bray-Curtis measure of dissimilarity to breakdown the contribution of each species to overall similarity to identify the species most important in contributing to patterns observed between clustered groups (Clarke et al. 2014).

2.4.2 Statistical modelling

Determining key environmental gradients as predictors

To reveal how macroinvertebrate community structure responded to environmental gradients, distance-based linear modelling (DISTLM) was employed using species abundance and environmental data from both ecological surveys with no a priori groups assigned. This multivariate linear regression approach is a favourable method for analysing and modelling the relationship between biological data and multiple predictor variables (McArdle & Anderson 2001). DISTLM using Bray-Curtis dissimilarities was conducted to identify environmental variables responsible for explaining the most variation in macroinvertebrate community structure within Tauranga Harbour. Square-root transformations were applied to abundance data to ensure any overpowering influence of dominant species was reduced, while still allowing the model to detect differences in community structure in response to environmental predictors (Anderson et al. 2008). The data distributions of environmental variables were explored by generating a draftsman plot and histogram for each environmental variable. Skewed distributions revealed by these plots indicated that transformations for several parameters were necessary to ensure the test assumptions were satisfied (i.e. normally distributed data).

Optimal transformations of each environmental predictor variable were applied following the recommendations from Anderson et al. (2008) (Table 2.3). In addition to initial draftsman plots, Pearson's correlations were determined to further assess multicollinearity between environmental predictors to ensure highly correlated variables would not cause misrepresentative DISTLM outputs (see Appendix 2; Table A2 for Pearson's correlations). Mud and sand content were strongly correlated (R= 0.93; Table A2), however I ran DISTLM by removing each of these variables independently which had little impact on the final fitted models, therefore I chose to include both variables in analysis. Using abundance data as the response variable, a DISTLM was fitted using a forward selection procedure (AIC selection criteria) to establish the key environmental predictors explaining variation in community structure. Backwards and stepwise selection procedures (AIC selection criteria) were also checked and each fitted similar final models. A distance-based redundancy analysis (dbRDA) ordination plot was used to illustrate the relationship between the set of environmental predictors (represented as vector overlays that indicate direction and strength) explaining the disparities in community structure.

All analyses described above were conducted in PRIMER 7 (version 7.0.13; Clarke et al. 2014) with the PERMANOVA+ add on (Anderson et al. 2008).

Table 2.3 Optimal transformations for environmental predictor variables (P).

Transformation performed	Environmental parameter (P)
Natural log: ln(P)	Chl-*a*, Cu, Pb, Zn, Gravel, Mud, Depth (ln(10+P))
Square-root: sqrt(P)	Gravel
Reverse natural log: ln(100-P)	Sand
No transformation	TN, TP, AFDW, Average current speed, Max current speed

Determining critical points of compositional turnover along key environmental gradients

To build on DISTLM to further explore the influence of environmental variables on macroinvertebrate communities, Gradient Forest (GF) modelling was employed. GF identifies critical points along environmental gradients where large shifts in rates of benthic macroinvertebrate compositional turnover occur (Ellis et al. 2012). GF models allow for identification of compositional turnover thresholds by aggregating regression-tree based Random Forest (RF) models. Species considered rare ($\leq$ 3 occurrences across all 120 sites) were excluded from GF analysis as models are constrained by limited data. The three sites where depth exceeded 6 m were also removed from GF models as there was not enough data to adequately model species turnover beyond this depth. Two key processes are undertaken for GF modelling. The first process uses an extension R package "extendedForest" (Liaw & Weiner 2002) which calls on R package "randomForest" to fit an ensemble of RF models for the input species. These RF models describe the relationship between the species distribution and a set of environmental variables. The second process uses R package "gradientForest" (Ellis et al. 2012) to aggregate all of the individual split points determined from these models, estimating the most important points of species turnover along each environmental gradient.

RF models (Breiman 2001) are a flexible and robust way of modelling non-linear predictor-response relationships. The RF models for individual species are built based on an ensemble of regression trees (in this study, 500) where observations are repeatedly partitioned based on the 'best' individual split. This split point is indicative of a measure of importance reflecting magnitude of change in abundance. The predictive power of individual RF models (R^2_f) is explained by the proportion of out-of-bag variance for each species f (Ellis et al. 2012), and the importance of each predictor variable (R^2; a dimensionless value representing cumulative importance) included in the model is determined by measuring model performance degradation as each environmental predictor is randomly permuted (Pitcher et al. 2012). Multicollinearity between predictor variables is accounted for by using a conditional approach, allowing RF models to be robust to highly correlated variables.

GF modelling aggregates split importance values across each environmental gradient that were determined by the RF models, where species models with positive fits ($R^2_f > 0$) are collated to form distributions reflecting compositional turnover relative to each environmental predictor (Ellis et al. 2012; Pitcher et al. 2012). As the distribution is formed, individual RF models with higher predictive importance (i.e. high R^2_f) have a greater influence on the turnover distribution than models with lower predictive importance (i.e. low R^2_f). The shape of the distribution constructed for each environmental variable indicates the predicted rate of compositional change along the respective gradient, where increased slope steepness indicates increased rate of community compositional turnover (Ellis et al. 2012; Pitcher et al. 2012). Each GF model was bootstrapped 100 times to gauge model performance and certainty. In each bootstrap iteration, a random subsample of the macroinvertebrate data was taken and each measure of compositional turnover was integrated when constructing final GF models for each environmental predictor. All GF analyses were conducted in statistical software R (version 4.1.0; R Core Team 2019).

2.5 Implications for ecosystem function

To explore how ecosystem function may be altered with shifts in environmental conditions associated with SLR, a set of analyses were re-run using functional group abundance data. Square-root transformed functional group abundance data was used for these analyses. An nMDS was generated where the grouping factor was derived from the assemblages of sites (sharing > 34% similar taxa-based community structure) determined by the initial cluster analysis on macroinvertebrate abundance data. To confirm if functional group community structure also differed between the initial cluster groups, a one-way PERMANOVA and PERMDISP were employed. Post-hoc pairwise tests were performed to distinguish which pairs of cluster groups significantly differed in functional group community structure. SIMPER analysis was performed using Bray-Curtis dissimilarities to identify contributions of each functional group to overall dissimilarity between clustered groups.

Functional group analyses were conducted in PRIMER 7 (version 7.0.13; Clarke et al. 2014) with the PERMANOVA+ add on (Anderson et al. 2008).

Chapter 3

Results

3.1 Community data

To assess if there was evidence of spatial patterns in macroinvertebrate community structure, a hierarchical cluster (CLUSTER) analysis was performed on the complete species abundance dataset using Bray-Curtis similarities. The analysis indicated three main clusters of survey sites based on 34-37.5% similarity in community structure (Fig. 3.1). The number of survey sites within each cluster varied, where the largest group included 69 sites, the second cluster contained 37 sites and the smallest cluster contained only 13. The two larger groups are separated based on a 37.5% similarity level, whereas the smaller group was formed at a 34% level of similarity.

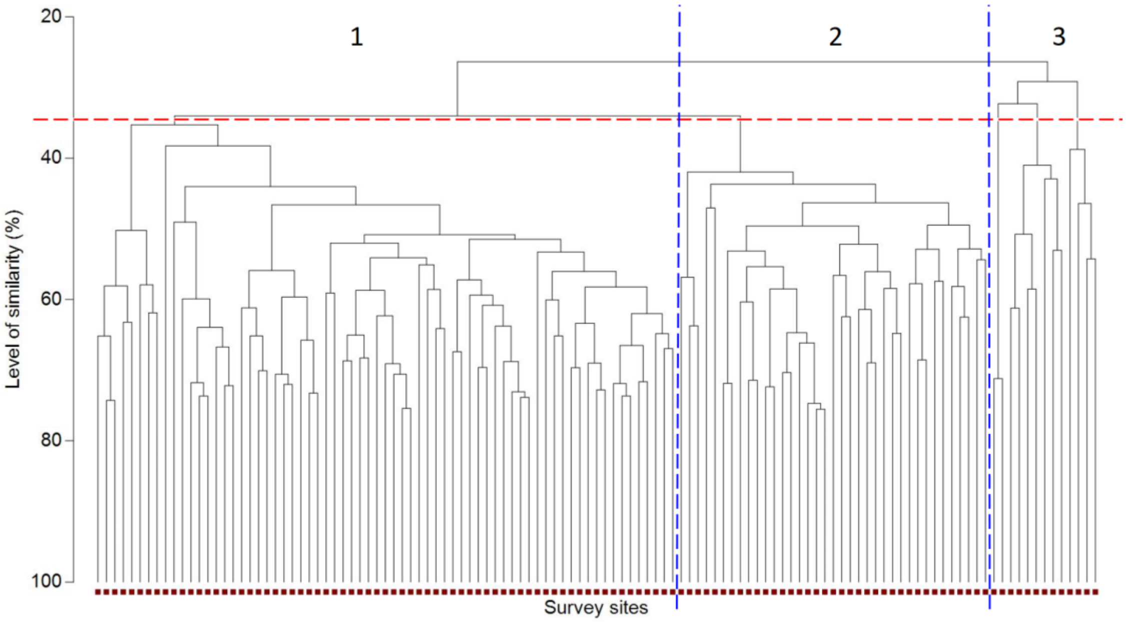

Figure 3.1 Hierarchical clustering of survey sites based on species abundance data. Clustering employed the Bray-Curtis method of similarity on site group averages. The red dashed horizontal line is indicative of 37% level of similarity. The blue dashed vertical lines show where cluster groups were separated at >34% level of similarity. The spatial distribution of the three identified clusters sites are shown in Figure 3.2. Site details and respective cluster can be found in Appendix 1; Table A1).

In general, the largest of the three groups (Cluster 1) had shallower water depths compared to the other two groups (Table 3.1); the mean depth for Cluster 1 was -0.71 m (range -1.99-1.71 m) compared to Clusters 2 and 3 which had mean water depths of 1.54 m (0.99-5.02 m) and 3.03 m (-0.16-9.00 m) respectively. Negative depth values indicate true intertidal sites (i.e. experiences tidal emergence). After considering the depth ranges of the three clusters and their spatial distribution throughout Tauranga Harbour (Fig. 3.2) I refer to Cluster 1 as representing the intertidal sites (IT), Cluster 2 as shallow subtidal sites (SS) and Cluster 3 as deep subtidal sites (DS). I acknowledge there is a small amount of sites that overlap in depth between clustered groups, however the average depths and position within the harbour allowed me to consider these clusters as generally representative of tidal zones.

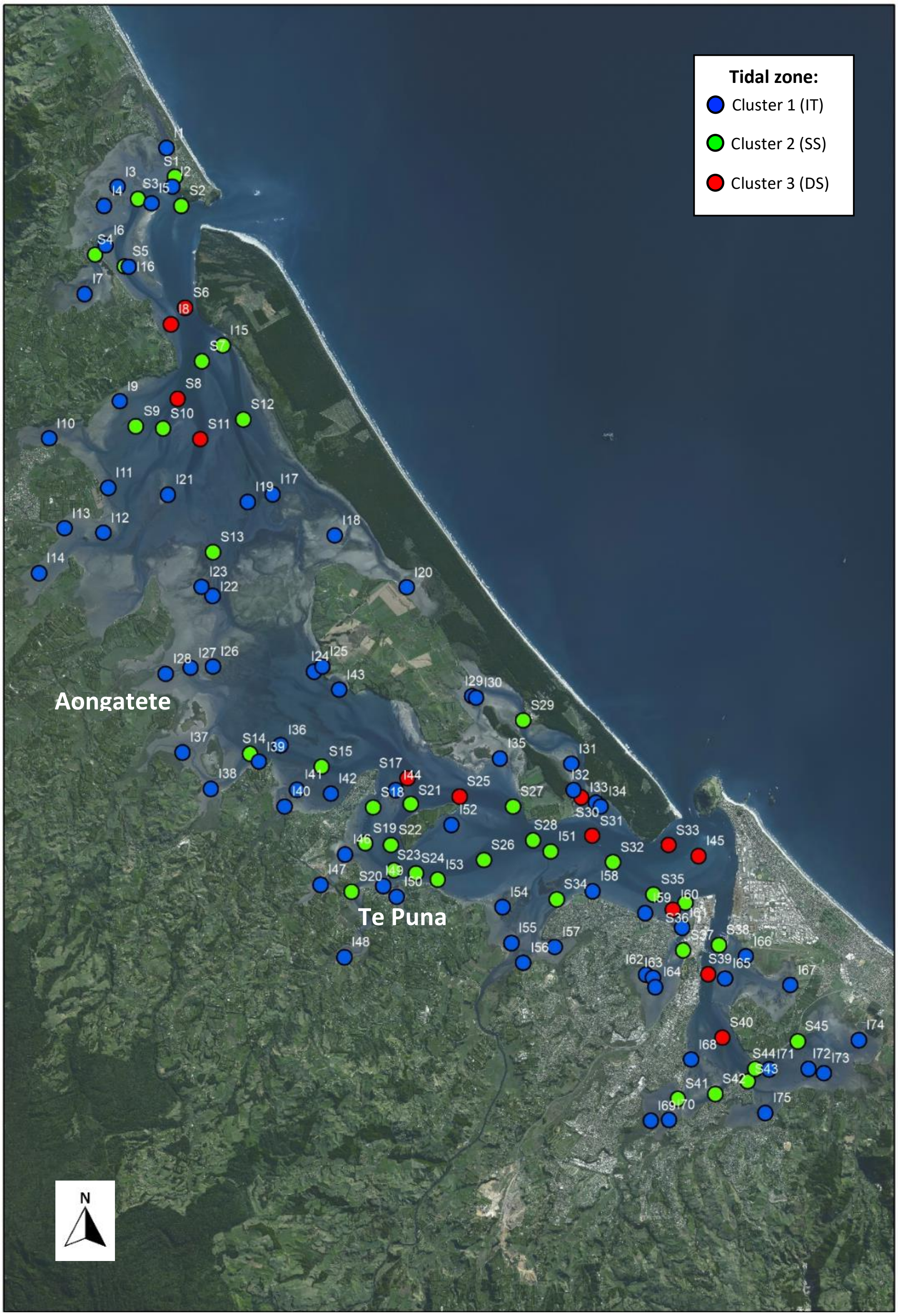

Figure 3.2 Map of Tauranga Harbour indicating the cluster group each individual site was assigned to based on overall dissimilarity in benthic macroinvertebrate community structure (blue = Cluster 1 – intertidal (IT), green = Cluster 2 – shallow subtidal (SS) and red = Cluster 3 – deep subtidal (DS)). Site number is indicated next to each site.

Table 3.1 Summary of mean environmental and univariate macroinvertebrate diversity measures (min-max) measured in Tauranga Harbour as a function of site clusters; intertidal (IT), shallow subtidal (SS) and deep subtidal (DS).

Environmental variables			
	Cluster 1 (IT)	**Cluster 2 (SS)**	**Cluster 3 (DS)**
Depth (m)	-0.71 (-1.99–1.71)	1.54 (-0.99–5.02)	3.03 (-0.16–9.00)
Chl-*a* (µg/kg)	6167 (210–16000)	16281 (1200–41300)	17685 (2000–56300)
Mud (%)	14.1 (0.1–76.4)	8.22 (2.6–23.4)	3.01 (0.6–5)
Gravel (%)	1.8 (0.1–14.6)	4.3 (0.1–15)	5.86 (0.1–17.8)
Sand (%)	84 (24–100)	88 (67–96)	91 (78–99)
TN (mg/kg)	491 (140–1900)	532 (340–1200)	452 (190–499)
TP (mg/kg)	171 (51–580)	147 (79–340)	121 (81–180)
Cu (mg/kg)	1.3 (1.0–6.1)	1.1 (0.4–3.5)	0.7 (0.3–1.0)
Pb (mg/kg)	3 (1–13)	2.9 (1.6–6.4)	2 (1–3.8)
Zn (mg/kg)	18 (3–55)	17 (8–37)	12 (6–25)
AFDW (g/100g)	3 (1–10)	3 (1–7)	2 (1–3)
Average speed (m/s)	0.15 (0.01–0.45)	0.34 (0.02–0.67)	0.53 (0.23–0.83)
Max speed (m/s)	0.63 (0.15–1.43)	0.83 (0.17–1.52)	1 (0.51–1.66)
Benthic community diversity			
Av. species richness (per core)	20 (6–33)	28 (21–40)	17 (11–23)
Av. abundance (per core)	113 (27–329)	242 (51–750)	80 (26–184)
Av. occurrence (% of sites species occurs in)	23 (45–100)	20 (3–100)	23 (8–100)
S-W Diversity (H’)	0.89	0.88	0.88

Chl-a Chlorophyll-*a*, *TN* total nitrogen, *TP* total phosphorus, *Cu* Copper, *Pb* Lead, *Zn* Zinc, *AFDW* organic content. H’=Shannon-Wiener diversity index

Sediment Chl-*a* concentrations varied greatly with values ranging from 210 to 56300 µg/kg (Table 3.1). On average, Chl-*a* values were around 2.6 times greater in SS and DS sites (mean= 16281 µg/kg and 17685 µg/kg, respectively) compared to IT sites (mean= 6167 µg/kg). In general, most sites were predominantly sandy (> 90%) and all sites except 11 had at least 70 % sand. The few sites where sand content was lower occurred at IT sites, with values as low as 24% (detected in Te Puna Estuary) however the average sand content for IT sites was still relatively high (84%). Mud content was generally higher in the IT regions of the harbour (mean= 14%), particularly in comparison to the DS sites (mean= 3%) (Table 3.1).

There was high variability in sediment nutrient concentrations across survey sites. Total nitrogen (TN) content ranged from 140 to 1900 mg/kg, with SS sites having generally higher TN concentrations compared to IT and DS sites (by 8% and 18%, respectively; Table 3.1). Total phosphorus (TP) concentrations across all sites ranged from 51 to 580 mg/kg, but unlike TN, higher TP content was generally associated with IT sites (mean= 171 mg/kg), compared to the SS and DS sites (147 and 121 mg/kg, respectively). Similarly, heavy metal concentrations (Cu, Zn) and organic content (AFDW) also tended to be higher in IT sediments than in the SS (by 18%, 4% and 7% respectively) and DS sediments (by 86%, 47% and 69% respectively) (Table 3.1). In general, average and maximum current speed were greatest at DS sites and lowest at IT sites, with average current speed of SS and DS sites (0.34 m/s and 0.53 m/s, respectively) more than double the average IT current speed (0.15 m/s) (Table 3.1).

3.1.1 Sampling effort adequacy

Prior to benthic community analyses species accumulation curves (SAC) were generated to provide evidence that IT, SS and DS clusters had been sampled adequately. For IT sites the SAC indicated that adequate sampling (i.e. a noticeable decrease in species accumulation rates with increasing sampling effort) occurred after 10 sites (30 cores), despite the curve never completely levelling off (Fig. 3.3). A similar result was observed for the SS cluster at around 12 sites surveyed (36 cores), however the curve did not plateau as sharply as exhibited by the IT SAC. For the DS cluster, species accumulation rates were more gradual than that observed for the IT and SS SAC. Despite no obvious plateauing, after around 10 sites had been surveyed (30 core samples) the rate of new species addition with additional sampling was beginning to decrease (Fig. 3.3).

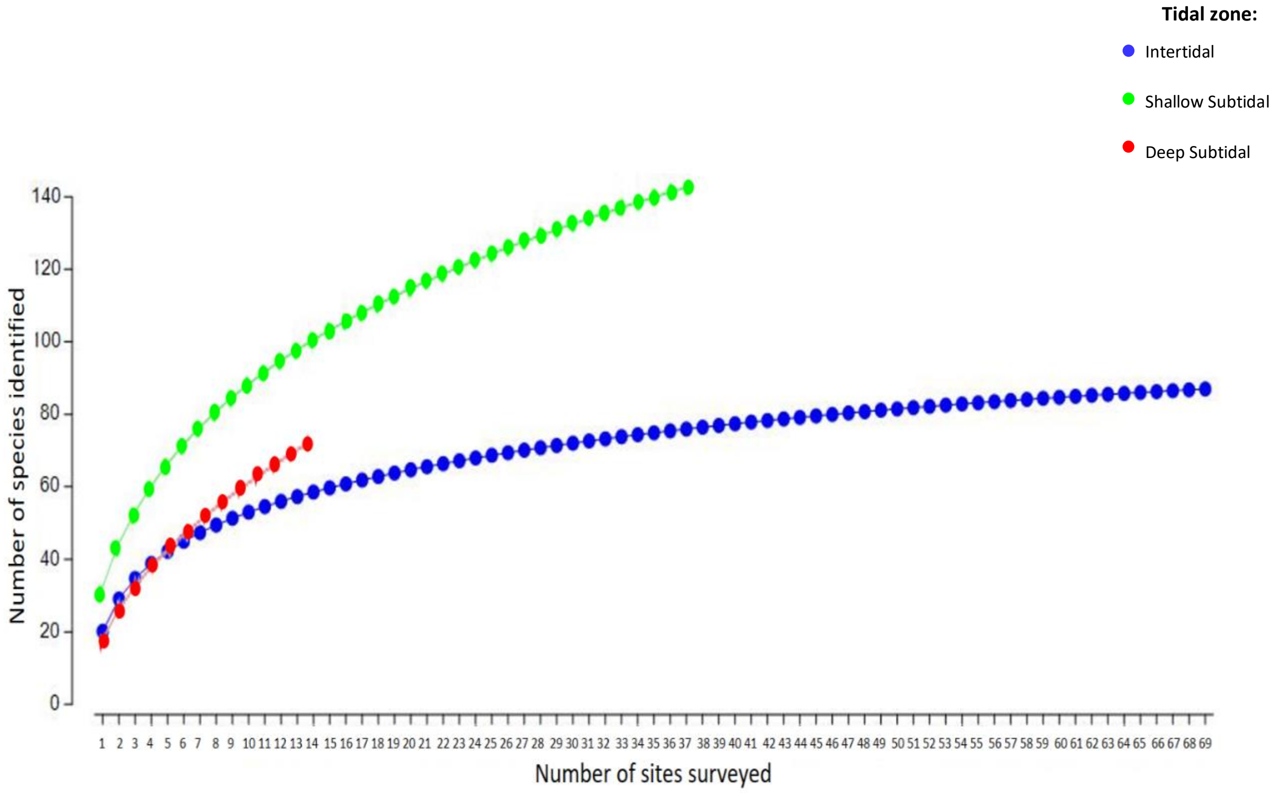

Figure 3.3 Species accumulative curves (SAC) for intertidal (IT; blue) (n = 69), shallow subtidal (SS; green) (n = 37) and deep subtidal (DS; red) (n =13) sampling sites.

3.1.2 Patterns in species richness, species diversity and total abundance

In this study, there were 175 different species identified across all sites in Tauranga Harbour. Species richness was greatest in the SS zone where mean species richness was 29% and 40% greater than that observed in IT and DS zones, respectively (Table 3.1). The lowest species richness measured was 6/core at an IT site in a sub-estuary, adjacent to Aongatete River, a source of freshwater input into the Harbour (Fig. 3.2). The greatest species richness was 40/core recorded at a SS site near the main channel at the southern end of the harbour, close to the Te Puna sub-estuary (Fig. 3.2). On average, SS (242 indiv./core) had more than double the average total abundance of benthic invertebrates than observed for both IT and DS (113 and 80 indiv./core, respectively) (Table 3.1). In contrast, Shannon-Wiener diversity indices for all three tidal zones were similar, despite the obvious differences in richness and abundance (Table 3.1). High total abundances at given sites were mostly driven by few dominant species (e.g. Amphipoda, Oligochaete worms, Spionid worms; Table 3.2).

Of the top five most abundant species determined for each zone, IT had three species in common with SS (Amphipoda, Spionidae and *Heteromastus filiformis*) and only one species (Amphipoda) shared with DS (Table 3.2). There were two species in common among the SS and DS top five most abundant (Amphipoda and Paraonidae). Overall, Amphipoda was the most abundant IT species (average = 25.8 ± 10.8) and the second most abundant species for both SS and DS (average = 38.9 and 13.3 indiv./core, respectively), with site occupancy ranging from 94% to 100% indicating this species is abundant and widespread. Similarly, Spionidae was the second most abundant species for IT (average = 17.4 indiv./core) and most abundant for SS (52.9 indiv./core) with 100% occupancy for both. However, Spionidae did not occur in the top five most abundant species for DS (Table 3.2). *Austrovenus stutchburyi* and *Linucula hartvigiana* only appeared in the top five most abundant species for IT, occupying 77% and 75% of IT sites, respectively (Table 3.2). Conversely, *Paphies australis* was the most abundant species for DS (average = 20.6 ± 18.8 indiv./core) despite only occupying 46% of DS sites, but did not appear in the top five most abundant species for either IT or SS (Table 3.2). High abundances observed for Amphipoda, Spionidae and Paraonidae may be attributed to multiple contributing species as taxonomic resolution was not at species level.

Table 3.2 Top five most abundant species in intertidal (IT), shallow subtidal (SS) and deep subtidal (DS) zones and their respective taxonomic group, average abundance (± 1 SE) and occupancy (% of sites within the zone where the species were present).

Species	Group	Average abundance (indiv./core)	Occupancy (%)
IT			
Amphipoda	Amphipod	25.8 (± 10.8)	94%
Spionidae	Polychaete worm	17.4 (± 3.6)	100%
Heteromastus filiformis	Polychaete worm	12.3 (± 3.9)	90%
Austrovenus stutchburyi	Bivalve (cockle)	7.7 (± 3.1)	77%
Linucula hartvigiana	Bivalve (nut shell)	7.6 (± 2.8)	75%
SS			
Spionidae	Polychaete worm	52.9 (± 23.5)	100%
Amphipoda	Amphipod	38.9 (± 32.9)	100%
Oligochaeta	Oligochaete worm	36.2 (± 30.5)	100%
Paraonidae	Polychaete worm	30.4 (± 9.2)	86%
Heteromastus filiformis	Polychaete worm	19.1 (± 6.6)	100%
DS			
Paphies australis	Bivalve (pipi)	20.6 (± 18.8)	46%
Amphipoda	Amphipod	13.3 (± 11.9)	100%
Nematoda	Nematode worm	9.2 (± 8.6)	77%
Hesionidae	Polychaete worm	6.6 (± 5.8)	69%
Paraonidae	Polychaete worm	5.4 (± 5.2)	54%

A non-metric multidimensional scaling (nMDS) plot was generated to visualise the differences in macroinvertebrate community structure between tidal zones in ordination space (Fig. 3.4). Clear differences in macroinvertebrate community structure between IT, SS and DS sites is indicated by distinct separation of groups in ordination space (i.e. no obvious overlap is observed). SS sites appear to share the most similar community structure (SIMPER; 47% within group similarity) closely followed by IT sites (SIMPER; 45% within group similarity), whereas DS sites appear relatively less homogeneous (SIMPER; 33% within group similarity).

SIMPER analysis revealed that overall dissimilarity between IT and SS was 68% and this is largely driven by differences in species abundance of Amphipoda (e.g. Caprellidae), Spionidae (e.g. *Aonides trifida*, *Boccardia syrtis*), oligochaete worms and *Heteromastus filiformis* which each are contributing to 4-7% of dissimilarity observed (Table 3.3A). Out of the seven highest contributing species to total dissimilarity between IT and SS, *Linucula hartvigiana* was the only species where IT average abundance was greater (by a factor of 68; Table 3.3A). Overall dissimilarity between IT and DS was 79%, where differences in community structure is primarily attributed to Spionidae (e.g. *A. trifida*, *B. syrtis*), Amphipoda (e.g. Caprellidae), *Paphies australis* and nematodes that each contribute to 4-7% of total dissimilarity between zones (Table 3.3B). IT average abundance was greater than DS for five of eight species contributing to the most dissimilarity, however this was not true for *P. australis* (Pipi) where DS average abundance was 34 times greater than IT (Table 3.3B). There was 71% dissimilarity between SS and DS, where 38% of overall dissimilarity can be attributed to Spionidae (e.g. *A. trifida*, *B. syrtis*), oligochaete worms, *H. filiformis*, *Aricidea sp*, Amphipoda (e.g. Caprellidae) and *P. australis* that each contribute to 4-10% of the total dissimilarity (Table 3.3C). Five of these six top contributing species had greater average abundance for SS than DS. This was notably true for oligochaetes, *H. filiformis*, Spionidae and *Aricidea sp*. (by factors of 5, 5, 8 and 9 respectively). Conversely, *P. australis* average abundance for DS was instead four times greater than SS (Table 3.3C). In general, this analysis indicates total dissimilarity is not attributed to large contributions of few species, but instead to a multitude of species each contributing a relatively small proportion.

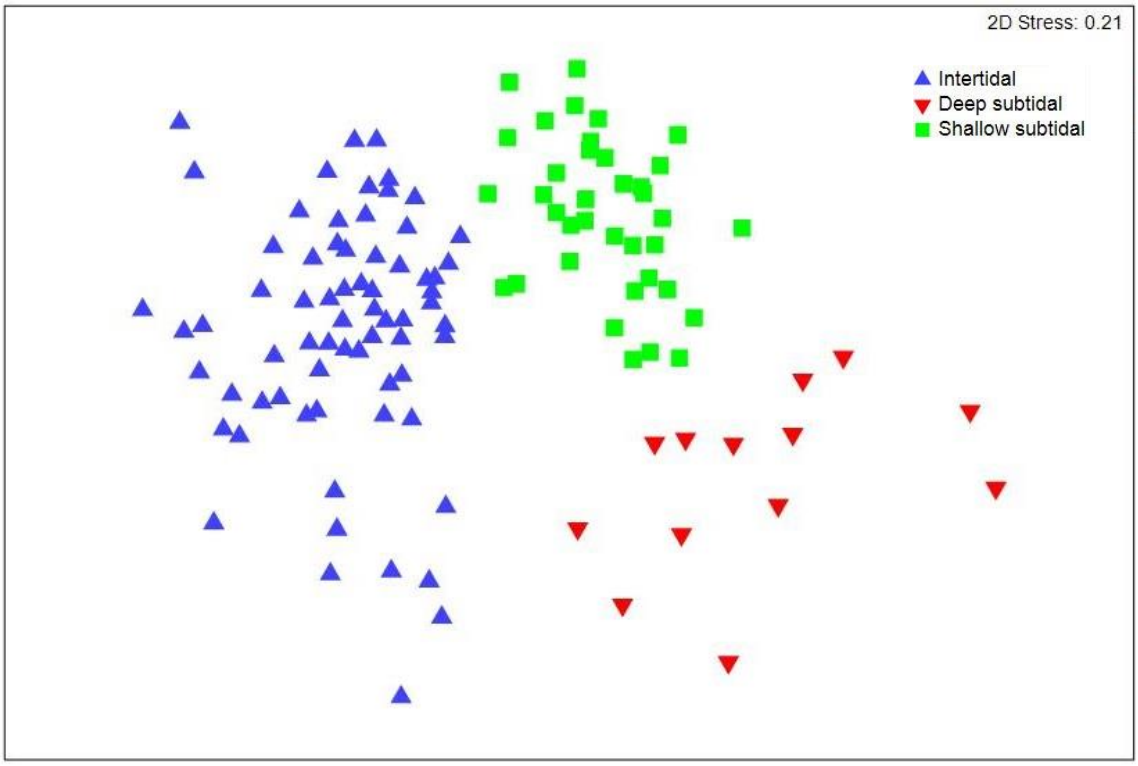

Figure 3.4 Non-metric multidimensional scaling (*nMDS*) plot visualising differences in macroinvertebrate community structure between intertidal (blue), shallow subtidal (green) and deep subtidal (red) zones based on Bray-Curtis dissimilarities between sites using square-root transformed abundance data. Note: Tidal zones were initially determined by CLUSTER analysis on community data therefore *nMDS* is intended for visualisation of community structure dispersion across sites and the referred tidal zones. Site details including assigned zone and depth are given in Appendix 1; Table A1.

Table 3.3 Similarity percentage (SIMPER) analysis results tables summarising key species contributing to the dissimilarities observed between **A)** IT and SS, **B)** IT and DS, and **C)** SS and DS macroinvertebrate communities based on square-root transformed macroinvertebrate abundance data. Overall dissimilarity between IT and SS was 68%, IT and DS was 79%, and SS and DS was 71%. Differences between tidal groups are shown to a 40% level. Av. Abund = average abundance (per core), Av. Diss = average dissimilarity, Diss/SD = ratio of average contribution divided by standard deviation, Contrib. % = contribution percentage, Cum. % = cumulative contribution percentage.

A. Species	IT Av. Abund	SS Av. Abund	Av. Diss	Diss/SD	Contrib. %	Cum. %
Amphipoda	4.03	4.26	4.26	0.92	6.30	6.30
Spionidae	3.80	5.91	4.16	1.15	6.15	12.45
Aricidea sp	0.68	3.50	3.72	1.18	5.51	17.96
Oligochaeta	2.03	4.43	3.50	0.90	5.18	23.14
Heteromastus filiformis	2.77	3.83	3.00	1.27	4.44	27.57
Syllidae	0.88	3.07	2.99	1.30	4.42	32.00
Linucula hartvigiana	2.03	0.03	2.21	1.13	3.27	35.27

B. Species	IT Av. Abund	DS Av. Abund	Av. Diss	Diss/SD	Contrib. %	Cum. %
Spionidae	3.80	0.69	5.46	1.72	6.93	6.93
Amphipoda	4.03	2.87	5.33	0.96	6.76	13.69
Paphies australis	0.07	2.43	4.19	0.61	5.31	19.00
Heteromastus filiformis	2.77	0.76	3.96	1.11	5.03	24.03
Nematoda	0.00	2.10	3.48	0.99	4.42	28.46
Linucula hartvigiana	2.03	0.00	3.16	1.17	4.01	32.47
Hesionidae	0.01	1.73	3.01	0.92	3.82	36.29
Austrovenus stutchburyi	1.89	0.04	2.81	1.04	3.57	39.86

C. Species	SS Av. Abund	DS Av. Abund	Av.Diss	Diss/SD	Contrib. %	Cum. %
Spionidae	5.91	0.69	6.49	1.38	9.15	9.15
Oligochaeta	4.43	0.94	4.47	1.04	6.29	15.44
Heteromastus filiformis	3.83	0.76	4.06	1.51	5.72	21.17
Aricidea sp	3.50	0.39	4.03	1.16	5.68	26.84
Amphipoda	4.26	2.87	3.98	0.89	5.61	32.45
Paphies australis	0.65	2.43	3.42	0.71	4.82	37.27

3.2 Determining important environmental predictors of macroinvertebrate community structure

Distance-based linear modelling (DISTLM) determined the most parsimonious predictive model explaining maximal variation in macroinvertebrate community structure in Tauranga Harbour. The final model included nine environmental predictors and explained 30% of total variation in community structure (Table 3.4). Depth was identified as the most important environmental predictor and explained 12.2%. Other significant environmental predictors included in the model were Chl-*a*, mud content, average current speed, gravel, sand, lead (Pb), total phosphorous (TP) and copper (Cu), although these each only explained between 4.6% and 1.3% of the variation in community structure (Table 3.4). The DISTLM results were illustrated by a dbRDA plot showing the direction of effect of each environmental predictor explaining variation in macroinvertebrate community structure. Separation of the tidal zones (indicative of depth) occurred along the x-axis on the output plot, aligning with variables depth, Chl-*a* and average current speed (Fig. 3.5).

Table 3.4 Results of the distance-based linear modelling (DISTLM) based on Bray-Curtis dissimilarities of the square-root transformed macroinvertebrate abundance data using forward selection based on Akaike's Information Criterion (AIC). P_{perm}-value for each environmental predictor is given with proportion of variance explained.

Variable	AIC	SS (trace)	Pseudo-F	P_{perm}	Prop.	Cumul.	Res. df
Depth	884	28412	16.09	0.0001	0.122	0.122	116
Chl-*a*	879	10837	6.42	0.0001	0.046	0.168	115
Mud	876	8365	5.14	0.0001	0.036	0.204	114
Average current speed	876	4799	3.00	0.0003	0.021	0.225	113
Gravel	875	3698	2.34	0.0043	0.016	0.241	112
Sand	874	4671	3.01	0.0002	0.020	0.261	111
Pb	873	3601	2.35	0.0024	0.016	0.276	110
TP	873	3603	2.38	0.0027	0.016	0.291	109
Cu	873	3057	2.04	0.0089	0.013	0.305	108

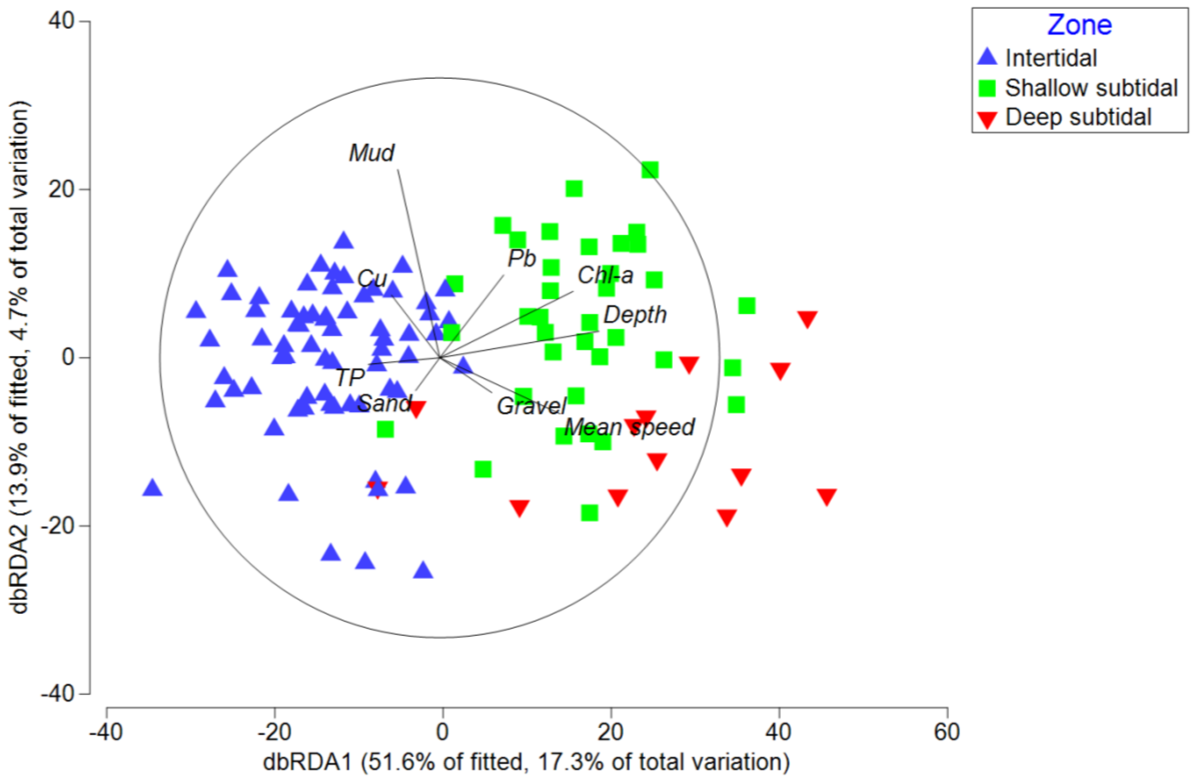

Figure 3.5 Distance-based redundancy analysis (dbRDA) plot visualising the direction and influence of environmental predictors on shifts in macroinvertebrate community structure.

3.3 Relative importance of environmental gradients for predicting compositional turnover

To build from DISTLM, Gradient Forest (GF) analysis was employed to investigate thresholds of community compositional turnover for environmental gradients known to influence community structure. GF effectively modelled species turnover for 92 (on average) of the 175 input species based on 100 bootstrapped model runs. All 13 environmental predictor variables included were considered important for predicting patterns of macroinvertebrate community compositional turnover, contributing to 47.9% combined cumulative importance. Depth was revealed as the most important predictor (6.1% of the conditional importance), closely follow by sediment Chl-*a* concentration (6.0% of the conditional importance) (Fig. 3.6). Other environmental gradients considered important predictors by GF were average current speed, gravel, maximum current speed, copper [Cu], mud content, lead [Pb], total phosphorous (TP), organic content (AFDW), total nitrogen (TN), zinc [Zn] and sand (Fig. 3.6).

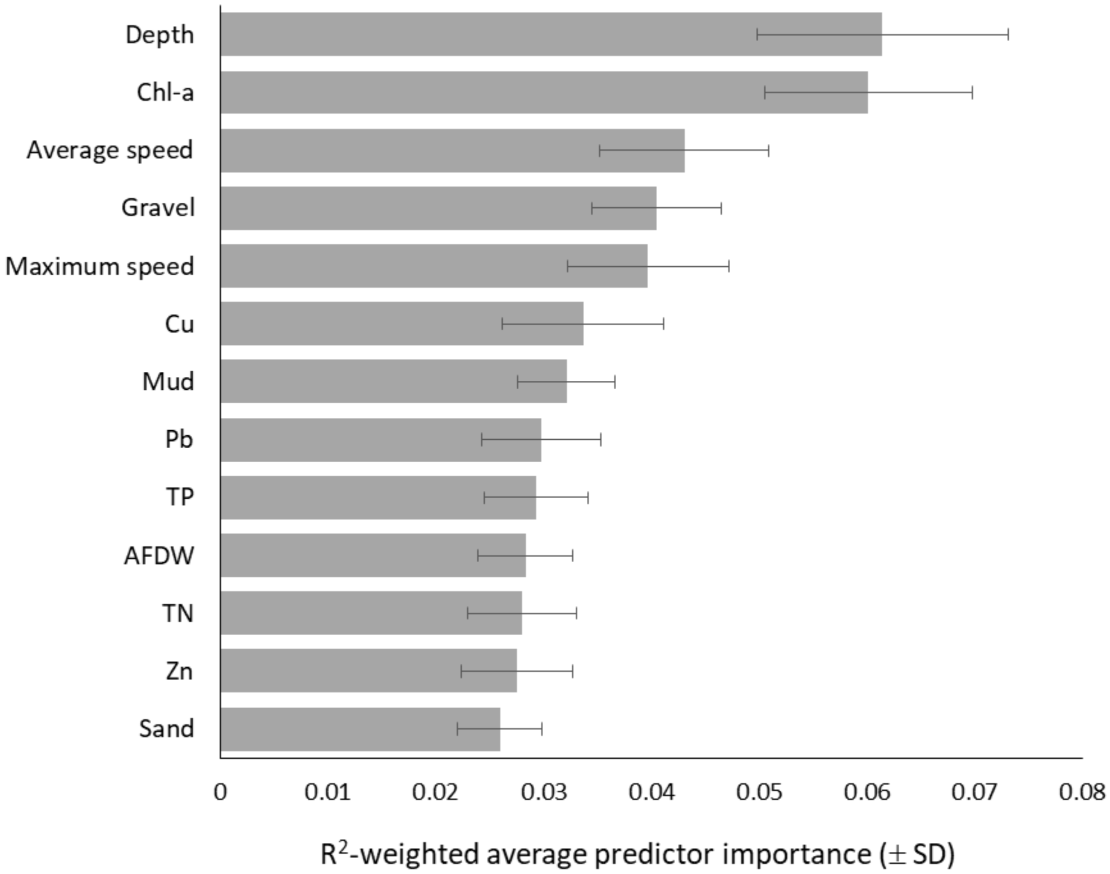

Figure 3.6 Overall importance (R^2-weighted importance across all species) of all environmental variables included in bootstrapped gradient forest models for predicting compositional turnover of benthic macroinvertebrate communities in Tauranga Harbour. Bars show mean contribution for depth, Chl-*a*, average current speed, gravel content, maximum current speed, copper [Cu], mud content, lead [Pb], organic content [AFDW], total nitrogen [TN], zinc [Zn] and sand content across 100 bootstraps. Error bars indicate the standard deviation (SD).

Non-linear curves representing rates of macroinvertebrate compositional turnover were observed for seven environmental gradients including depth, Chl-*a*, mud content, average current speed, copper, AFDW and maximum current speed. The remaining environmental gradients (TN, TP, gravel and sand) had comparatively linear relationships indicating a constant rate of compositional turnover for these predictors (Fig. 3.7). Steep sections in the cumulative importance curves indicated large shifts in community structure (i.e. rapid compositional turnover) along depth, Chl-*a*, Cu, maximum current speed and AFDW gradients, where plateaued sections of the curves indicate more comparable communities. For depth, relatively constant rates of compositional turnover were observed until around 1 m, before small rapid increases occurred periodically at 1.1 m, 2.1 m, 3.1 m and 3.9 m (Fig. 3.7). Similar patterns were observed for Chl-*a*, where compositional turnover rates increased relatively constantly until around 22000 µg/kg before levelling off, then displayed rapid increases at 28000 µg/kg, 37000 µg/kg and 45000 µg/kg (Fig. 3.7).

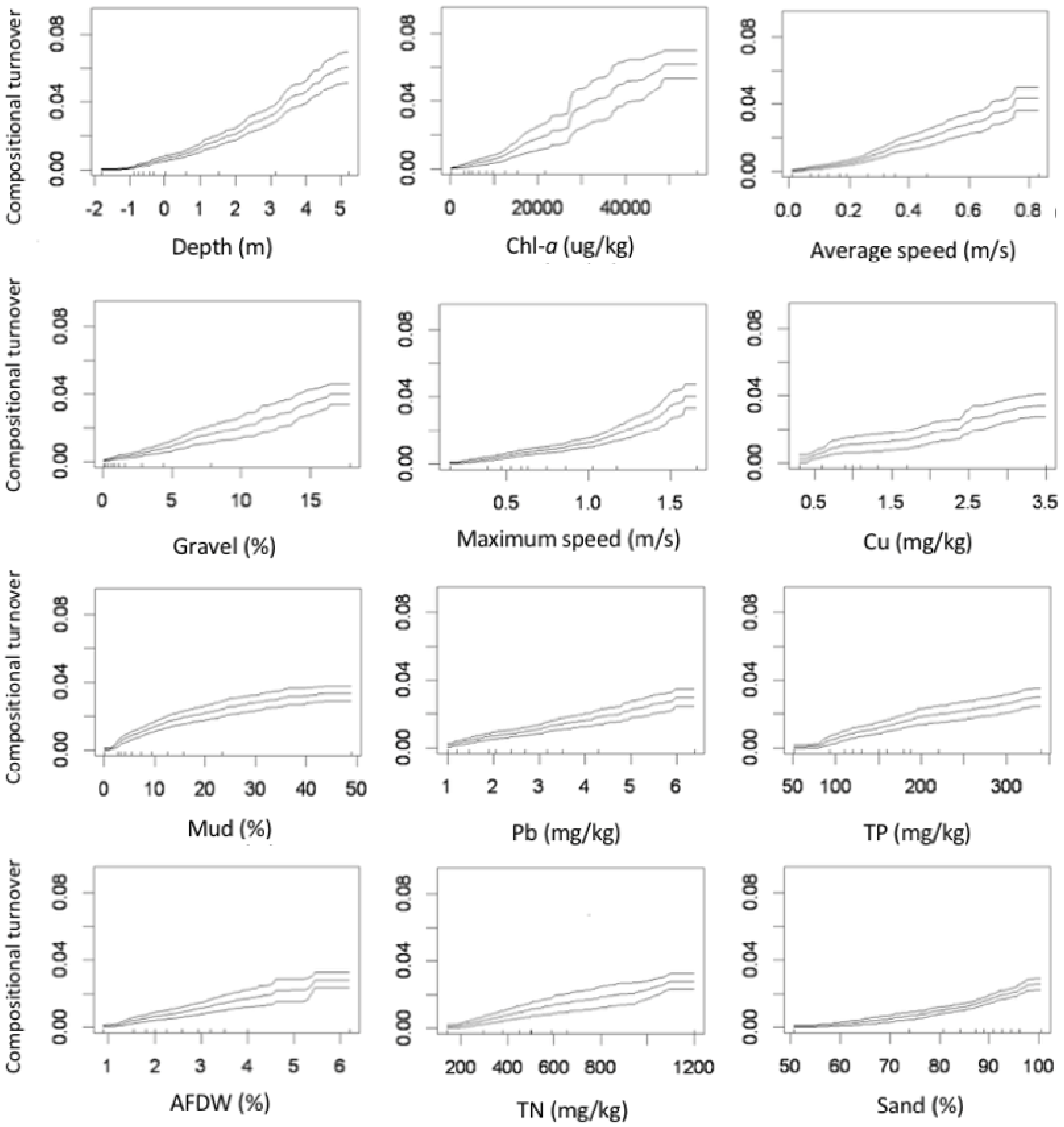

Figure 3.7 Cumulative importance curves (with 95% prediction intervals) visualising the overall pattern of compositional turnover (in R^2-importance units) for all species across all environmental predictors included in gradient forest models. Rug plots along x-axis represent deciles across each environmental gradient.

3.4 Functional group analysis

A non-metric multidimensional scaling (nMDS) plot was generated to visualise the differences in functional group community structure between tidal zones in ordination space (Fig. 3.8). Evidence of differences in functional group community structure between IT, SS and DS sites is indicated by general clustering of the tidal zone sites, despite some overlap observed between zones. A PERMANOVA indicated significant differences in functional group community structure between tidal zone (Pseudo-F=

21.047; $P < 0.001$) and post-hoc pairwise tests revealed significant differences between all pairs of tidal groups ($P < 0.001$) (Table 3.5). IT and SS sites share the most similar community structure, in comparison to the DS sites that exhibit comparatively less homogeneity in functional group community structure. A PERMDISP revealed significant differences in dispersion between IT and DS ($t=3.8$; $P < 0.001$), and SS and DS ($t=3.53$; $P < 0.01$) suggesting that differences observed in community structure between these zones should be interpreted with caution, whilst no significant differences in dispersion were identified between IT and SS.

A SIMPER analysis revealed that overall dissimilarity between the IT and SS functional group communities was 46% and was largely driven by differences in functional group abundance of FG13 (limited mobility, soft-bodied, deposit-feeding; e.g. *H. filiformis*), where average abundance was 80% greater for SS than IT, contributing 11% of the overall dissimilarity alone. The next most influential functional groups for driving differences in community structure between IT and SS were FG22 (mobile, rigid, deposit-feeding, predator/scavenger; e.g. Amphipoda, Isopoda), FG17 (limited mobility, soft-bodied, predator/scavenger; e.g. Oligochaeta), FG15 (soft-bodied, below surface, tube structure; e.g. Spionidae) and FG10 (soft-bodied, suspension-feeding, tube structure; e.g. *Euchone* sp.) each contributing 8-9% of the overall dissimilarity (Table 3.6A). In most instances, functional group abundance tended to be lower in IT compared to SS, with the exception of FG2 (mobile, calcified, suspension-feeding; e.g. *A. stutchburyi*) and FG6 (limited mobility, calcified, deposit-feeding; e.g. *L. hartvigiana*), where average abundance per core was greater for IT than SS (by factors of 1.7 and 3.1 respectively; Table 3.6). Overall dissimilarity between IT and DS was 60%, where FG12 (mobile, soft-bodied, deposit-feeding; e.g. *Scoloplos* sp.), FG13 (limited mobility, soft-bodied, deposit-feeding; e.g. *H. filiformis*), FG10 (soft-bodied, suspension-feeding, tube structure; e.g. *Euchone* sp.), FG22 (mobile, rigid, deposit-feeding, predator/scavenger; e.g. Amphipoda, Isopoda), FG15 (soft-bodied, below surface, tube structure; e.g. Spionidae) and FG2 (mobile, calcified, suspension-feeding; e.g. *A. stutchburyi*) cumulatively contributed to 50% in overall dissimilarity (8-9% individually) (Table 3.6B). There was 60% dissimilarity between SS and DS, where FG13 (limited mobility, soft-bodied, deposit-feeding; e.g. *H. filiformis*) alone contributed to 15% of the overall dissimilarity. Functional groups FG15 (soft-bodied, below surface, tube structure; e.g. Spionidae), FG10 (soft-bodied, suspension-feeding, tube structure; e.g. *Euchone* sp.) and FG12 (mobile, soft-bodied, deposit-feeding; e.g. *Scoloplos* sp.) were the next most influential contributors to overall dissimilarity, where 10-11% of overall dissimilarity between SS and DS can be attributed to each of these functional groups (Table 3.6C).

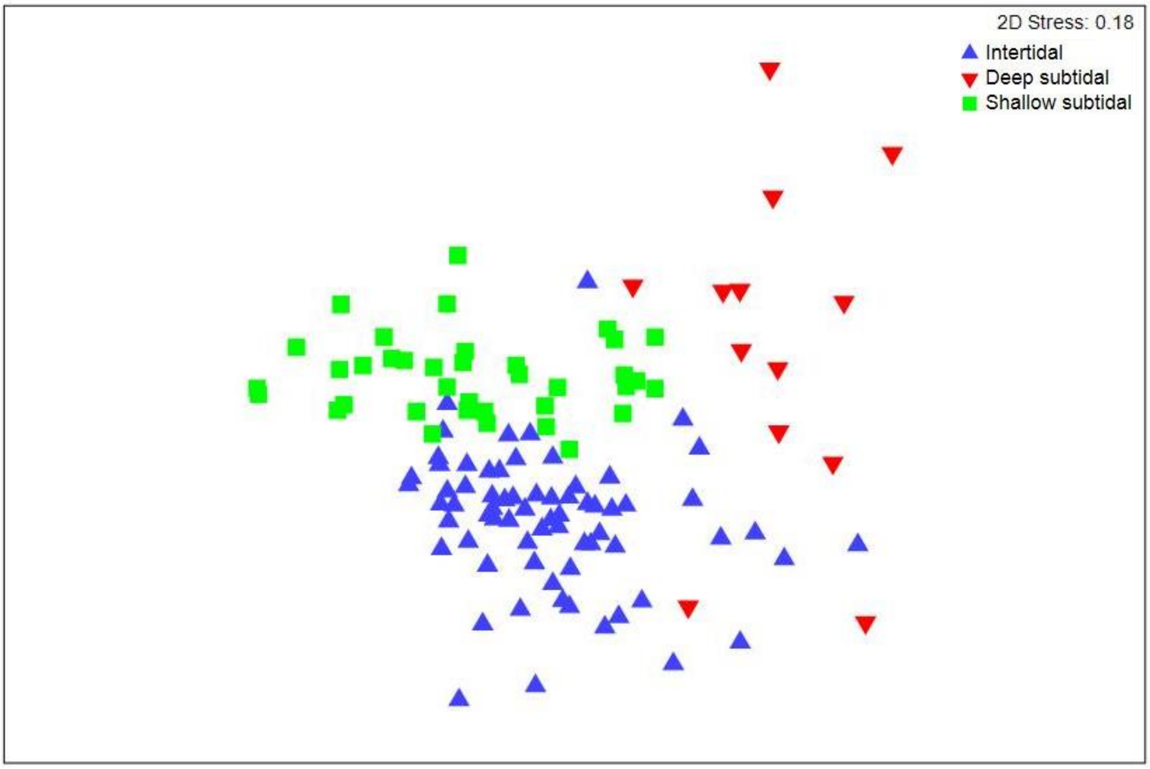

Figure 3.8 Non-metric multidimensional scaling (*nMDS*) plot visualising shifts in macroinvertebrate functional group structure between intertidal (blue), shallow subtidal (green) and deep subtidal (red) zones (as determined by initial cluster analysis on species abundance data) based on Bray-Curtis dissimilarities between survey sites of the square-root transformed abundance data.

Table 3.5 Summary of one-way PERMANOVA comparing functional group abundance data between tidal zones (Intertidal, IT; Shallow subtidal, SS; Deep subtidal, DS).

Source	df	SS	MS	Pseudo-F	P(perm)	Post-hoc pairwise tests
Zone	2	33091	16545	21.047	0.0001	I ≠ SS ≠ SD
Residuals	116	91189	786			
Total	118	1.24×10^5				

Table 3.6 Similarity percentage (SIMPER) analysis results table summarising key functional groups (FG) contributing to the dissimilarities observed between **A)** IT and SS, **B)** IT and DS, and **C)** SS and DS macroinvertebrate communities based on square-root transformed functional group abundance data. Overall dissimilarity between IT and SS was 46%, IT and DS was 60%, and SS and DS was 60%. Differences between tidal groups are shown to a 70% level. Av. Abund = average abundance (per core), Av. Diss = average dissimilarity, Diss/SD = ratio of average contribution divided by standard deviation, Contrib. % = contribution percentage, Cum. % = cumulative contribution percentage. For corresponding functional group attributes see Table 2.2.

A. Functional group	IT Av. Abund	SS Av. Abund	Av. Diss	Diss/SD	Contrib. %	Cum. %
FG13	5.34	9.70	5.16	1.46	11.30	11.30
FG22	4.04	4.39	3.94	0.91	8.62	19.92
FG17	2.50	5.66	3.86	1.10	8.45	28.37
FG15	3.90	6.35	3.74	1.32	8.19	36.56
FG10	3.80	5.99	3.67	1.30	8.04	44.60
FG12	3.95	5.96	3.63	1.29	7.94	52.54
FG19	2.04	4.68	3.38	1.03	7.40	59.94
FG23	2.10	3.52	2.34	1.29	5.12	65.06
FG6	2.15	0.70	2.01	1.11	4.39	69.45
FG2	1.92	1.08	2.00	1.12	4.37	73.82

B. Functional group	IT Av. Abund	DS Av. Abund	Av. Diss	Diss/SD	Contrib. %	Cum. %
FG12	3.95	0.77	5.22	1.91	8.68	8.68
FG13	5.34	2.42	5.10	1.52	8.48	17.16
FG10	3.80	0.73	5.00	1.93	8.32	25.48
FG22	4.04	2.95	5.00	0.97	8.31	33.80
FG15	3.90	0.83	4.99	1.95	8.31	42.10
FG2	1.92	2.43	4.83	0.89	8.03	50.14
FG19	2.04	2.95	3.84	1.26	6.38	56.52
FG6	2.15	0.04	3.33	1.22	5.55	62.06
FG11	0.00	2.10	3.32	1.01	5.53	67.59
FG5	1.73	0.45	2.74	1.54	4.56	72.15

C. Functional group	SS Av. Abund	DS Av. Abund	Av. Diss	Diss/SD	Contrib. %	Cum. %
FG13	9.70	2.42	9.08	2.18	15.12	15.12
FG15	6.35	0.83	6.63	1.80	11.04	26.16
FG10	5.99	0.73	6.26	1.66	10.42	36.58
FG12	5.96	0.77	6.16	1.63	10.26	46.84
FG17	5.66	1.99	4.71	1.20	7.84	54.68
FG22	4.39	2.95	4.07	0.89	6.78	61.46
FG19	4.68	2.95	3.84	1.05	6.39	67.85
FG2	1.08	2.43	3.64	0.76	6.07	73.92

Chapter 4

Discussion

This study was carried out with the intention to fill gaps in the scientific literature around the implications of sea-level rise (SLR) on estuarine biodiversity and ecosystem functioning. Considering the evolving relevance of diffuse climate change related stressors, to date there has been little research addressing this aspect of coastal climate change ecology. The findings of this thesis indicate that there will be significant shifts in estuarine macroinvertebrate community structure with future SLR. Furthermore, I demonstrated that localised gains and losses of individual species and functional traits within the community will likely have implications for ecosystem function. This chapter will summarise key findings from this study and provide a contextualised discussion of the relevant repercussions. Finally, recommendations for future research and management will be provided, followed by concluding remarks.

4.1 Environmental drivers of macroinvertebrate community structure and compositional turnover

4.1.1 Water column depth

In this study, water column depth was identified as the most important predictor of variation in macroinvertebrate community structure (Table 3.4) and rates of community compositional turnover (Fig. 3.6). The influence of depth on the spatial distribution of marine organisms has been well studied (e.g. Mindel et al. 2016; Kramer et al. 2020; Villalobos et al. 2021), however links to SLR are generally ignored. In estuaries, increasing depths will be a key outcome of SLR (Holleman & Stacey 2014), therefore gaining an understanding how macroinvertebrate communities shift with depth allows us to gauge prospective implications of SLR.

The observed influence of depth on species abundance and distributions, and therefore overall community structure can be attributed to a multitude of factors. The high relative importance of depth may be owed to relationships with water column and sedimentary environment characteristics such as sea temperature, salinity, sediment grain size and nutrient content, which are all known to also influence patterns of macroinvertebrate biodiversity (Ysebaert et al. 2003; Liao et al. 2016; Clark et al. 2021). This suggests that depth can represent a host of co-varying environmental parameters that will also shift with SLR, reinforcing the suitability of depth as a predictor of species distributions under future SLR scenarios. Previous studies have demonstrated depth can effectively predict the spatial distribution of marine species (e.g. O'Hara et al. 2017; Zhang et al. 2019; Simon-Nutbrown et al. 2020). Moreover, Rullens et al. (2021) developed species distribution models of a key bivalve *Austrovenus stutchburyi* in Tauranga Harbour, also identifying depth as an important predictor. Specifically, the study found that *A. stutchburyi* was generally limited to depths representative of intertidal habitats throughout the estuary, consistent with findings of this thesis (see Table 3.2; Table 3.3). These findings support the suitability of depth as an effective predictor of species and community responses to SLR. However, is unlikely that depth alone is driving observed responses, but instead acts as a surrogate for a combination of co-varying factors known to shape patterns of estuarine macroinvertebrate biodiversity.

In my study of Tauranga Harbour, GF modelling indicated accelerated compositional turnover rates of macroinvertebrate communities occurred periodically with approximately 1 metre increments as depth exceeded 2 metres and a small raise in turnover rate when depth was ~1.1 metres (Fig. 3.7). Using SLR predictions with current global emission rates, we can expect between 0.6 to 1.1 metres of sea level rise by 2100 (Oppenheimer et al. 2019). Using depth as a proxy for SLR (assuming spatial and temporal variability is equal; Picket 1989), my results indicate the upper prediction reflects a threshold where a small increase in SLR at 1.1 metres will drive a disproportionately greater change in macroinvertebrate community structure than that perceived for preceding SLR scenarios. This may be explained by the expected reductions suffered by intertidal species that are constrained by their optimal spatial distribution (Kraan et al. 2010; Puls et al. 2012; Rullens et al. 2021), impeding their ability to thrive in deeper submerged habitats that reflect SLR. This shift observed in macroinvertebrate community structure would also align with that expected of the projected intertidal habitat loss under a 1.1 metre SLR scenario (~85% reduction by 2100; Mangan et al. 2020). Nonetheless, steady rates of compositional turnover were still observed approaching 1.1 metre depth, providing an indication that any amount of SLR will alter macroinvertebrate community structure, perhaps irreversibly, within Tauranga Harbour. Therefore, to ensure the contributions to estuarine ecosystem function by intertidal communities are not lost, proactive management actions to promote ecological resilience in these environments should be prioritised.

4.1.2 Sediment Chlorophyll-*a*

Sediment chlorophyll-*a* (Chl-*a*) concentration was identified as the second most important predictor of variation in community structure (Table 3.4) and rates of macroinvertebrate community compositional turnover (Fig. 3.6). Chl-*a* concentration is indicative of primary producer abundance and biomass and in the sediments, this consists of microphytobenthos (MPB) and phytoplankton settled from the water column. In my study, rates of compositional turnover were relatively constant until Chl-*a* concentration reached around 22000 µg/kg, in which a sharp increase in rate was observed (Fig. 3.7). This abrupt increase in compositional turnover rate suggests a threshold level of plant biomass where a disproportionately large shift in macroinvertebrate community structure occurs. However, multiple factors are likely to play a role in this perceived shift as Chl-*a* is known to co-vary with other environmental variables such as estuary flushing time, temperature, mud content, nutrient concentrations (i.e. total phosphorus, total nitrogen) and depth (Ferreira et al. 2005; Reiss et al. 2007; Fowler et al. 2013; Pratt et al. 2014a; Woodland et al. 2015). Thus, establishment of a cause-and-effect relationship is challenging and any interpretation should be made with caution despite GF models high tolerance to highly correlated variables.

Benthic primary producer biomass, indicated by sediment Chl-*a*, is often regulated by macroinvertebrate grazing activity, light climate, sediment properties and nutrient concentrations (Cloern 1999; Grinham et al. 2011; Weilhoefer et al. 2017; Bruschetti et al. 2018). The influence of grazing activity on primary producer biomass suggests greater Chl-*a* concentrations will occur where macroinvertebrate grazer abundance is lower. In my study, this effect was not observed as deposit-feeder abundance (e.g. grazing spionids, oligochaetes, polychaetes) tended to be much greater within shallow subtidal sites (often more than double) than that observed at intertidal sites, despite high Chl-*a* concentrations observed at subtidal sites. However, high MPB turnover rates could explain the seeming lack of a significant grazing effect if macroinvertebrate grazing intensity did not considerably exceed MPB turnover (Smith & Underwood 2000). Alternatively, the direct effects of grazing may be less important for influencing MPB biomass than other interactions carried out by deposit-feeders (e.g. bioturbation) (Pratt et al. 2014b).

As Chl-*a* concentrations tended to be greater at deep subtidal sites (Table 3.1), it could be argued that increased depths associated with SLR would promote higher Chl-*a* concentrations and therefore enhance the trophic state of an estuary. However, increased depth may entertain a counteractive effect by reducing productivity if less light is able to reach the seafloor (Mangan et al. 2020; Thrush et al. 2021), although depth may be less important if the water column of deeper channels is sufficiently clear. Additionally, SLR may have a disproportionate negative effect in highly turbid estuaries due to reduced intertidal areas. This is because emerged periods (which is unique to intertidal habitats) provide resilience in turbid estuaries by enabling light to reach benthic primary producers such as MPB and seagrasses (Drylie et al. 2018). Therefore, it is possible high Chl-*a* concentrations observed at deep subtidal sites may be attributed to contributions of pelagic phytoplankton, lower grazing activity by macroinvertebrates or a clear water column. Although high Chl-*a* concentrations are often considered favourable as they indicate greater productivity, this is not always true. It is important to recognise that extreme quantities of Chl-*a*, caused by eutrophication for example, may pose a threat to estuarine health due to excessive oxygen consumption through decomposition which can compromise water quality (i.e. hypoxia; Chen et al. 2017). Thus, determining whether heightened Chl-*a* concentrations will be considered beneficial or harmful is a complex issue and likely to be context (and threshold) dependent. Overall, we can deduce that patterns in primary producer biomass will be influenced by future SLR in estuaries. However, in what way SLR may contribute to structural shifts in macroinvertebrate communities and whether these shifts will be valued will likely be due to multiple aspects of environmental change.

4.1.3 Current speed

Results of this thesis indicated average current speed is also an important factor for predicting patterns in macroinvertebrate community structure (Table 3.4) and compositional turnover (Fig. 3.6). Flow rates are often highly variable throughout estuaries, largely owed to the complex bathymetry of the seafloor (e.g. channels) and bordering landforms (e.g. tombolos) that influence flow dynamics (Lee & Valle-Levinson 2012; Conroy et al. 2020). In my study, average current speeds measured at each site varied from 0.01—0.83 m/s (Table 3.1), with a rapid increase in compositional turnover rate as current speed reached 0.75 m/s (Fig. 3.7). Average current speeds exceeding this value generally existed at deeper sites in Tauranga Harbour, often in the centre of channels (Fig. 3.2) and is likely explained by the strong influence of tidal exchange on current speeds in main channels (Chadwick & Largier 1999; Bolaños et al. 2013).

The flow dynamics associated with these channels often support increased delivery rates of particulate food which is favourable to filter-feeding organisms (Norkko et al. 2006). This may explain why high densities of filter-feeding *Paphies australis* were generally restricted to deep subtidal sites in this study. This finding is supported by Rullens et al. (2021) that used species distribution models to demonstrate *P. australis* is mostly limited to these fast-flowing channels within Tauranga Harbour. As estuary depth is expected to increase with future SLR, we can therefore anticipate altered current speeds (i.e. likely reduced in deep channels) due to the influence of basin geometry (e.g. degree of channel constriction) and depth on flow dynamics (Zarzuelo et al. 2017; de Ruiter et al. 2019). This indicates that although overall water column depth will increase with SLR, which could suggest *P. australis* will extend their spatial distribution, their distribution is likely to be constrained if altered current speeds do not match those required to support high densities of this ecologically and culturally important species. From this we can deduce that some species will not necessarily extend their spatial distribution to ‘follow’ their optimal depth range if other environmental factors are altered that may limit their distribution.

4.2 Comparisons across tidal zones

This study provided evidence that estuarine benthic macroinvertebrate community structure does differ across intertidal (IT), shallow subtidal (SS) and deep subtidal (DS) zones. Sampling sites that shared significantly similar macroinvertebrate community structure were clustered together and the respective site depths within each cluster resulted in the supposition they were representative of IT, SS and DS zones (Fig. 3.1). Allowing this analysis to tease apart groups of sites based on community structure similarity removed bias associated with arbitrary assignment of sites to a priori groups.

My findings demonstrate that species richness and average abundance are generally greater at SS sites in Tauranga Harbour (mean depth = 1.5 m ± 0.5 SD; Appendix 1) (Table 3.1). An explanation for this is that SS represents a transitional zone comprising a mixture of species that occur in IT and DS habitats. Therefore, increased species richness and diversity, which are defining characteristics of transition zones (Schilthuizen 2000; Kark & van Rensburg 2006), may be attributed to overlapping distribution between IT and DS species ranges. Conversely, my findings show that species richness and average abundance tended to be lower at IT sites (Table 3.1). This was expected as many estuarine species lack unique adaptations (e.g.

desiccation prevention) required to endure environmental circumstances typical of IT habitats (e.g. air exposure during periods of tidal emergence) (Newell 1976), therefore their spatial distribution is generally limited to subtidal regions. Although the general consensus within ecological studies is that increased diversity positively influences ecosystem function (Hooper et al. 2005; Danovaro et al. 2008), this can be context dependent (Stachowicz et al. 2007; Grman et al. 2010). In estuarine ecosystems, this may be attributed to disproportionate contributions of certain species to ecosystem function (e.g. *A. stutchburyi*; Thrush et al. 2006) owed to key factors (e.g. abundance/dominance, functional traits) influencing important ecological processes and functions (e.g. sediment destabilisation, primary production, ecosystem engineering) (Welsh 2003; Lohrer et al. 2004; Luck et al. 2009; Lohrer et al. 2010; O'Gorman et al. 2010; Hillman et al. 2020). Therefore, it is critical to recognise that greater species richness does not always reflect better ecosystem performance, particularly when functionally important or unique species are reduced or lost (Grman et al. 2010).

Under future SLR conditions, it is suggested that intertidal areas will essentially become subtidal as they become permanently inundated (Holleman & Stacey 2014). In this study, functional group community structure significantly differed between IT, SS and DS habitats (PERMANOVA; Table 3.5), indicating dominant IT functional groups may experience reductions whilst those of SS will become more widespread. Based on my results, such a shift would suggest a nearly two-fold increase in FG13 (limited mobility, soft-bodied, deposit-feeding; e.g. *H. filiformis*, spionids) average abundance in areas where this habitat shift occurs. Species included in this functional group are considered important drivers of community structure and many are key bioturbators that contribute to ecological processes and promote ecosystem function (e.g. nutrient cycling, sediment destabilisation) (van der Linden et al. 2017; Wouters et al. 2018), which at a glance suggests this shift could be desirable. Additionally, this functional group was relatively abundant across all tidal zones and had a high degree of redundancy, indicating high ecological resilience to environmental change. However, my results suggest FG2 (mobile, calcified, suspension-feeding; e.g. *A. stutchburyi*) and FG6 (limited mobility, calcified, deposit-feeding; e.g. *L. hartvigiana*) will experience reductions in average abundance (by 43% and 67%, respectively) in areas that shift from IT to SS, indicating this shift is not likely favourable. A dominant species of FG2 (*A. stutchburyi*) plays an important role in intertidal habitats as ecological engineers and positively influences ecological processes such as primary production (Thrush et al. 2006; Smith et al. 2010; Lohrer et al. 2016; Woodin et al. 2016). However, the distribution of species contributing to these dominant IT functional groups are generally more constrained and display lower redundancy, therefore the expected habitat shifts associated with SLR indicate implications for ecosystem function due to the predicted reductions suffered by these groups.

Understanding the environmental conditions that characterise each tidal zone may help explain why differences in macroinvertebrate community structure was observed. In my study, coarser sediments (i.e. higher proportion of gravel and sand) were generally associated with deeper subtidal sites, whereas intertidal sites tended to have finer sediments (i.e. higher proportion of mud). These disparities were expected as sediment characteristics are often shown to vary with habitat type and depth (Brown & McLachlan 1990; van Houte-Howes et al. 2004; Fujii & Raffaelli 2008; Pratt et al. 2014a; Bartoli et al. 2021). Moreover, as sediment mud content is a known driver of patterns of macroinvertebrate diversity (e.g. Sakamaki & Nishimura 2009; Pratt et al. 2014a; Robertson et al. 2015), we can deduce that the disparities in community structure observed between tidal zones may be at least partially attributed to sedimentary characteristics. This is also supported by findings of this study that determined mud content as a significant predictor for explaining variation in macroinvertebrate community structure (DISTLM; Table 3.4). Therefore, as SLR is expected to alter the sedimentary environment in estuaries (Fujii & Raffaelli 2008), having this understanding of how depth-associated shifts in habitat characteristics will impact patterns of macroinvertebrate biodiversity helps us predict ecological consequences of SLR.

4.3 Implications of reduced intertidal area

In this study, *A. stutchburyi* was very abundant within IT sites, yet abundance and occurrence was substantially reduced in SS and DS sites (Table 3.2; Table 3.3). This is consistent with other studies that demonstrate dominance of *A. stutchburyi* within intertidal soft-sediments (Thrush et al. 2006; Lohrer et al. 2016). *A. stutchburyi* plays a critical role within intertidal macroinvertebrate communities contributing to key ecosystem processes such as primary production, denitrification and ecological engineering of the sedimentary environment (Smith et al. 2010; Jones et al. 2011; Lohrer et al. 2016). Using future SLR scenarios, intertidal coverage of Tauranga Harbour is projected to experience a nearly 80% reduction due to inundation (Mangan et al. 2020), indicating major consequences for *A. stutchburyi* populations. As intertidal regions become permanently inundated due to SLR, we can expect that these functions performed by *A. stutchburyi* are also reduced. However, there is often a degree of functional redundancy within estuarine taxa where multiple species can offer similar contributions to ecosystem processes (Greenfield et al. 2016). In this study, *A. stutchburyi* and *P. australis* (pipi) were the only species characterised by FG2 (large mobile suspension-feeding bivalves), indicating low redundancy and resilience despite occurring in high abundances. Furthermore, as *P. australis* is generally restricted to subtidal regions, particularly where depth and current speeds are greater (Rullens et al. 2021), it is unlikely to be a suitable functional replacement for intertidal *A. stutchburyi*. Lack of overlap of these species realised distributions suggests that despite similar contributions to functionality, *P. australis* is unlikely to provide resilience for intertidal habitats should *A. stutchburyi* populations be reduced or lost. Furthermore, this study reveals an absence of functionally equivalent shallow subtidal species to potentially replace *A. stutchburyi*. This is concerning as SLR will reduce intertidal area, whilst shallow subtidal coverage is expected to increase. This highlights the vulnerability of *A. stutchburyi* and their functional role to intertidal habitat loss, thus we can anticipate significant implications on ecosystem function due to SLR.

As significant reductions of intertidal areas will be one major consequence of SLR faced by coastal ecosystems globally (Galbraith et al. 2002; Jackson & McIlvenny 2011; Elmilady et al. 2018; Mangan et al. 2020), we can also anticipate implications for other species that are primarily found in these regions. Results of this study also suggest that *Linucula hartvigiana* is generally limited to intertidal habitats (Table 3.2; Table 3.3). In this study, *L. hartvigiana* was the most abundant species of the four assigned to FG6 (limited mobility deposit-feeding bivalves). However, the other species such as *Euphilomedes* sp. and *Solemya parkinsoni* occurred in substantially lower densities than that observed of *L. hartvigiana* (only 4.7% and 0.43% the average abundance per core, respectively). The other contributor to this functional group was *Potamopyrgus estuarinus* which was also predominantly limited to intertidal regions, and therefore not a likely replacement species for *L. hartvigiana* in the case that intertidal regions become permanently inundated (i.e. becomes subtidal). If *L. hartvigiana* populations are substantially reduced due to SLR, functional group resilience will therefore depend upon the compensation capacity of functionally similar species. If poorly abundant shallow subtidal occurring species (i.e. *Euphilomedes* sp., *S. parkinsoni*) thrive and increase abundance under SLR conditions (e.g. if there is less competition for resources; Kunte 2008), they may compensate for reductions experienced by *L. hartvigiana*. However, as losses of dominant species cannot always be compensated for (e.g. Smith & Knapp 2003), it is unlikely redundancy effects of other functionally similar species if they cannot achieve adequate abundance. Overall, this highlights that redundancy potential of a functionally similar species will only be realised if abundance can increase to compensate for dominant species reduction/loss and the spatial distribution of the potential replacement is not also compromised by SLR.

Although *L. hartvigiana* is typically a widespread and highly abundant species throughout soft-sediment habitats (Morley & Hayward 2016), their exact contribution to ecosystem function has not yet received attention. Thus, it is challenging to quantify the ecological implications of reductions of this species and the lack of suitable functional replacements. Nevertheless, a high degree of functional redundancy between intertidal and shallow subtidal habitats where species generally limited to intertidal such as *L. hartvigiana* are represented is fundamental to ensure the respective functions they likely uphold are maintained when faced with SLR. This study indicates that this is not the case for these intertidal limited mobility deposit-feeding bivalves, suggesting there will be implications that are not yet fully recognised for ecosystem function if intertidal habitat is lost to SLR. We do however know that intertidal habitats hold a significant role in maintaining important ecological processes (e.g. primary production, denitrification; Drylie et al. 2018; Sigleo 2019), often exceeding that of the adjacent subtidal habitats (Piehler & Smyth 2011). Additionally, species abundance has been shown to strongly influence these processes (e.g. Dangles & Malmqvist 2004; Schenone & Thrush 2020). Therefore, it is reasonable to extrapolate that highly abundant intertidal species will have a significant influence on ecological processes, although the nature of the effect will likely depend on species identity. To obtain an extensive understanding of the implications we can expect to arise under future SLR conditions, which will be critical for future ecosystem management, we must understand the unique roles of all species and their functional groups that are vulnerable to expected habitat shifts. This highlights the importance of directly measuring the unknown species-specific and functional group-specific contributions to ecosystem function in future research.

An important aspect to acknowledge is the possibility that time scales associated with geomorphic and ecological shifts due to SLR may differ. Generally, ecological shifts can occur very rapidly as changed environmental conditions can often have a direct impact on species distributions (Pollard & Reed 2004). Changes to geomorphology however, can take place over a much longer period of time (Tullos et al. 2014). This suggests that if intertidal habitats become flooded by SLR, the projected changes to the sedimentary environment (i.e. lower mud content/coarser sediments) may display a time lag, whereas the response of species distributions and their respective communities to SLR is expected to be much more immediate. Moreover, there is the possibility of intertidal habitat ‘legacy effects’ (i.e. residual qualities of the former habitat; Bain et al. 2012) hindering the transition of ‘muddy’ sediments to ‘sandy’ sediments typical of the shallow subtidal habitats observed in my study. This suggests that species currently thriving in shallow subtidal habitats (e.g. Oligochaetes) may not necessarily occur in the same densities in inundated intertidal areas if sediment composition limits their distribution. As I employed a space-for-time approach, key findings of this thesis heavily rely on the assumption that intertidal habitats will essentially become shallow subtidal as they become permanently inundated by SLR. Therefore, unknown legacy effects of intertidal habitats may influence macroinvertebrate community responses to SLR that have not been accounted for in this study.

4.4 Other sources of environmental variability

Coastal marine environments, as with most natural systems, are subject to an extremely high degree of environmental variability. Despite the high significance of my DISTLM predictive model for explaining variation in macroinvertebrate community structure, it only explained 30% of observed variation. This leaves a large proportion unexplained. Although high proportions of unexplained variability are not uncommon among studies assessing environmental drivers of community structure (e.g. Turner et al. 1999; Bowden et al. 2001; van Houte-Howes et al. 2004; Botwe et al. 2015; Berthelsen et al. 2018), we must acknowledge that there are other factors not accounted for in my study that are having an undetected influence.

In Tauranga Harbour, it is likely that small-scale drivers (i.e. local) were contributing to most of the unexplained variation. For example, biotic interactions (e.g. predator-prey relationships; Thrush 1999), wind-wave exposure (Hewitt et al. 2016) and fishing pressure (e.g. overharvesting of key shellfish species; Marsden & Adkins 2010) can all have strong direct and indirect influences on the structure of macroinvertebrate communities. Salinity is also known to shape patterns of biodiversity (Zettler et al. 2007; Clark et al. 2021), therefore may contribute to the unexplained variation. It could also be argued that an effect of salinity may be amplified with SLR as altered tidal exchange flows are expected to promote migration of saline water into estuaries (i.e. saline intrusion) (Hilton et al. 2008).

Other factors acting on a global-scale such as sea surface and water column temperature are also known to strongly influence patterns of biodiversity in marine environments (Southward et al. 1995; Hewitt et al. 2016; Denis-Roy et al. 2020; Clark et al. 2021). Temperature was one important factor that was not included in my analyses due to a lack of relevant data for each site. However, Tauranga Harbour is subject to large tidal exchange so water temperature is expected to remain relatively constant through the estuary (Tay et al. 2013), although seasonal sampling may have allowed an effect of temperature to be detected. This suggests temperature would not have been a key driver of dissimilarity between macroinvertebrate communities within this study, unlike if sampling was conducted over a broader geographic-scale (e.g. across latitudinal gradient). As my study does not account for these factors known to shape patterns of biodiversity, further research could consider interactive effects between drivers acting on local (e.g. sediment composition, salinity) and global scales (e.g. climate, SLR) to influence macroinvertebrate community structure.

4.5 Recommendations for future research and management

This study was based on biological and environmental data from a single temperate estuary, where all sampling was conducted at unvegetated soft-sediment habitats during austral summer. Additionally, there was a four-year gap between the two ecological surveys that data were obtained from and used for my study. This requires acknowledgement that findings must be interpreted with caution and care must be taken when inferring conclusions for other habitat types and estuaries around the globe. Therefore, to increase the generality of the results of this thesis, further research is fundamental.

Firstly, I recommend that future research should encompass ecological data from a range of estuaries to confirm if shifts in macroinvertebrate communities and their contributions to ecosystem function will be comparable across estuaries. As estuarine environments differ substantially in terms of their complexity and environmental variability, we must consider that environmental change will impact individual estuaries and their respective communities differently. However, gaining evidence that individual estuaries will respond similarly to SLR could help inform management actions as a generalised framework for mitigating impacts could be established. Secondly, results of this thesis are currently restricted to austral summer. Seasonal sampling would uncover the impacts of seasonal variation on macroinvertebrate diversity and whether community shifts expected with SLR are influenced by this variation. Furthermore, results of this thesis could be complemented by future research encompassing a wider range of habitat types (e.g. seagrass beds). This would allow for generalised conclusions to be drawn for other estuarine habitats and would not be limited to unvegetated soft-sediments.

Assessing the potential impacts of climate change stressors such as SLR is particularly challenging as before-after study designs would have to take place over large time scales. Furthermore, by the time conclusions can be drawn, irreversible ecological changes are already likely to have occurred. Although employing a space-for-time approach can be advantageous, it relies on the assumption that spatial and temporal variation are equal (Picket 1989). An alternative approach could be employment of time-series data on biological communities and the environmental parameters at estuarine habitats. This could allow for early detection of trends in ecological responses to SLR. Therefore, as a final recommendation for future research, I encourage utilization of a national environmental monitoring programme (Hewitt et al. 2014) to monitor temporal trends in macroinvertebrate community structure focusing on sites located at the intertidal-shallow subtidal interface. This would be a valuable tool to assess ecological responses to SLR occurring over time and allow predictions for the future based on observed trends.

Understanding the anticipated challenges that biological communities within estuarine habitats will face under future SLR conditions will be critical for successful management actions. To ensure longevity of ecosystem function and the respective services that society value, management should prioritise ecological resilience by mitigating localised anthropogenic stressors where there is greater control (e.g. overfishing, sedimentation, eutrophication) and consider allowing intertidal areas to undergo natural migration inland to offset coastal squeeze (e.g. removing man-made sea defenses).

A proactive and transdisciplinary approach to management should be employed that considers local indigenous knowledge and practices in concert with global approaches such as an ecosystem-based management. In Aotearoa New Zealand, this is particularly important as the cultural services delivered by coastal habitats are often disproportionately valued by indigenous communities whom have utilised these environments over past generations and possess a strong sense of kaitiakitanga (guardianship and conservation of the environment).

This is fundamental for recognising indigenous-Māori rights to contribute to governmental environment management that were assured under the Treaty of Waitangi, 1840.

Management efforts targeting biodiversity in coastal environments should recognise the expected shifts in community structure that will occur through habitat loss. This will be fundamental for ensuring management strategies are indeed effective for maintaining biodiversity, particularly for systems such as Marine Protected Areas (MPAs) that often treat habitats as fixed in space over time. Well-informed management of coastal environments and the biological communities that reside there will be critical for ensuring that the ecosystem functions and services valued by society are conserved for future generations.

4.6 Concluding remarks

There is no denying that SLR resulting from a warming planet will significantly modify coastal geomorphology, influencing tidal dynamics, currents and the sedimentary environment. Hence, it is surprising that ecological responses to the expected changes to occur in coastal abiotic environments have received little attention. This study demonstrates that macroinvertebrate community structure differs significantly across tidal zones in Tauranga Harbour and that patterns in macroinvertebrate biodiversity will shift in response to altered depth and the concomitant changes to the water column and sedimentary environment. Furthermore, even though reduced intertidal coverage will impact estuarine ecosystems and their communities at local and global scales, the ecological repercussions have been largely dismissed despite their prospective significance. A key aim of this study was to address these implications and facilitate further discussion concerning intertidal habitat loss. Throughout this thesis, I identify ecologically and culturally important species and their respective contributions to ecosystem function that are generally limited to intertidal habitats in Tauranga Harbour and demonstrate the consequences we can expect to encounter when faced with future SLR. Analysis using functional trait based groups suggested that already low functional redundancy will not be realised for a key intertidal species indicating concerns for ecosystem function with SLR due to the absence of a functionally equivalent shallow subtidal substitute. Furthermore, the results of the thesis underpin the idea that the ecological impacts of species loss will be dependent on the species-specific contributions to ecosystem function. Overall, this study strongly suggests SLR will significantly alter estuarine macroinvertebrate communities, indicating repercussions for ecosystem function and resilience of valued coastal environments. Key findings of this study will be essential for ensuring management actions do not treat coastal areas as static systems due to ecological shifts with SLR over time.

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Appendices

Appendix 1: Site Information

Table A1 Site information for the sampling sites this study was based on. Data were obtained then collated from MTM and OTOT research programmes. Cluster # = CLUSTER analysis assigned group number, tidal zone = referred tidal zone derived from depth ranges of clustered groups (IT = intertidal, SS = shallow subtidal, DS = deep subtidal), depth = model grid depth corrected to chart datum (metres; negative values is reflects periods of emergence), Chl-*a* = Chlorophyll-*a* concentration (μg/kg), mud = sediment grain size < 63μm (%), gravel = sediment grain size ≥ 2mm (%), sand = sediment grain size ≥ 63μm and < 2mm (%), Pb = lead (mg/kg), Zn = zinc (mg/kg), TP = total phosphorus concentration (mg/kg), TN = total nitrogen (mg/kg), AFDW = organic content; ash-free dry weight (g/100g).

Site ID	Sampling date	NZTME	NZTMN	Cluster #	Tidal zone	Depth	Chl-*a*	Mud	Gravel	Sand	Pb	Zn	TP	TN	AFDW
I1	01/02/2012	1862844	5850790	1	IT	-0.84	4600	3.6	0.4	96.0	1.1	8	110	380	1.6
I2	02/02/2012	1863039	5849578	1	IT	0.27	6600	2.5	10.2	87.3	1.4	9	210	590	2.4
I3	01/02/2012	1861313	5849572	1	IT	-0.87	4600	3.9	1.7	94.5	1.0	6	110	380	1.9
I4	01/02/2012	1860898	5848973	1	IT	-1.12	3200	5.6	0.4	94.0	1.0	6	120	350	2.5
I5	24/02/2012	1862374	5849061	1	IT	-0.32	2400	1.5	1.2	97.4	1.0	7	140	290	1.6
I6	01/02/2012	1860947	5847735	1	IT	-0.68	8600	7.3	0.7	91.9	1.3	11	180	530	3.8
I7	01/02/2012	1860284	5846213	1	IT	-0.91	10000	10.2	1.1	88.7	1.0	11	180	640	3.0
I8	15/02/2012	1862990	5845258	3	DS	0.39	5300	2.9	0.3	96.7	1.3	10	160	380	3.0
I9	23/01/2012	1861385	5842837	1	IT	-0.71	2200	3.6	1.5	94.9	1.4	27	78	180	1.0
I10	23/01/2012	1859160	5841668	1	IT	-0.78	1100	30.9	2.9	66.2	5.6	34	340	1000	4.4
I11	15/02/2012	1861019	5840122	1	IT	-0.60	4400	6.5	0.9	92.5	1.1	12	120	390	2.8

Site ID	Sampling date	NZTME	NZTMN	Cluster #	Tidal zone	Depth	Chl-*a*	Mud	Gravel	Sand	Pb	Zn	TP	TN	AFDW
I12	18/01/2012	1860872	5838709	1	IT	-0.55	1900	8.9	0.1	91.0	1.9	9	120	300	2.0
I13	18/01/2012	1859645	5838849	1	IT	-0.97	2800	14.3	0.6	85.1	3.4	22	250	540	3.1
I14	18/01/2012	1858852	5837443	1	IT	-1.05	5600	24.7	1.0	74.3	4.6	26	330	830	4.5
I15	18/01/2012	1864615	5844595	2	SS	1.11	1200	3.7	0.4	95.9	2.2	13	160	340	2.1
I16	18/01/2012	1861664	5847064	1	IT	0.46	7000	3.3	0.7	96.1	1.5	11	180	310	1.8
I17	16/02/2012	1866194	5839926	1	IT	-0.29	4200	3.9	2.0	94.1	1.0	8	110	370	2.1
I18	17/01/2012	1868133	5838623	1	IT	-1.26	210	1.3	0.2	98.5	1.1	3	53	140	0.9
I19	17/01/2012	1865401	5839681	1	IT	-0.07	3000	4.3	0.1	95.6	1.2	7	91	310	2.1
I20	17/01/2012	1870400	5836995	1	IT	-1.30	1200	0.1	0.1	100	1.3	10	92	340	1.6
I21	16/02/2012	1862901	5839911	1	IT	-0.58	5100	6.5	2.0	91.3	1.3	11	180	540	3.8
I22	05/01/2012	1864304	5836733	1	IT	-0.51	3300	17.5	0.9	81.6	3.5	18	220	700	4.2
I23	05/01/2012	1863958	5837013	1	IT	-1.02	7900	34.2	0.8	64.9	3.1	14	200	430	3.1
I24	17/01/2012	1867485	5834361	1	IT	-0.17	5600	15.7	0.8	83.5	3.1	19	200	390	2.6
I25	17/01/2012	1867748	5834506	1	IT	-0.86	3800	1.4	1.4	97.2	1.4	6	51	180	0.9
I26	20/12/2011	1864309	5834506	1	IT	-0.81	3600	23.3	0.1	76.5	2.7	13	130	590	4.0
I27	20/12/2011	1863615	5834467	1	IT	-0.52	7300	18.7	0.1	81.3	4.3	20	180	580	4.2
I28	02/02/2012	1862821	5834277	1	IT	-0.95	8600	22.4	0.1	77.5	2.8	14	160	520	3.5
I29	20/12/2011	1872451	5833584	1	IT	-0.59	3900	16.2	1.2	82.6	2.5	16	150	690	2.7
I30	20/12/2011	1872580	5833532	1	IT	-0.48	4000	8.9	0.5	90.7	1.9	9	97	450	1.8

Site ID	**Sampling date**	**NZTME**	**NZTMN**	**Cluster #**	**Tidal zone**	**Depth**	**Chl-*a***	**Mud**	**Gravel**	**Sand**	**Pb**	**Zn**	**TP**	**TN**	**AFDW**
I31	19/12/2011	1875571	5831455	1	IT	-0.84	4800	13.0	1.0	86.1	1.9	10	120	490	3.2
I32	19/12/2011	1875642	5830632	1	IT	-0.57	8100	7.7	1.1	91.2	2.5	12	160	490	2.3
I33	19/12/2011	1876347	5830239	1	IT	-0.61	7200	6.3	2.3	91.5	2.2	12	190	550	2.6
I34	19/12/2011	1876500	5830117	1	IT	-0.36	5400	3.2	0.7	96.2	1.9	8	130	350	1.8
I35	21/12/2011	1873330	5831630	1	IT	-1.23	3300	3.3	0.7	96.0	1.2	5	93	290	1.4
I36	20/12/2011	1866432	5832044	1	IT	1.71	4700	12.6	0.2	87.3	3.1	15	180	530	3.3
I37	21/12/2011	1863362	5831812	1	IT	-0.93	3300	47.5	1.5	51.0	4.5	26	310	760	4.5
I38	21/12/2011	1864247	5830677	1	IT	-0.63	4100	48.9	0.3	50.7	4.1	21	260	620	4.2
I39	20/12/2011	1865756	5831517	1	IT	-0.71	4300	15.0	0.8	84.2	2.0	12	130	460	2.6
I40	19/12/2011	1866557	5830113	1	IT	-1.32	6100	31.5	0.2	68.4	4.0	19	220	650	3.8
I41	19/12/2011	1866954	5830644	1	IT	-0.67	5000	15.1	0.6	84.3	2.3	15	140	450	3.5
I42	21/12/2011	1868018	5830518	1	IT	-0.17	5900	25.4	0.9	73.9	4.3	27	280	760	4.0
I43	17/01/2012	1868270	5833779	1	IT	0.75	5000	4.9	0.6	94.5	2.6	14	120	310	1.6
I44	08/12/2011	1870057	5830629	1	IT	-0.36	5000	20.9	1.6	77.6	5.1	21	220	450	4.3
I45	03/02/2012	1879574	5828564	3	DS	0.33	11000	1.5	1.0	97.5	1.0	6	180	320	1.2
I46	20/12/2011	1868460	5828617	1	IT	-0.90	4900	38.6	1.5	60.0	3.7	22	240	620	3.8
I47	20/12/2011	1867687	5827666	1	IT	-2.00	8800	29.2	10.2	60.5	3.3	18	220	660	4.0
I48	08/12/2011	1868434	5825385	1	IT	-0.97	11000	76.4	0.1	23.7	13.0	46	580	1900	10.0
I49	07/12/2011	1869659	5827627	1	IT	-1.01	5600	17.3	5.6	77.2	5.4	55	210	680	3.0

Site ID	**Sampling date**	**NZTME**	**NZTMN**	**Cluster #**	**Tidal zone**	**Depth**	**Chl-*a***	**Mud**	**Gravel**	**Sand**	**Pb**	**Zn**	**TP**	**TN**	**AFDW**
I50	08/12/2011	1870076	5827281	1	IT	-1.47	9600	27.9	3.9	68.2	4.2	34	290	920	4.5
I51	15/02/2012	1874915	5828700	2	SS	2.95	6700	3.8	0.4	95.7	1.7	12	120	380	2.7
I52	08/12/2011	1871810	5829542	1	IT	-0.25	4500	8.9	1.4	89.7	4.3	20	200	450	2.7
I53	16/02/2012	1871371	5827820	2	SS	0.91	7500	9.5	1.6	88.9	2.1	17	170	590	3.1
I54	08/12/2011	1873409	5826958	1	IT	-1.05	6000	10.9	1.5	87.6	3.4	24	120	350	3.4
I55	08/12/2011	1873681	5825837	1	IT	-0.95	16000	12.6	0.3	87.0	4.3	21	180	590	3.0
I56	08/12/2011	1874059	5825206	1	IT	-1.24	15000	12.5	0.1	87.5	4.3	35	130	520	3.3
I57	07/12/2011	1875042	5825703	1	IT	-1.20	11000	6.4	0.1	93.5	2.0	13	150	460	3.2
I58	07/12/2011	1876239	5827455	1	IT	-0.78	8700	5.9	5.9	88.1	2.6	22	180	410	3.5
I59	16/12/2011	1877894	5826769	1	IT	-0.99	4000	1.8	4.0	94.2	1.6	8	91	200	1.3
I60	16/02/2012	1878761	5826878	3	DS	0.02	3600	0.6	0.1	99.3	1.0	11	110	190	1.8
I61	07/12/2011	1879047	5826309	1	IT	-0.61	8400	4.0	6.4	89.5	2.3	20	180	390	2.1
I62	07/12/2011	1877913	5824841	1	IT	-1.06	6600	12.4	0.3	87.2	2.1	16	120	380	2.5
I63	07/12/2011	1878131	5824740	1	IT	-1.04	7500	18.5	0.4	81.3	3.0	45	180	500	3.1
I64	07/12/2011	1878213	5824451	1	IT	-1.09	11000	5.1	2.1	92.7	1.8	14	100	460	2.5
I65	08/12/2011	1880395	5824712	1	IT	-0.83	5400	9.1	1.0	90.0	2.5	22	160	450	3.2
I66	16/12/2011	1881055	5825407	1	IT	-0.80	4100	4.4	0.8	94.7	1.8	15	120	250	1.5
I67	07/12/2011	1882458	5824505	1	IT	-1.47	2600	7.0	0.4	92.7	1.4	10	89	220	1.9
I68	07/12/2011	1879334	5822166	1	IT	-0.77	9000	9.5	7.1	83.4	2.5	20	150	410	2.2

Site ID	Sampling date	NZTME	NZTMN	Cluster #	Tidal zone	Depth	Chl-*a*	Mud	Gravel	Sand	Pb	Zn	TP	TN	AFDW
I69	08/12/2011	1878074	5820248	1	IT	-0.89	8200	32.4	4.2	63.4	4.4	44	210	560	4.0
I70	07/12/2011	1878638	5820282	1	IT	-1.12	10000	21.2	0.5	78.2	3.1	38	160	280	3.2
I71	14/02/2012	1881779	5821870	1	IT	0.41	11000	2.6	14.6	82.8	1.2	18	150	470	2.0
I72	20/02/2012	1883024	5821883	1	IT	-0.41	9700	10.3	0.9	88.8	2.7	20	190	580	2.4
I73	20/02/2012	1883502	5821744	1	IT	-0.56	9800	14.1	4.0	82.0	2.7	19	180	640	2.5
I74	07/12/2011	1884604	5822782	1	IT	-0.94	9100	3.5	0.3	96.3	1.2	10	93	180	1.8
I75	06/12/2011	1881669	5820495	1	IT	-0.86	9100	12.2	0.9	86.9	2.7	28	180	280	2.8
S1	21/04/2016	1863119	5849891	2	SS	-0.81	13000	2.9	4.6	92.4	1.7	10	98	499	1.4
S2	21/04/2016	1863324	5848985	2	SS	5.02	13000	3.3	0.2	96.3	1.9	9	150	499	2.2
S3	21/04/2016	1861965	5849197	2	SS	1.64	23200	2.6	1.3	96.0	1.6	8	152	499	1.9
S4	21/04/2016	1860615	5847444	2	SS	-0.25	12400	2.9	9.3	87.6	1.7	8	87	499	1.9
S5	22/04/2016	1861538	5847070	2	SS	0.83	31800	6.2	0.1	93.7	2.2	12	167	500	4.2
S6	21/04/2016	1863438	5845776	3	DS	8.12	12900	2.9	12.6	84.5	1.8	8	109	499	1.4
S7	22/04/2016	1863971	5844105	2	SS	4.22	22100	2.7	3.3	93.9	2.0	8	119	499	1.5
S8	22/04/2016	1863208	5842925	3	DS	3.09	21000	3.3	2.4	94.4	2.0	10	118	499	1.8
S9	02/05/2016	1861889	5842056	2	SS	0.29	14800	8.0	0.8	91.3	2.0	10	114	499	2.0
S10	02/05/2016	1862749	5841987	2	SS	1.39	22700	14.7	1.5	83.9	2.4	12	141	700	3.2
S11	02/05/2016	1863916	5841646	3	DS	2.93	15900	4.1	6.9	89.0	2.0	9	110	499	1.8
S12	02/05/2016	1865267	5842276	2	SS	1.31	12600	5.1	0.8	94.2	1.7	9	79	499	1.8

Site ID	**Sampling date**	**NZTME**	**NZTMN**	**Cluster #**	**Tidal zone**	**Depth**	**Chl-*a***	**Mud**	**Gravel**	**Sand**	**Pb**	**Zn**	**TP**	**TN**	**AFDW**
S13	02/05/2016	1864312	5838107	2	SS	-0.18	16300	12.6	0.5	86.9	2.7	13	132	600	3.3
S14	16/03/2016	1865477	5831782	2	SS	0.47	22300	6.2	0.4	93.4	3.2	17	153	499	3.2
S15	16/03/2016	1867728	5831371	2	SS	1.29	16500	11.3	2.8	85.9	3.2	19	154	499	3.3
S17	16/03/2016	1870415	5831000	3	DS	3.10	56300	5.0	8.3	86.7	2.8	19	115	499	2.1
S18	31/03/2016	1869343	5830086	2	SS	0.81	15600	10.8	1.2	87.9	2.9	20	117	499	2.7
S19	31/03/2016	1869104	5828958	2	SS	0.96	17600	18.7	2.9	78.4	3.6	24	175	600	3.9
S20	31/03/2016	1868665	5827445	2	SS	0.21	19200	22.9	9.8	67.4	6.4	28	340	1200	6.2
S21	18/05/2016	1870527	5830195	2	SS	2.67	19100	11.9	2.0	86.0	3.2	19	143	499	3.1
S22	18/05/2016	1869904	5828906	2	SS	3.32	14000	9.2	2.8	87.9	3.2	20	147	499	2.8
S23	08/04/2016	1869999	5828115	2	SS	3.13	8100	7.9	2.2	89.8	3.3	17	100	499	3.6
S24	01/04/2016	1870693	5828013	2	SS	3.49	12400	23.4	3.2	73.4	4.6	28	189	700	4.7
S25	21/03/2016	1872057	5830430	3	DS	3.56	39400	3.4	0.5	96.1	2.0	9	114	499	1.7
S26	01/04/2016	1872819	5828436	2	SS	4.44	8400	7.9	0.5	91.6	3.7	22	187	499	3.3
S27	18/03/2016	1873732	5830110	2	SS	2.51	32800	5.1	4.2	90.8	3.3	20	111	499	1.8
S28	18/03/2016	1874368	5829059	2	SS	1.87	10200	7.0	12.8	80.2	3.3	16	180	500	2.7
S29	16/03/2016	1874058	5832821	2	SS	-0.65	19100	6.2	2.4	91.5	2.2	11	115	500	1.8
S30	18/05/2016	1875880	5830399	3	DS	-0.16	34700	3.0	0.1	97.0	1.7	8	136	499	1.3
S31	18/03/2016	1876229	5829192	3	DS	9.00	2000	2.6	12.5	85.0	2.1	14	81	499	1.0
S32	03/05/2016	1876881	5828367	2	SS	2.39	22800	5.3	5.0	89.9	2.4	14	182	500	2.4

Site ID	Sampling date	NZTME	NZTMN	Cluster #	Tidal zone	Depth	Chl-*a*	Mud	Gravel	Sand	Pb	Zn	TP	TN	AFDW
S33	03/05/2016	1878625	5828901	3	DS	4.91	2200	2.4	4.3	93.3	1.4	8	111	499	1.1
S34	03/05/2016	1875108	5827203	2	SS	-0.27	22900	5.5	3.0	91.5	1.7	10	104	499	2.1
S35	18/05/2016	1878151	5827359	2	SS	3.21	9100	3.3	5.9	90.8	2.1	12	134	499	1.3
S36	28/04/2016	1879150	5827089	2	SS	1.41	7200	5.6	12.7	81.8	2.6	15	85	499	2.2
S37	04/05/2016	1879087	5825602	2	SS	0.15	19500	3.8	10.4	85.7	2.8	19	91	499	1.9
S38	04/05/2016	1880201	5825764	2	SS	2.84	14700	9.4	0.7	89.9	3.5	20	182	499	2.9
S39	04/05/2016	1879878	5824854	3	DS	2.73	15200	4.2	17.8	78.0	3.2	22	108	499	2.4
S40	15/03/2016	1880318	5822864	3	DS	1.43	10400	3.2	9.4	87.5	3.8	25	117	499	1.7
S41	28/04/2016	1878919	5820940	2	SS	-0.53	41300	5.0	15.0	80.1	3.0	18	152	499	2.9
S42	28/04/2016	1880085	5821093	2	SS	-0.99	14100	4.9	6.2	88.9	2.1	28	117	499	2.0
S43	30/03/2016	1881102	5821482	2	SS	-0.53	11200	14.7	6.9	78.5	6.4	37	183	500	3.0
S44	30/03/2016	1881346	5821885	2	SS	0.82	13000	8.0	12.4	79.6	5.5	31	177	499	2.6
S45	30/03/2016	1882682	5822747	2	SS	-0.29	14000	12.3	7.0	80.8	4.2	27	250	600	2.9

Appendix 2: Pearson’s correlations of environmental variables

Table A2 Pearson’s correlation coefficient (r) between environmental variables. Correlations where, r > 0.70, in bold.
Abbreviations used in Table A2 represent total phosphorus, TP; total nitrogen, TN; chlorophyll-*a*, Chl-*a*; copper, Cu; lead, Pb; zinc, Zn; arsenic, As; cadmium, Cd; chromium, Cr; mercury, Hg; nickel, Ni; and ash-free dry weight, AFDW

	TP	**TN**	**Chl-*a***	**Cu**	**Pb**	**Zn**	**As**	**Cd**	**Cr**	**Hg**	**Ni**	**AFDW**	**Gravel**	**Sand**	**Mud**	**Depth**	**AS**	**MS**
TP	1.00																	
TN	**0.72**	1.00																
Chl-*a*	-0.10	0.19	1.00															
Cu	0.64	0.46	-0.19	1.00														
Pb	0.67	0.64	0.08	**0.71**	1.00													
Zn	0.53	0.67	0.01	0.63	**0.78**	1.00												
As	0.42	0.29	0.20	0.07	0.25	0.04	1.00											
Cd	0.53	0.41	-0.08	**0.71**	0.61	0.58	-0.09	1.00										
Cr	0.42	0.36	0.03	0.11	0.17	-0.03	0.45	0.13	1.00									
Hg	0.37	0.19	-0.13	0.35	0.33	0.27	0.20	0.13	-0.09	1.00								
Ni	**0.70**	0.60	-0.10	0.54	0.59	0.39	0.48	0.50	**0.80**	0.13	1.00							
AFDW	**0.75**	0.53	-0.05	0.58	0.68	0.52	0.30	0.60	0.56	0.13	**0.81**	1.00						
Gravel	0.02	0.22	0.30	0.12	0.21	0.22	-0.20	-0.01	-0.48	0.17	-0.23	-0.04	1.00					
Sand	**-0.70**	-0.65	0.07	-0.53	**-0.71**	-0.59	-0.04	-0.54	-0.05	-0.29	-0.48	**-0.71**	-0.25	1.00				
Mud	**0.71**	0.58	-0.19	0.50	0.65	0.53	0.24	0.69	0.46	0.22	**0.81**	**0.75**	-0.12	**-0.93**	1.00			
Depth	-0.16	0.07	0.41	-0.31	0.00	-0.14	0.30	-0.39	0.10	-0.07	-0.01	-0.16	0.16	0.22	-0.29	1.00		
Average Speed	-0.16	-0.02	0.48	-0.29	-0.13	-0.19	0.06	-0.41	-0.37	0.08	-0.42	-0.27	0.34	0.27	-0.41	0.55	1.00	
Max Speed	-0.09	-0.07	0.21	-0.13	-0.11	-0.20	-0.18	-0.19	-0.36	0.26	-0.37	-0.17	0.25	0.22	-0.32	0.19	**0.76**	1.00