Consequences of shellfish die-offs on seafloor biodiversity

A thesis

of

Master of Science (Research) in Environmental Science

at

The University of Waikato

by

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2023

Abstract

Coastal soft sediment habitats contain highly productive benthic communities that provide numerous ecological services. Many of these functions, processes and services are underpinned by the behaviour, density and diversity of the resident macrofaunal community. Climate change has caused heat waves to become more regular and extreme, causing die-off's of functionally important shellfish beds, potentially generating large shifts in benthic community structure and functioning. Recent studies of the New Zealand intertidal cockle (*Austrovenus stutchburyi*) die-off events have focused on cockle population recovery, but there is very little understanding of how the rest of the macrofaunal community responds. To understand how the macrofaunal communities respond to cockle-die offs, a manipulative experiment was undertaken at 23 sites in four estuaries on the northeast coast of the North Island. In late summer, at each site we established a 9m^2 control and 9m^2 exclusion plot. One year later, we sampled all plots for macrofauna and sediment properties. Results indicate a strong relationship between treatment type and community composition, with none of the exclusion treatments returning to pre-disturbance community compositions. Furthermore, that recovery was largely estuary specific and community composition following disturbance was highly variable within exclusion treatments. Statistical analysis highlighted that exposure to high intensity wind-wave activity and polychaete dominance within estuaries could explain the relatively improved recovery of Ongare sites within Tauranga harbour. Additionally, there are observable variations in cockle recruitment between sites for both adults and juveniles. This experiment explores whether the removal of cockles, as key habitat forming species, selects for a different macrofaunal community type. The observed changes in community structure can be linked to shifts in ecosystem functioning in these soft sediment habitats.

Acknowledgements

Firstly, I would like to acknowledge the scholarships that allowed me to complete and commit to my Masters. I would like to thank the University of Waikato, Waikato Regional Council and the Embling Memorial Fund for making it possible for me to continue exploring my passion in environmental science. Secondly, I would like to acknowledge all of the other post-graduate students and my friends who have been there to either support me directly with my research or provide solace throughout the course of my degree. It would not have been possible without your support. Additionally, I would like to thank my supervisors Joanne Ellis, Conrad Pilditch and Rebecca Gladstone-Gallagher for all their insight and guidance throughout this entire process. Finally, I would like to thank the University of Waikato for all of the teaching and outreach opportunities I was able to partake in throughout my degree, those experiences have been truly eye opening and some of the highlights from my time at university.

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1 Introduction

Coastal regions make up some of the most productive and complex environmental systems globally. These regions are unique to the specific set of environmental conditions (Thrush, 1991), which often results in highly specialised community systems (Woodin et al., 2016a). Intertidal sections of coastline have an extremely diverse range of conditions which are heavily influenced by tidal regimes (Bell et al., 1997). Depending on their substrate type, wave exposure and the horizontal area between high and low tide marks intertidal systems can be placed into two main categories: rocky shore and soft sediment (Nordstrom & Roman, 1996; Turner et al., 1999; Woodin et al., 2016a). Unlike rocky shore systems soft sediment intertidal zones are horizontally expansive and allow for complex and highly productive infaunal and meiofaunal communities (Greenfield et al., 2016; Morrison, 2021)

Due to New Zealand’s unique topography and high erosion rates, soft sediment coastal environments are present along many of its shorelines (Ryan et al., 2003). These estuaries are essential to maintaining healthy marine communities both locally and internationally due to the extensive ecological services they provide (Apri et al., 2021; Smaal et al., 2019; Woodin et al., 2016b). They have provided crucial economic, social and cultural resources since the arrival of humans to Aotearoa (Li et al., 2023; Smaal et al., 2019). This proximity and interaction with humans however, has exposed these systems to an increasing frequency and intensity of direct and indirect anthropogenic stressors (Nordstrom & Roman, 1996; Tricklebank et al., 2021) resulting in the degradation of ecosystem function and health, which ultimately leads to a reduction in the provision of ecosystem services (Gladstone-Gallagher et al., 2019; Thrush et al., 2021).

1.1 Physical properties of estuaries

Soft sediment intertidal systems are largely found within estuaries and form on transgressive coasts (Walker, 1992). Estuaries are highly complex structures and are a combination of the terrestrial properties (such as bedrock type) and the type of exposure they have to tides and waves (Pritchard, 1952; Ryan et al., 2003).

An estuary is defined as the seaward portion of a drowned river valley system which receives sediment from both fluvial and marine sources, and which contains facies influenced by tide, wave and fluvial processes. The estuary is considered to extend from the landward limit of tidal facies at its head to the seaward limit of coastal facies at its mouth (Dalrymple et al., 1992)

In New Zealand, there are a variety of estuary types with many originating as flooded river valleys or embayment's as a result of fluctuations in relative sea level (Kennedy et al., 2022). There is also a lot of variability in the forming factors of estuaries. Furthermore, the definition is unable to account for the unique ecological influences that contribute to the development of estuaries (Ryan et al., 2003). Estuarine ecosystems are often established on rich fluvial planes which undergo progressive evolution depending on specific coastal morphology and their exposure to wind-wave activity (Nordstrom & Roman, 1996). Many New Zealand estuaries are initially dominated by marine influences due to tidal asymmetry (difference in velocity between ebb and flood tides), resulting in the deposition of sands on incoming tides (Nordstrom & Roman, 1996). In other instances, estuaries can be formed under a wave dominance which relies heavily on particles being transported through wave energy and littoral drift (Ryan et al., 2003). Regardless of how soft sediment estuaries form, they all undergo a maturation through their gradual infilling from both marine and terrestrial sources (Figure 1).

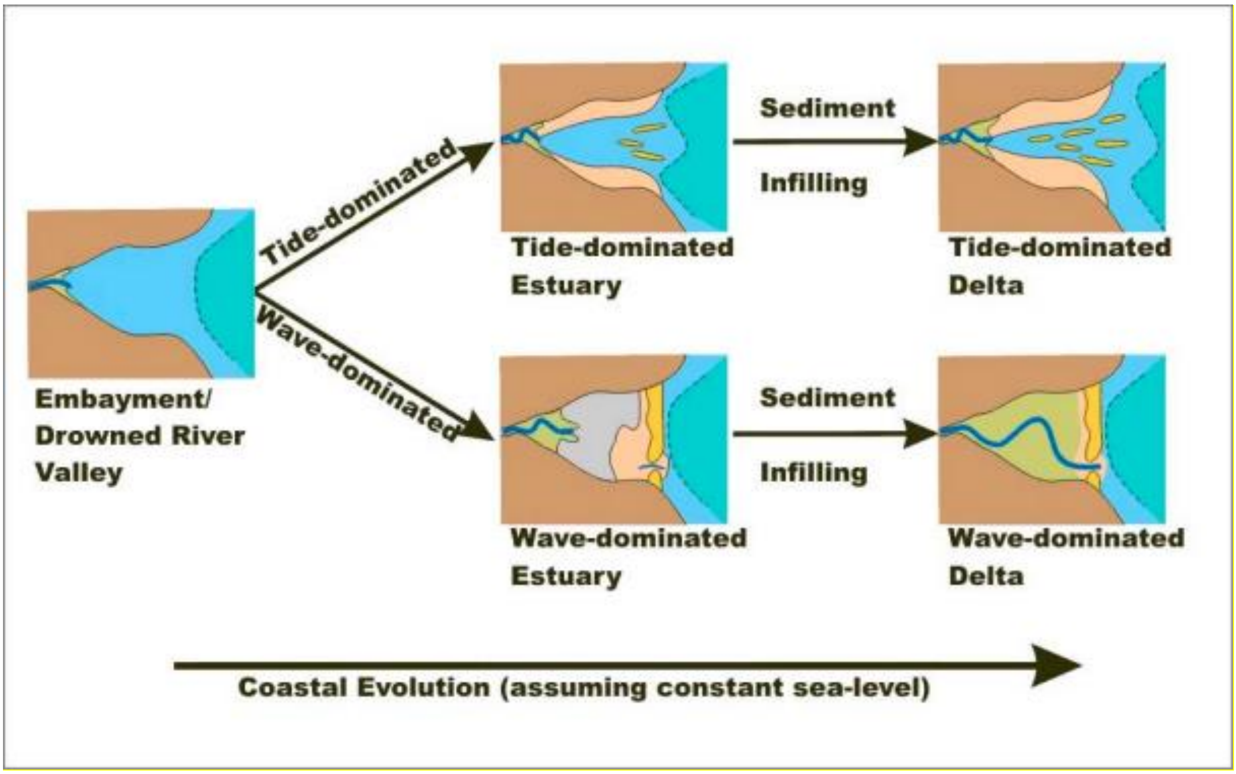


Figure 1: Diagram displaying the summarised evolution of estuaries depending on whether they are tide or wave dominated (Ryan et al., 2003).

The highly variable sources and velocity of water transporting sediment from both fluvial and marine regions (Figure 2) results in highly heterogenous sediment properties within a single estuary (Ryan et al., 2003). These sediment sources vary on a temporal scale, as shifts in weather, mean sea level and climate result in different physical conditions that influence the substrate inputs to estuaries (Kennedy et al., 2022; Nordstrom & Roman, 1996). These historic dynamic states in estuary conditions have been recorded through the examination of sediment cores, illustrating the connection between different sediment compositions, global weather patterns and community composition (Kennedy et al., 2022).

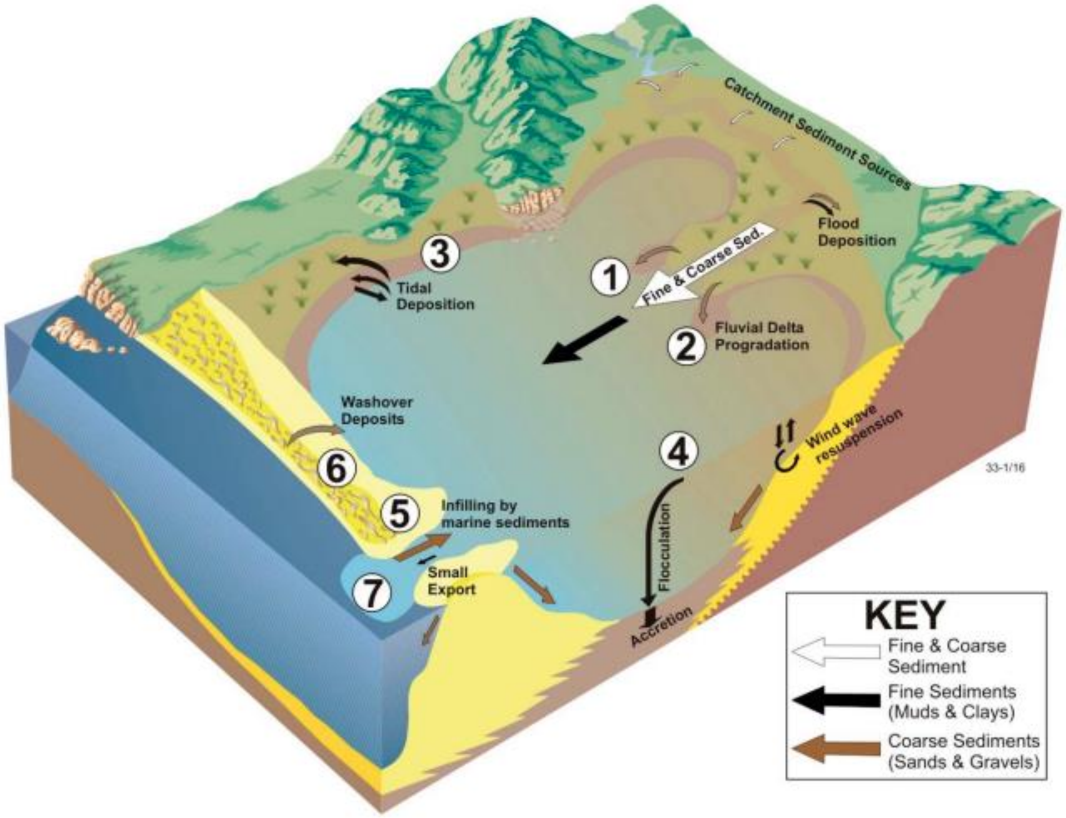


Figure 2: Model displaying how marine and fluvial sediments enter soft sediment estuaries. Furthermore, the different actions which result in the deposition and transport of sediment within the estuary (Ryan et al., 2003).

These forming conditions have a large influence on the physical oceanographic properties of soft sediment estuaries, determining water velocity, water source, and ultimately sediment transport (Figure 2). However, the sediment composition specifically with more established estuaries like those in New Zealand can be largely dictated by the more recent fluvial inputs from the catchment area (Nordstrom & Roman, 1996). The daily cycles of tides exposing and covering these environments, result in only the top 10-20 centimetres of sediment being suitable for most organisms (Glud, 2008; Kemp & Boynton, 1980). This due to limitation in oxygen penetration depending on sediment properties such as mean grain size, porosity, and bioturbation (Glud, 2008). This in turn dictates benthic community composition and associated ecosystem services that soft sediment ecosystems provide, with the current state and composition of the surface sediment layers (Ellis et al., 2004; Hope et al., 2020; Smaal et al., 2019; Vieillard, 2020). These ecosystems are essential for providing services such as: carbon sequestration, nutrient cycling, coastal protection and biodiversity hotspots (Byers & Grabowski, 2014; Smaal et al., 2019).

Land use within the catchment areas has a significant influence on the surface layers within these environments (Kennish, 2002; Li et al., 2023; Thrush et al., 2003) resulting in significant shifts in the surface sediment layers due to anthropogenic activity in estuary catchment areas (Flowers et al., 2023; Kennish, 2002). New Zealand terrestrial areas are naturally susceptible to erosion due to soil/ bedrock types and temperate climate conditions, which historically contribute large amounts of fine material input to coastal regions (Green & Coco, 2014; Thrush et al., 2004). However, significant land use change and anthropogenic induced climate change weather events have increased terrestrial erosion rates (Flowers et al., 2023; Green & Coco, 2014; Thrush et al., 2003) substantially increasing the suspended sediment loads being introduced to estuaries and ultimately increasing fine sediment deposition in estuaries (Figure 2). Increased fine sediment concentrations reduce oxygen penetration into coastal sediments, reducing the vertical depth of sediment which can support benthic communities (Flowers et al., 2023). Any losses or shifts in soft sediment benthic communities, can cause significant reduction in the ecological service provision and result in community composition shifts (Jones et al., 2017; Thrush et al., 2003; Vieillard, 2020).

1.2 The biotic factors of soft sediment communities

Soft sediment communities are diverse and versatile groups of organisms that can be more productive than any terrestrial ecosystem (Byers & Grabowski, 2014; Gladstone-Gallagher et al., 2019). Despite their compositions varying greatly both within and between estuaries due to variation in physical parameters, there are some key functions that specific species classes undertake (Greenfield et al., 2016; Lundquist et al., 2018; Thrush, 1991). Diversity among species that share functional traits ensures that despite shifts in individual abundances, the ecosystem health and essential functions are maintained (Kraan et al., 2010; Lundquist et al., 2018). There are many ways in which to organise these complex communities, grouping organisms by their class is a simple and comprehensive way to summarise the complexity (Apri et al., 2021). In these ecosystems there are 5-9 classes of organisms that can be identified. Here, the main five that will be focused on are: Anthozoa, Bivalvia, Gastropoda, Malacostraca and Polychaeta (Drylie et al., 2020). Benthic polychaetes are an extremely diverse class of organisms within these ecosystems, acting as subsurface deposit feeders, predators/ scavengers and suspension tube feeders (Drylie et al., 2020; Greenfield et al., 2016; Miri et al., 2023). The mobility of polychaetes varies greatly depending on species, all acting as bioturbators to some degree through the building of burrows or actively moving through sediment (Martins & Barros, 2022). They are a crucial part of soft sediment communities and have been found to thrive in variable sediment compositions, particularly those with higher mud contents (Fauchald & Jumars, 1979; Martins & Barros, 2022).

The Malacostraca class is comprised of multiple types of crustaceans, ranging from amphipods (e.g. shrimps) to decapods (e.g. crabs) and isopods (Cumberlidge et al., 2015). Like polychaetes, malacostracans have a variety of physical shapes and sizes and can reside within sediments (infaunal), on the surface of sediment (epifaunal), or between the sediment and the surface (meiofaunal) (Würzberg, 2011). Their variety in positioning within soft sediment environments and their physical characteristics allows this class of organisms to provide a plethora of ecosystem services (Drylie et al., 2020; Jayachandran et al., 2019). They are generally highly mobile detritovores and scavengers, through both suspension and deposit feeding and in some instances creating large burrows (Needham et al., 2011). These activities are crucial for carbon sequestration, nutrient recycling and sediment oxygenation (Jayachandran et al., 2019). They also have ability to overturn large amounts of surface sediment in a short period of time and stabilise sediment against hydrological disturbance (Jayachandran et al., 2019; Needham et al., 2011). However, their particular functions that provide ecological services can be heavily influenced by the environmental characteristics in different estuaries (Needham et al., 2011), shifting what role individuals from the same species play in the greater benthic community web between estuaries (Needham et al., 2011).

The calcium shells of gastropods are another common sight within soft sediment systems, occurring in variable abundances depending on sediment characteristics and community composition (Greenfield et al., 2016). Due to their vulnerability within soft sediment environments, their hard calcium shells serve as defensive structures against predation and desiccation (McLean, 1983). Gastropods have a variety of roles which directly and indirectly interact with the greater benthic food web. With different species occupying multiple trophic levels (Suratissa & Rathnayake, 2017), gastropods can be herbivores, carnivores, filter-feeders and parasites within the estuarine communities (Drylie et al., 2020; Greenfield et al., 2016; Suratissa & Rathnayake, 2017). Directly impacting the cycling of nutrients, the sequestration of carbon within their shell structures, and bioturbation as they move through surface sediments, gastropods play a vital role in soft sediment ecosystem functioning (Greenfield et al., 2016; Suratissa & Rathnayake, 2017). Their shells also provide essential substrate and habitat for a variety of benthic species who are unable to produce their own shells (McLean, 1983). It has been found that individual gastropod abundances are dependent on sediment properties, as the sediment properties influence microphytobenthos (MPB) mats (Forbes & Lopez, 1989; Orvain & Sauriau, 2002). These changes in mean grain size cause shifts in gastropod grazing behaviours and the abundance (Forbes & Lopez, 1989; Orvain & Sauriau, 2002).

Bivalves and anthozoans are generally linked in their abundances within soft sediment estuaries, with bivalves providing the necessary substrate for anthozoans to bind (McLaverty et al., 2020). Anthozoans, like *Anthopleura aureoradiata*, are filter feeding organisms which need a hard substrate to attach themselves to, often forming symbiotic relationships with hard shelled organism (Hopper et al., 2008). They play a role in removing organic material from the water column as well as protective buffers from parasites for the whole benthic ecosystem (Hopper et al., 2008), highlighting them as a possibly essential member of healthy benthic communities that have suitable substrate or are dominated by large bivalves (Hopper et al., 2008). Bivalves in many instances form the backbone of these soft sediment ecosystems, influencing the settlement of other species, nutrient/ oxygen availability and bioengineering surface sediment properties (Jones, Pilditch, Bruesewitz, et al., 2011; Jones, Pilditch, Bryan, et al., 2011; Volkenborn et al., 2012). Bivalves can be both mobile (passive and active) or burrow deep into soft sediments, bringing nutrients and oxygenated rich water from the surface and pumping it through anoxic deeper sediments (Norkko & Shumway, 2011; Smaal et al., 2019). They also can change the near-bed flow of estuaries; high density cockle beds (*Austrovenus stutchburyi*) increase the bed shear stresses which reduces the flow speed in these areas (Jones, Pilditch, Bryan, et al., 2011; Smaal et al., 2019). Additionally, bivalves are essential food resources for migratory and larger coastal megafauna species, allowing for communities outside of the benthic ecosystem to benefit from their productivity (Thrush et al., 1991).

1.3 Backbone of soft sediment communities

There are many definitions for keystone species which vary depending on the specific role that a certain species has within a designated ecosystem (Mills et al., 1993). A keystone species is defined as a species having a disproportionate importance in their community, like the grey wolf in Yellowstone National Park ecosystem for example (Mills et al., 1993; Mouquet et al., 2013; Ripple & Beschta, 2012). Directly and indirectly influencing species abundances within the ecosystem through their reintroduction, causing trophic cascades that brought abiotic and biotic factors back into natural balance (Ripple & Beschta, 2012). *Austrovenus stutchburyi* in many New Zealand estuaries acts as a keystone species for the soft sediment benthic communities. They provide multiple functions that facilitate the presence of other species, such as the provision of substrate, cycling of nutrients and bioengineering (Jones, Pilditch, Bryan, et al., 2011; Smaal et al., 2019; Woodin et al., 2016b), improving the physical conditions so that the surface sediment layers can support a greater abundance and diversity of life (Jones, Pilditch, Bryan, et al., 2011; Whitlatch et al., 1997). However, *A. stutchburyi* can also have an inhibitory impact on the soft sediment community in high density beds, restricting the settlement of new species and bivalve juveniles through their deposit feeding (Sandwell et al., 2009; Whitlatch et al., 1997). Under natural conditions in healthy estuaries, *A. stutchburyi* are predicted to aid the recovery following disturbance events through their facilitation of hospitable environmental conditions and by being a food resource themselves (Van Colen et al., 2012; Zajac et al., 1998). Additionally, *A. stutchburyi* dominated communities require significant changes in environmental conditions or large weather events to cause a permanent shift in community structure (Hines et al., 1997; Tricklebank et al., 2021; Vieillard, 2020).

Herein lies the problem, even though soft sediment species like *A. stutchburyi* can thrive and adapt to the highly variable natural conditions and provide an abundance of ecological services (Ellis et al., 2000; Salmond, 2020; Smaal et al., 2019), their position between marine and terrestrial inputs makes them vulnerable to anthropogenic stressors such as heatwaves (Baux et al., 2019; Grilo et al., 2011). Additionally, due to climate change, heat wave induced die-off's of keystone shellfish species on local scales are increasing in frequency (Tricklebank et al., 2021). This has the potential to cause ecological shifts in benthic community structures and the resulting ecological services that they provide. Recent studies of intertidal cockle (*Austrovenus stutchburyi*) die-off events have been centred around cockle population recovery (Cummings & Thrush, 2004; Jones et al., 2017; Tricklebank et al., 2021). The studies generally found lags and hysteresis in population recovery with concerns that they are not reaching historic sizes as mature adults (Morrison, 2021; Quinn, 2009). However, there is still very little known about how the rest of the macrofaunal community responds, which is the knowledge gap that this research thesis aims to fill. The response of the whole macrofaunal community may provide essential insight into the observed delayed impact in cockle population recovery and shifts in function. This study will be looking directly at how the density of adult cockles affect community composition in different estuaries across the North Island of New Zealand and what role they play in the recovery of these communities following a heat-wave induced die-off event. This will be achieved by simulating a heatwave induced die-off event in four estuaries across the North Island of New Zealand. Through the removal of adult cockles from surface sediments followed by macrofaunal community and sediment characteristic analysis one year post disturbance. Only adult cockles will be removed due to the significantly larger influence on the rest of the benthic community compared to juveniles. I hypothesize that the removal of adult cockles from these communities will result in decreases in both diversity and species abundances as well as the exclusion treatment having the greatest impact in cockle dominated estuaries.

2 Methods

To understand how the macrofaunal communities respond to cockle-die offs, a manipulative experiment at 23 sites in four estuaries on the northeast coast of the North Island was undertaken. At each site we established a 9 m^2 control and a 9 m^2 cockle exclusion plot where adult cockle densities varied from several hundred to several thousand per m^2 (Figure 1). The experiment covered both large spatial and temporal scales, to account for greater variability in co-variables (Figure 3).

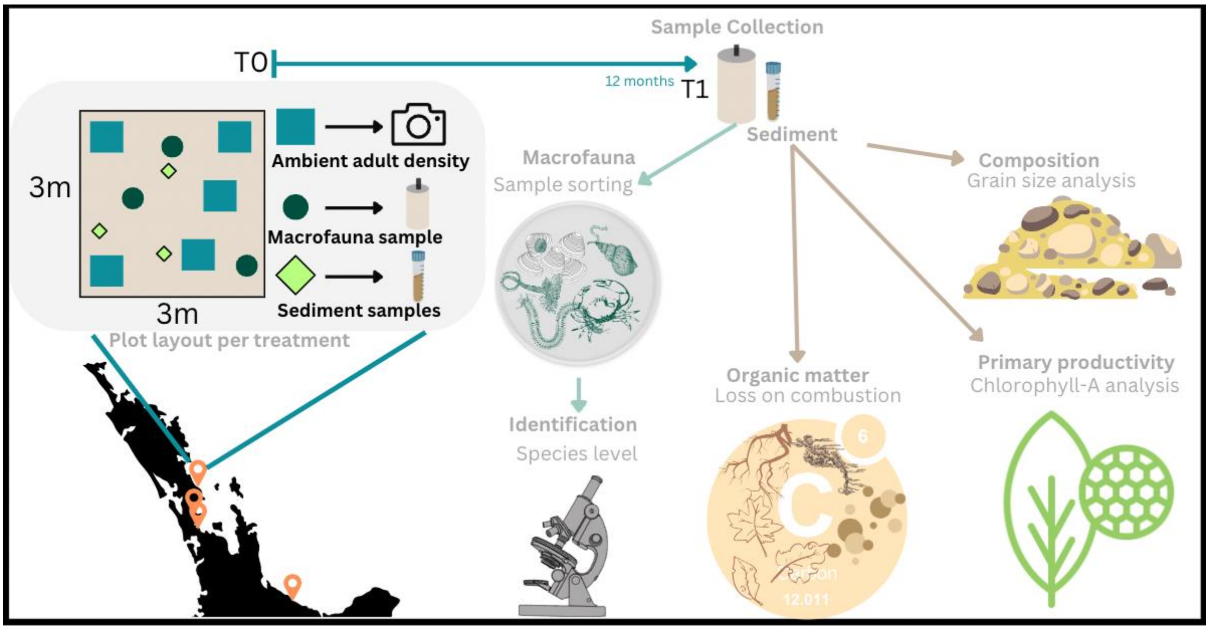


Figure 3: Diagram displaying the experimental set, sample collection, and general processing technique for data collection.

2.1 Site selection and treatment implementation

Five sites across four estuaries were selected along the north-east coast of the North Island of New Zealand. These sites were selected due to their ease of access and being known to have existing cockle beds. A cockle density gradient was then established within each estuary, sites that had a density range of 300-600 adults/m^2 were labelled "medium density", sites that had densities >1000 cockles/m$^{2.}$ were labelled as "high density" regions. Following a paired study structure, a total of 46 3x3m plots were established in four estuaries between the 12-16th April 2021 covering an even split of both high and medium density sites. Figure 4 displays the location of the five sites and the plots which samples were collected from.

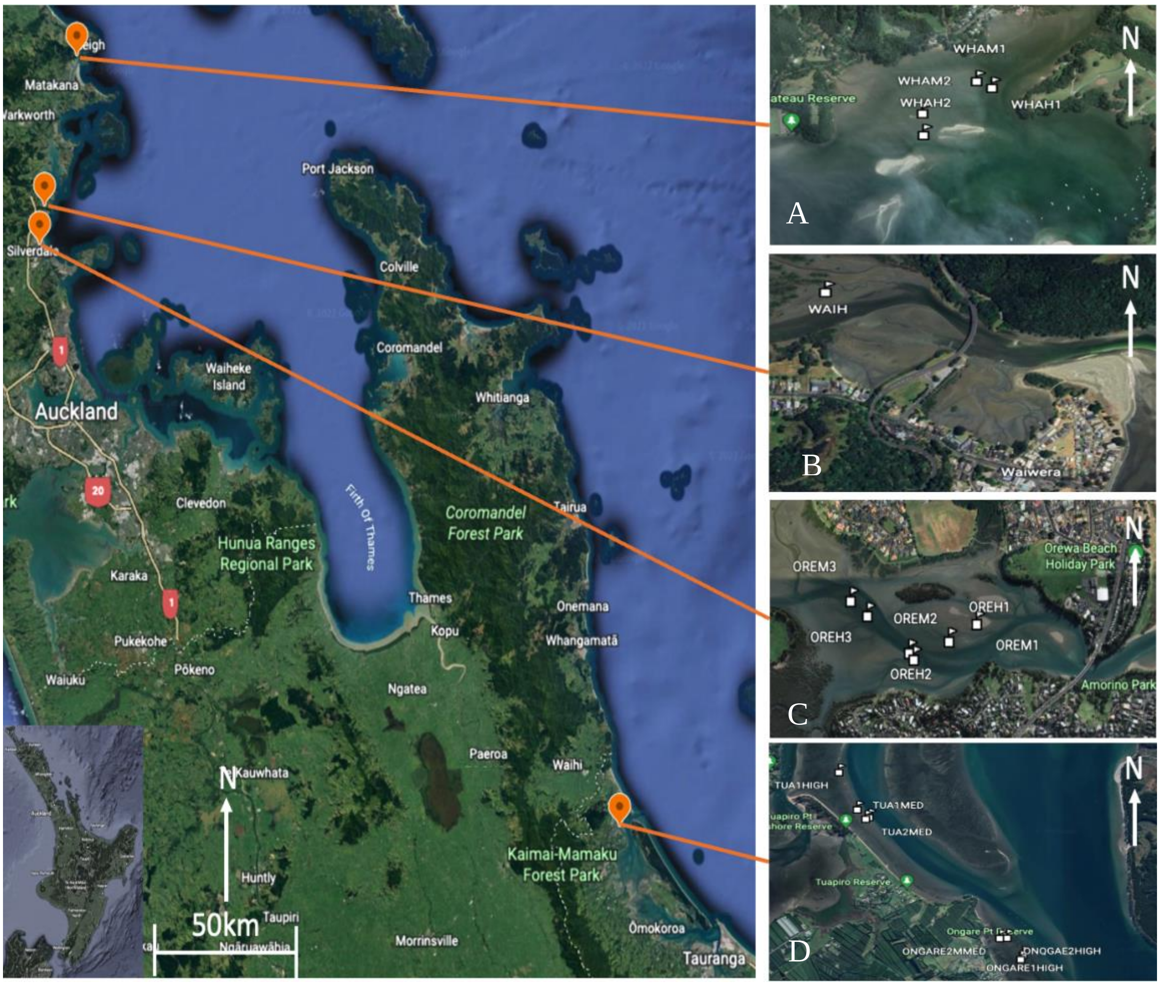
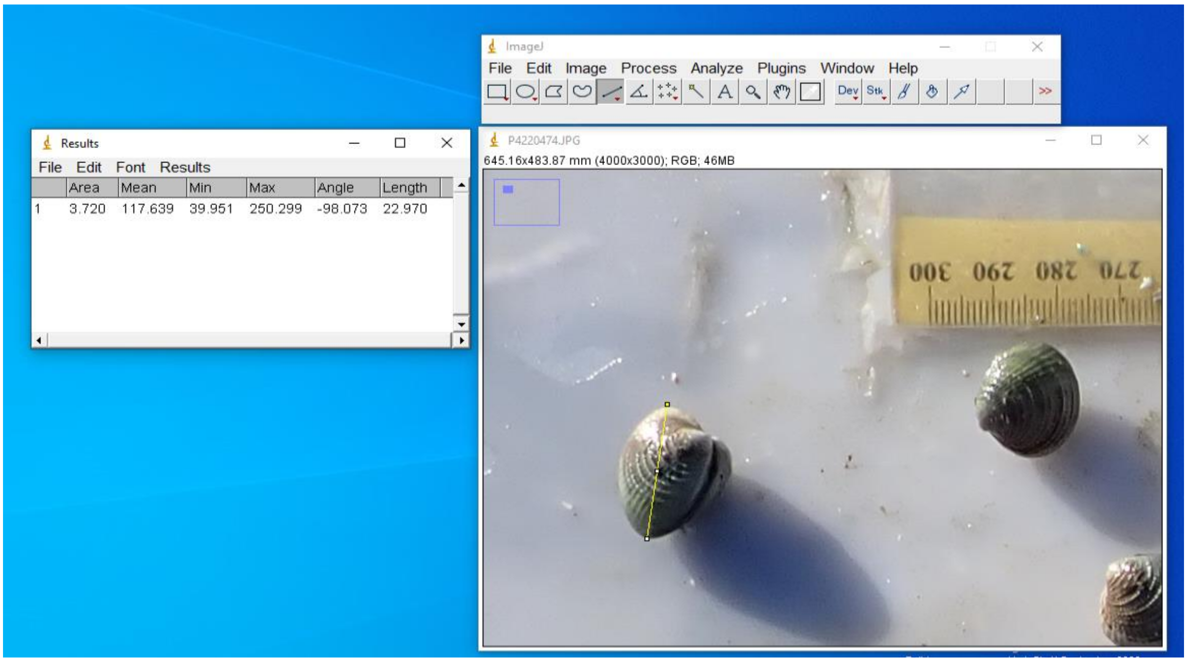


Figure 4: Map displaying the spatial spread of the four investigated estuaries. Attached are location of each site that was sampled. Individual estuaries are highlighted to the right, beginning with Whangateau Harbour (A), Waihou (Waiwera) estuary (B), Orewa estuary (C), and Tauranga Harbour (D) with two sites (Tuapiro and Ongare). High density plots are displayed as either "HIGH" or "H" at the end of site code, the medium density plots are denoted by either "MED" or "M" as a suffix to site name.

The replicates for each treatment vary between estuary with Orewa having higher replicates (8 pairs) compared to the other sites, such as Tuapiro (2 pairs). Environmental conditions and working conditions are responsible for the variety in replicates between sites. Cockle exclusions was achieved by sieving surface sediments 0-3 cm on 1 cm mesh to remove large cockles from 3x3 m plots as seen in Figure 4. The removed cockles were transported a significant distance from where they were removed to mitigate their immediate return into the disturbed plots. Control plots were disturbed in a similar way by hand plowing the surface sediment, trampling, and sieving quadrats but no cockles were removed. The generalized experimental set up is illustrated in Figure 3, highlighting the specific processes for different sample collection and processing within each treatment plot. This process was replicated for each treatment across all five sites.

Before removing cockles from the exclusion treatment, five 25 x 25 cm quadrats in each plot were photographed for density and size (sieved on a 500 µm mesh) to get a measure of ambient cockle density and size range (Figure 5). The ambient cockle density was measured again one year later during the rest of the sample collection by taking the sum of five 25 x 25 cm quadrats within each plot. This was crucial to measure the success of the treatment one year post disturbance. Figure 5 demonstrates how the photographed cockles were sized.



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 	Area	Mean	Min	Max	Angle	Length
1	3.720	117.639	39.951	250.299	-98.073	22.970
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645.16x483.87 mm (4000x3000); RGB; 46MB

Figure 5: Photo analysis of ambient cockle cores displaying how the measuring of A. stutchburyi was conducted.

2.2 Sample collection

One year after the experimental set up, the sample collection took place between 28th of March and 1st of April 2022. Three randomly selected locations within each plot were identified for the collection of a sediment core (13cm in diameter and 10 cm deep volume of roughly 1327 cm^3), this is illustrated by the dark green circles on Figure 3.

Each sediment core was placed onto a 500 µm sieve to remove microfauna and fine sediment which was not of interest for this study. Following preliminary sieving in situ, each core was stored within a plastic container and preserved with a 50% isopropanol (IPA) solution to prevent degradation of organic material. In addition to the collection of macrofauna, five 2.5cm diameter 2cm deep cores were taken for sediment properties (randomly distributed around the plot and pooled into one container) and frozen for later analysis of grain size, chlorophyll *a*, and organic content.

2.3 Macrofauna core processing and macrofaunal identification

Once each replicate had been correctly collected and stored, each macrofauna container was dyed with 2-4 ml of concentrated rose bengal solution, this highlights the individual macrofauna specimens to better aid the sorting process. After allowing at least twelve hours for the dye to be properly absorbed, each individual sample was passed through a sieve tower with mesh sizes ranging from 1 mm to 500 µm.

Any material that passed through the 500 µm sieve was not recollected or examined since initial sample collection discarded anything smaller than 500 µm in size. Once the core had been sorted by mesh size, each sieve layer was emptied onto a white sorting tray. Depending on the density of the sediment, shell hash or sea grass within each core the number of trays used varied from 2 to 9 to increase clarity during the sorting process.

Each sample was then manually processed with a microscope and soft tweezers under a lamp to remove whole and fragmented pieces of dyed organisms to be later identified. These organisms were stored in a 50% IPA solution to ensure that they would not degrade. An important detail was to make the best attempt to pair the bivalve innards with a complete shell to aid the identification process. Additionally, to collect all fragments of polychaetes and any gastropods that could have been alive or storing other macrofauna within their shells. Each sample was sorted into three individual containers to separate juvenile bivalves, small macrofauna, and large bivalves and macrofauna. The remaining sediment and “waste” from the sample was then reviewed by a senior researcher for a quality assessment. Additionally, one replicate of each site that had gone through this process was then sent to NIWA for a final round of quality assessment to ensure no specimens were missed in the sorting stage. Any specimens that were collected during either stage of the quality assessment were added to the respective macrofauna container for that sample.

The identification process began with the small macrofaunal and juvenile bivalve containers as they contained the greatest abundance of individuals and diversity of species. Individual specimens were identified down to species level in all applicable situations under a microscope and tallied for each sediment core. When sizing the juvenile bivalves, a graticule eye piece was used, it was calibrated with a ruler where 1x magnification = 5mm, 0.63x magnification = 7mm. If individuals were larger than 7mm then a digital calliper was used. The same process was followed for the larger containers and the measuring of the bivalves in the larger containers.

2.4 Environmental characteristics processing

2.4.1 Sediment particle size

Sediment samples are homogenised and a subsample of approximately 5 g was placed in 9% hydrogen peroxide for organic matter digestion, until bubbling ceased. The sediment sample was then wet sieved through nested 2000 µm, 500 µm, 250 µm and 63 µm mesh sieves. Pipette analysis is used to find the proportion of the <63 µm fraction that was >3.9 µm (silt) and <3.9 µm (clay) using Stoke’s Law. All fractions are then dried at 60 C° until a constant weight was achieved (fractions are weighed at 40 h and then again at 48 h to ensure a constant weight was achieved). The results of the analysis are presented as a percentage weight of gravel/shell hash (>2000 µm), coarse sand (500 – 2000 µm), medium sand (250 – 500 µm), fine sand (125 – 250 µm), very fine sand (63 – 125 µm), silt (3.9 – 63 µm), and clay (<3.9 µm). Mud content was calculated as the sum of the silt and clay content.

2.4.2 Organic matter content:

Approximately 5 g of sediment was placed in a dry, pre-weighed tray. The sample was then dried at 60 °C until a constant weight was achieved (as above), combusted for 5.5 h at 400 °C, and then reweighed. Percentage loss on ignition was calculated by the loss of weight between the dried sediment and the sediment post combustion at 400 °C.

2.4.3 Chlorophyll-A:

Within one month of sampling, the full sediment sample was freeze dried, then homogenised and a subsample (5 g) taken for analysis. Chlorophyll-A and its degradation product (phaeophytin) are extracted by boiling the sediment in 90% ethanol. An acidification step was used to remove phaeophytin before reading the extract on a spectrophotometer (measured in µg/g of sediment) (Sartory, 1982).

2.4.4 Wave exposure analysis:

Wave exposure analysis (WEA) was calculated following the methodology from Turner et al. (1999) detailing the equations and process which can be seen below.

$$E_M = \sum_{i=1}^{12} \text{mean wind } velocity_{20i^\circ} \times \ percent\ frequency_{20i^\circ} \times \ fetch_{20i^\circ}$$

$$E_E = \sum_{i=1}^{12} exceedance_{20i^\circ} \times fetch_{20i^\circ}$$

Wind speed from 2003 through to 2012 was taken from 3 NIWA weather stations listed in table 1 and used for the WEA in this thesis. The wind records from each station were variable with all stations having at least 8200 data points within that timeframe. The WAE begins by calculating the mean wind velocity (E_M) for a series of fetches at 20° compass bearing increments (20-40, 50-70, 80-100, 110-130, 140-160, 170-190, 200-220, 230-250, 260-280, 290-310, 320-340, 350-10). The compass bearings are used to measure the distance to land or mouth of harbour from each sampling location within each estuary. Mean wind velocity = mean wind speed in m/s for each compass bearing over the 30-d period preceding each sampling date. Percent frequency = percent frequency with which the wind occurred from each compass bearing over the 30-d period preceding each sampling date. Exceedance (E_E) was the percent of time for each 30-d period and each compass bearing, that mean wind speeds exceeded 16 m/s (approximately 33 knots). The exceedance of 16 m/s was selected as only 19% of winds recorded within the Manukau Harbour exceeded this speed (Bell et al., 1997; Turner et al., 1995). Due to the similar characteristics of the estuaries used within this thesis and those referenced by *Turner et al. (1999)* the WAE was applicable.

Table 1: Table displaying the details of NIWA weather station where wind data collected for the wave exposure analysis.

Sample Estuary – station name	Agent number	Network number	Latitude	Longitude
Tauranga sites – Katikati 2	1569	B75592	-37.677	175.945
Orewa & Waiwera – Whangaparaoa Aws	1400	A64683	-36.60268	174.83458

Whangateau – Takatu, Matakana	1358	A64372	-36.375	174.747

From the WEA the mean exposure (E_m) and upper (75th) quantile (E_{75}) wind speed for 10-year annual average ($E_{m\text{-}A}$ & $E_{75\text{-}A}$) were used within the statistical analysis within the distanced based reducing analysis.

2.5 Statistical analysis

Firstly, to account for variability between estuaries Excel was used to visualise the broad community compositions and environmental variation. Additionally, it was used to calculate summary statistics (means, standard deviations, proportions, etc) that were used to compare community and environmental characteristics between estuaries. Excel was further used to assess the impact of treatment type on community abundances, diversity with ambient cockle density. This was followed by Non-Metric Multidimensional Scaling (nMDS) plots in R to assess how treatment influenced community grouping of sites at varying scales and over time. Cockle counts were removed from the community data prior to multivariate statistical analyses to best evaluate community shifts between treatments. To understand which species were responsible for driving the differences between treatments, similarity percentage (SIMPER) analyses was conducted. The SIMPER analysis was used to identify significant species and the cumulative sum of all species between control and exclusion treatment.

When investigating the impact of environmental factors (sediment properties and exposure factor) and ambient adult cockle densities, distance-based redundancy analyses (dbRDA) was conducted. All multivariate analyses were conducted using PRIMER V7 with no transformations applied to the data. The dbRDA highlights the environmental parameters that are responsible for the variability in community data. The dbRDA was used to investigate the impact of environmental parameters for each treatment type at each site, linking key factors with specific community clusters.

3 Results

This experiment identified nearly 16,000 individual organisms across 130 samples from the four estuaries investigated. This section will provide an overview of the general trends between community and environmental variations, addressing the estuary specific biotic and abiotic factors, followed by assessing the impact that the exclusion treatment had on community assemblage and how both community diversity and abundances varied with ambient adult cockle density. These results highlight the effect that adult cockle presence has on both community diversity and abundance, through the comparison of treatment type. Next, I identify key species that drove differences between treatment types, possibly highlighting direct community influences associated with the removal of adult cockles. Finally, I evaluate the specific role that measured environmental variables had in separating community clusters and their estuary specific influences. This allows for specific environmental parameters to be associated with communities that displayed greater or reduced recovery one year post adult cockle removal, which addresses the impact that environmental factors and key community drivers have on the recovery soft sediment communities following a simulated cockle die-off event.

3.1 Summary Data

When looking generally at the variation in community assemblage and environmental characteristics between locations it appears to be linked to their physical location, with no significant variability in biotic or abiotic properties between treatment types. The impact of site proximity is apparent with both sites within Tauranga Harbour (Tuapiro and Ongare) and the sites at Orewa and Waiwera respectively, with both sets of sites exhibiting extremely similar community proportions and sedimentary characteristics (Figure 6). Whereas sites within Whangateau harbour share few similarities in either community of sediment proportions from the two other groupings (Figure 6), representing a relatively unique set of estuary conditions within this study. From the two Tauranga sites (Tuapiro and Ongare) it is noticeable that they are dominated by polychaetes, making up at least 66% of their recorded organisms, followed by bivalves which only made up between 12-16.8% of their total abundance on average (Figure 6). The mud and sand content from Tuapiro and Ongare are not significantly different from the other three sites, however they possess far higher proportions of chlorophyll a in comparison, suggesting that these two sites experience a greater amount of primary productivity than the other estuaries, especially samples collected from Ongare.

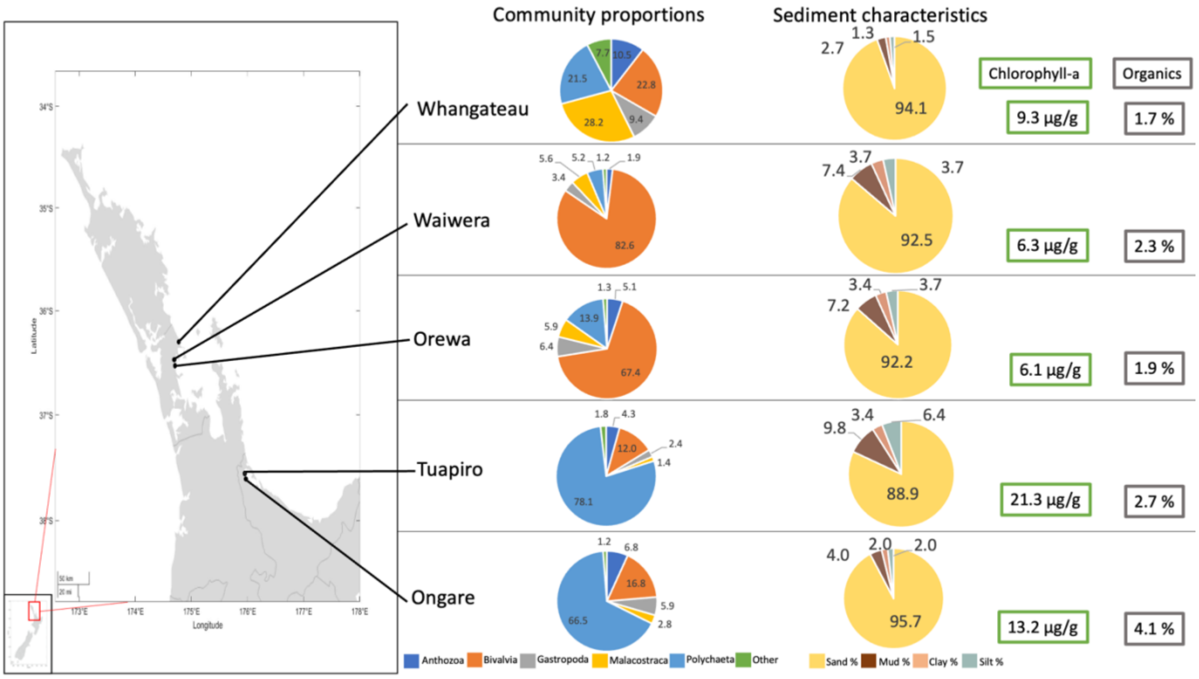

Figure 6: Plot summarising the key community groups and sediment characteristics across all five sites. Highlighting spatial variability between sites physically and ecologically. The percentages for community proportions were calculated by taking the average abundances of each Class and dividing that by average total abundance. Full data found in Appendices 1.

The Orewa and Waiwera sites have the inverse pattern in their community composition, with between 67-82% of their total abundance attributed to bivalves and only between 5 -12% polychaete abundance. Unlike the sites from Tauranga harbour, they have greater proportions of malacostracans (5.2-5.9%) within their communities. The sediment properties between these two sites are almost identical despite not being collected from the same estuary. This suggests that although they do not share the same intertidal area, their catchments areas have similar land use, soil profiles, sediment sources and similar marine influences. The similarity in their physical benthic properties could explain why their community compositions are so similar in terms of the dominance of main taxonomic groups.

Whangateau is largely the outlier from the five sites for both community composition and sediment characteristics. The average proportions of bivalves (22.8%), polychaetes (21.5%) and malacostracans (28.5%) are relatively similar. Additionally, they on average had greater amounts of anthozoans (10.5%) and gastropods (9.4%) in comparison to other four sites. The communities from Whangateau Harbour appear to be more evenly balanced and not dominated by a single class of organisms. Even though the Whangateau sites have a similar proportion of sand within their sediment, they have much lower proportions of all the other physical sediments (mud, silt, clay, organics) in comparison to the other estuaries. On average however, they exhibited higher concentrations of chlorophyll a (9.3 µg/g) than Waiwera and Orewa but less than the sites from Tauranga Harbour. This supports the trend from the Tauranga sites between polychaete abundance and chlorophyll a concentration.

3.2 Exclusion experiment results

Although many trends can be extracted from community proportions it does not give insight to how the different treatments impacted their assemblages and how ecological factors such as ambient cockle density influenced these communities. Figure 7 highlights the impact treatment and ambient cockle density have on the average diversity from each plot. The control treatments have generally higher diversities across all sites with smaller variation on average, especially when ambient adult cockle density exceeded 501 cockles per 0.3125m^2. In addition to this, most exclusion plots where the adult cockle density was greater than 272 per 0.3125m^2 had an average diversity of seven species per plot. This supports the relationship between the presence of cockles and higher diversity rates. However, in communities with less than 215 adult cockles per 0.3125m^2 average diversity was significantly higher than all other sites. These sites were largely Ongare and Tuapiro with a few Whangateau plots which were dominated by polychaetes (Figure 6). This could demonstrate that when there are low cockle abundances, benthic communities are dominated by a highly diverse group of polychaetes. Furthermore, these sites experienced a reduced treatment effect when comparing control to exclusion plots which supports the trend that these sites are not largely dominated by bivalves or influenced by their absence.

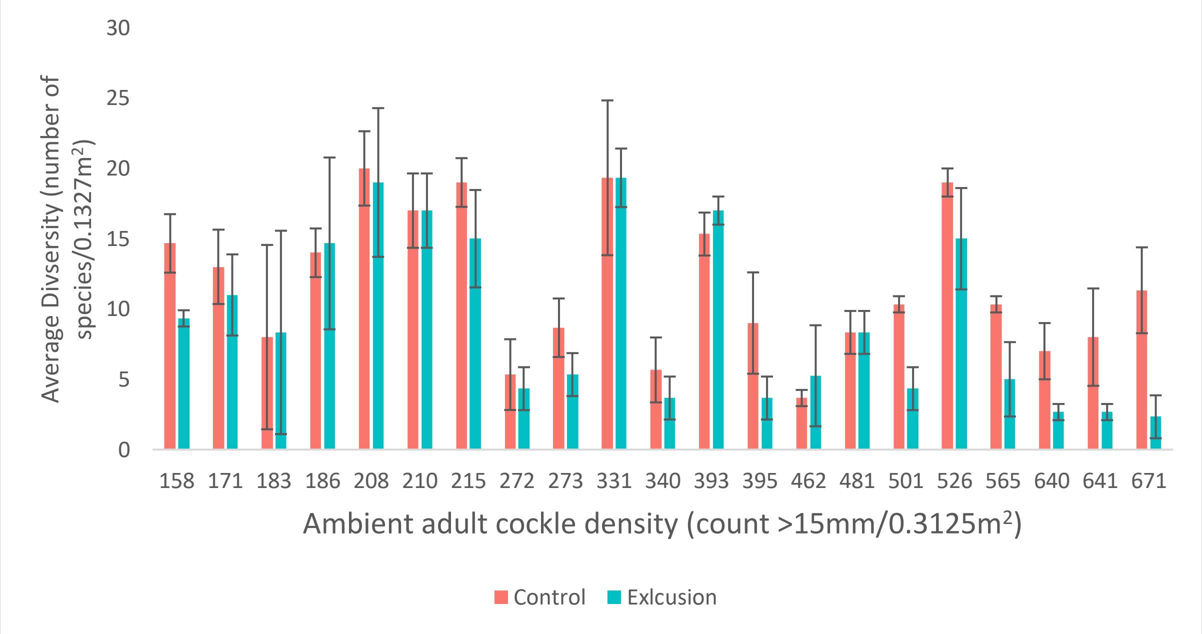

Figure 7: Plot displaying the relationship between ambient cockle density from five 25 x 25 cm (0.3125m^2) quadrats (from non-treatment areas) and average diversity of species from control and exclusion plots at each site. A. stutchburyi *was removed from the diversity calculations to better measure treatment impact. Raw data can be found in appendix 2.*

This trend continues when examining the average total abundance shifts in response to treatment type and ambient adult cockle density (*Figure 8*). Average total abundances within control treatments tend to be higher than those from exclusion treatments regardless of ambient adult cockle density. The plots that exhibit higher abundances are from Tuapiro, Ongare and Whangateau sites which follows a similar pattern to that previously seen in respect to average diversity (*Figure 7*). These sites generally had a low ambient adult cockle density (< 215), suggesting that the high abundance of organisms could be attributed to the dominance of polychaetes (*Figure 8*). At sites that had ambient adult densities greater than 215 which are dominated by bivalve species, the impact of removing *A. stutchburyi* resulted in a massive reduction in overall abundance. Furthermore, sites that were dominated by polychaetes had less variation between the two treatments in both average diversity and total abundance.

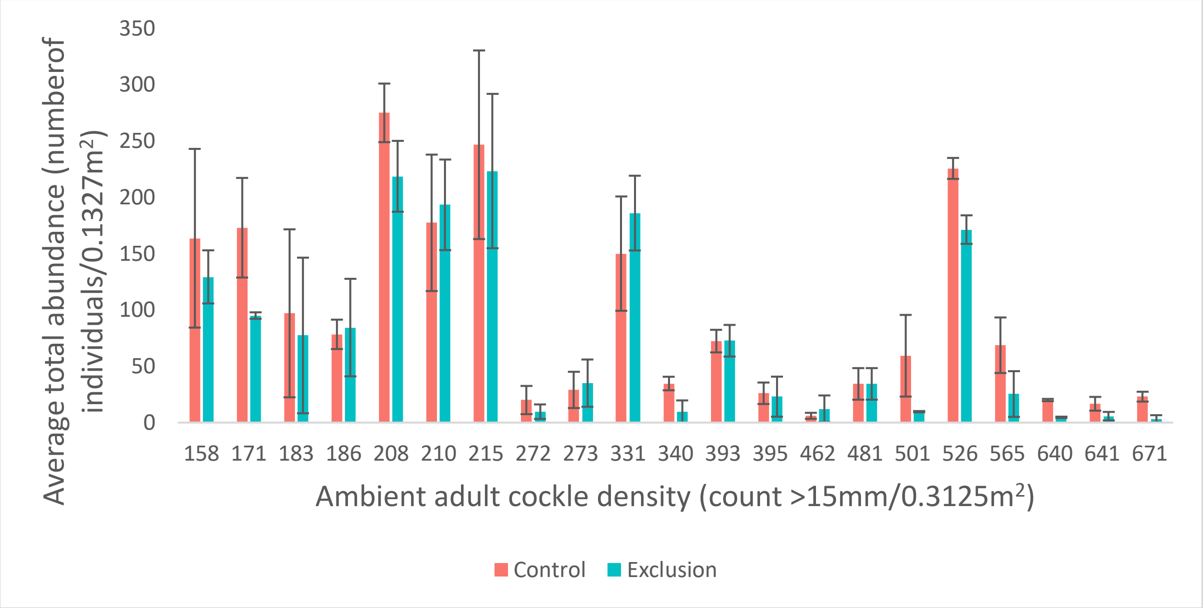

Figure 8: Plot displaying the relationship between ambient cockle density (from non-treatment areas) and average total abundance of species from control and exclusion plots at each site. A. stutchburyi *adult and juvenile abundances were removed from the average total abundance calculations to better measure treatment impact. Raw data can be found in appendix 2.*

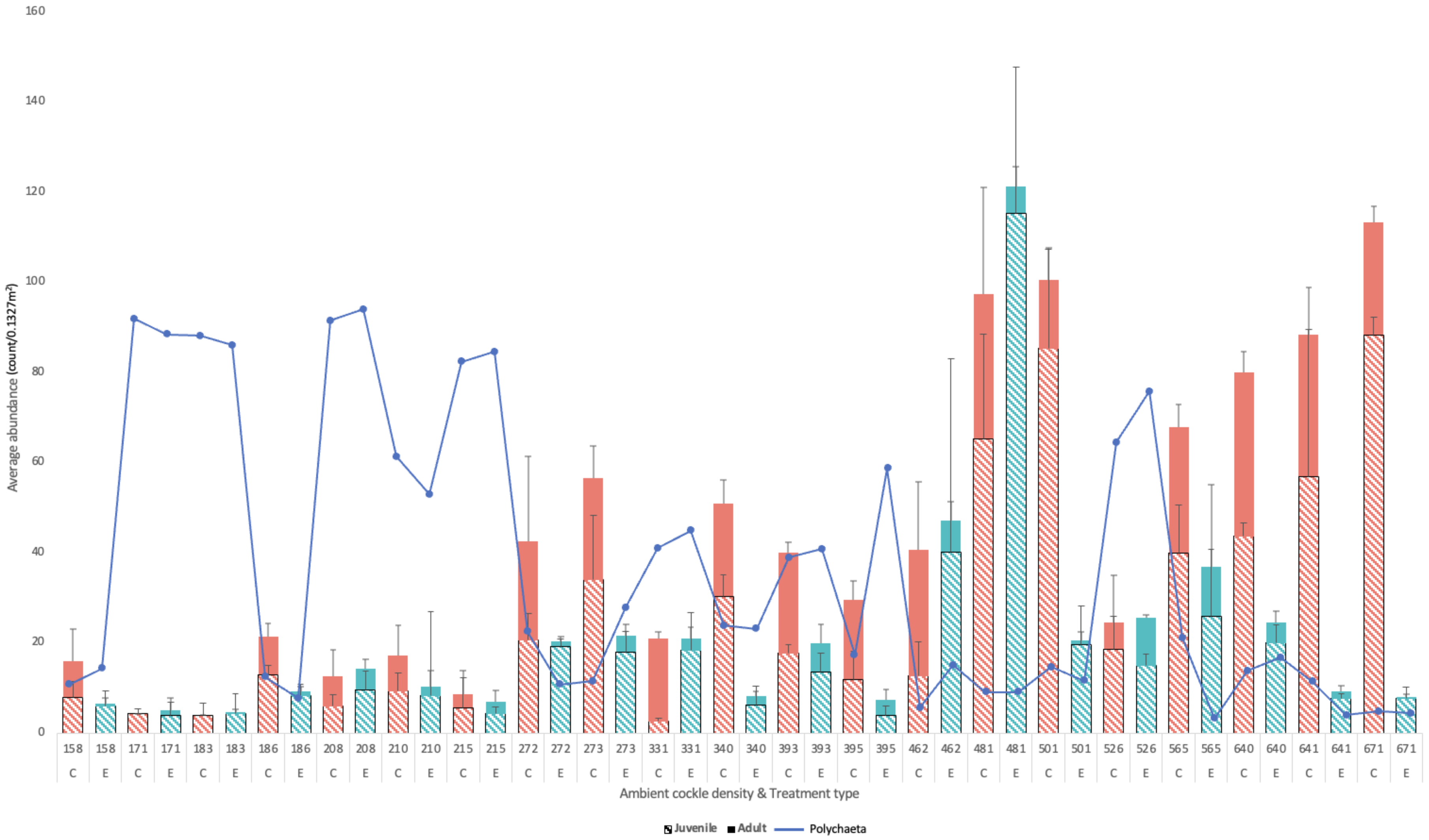

Figure 9: The plot displays the average abundance of A. stutchburyi against ambient cockle density and treatment type (C = control, E = exclusion). The stacked bar graphs highlight what proportion of the cockles present are adults (>15mm) or juveniles (15mm<), this is illustrated by the dashed (Juvenile) and solid (Adult) sections of each bar. Standard deviation for each section of was also included. Average polychaete abundance was plotted on top of this to display their relationship with cockle abundance and ambient adult densities (Appendix 2).

Finally, the impact that the treatment had on *A. stutchburyi* specifically and how the adult juvenile proportions of the population varied was examined (Figure 9). The stacked bar charts represent the total average abundance for each site, with the two segments representing the proportion of adults (15mm>) and juveniles (<15mm). When looking at the total average abundance, there is a positively correlated trend as ambient adult cockle density increases especially in control treatment plots. Unsurprisingly, the exclusion treatments had substantially lower average abundances of *A. stutchburyi* with far fewer adults regardless of the ambient cockle density. Across both treatment types and when ambient adult densities were less than 565 cockles per $0.3125m^2$, the abundance of juvenile cockles was relatively more consistent compared to adult abundance. Suggesting that juvenile cockles experience a more stable recruitment into plots regardless of treatment type compared to adults. The control plots had a far greater abundance of both adults and juveniles when ambient cockle density was greater than 272, this aligns with previous trends seen with estuary specific cockle abundances (Figure 7 & Figure 8). This is further highlighted by the line superposed on the plot to representing the average polychaetes abundance with increasing ambient cockle density. It appears that the abundance of polychaetes is inversely proportional to the abundance of *A. stutchburyi*. This further substantiates the diversity and abundance trends from previous plots and clearly illustrates the antithetical relationship between the two organism classes.

3.3 Community Data

The nMDS analysis allows for further clarity around the differences between estuaries and treatments, further highlighting the three preliminary clusters identified through excel exploration (Figure 10). These groupings from the full experiment appear to separate communities by estuary and site proximity (Waiwera & Orewa, Tuapiro & Ongare, and Whangateau) regardless of what treatment the site was exposed to. Indicating that even though diversities and abundances shifted significantly between treatment types at each site, that they are still more similar to other sites within their estuary than those from other locations. Although, the clusters for the Tauranga sites (Ongare & Tuapiro) exhibit far less variability compared to the other two estuary groupings including both treatment types. This could suggest that these sites were not as greatly impacted by the removal of *A. stutchburyi* in comparison to the other estuaries. Contrarily, the Waiwera and Orewa sites appear to have a wider spread in variance between the two treatments (Figure 8). Which could indicate that the communities within Orewa and Waiwera were more strongly influenced by treatment type.

However, due to the lack of heterogeneity within estuaries site level nMDS analyses requires deeper unpacking of the variation between treatments at each site to fully identify key drivers in community variability.

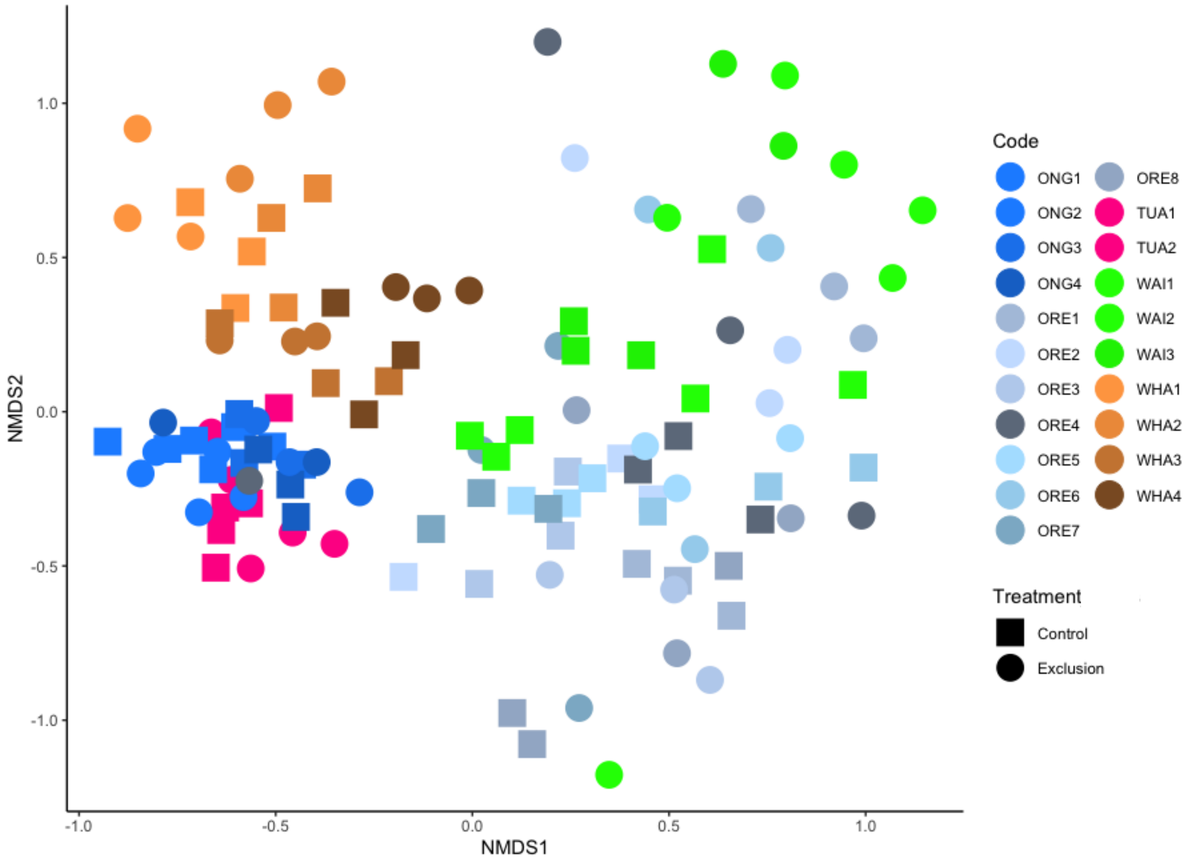

Figure 10: nMDS plot of entire community data set from all sites. Each site is grouped by similar colours and treatment is denoted by either a square (Control) or a circle (Exclusion).

Subsequent figures highlight the community variance within each estuary between the two treatment types, beginning with the southernmost site Ongare (Figure 11), displaying the four experiment plots that were sampled. Overall, the control treatment replicates experienced substantially less variability in community composition one year post disturbance in comparison to the exclusion plots. This indicates that in response to the exclusion treatment that communities in proximity recovered dissimilarly despite being exposed to similar conditions. Furthermore, the overlap between the two communities from both treatments is minimal or does not occur, suggesting that the exclusion treatment had a strong impact on species composition within Ongare sites. Furthermore, one year post disturbance the exclusion communities were substantially different to those from the control. SIMPER analysis of the four sites found that the species that were significant in explaining the variance between the two treatments varied between plots (Appendix 3). However, it was able to identify

Phoxocephalidae and *Nemertea* as significant in explaining the differences between treatments for plots 1 & 3 as well as Ongare as a whole. It is also important to note that all four plots were dominated by *Prionispio aucklandia* and other polychaetes, which were not identified to occur significantly different abundances between treatments except plot 3. Further supporting the trends that Ongare sites were not dominated by bivalve species (Figure 6). These Polychaeta species also generally occurred in higher abundances within the control treatment plots, indicating that the exclusion treatments did have some influence on the Polychaeta population (Appendix 4).

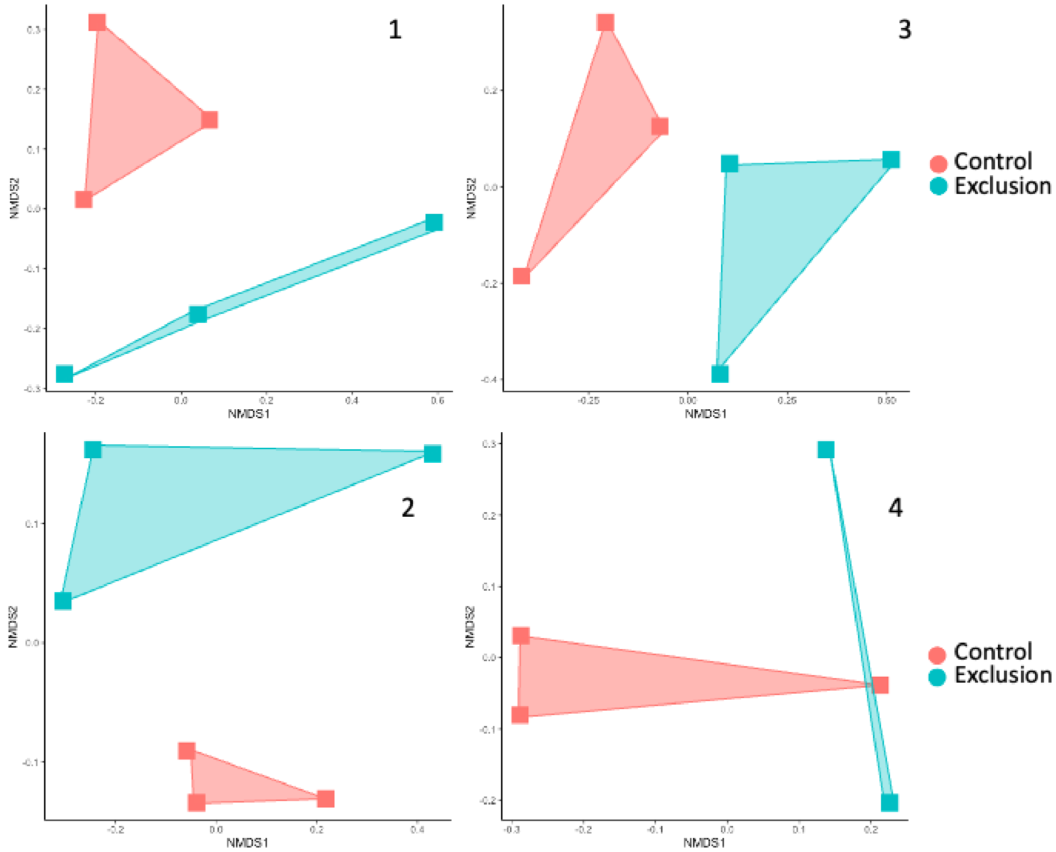

Figure 11: nMDS plot of the four Ongare sites. Within each individual nMDS plot there are three control (red) and three exclusion (blue) squares representing the three replicates from each treatment plot. The grided area represents the spread in community variance between the three replicates. In plot 4 only two exclusion points are visible due to an overlap in values.

Tuapiro sites (Figure 12) exhibited similar trends to those from Ongare, with control plots producing tighter clusters from the three plots compared to exclusion plots. The control plots from Tuapiro 1 experienced such small variability that they produced nMDS values that overlapped. Additionally, there were some issues with the second Tuapiro plot due to only two replicates of the exclusion treatment being valid producing inconsistent findings. When exploring the SIMPER analysis for Tuapiro 1, *Anthopleura aureoradiata* was identified to be a significant driver for the differences between the treatment types (Appendix 3). The raw data further supports this and highlights that anthozoans like *A. aureoradiata* occurred in significantly higher abundances in the control treatments (Appendix 4). This combined with the knowledge that abundances and diversity were higher under control treatments in Tuapiro 1 (Figure 7 & Figure 8) suggest that the exclusion of *A. stutchburyi* had a clear impact on the benthic community within Tuapiro.

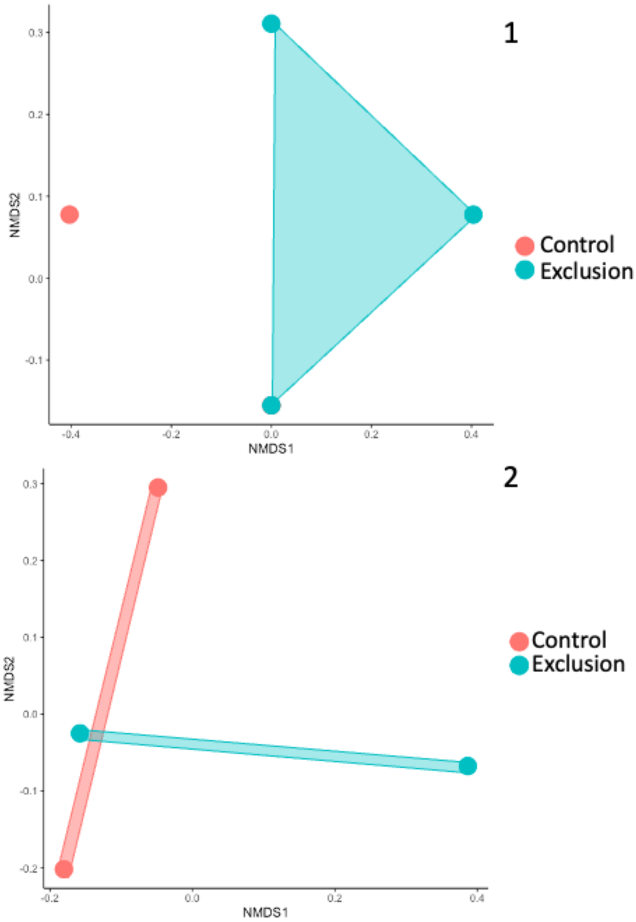

Figure 12: nMDS plot for the two Tuapiro sites. Each nMDS plot consists of three exclusion (blue) and three control (red) replicates. The grided area represents the spread in community variance between treatment replicates at one site. Overlap in values occurred which is why there are only one or two of the three replicates visible in the plots above.

Orewa had the highest number of sites within a single harbour, allowing for a greater amount of heteroscedasticity to be accounted for within the estuary. Although Orewa experienced a large amount of variability overall (Figure 10), the individual Orewa plots (Figure 13) highlight that there was more significant community variance between treatment types. Like the two sites from Tauranga harbour, the control treatment plots experienced reduced dissimilarity compared to the exclusion plots as they formed tighter clusters. There was generally no or minimal overlap in the community clusters for both treatments across the eight plots. The specific species that were identified through SIMPER analysis varied greatly across the eight plots, although there are some trends in their roles in the community. The SIMPER analysis found that for most plots within Orewa harbour that species which were associated with *A. stutchburyi* such as barnacles (*Austrominius modestus*) and limpets (*Notoacmea scapha*) were significant in explaining the difference between treatment communities (Appendix 3). Additionally, crab species (*Hemiplax hirtipes*, *Hemigrapas crenulatus*, *Hemigrapas sexdentatus*) and other bivalves (*Macomona liliana* & *Nuculidae gray*) abundances were also significant between treatment communities and much higher in control plots. Finally, there were some plots which had identified some polychaetes to also be significant in explaining the differences between the two treatments. All the species that were found to be significant through the SIMPER analysis occurred in higher abundances within the control plots (Appendix 4). Additionally, the high number of key species identified through the SIMPER analysis indicates that cockles played a significant role in community biodiversity, as previously suggested by trends in section 3.1.

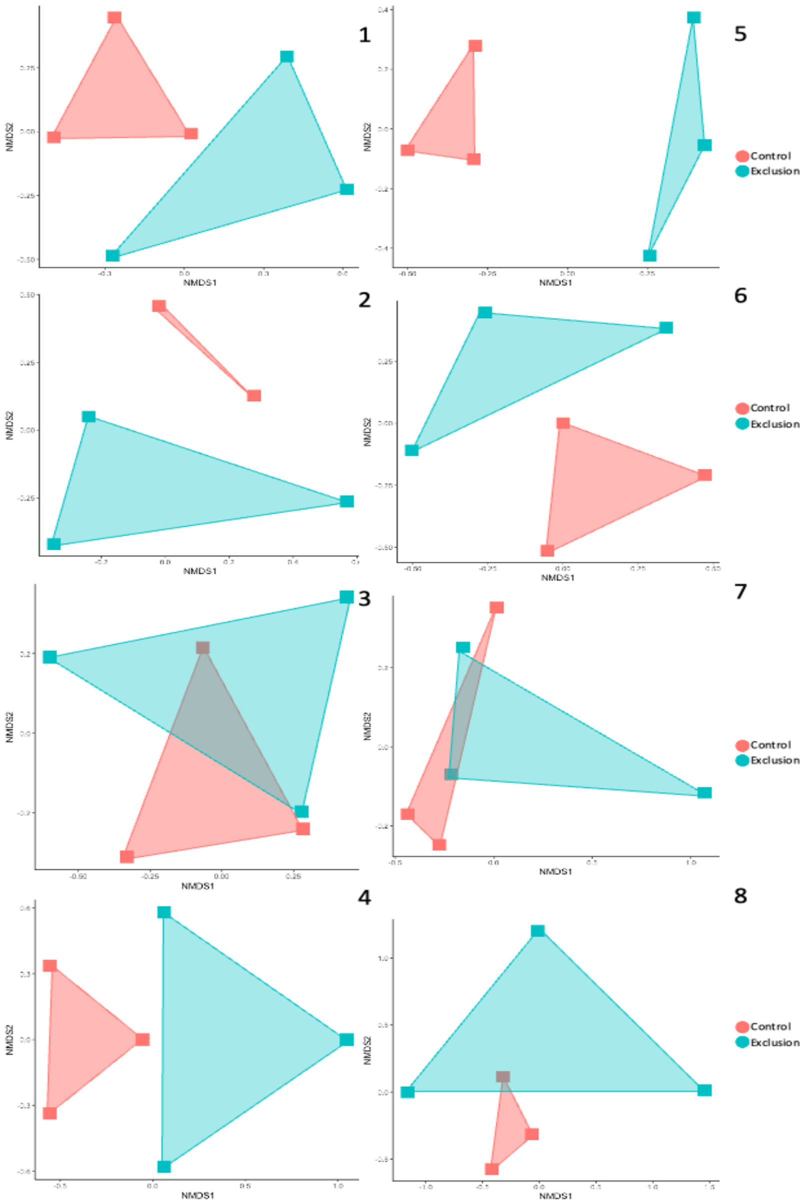

Figure 13: nMDS plots for all eight Orewa sites. For each site (1-8) there are three exclusion (blue) and three control (red) replicates. The grided area represents the community variance between the three replicates of each treatment at each plot. Overlap in points in plot 2 is due to similarity in values for two of the replicates.

The Waihou estuary which housed the Waiwera treatments fell within the same community cluster as Orewa (Figure 10), supporting that they share similar species compositions (Figure 6). However, when examining how the two treatments impacted community assemblage after one year (Figure 14) the control communities experienced almost no variation between the three plots. Suggesting that even though Orewa and Waiwera share similar community composition, at least the control plots within Waihou estuary (Waiwera) were far more homogenous. As with other previous sites, the exclusion plots displayed far greater variation both from the control plots and other exclusion communities within the same plot. This indicates that within Waiwera sites that the exclusion of cockles had the greatest impact and destabilized the benthic community. The second site at Waiwera highlights that even one year post disturbance, the resulting control and exclusion communities share some similarity. Nonetheless, despite the fact the two treatment communities share some similarity the exclusion plots failed to return to pre-disturbance composition. SIMPER analysis of the nMDS results identified a substantial number of species that were significant in explaining the differences between treatment communities, including various species of gastropods, malacrostracans and polychaetes (Appendix 3). These species like those identified in the Orewa sites were both directly and indirectly linked to the presence of *A. stutchburyi* (limpets, anemones & barnacles). The raw data highlights that all the species identified to be significant through the SIMPER analysis to have occurred in higher abundances in all three control plots (Appendix 4). This supports the trend at the Orewa sites that adult cockles promote the abundance and diversity of multiple other species (Figure 7& Figure 8) and reinforces the community proportion data (Figure 6).

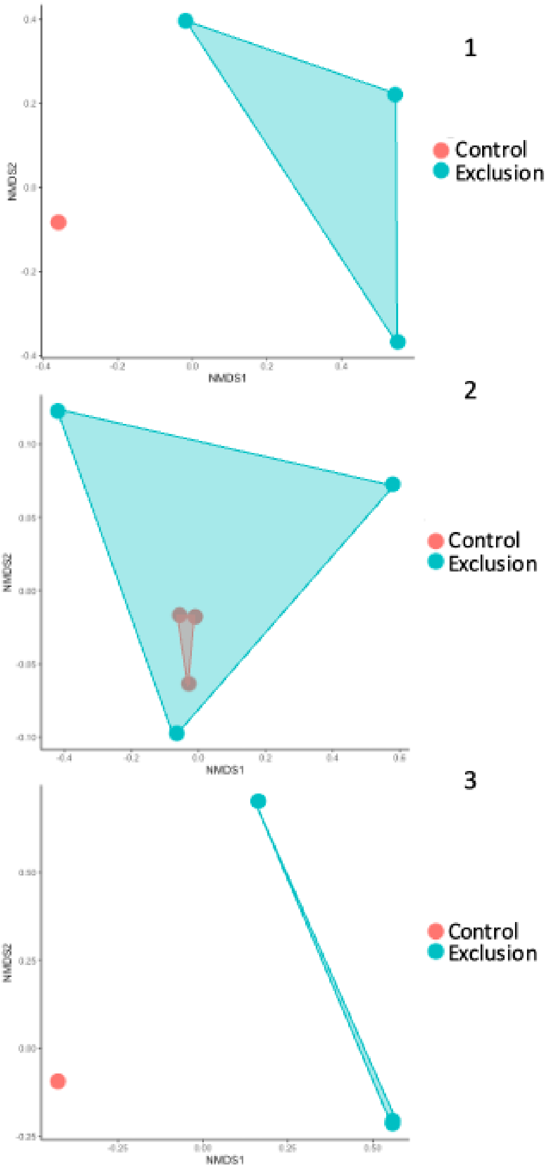

Figure 14: nMDS plots for all three Waiwera sites. For each site (1-3) three replicates of control (red) and three exclusion (blue) treatments were plotted. The grided area between points indicates the community variance between the three replicates. Overlap in points in sites 1 & 3 resulted in only one or two of the replicates to be visible.

Whangateau had a vastly different community composition compared to the other two estuary clusters (Figure 10). Regardless, the nMDS analysis of the treatment impact followed the same pattern as all the other sites, with the control plots exhibiting less variance and no overlap between the two treatment community compositions (Figure 15). The response at the Whangateau sites were not as pronounced, with the control treatments experiencing some large variation within their treatment communities. The controls additionally did not display the characteristic spread between the three control plots, with some overlap of occurring in plots 2,3 and 4 of Figure 15. Whangateau was not dominated by cockles or any single organism class (Figure 10), which could explain the variable response to the exclusion treatment seen in plots 2,3 & 4 (Figure 15).

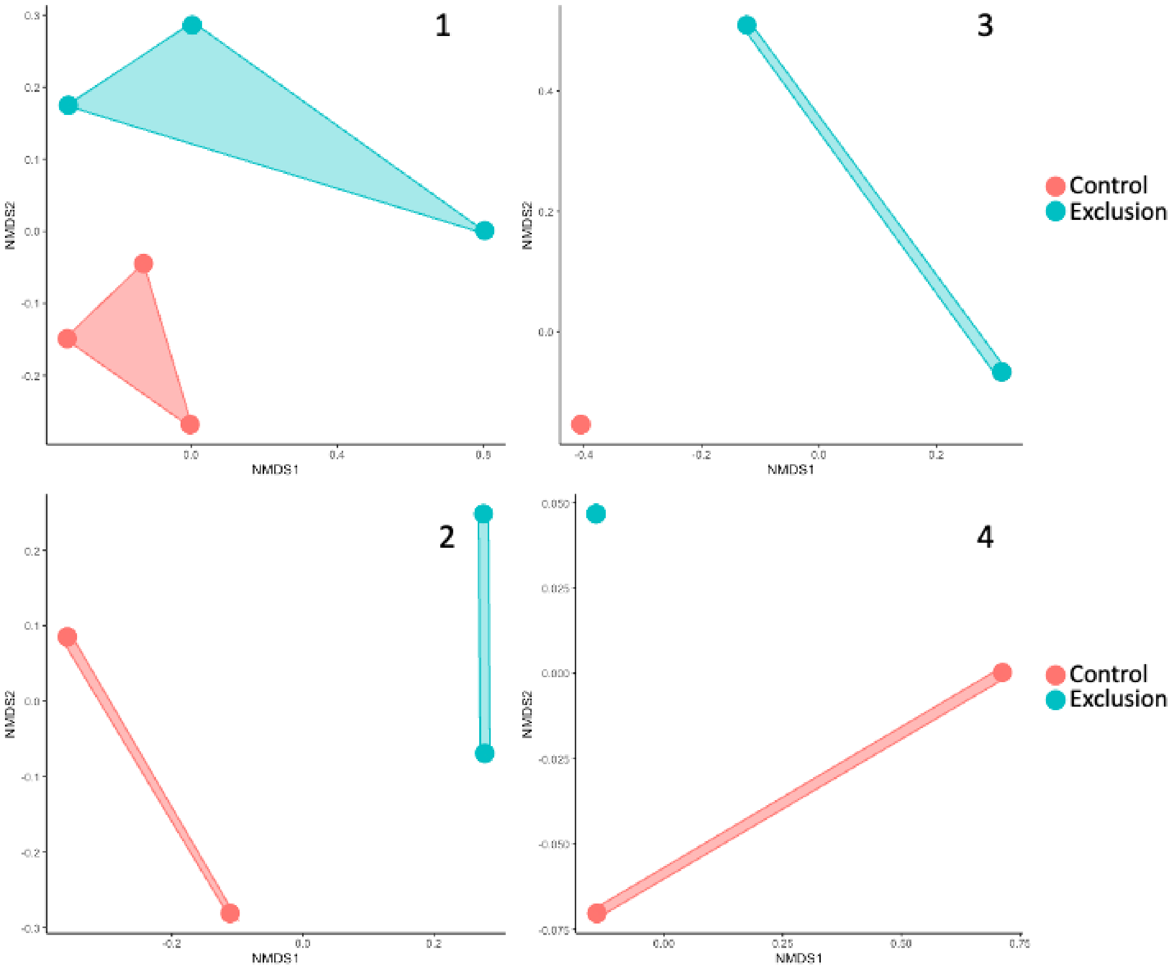

Figure 15: nMDS plots for the four sites within Whangateau harbour. Each site (1-4) has three replicates of control (red) and exclusion (blue). The grided area between the replicates represents the community variances at for each treatment at each site. Overlap in values in sites 2,3 & 4 resulted in either one or two of the three replicates to be visible.

The SIMPER analyses of these plots further support the nMDS by highlighting the significant species variability between the four plots (Appendix 3). Plot 1 which follows a similar trend as other cockle dominated sites (Figure 13 & Figure 14) identified anemones (*Anthopleura aureoradiata*) as a significant species in explaining the difference between the two treatments. Interestingly, the other three plots also found *A. aureoradiata* to be a significant species despite the nMDS not exhibiting the same pattern. These plots also identified multiple species of polychaetes and gastropods to be significant in explaining differences between the treatments. Where the Whangateau sites really differ from the other estuaries is the significant malacostraca (*Torridoharpinia hurleyi, Lysianassidae* spp. & *Halicarcinus whitei*) that were identified through SIMPER analysis. This class of organism also occurred in their highest proportional abundances in Whangateau harbour (Figure 10), dominated largely by *Paracorophium excavatum*. Unlike the other estuaries, the identified significant species did not always occur in higher abundances in the control treatments, with some polychaetes occurring in higher abundances in the exclusion plots (Appendix 4).

3.4 Influence of environmental characteristics

After accounting for the biotic influence that explained some of the variability between treatment communities, it is essential to explore the environmental characteristics that could have impacted community recovery post disturbance. The following plots display the dbRDA that was conducted to examine how physical characteristics like sediment composition, exposure to wind wave action, and ambient adult cockle density influenced community clusters. Due to the large spatial scale between estuaries and heteroscedasticity of environmental characteristics within estuaries, being able to identify key physical factors that impact community clustering ultimately helps understand what influences their recovery. The dbRDA has been intentionally separated by the control & exclusion treatments to highlight key environmental characteristics within each treatment. Since paired treatments plots are situated near each other, the physical parameters that influence them will be extremely similar. The differences between the two treatments will indicate how the removal of *A. stutchburyi* significantly shifts how environmental conditions influence the recovery of benthic communities.

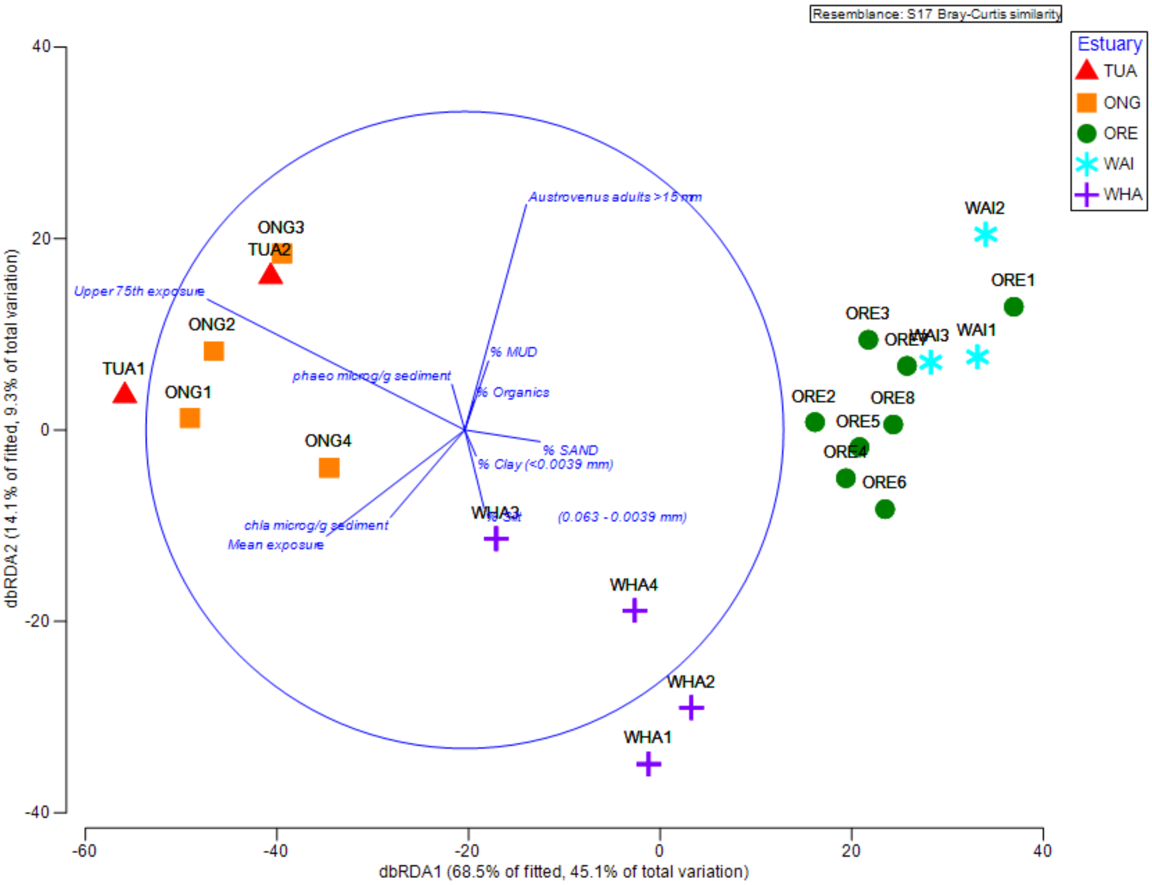

Figure 16: dbRDA plot for all control sites with environmental parameters and ambient adult cockle density as predictor variables.

As demonstrated throughout the nMDS control treatments in section 3.3, the dbRDA further supports the small amount of variance that control treatments experienced both biotically and abiotically (Figure 16). There is such minimal variance between the three replicates at each site that there is complete overlapping of values for all estuaries. The upper 75th percentile and mean exposure strongly influence the plots within Tauranga harbour (Tuapiro and Ongare) with some influence from photosynthetic organisms (chlorophyll-A and phaeo pigments). Suggesting that these sites are exposed to substantially more wind wave action than the other estuaries with higher levels of primary productivity within surface sediments. Ambient cockle density appears to separate community clusters across the other axis, clearly setting Whangateau sites apart from the rest. Waiwera and Orewa estuaries once again clustered together, further supporting the previously identified sedimentary and community patterns between the two sites. Furthermore, both sites exhibited relatively small amounts of variance within their respective estuaries with the presence of adult cockles, supporting the trends seen through nMDS analysis (Figure 13 & Figure 14). Finally, the Whangateau sites illustrate that they were also influenced by silt and clay sediment content, which is vastly different from the other two estuary clusters.

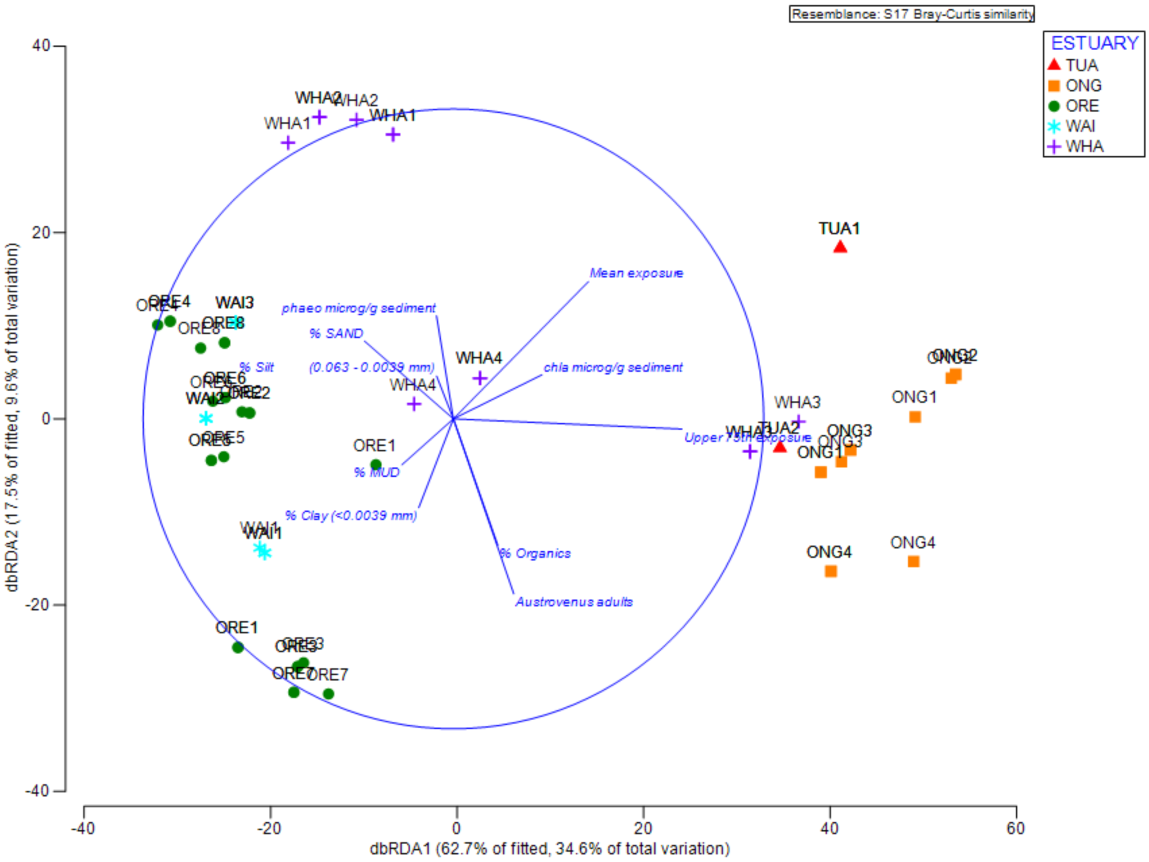

Figure 17: dbRDA plot for all exclusion sites with environmental parameters and ambient adult cockle density as predictor variables.

The exclusion dbRDA analysis produced a largely different plot compared to those from the control analysis. Most of the sites experienced significant variation within each estuary with only a few overlapping replicate communities (Figure 17). Like in the control dbRDA analysis, the upper 75th exposure had the most significant impact for both Ongare and Tuapiro sites. With chlorophyll a content and mean exposure having larger influences on the clustering of some the Tauranga replicates. Interestingly, some of the Whangateau replicates were also found to be influenced by the upper 75th exposure and clustered with the Tauranga estuary sites. Additionally, that Ongare and Tuapiro sites experienced the least amount of variance between exclusion treatments. Whangateau exclusion plots experienced the greatest amount of variation, notably greater than what their control plots exhibited, with some replicates even being grouped near Orewa and Waiwera sites. This proximity to the two other estuary clusters is not surprising as some of the Whangateau replicates shared highly similar communities to both Tauranga and Orewa/ Waiwera clusters. Waiwera and Orewa replicates also experienced substantially more variation between replicates than within the control treatment. With amounts of sand, mud, and clay playing the largest roles in influencing the replicate clusters.

A few of the sites were pulled down by ambient adult cockle density and/ or percentage of organics but not enough to exceed that of the sediment properties. Discussion

This research addresses the impact of adult cockle removal on the wider macrofaunal community, highlighting key environmental and ecological impacts that influence benthic community recovery. These findings have important implications that recovery and resilience are driven by existing community composition and connectivity factors (Thrush, Halliday, et al., 2008). This brings attention to the fragmentation and ecological homogenization of benthic communities as a result of losing a keystone species such as *A. stutchburyi* (Gladstone-Gallagher et al., 2021; Thrush, Hewitt, et al., 2008). Additionally, there is a degree of estuary specific environmental conditions that influence the recovery of these communities following a cockle die-off event. The sediment compositions serve as indications of estuary health, determining to some degree what community composition can be supported (Ellis et al., 2000; Vieillard, 2020). Combining both these biotic and abiotic factors with the intensity and exposure of wind-wave at each site, can lead to highly variable estuary specific recovery rates for both adult and juvenile cockles as well as the greater macrofaunal community.

3.5 Impact of sediment composition on recovery

Environmental parameters are influential in determining community composition, dictated by the range in physical conditions that are present (Thrush, 1991). In terms of healthy ranges for sediments within estuaries, silt and clay can only be tolerated in low proportions due to their ability to clog gills and inhibit multiple feeding methods (Robinson et al., 1984; Stevens, 1987). The levels recorded within the five estuaries were not high enough to be considered uninhabitable, but were all found to be outside hypothised pre-anthropogenic levels except for Whangateau (Robinson et al., 1984; Stevens, 1987). A recent intertidal study found that there were different stable states dictated by different sediment mud %, with sites with less than 3 % mud content representing healthy and non-degraded estuaries (Vieillard, 2020). Suggesting that out of all five sites from this study, Whangateau harbour represents the only place within the healthy non-degraded mud content threshold. The study also found that there were tipping points correlated with different mud proportions that would result in tipping point cascades (Vieillard, 2020). Furthermore, consecutive mud content stable states would result in decreasing diversity and abundance of macrofauna species and a reduction in the provision of ecological services (Norkko et al., 2006; Vieillard, 2020). Additionally, increased terrestrial sediment can lead to higher rates of organic material and chlorophyll, possibly explaining why

Ongare had substantially higher amounts of chlorophyll-a compared to other sites (Norkko et al., 2006; Vieillard, 2020). Tuapiro experienced substantially more exposure compared to Ongare, which could explain the differences between their mud contents and chlorophyll-a levels considering the sites share very similar catchment areas (Reise et al., 2001; Vieillard, 2020). However, the Tauranga sites did not experience a decrease in species abundance which can be associated with increasing mud content (Tricklebank et al., 2021; Vieillard, 2020). It could also be that there is a link between muddier and lower cockle density sites possessing extensively higher abundance and diversity of polychaetes. The could possibly represent a new stable benthic community, in which polychaetes are able to relatively quickly respond to the loss of larger macrofauna without significant losses to community diversity or abundance (Ellis et al., 2017; Ólafsson et al., 1994; Van Colen et al., 2012; Vieillard, 2020). It could also suggest that the soft sediment communities within Tauranga harbour are better at returning to their pre-disturbance cockle populations faster than the other estuaries (Zajac et al., 1998) due to their lower diversity of organism classes and more homogenous physical conditions (Thrush, Halliday, et al., 2008). On the otherhand, both Orewa and Waiwera estuaries also fell outside the hypothesised healthy state with their mud content (less than 3%) but were less exposed than the sites from Tauranga harbour which could explain their reduced recovery following disturbance (Norkko et al., 2002; Van Colen et al., 2012; Vieillard, 2020). This suggests that although they do not share the same intertidal area, that their catchments areas have similar land use, soil profiles, sediment sources and similar marine influences, relating the similarity in their community compositions to indistinguishable sedimentary and hydrological conditions (Thrush, Halliday, et al., 2008).

3.6 Ecology driven recovery

The impact of the treatment was significant for diversity and abundances for communities dominated by *A. stutchburyi* which occurred alongside higher ambient adult cockle densities (greater than 215 cockles per 0.3125m^2). It was identified that the recovery of community diversity, species richness and community composition was largely linked to the presence of adult cockles and ambient cockle density. This coincides with literature that identifies the removal of *A. stutchburyi* as having a destabalising impact on the greater macrofaunal community, due to the multitude of facilitory services they provide (Ellis et al., 2000; Van Colen et al., 2012; Whitlatch et al., 1997; Zajac et al., 1998). The presence of adult cockles within control treatments reduced the variability and increased diversity across all sites on average, especially at higher ambient cockle densities (exceeding 500 cockles per 0.3125m^2), reinforcing the idea that in high density adult cockle sites *A. stutchburyi* act as a benthic diversity facilitator. This aligns directly with literature identifying larger bioturbators like cockles to have a disproportionately larger influence in restoring estuarine conditions to pre-disturbance states (Van Colen et al., 2012), which is evident in three of these four estuaries.

The community composition and diversity also varied greatly in both treatment types with an ambient cockle density gradient, displaying a clear community shift at lower cockle densities (less than 215 cockles per 0.3125 m^2). Lower cockle densities exhibited communities dominated by polychaetes. Adult cockles are known to have an inhibitory impact on benthic communities at higher densities (Turner et al., 1997; Whitlatch et al., 1997), highlighted by substantially greater species richness and abundance in Tauranga harbour. This could be attributed to both their low ambient adult cockle densities and low cockle abundances observed within both treatment types in this study. The inhibitory effect of cockles was also observed within Whangateau harbour. It had the most unique community compositions compared to the other estuaries, a limited exposure to wind-wave activity and a relatively healthier mud content (Tricklebank et al., 2021; Vieillard, 2020). The increased levels of species richness and abundances within Whangateau exclusion plots further supports the inhibitory effects that adult *A. stutchburyi* could have on the abundances and settlement of some species estuaries (Turner et al., 1997; Whitlatch et al., 1997). Especially because Whangateau harbour relies heavily on internal recruitment, it is likely that organisms that experience inhibition by adult cockles in neighbouring sediment migrated into the disturbed plots (Fisheries, 2009; Tricklebank et al., 2021; Zajac et al., 1998). This could explain the highly variable recovery within exclusion treatment plots, aligning with the theory that in relatively healthy estuaries, ecological controls play a significant role in the self-regulation of community composition (Ólafsson et al., 1994; Tricklebank et al., 2021). Despite the elevated abundance and diversity levels in some plots, community composition was unable to recover to pre-disturbance levels like the rest of the exclusion treatment sites. Even though the lack of recovery of these sites was largely linked to the absence of adult cockles within the system, there were a multitude of other site specific significant species which occurred in variable abundances between treatments. In some cases, species directly associated with the presence of *A. stutchburyi* like *A. modestus* and *A. aureoradiata* occurred in significantly different abundances between treatments. Which is consistent with literature that has identified a link between the presence of cockles and both anenomes and barnacles, due to the provision of substrate (Foster, 1986;

McLaverty et al., 2020). Additionally, cockle dominated communities experienced a greater number of significant differences in species abundances across all classes between two treatments. Some plots finding a greater number of species with significant differences between the two treatments than species that were not. Furthermore, there were no consistent trends for other significant species as each plot within each estuary often identified different significant species. This is consistent with the highly variable nature of these environments being highly variable at larger scales (Thrush, 1991).

The exclusion treatment also had a strong impact on cockle adult-juvenile proportions with higher ambient cockle density, with the presence of adults in the control plots facilitating greater juvenile abundances (Hewitt et al., 1997; Tricklebank et al., 2021; Whitlatch et al., 1997). A recent study investigating cockle populations following a die-off event found juvenile cockle abundances relatively constant (Tricklebank et al., 2021), which we found only occurred in sites that were polychaete dominated. This suggests that the recruitment of juveniles within polychaete dominated estuaries is not merely linked to the presence of adult cockles. This could be explained by the higher wind-wave exposure within these sites which facilitates the dispersal of juveniles (Lundquist et al., 2004; Reise, 2012), enabling a more even juvenile concentration regardless of treatment.

Despite the removal of adult cockles having an observable impact in reshaping community composition one year post-disturbance, it appears to have minimally influenced the recovery of both the benthic community and cockle populations overall. Suggesting that the relatively more successful community recovery displayed within Tauranga harbour (Tuapiro and Ongare) can be attributed to the benthic community and environmental parameters. However, The increased variation within the exclusion treatments indicates that both these sites experienced a significant decline in the integrity of their community structure, causing there to be highly variable and inconsistent community recovery following the disturbance event, further highlighting the importance of *A. stutchburyi* as a keystone species within these two sites. On the other hand, the substantially less variability in community composition between control plots compared to exclusion plots, highlights that the removal of adult cockles from the communities had a destabilising effect. Furthermore, that exclusion plots had an unpredictable recovery one year post disturbance and an overall reduction in diversity. The reduced diversity and greater dominance by a few species in the cockle exclusion plots could indicate a decline in the communities resilience and explain the exhibited slow rates of recovery (Gladstone-

Gallagher et al., 2021; Thrush, Halliday, et al., 2008). The continuation of degradation linked with sediment composition accompanied with a large disturbance event (i.e. cockle die-off event), has the ability to push communities past thresholds into another stable state (Thrush, Halliday, et al., 2008; Vieillard, 2020). Additionally, leading to more homogenised communities with reduced capacities for recovery, switching from community driving recovery to it being limited to the individual species ability to adapt to the conditions within the disturbed region (Ellis et al., 2000; Gladstone-Gallagher et al., 2021).

3.7 Wind-wave driven recovery

The distanced based redundancy analysis reinforced the spatial proximity grouping of sites and identified key environmental factors like wave exposure and ambient cockle densities to be influential. Tauranga sites which were dominated by polychaetes experienced the smallest amount of variability and were largely influenced by the upper 75th quartile of exposure events. Suggesting that the more powerful wind-wave events strongly influenced the recovery of these replicates. Additionally, Ongare and Tuapiro sites experienced the least amount of variance between exclusion treatments, indicating that the exposure to wind-wave energy helped facilitate recovery. Supporting the impact that intense wind-wave exposure helps facilitate recovery within soft sediment ecosystems, as these high energy events cause greater organism transportation through bed-load transport and suspension (Ellis et al., 2000; Reise, 2012; Turner et al., 1997) . There is also evidence that deposition of medium sized particles which occurs during higher energy events by facilitating the colonization of microphytobenthos, which in turn attracting heterotrophic polychaetes (Norkko et al., 2002). The opposite trend was exhibited within Whangateau harbour, which relies heavily on internal recruitment because it has a narrow harbour entrance and is far from other estuaries (Fisheries, 2009; Tricklebank et al., 2021; Zajac et al., 1998). This lack of wind-wave disturbance could explain the highly heterogeneous community composition and the variable recovery within exclusion treatment plots. This suggests that through the exclusion of adult cockles, that some locations within Whangateau harbour assimilated to resemble either communities dominated by polychaetes or bivalves, which appears to be largely influenced by the physical characteristics that specific replicates were exposed to.

4 Conclusion

The hypothesis was initially correct; cockles did have a significant influence on some of the soft sediment communities, but the impact is estuary dependant. This variance associated with site was evident through all stages of analysis with different plots within the same estuary identifying different significant species both between and within treatment types. All sites experienced extensive variation between control and exclusion treatments, with the recovery of exclusion communities being largely unpredictable and inconsistent one year post disturbance. The reduced recovery within Whangateau and Orewa/ Waiwera clusters could also be possibly attributed to the lack of wind-wave exposure within these estuaries, reducing bed load transport and the ability for larger macrofauna to recolonise the disturbed areas. The hypothesis was also correct in that non-cockle dominated communities like those found within Tauranga harbour (Tuapiro and Ongare) were less impacted by the removal of adult cockles.

There are multiple reasons that could explain why Tauranga exclusion treatment sites experienced relatively less variability compared to the other estuaries. The two prominent variables are linked to polychaete community dominance and more frequent and intense wind-wave activity facilitating bed load transport and the recolonisation of disturbed plots. This study however does not account for few variables which could have substantial influences on the community. Such as the impact of shell hash from a real adult cockle die-off event, which could provide substrate to facilitate the recolonisation. Additionally, the changes in nutrient fluxes pre and post disturbance, helping narrow down the specific geochemical services associated with a cockle die-off event. From this study it is clear that any cockle die-off event within soft sediment environments would have a largely negative impact overall, with a variable and highly estuary specific recovery period. It is clear that recovery and resilience are dictated by environmental conditions and existing species composition. The successional recovery aspects will be influenced by community dynamics with implications for rates of recovery following disturbance regimes (such as heatwave events). It can be postulated that increasing disturbance regimes could increase ecological fragmentation resulting in lower resilience and recovery. This would likely result in progressively worsening community functioning alongside the degradation in estuarine health, reducing the ability to provide ecosystems services.

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Appendices

Appendix 1 – Sediment and community proportions data

Table 2: Table displaying the raw data for sediment composition.

Site name	Treatment	% SAND	% MUD	% Clay (<0.0039 mm)	% Organics	% Silt (0.063 - 0.0039 mm)	chla microg/g sediment
TUA1	Control	95.552	4.448	2.43	3.38	2.02	15.45
TUA2	Control	95.212	4.314	2.16	2.33	2.16	9.71
TUA1	Exclusion	96.414	3.471	1.32	2.74	2.15	16.06
TUA2	Exclusion	95.555	3.790	2.274	2.50	1.516	11.75
ONG1	Control	88.501	10.205	3.51	3.88	6.70	23.14
ONG2	Control	84.959	14.836	5.93	5.01	8.90	24.34
ONG1	Exclusion	89.965	9.959	3.984	4.66	5.976	19.53
ONG2	Exclusion	86.993	13.007	2.409	5.35	10.599	24.57
ONG3	Control	89.144	9.404	3.583	3.87	5.822	19.94
ONG4	Control	89.198	6.782	2.81	3.19	3.98	18.66
ONG3	Exclusion	90.786	8.130	2.602	3.95	5.528	21.88
ONG4	Exclusion	91.624	6.017	2.28	2.61	3.73	18.21
ORE1	Control	95.618	4.275	1.283	1.79	2.993	6.07
ORE2	Control	92.408	6.157	3.941	1.73	2.217	8.30
ORE1	Exclusion	89.734	10.257	6.312	2.02	3.945	7.03
ORE2	Exclusion	92.862	6.884	2.98	1.75	3.91	6.53
ORE3	Control	92.790	4.754	2.237	1.98	2.517	6.11
ORE4	Control	93.018	5.459	2.50	1.83	2.96	5.60
ORE3	Exclusion	89.823	9.019	3.22	1.60	5.80	2.98
ORE4	Exclusion	92.227	7.675	3.15	1.75	4.53	5.50
ORE5	Control	92.881	5.394	2.360	1.89	3.034	5.21
ORE6	Control	94.856	4.936	3.085	1.57	1.851	5.76
ORE5	Exclusion	93.563	6.242	3.12	1.90	3.12	4.11
ORE6	Exclusion	95.403	4.569	2.47	1.58	2.09	6.07
ORE7	Control	90.269	9.010	5.631	1.60	3.379	6.24
ORE8	Control	91.255	8.022	3.438	2.13	4.584	6.64
ORE7	Exclusion	87.326	12.534	5.88	2.44	6.66	8.16
ORE8	Exclusion	90.528	9.427	3.57	2.10	5.86	7.95
WAI3	Control	94.555	5.159	2.580	1.92	2.580	4.12
WAI3	Exclusion	91.237	8.693	4.04	2.50	4.65	4.69
WAI1	Control	94.168	5.832	3.791	2.66	2.041	6.82
WAI1	Exclusion	93.689	6.291	3.06	1.87	3.23	6.20
WAI2	Control	91.214	8.702	4.873	2.40	3.829	7.79
WAI2	Exclusion	90.317	9.683	3.60	2.20	6.09	8.06
WHA1	Control	94.898	4.460	2.00	2.37	2.46	9.92
WHA2	Control	94.201	4.929	1.87	1.89	3.06	9.01

WHA2	Exclusion	94.959	3.440	1.56	1.66	1.88	10.89
WHA2	Exclusion	93.839	4.530	1.56	1.91	2.97	8.14
WHA3	Control	91.204	1.510	1.510	1.66	0.000	9.54
WHA4	Control	95.755	1.517	0.337	1.71	1.180	9.91
WHA3	Exclusion	90.575	0.713	0.55	1.33	0.16	8.41
WHA4	Exclusion	97.025	0.755	0.755	1.29	0.000	8.90

Table 3: Table displaying raw community class proportions per site used to calculate average class proportions per estuary.

Site	**Treatment**	**Anthozoa %**	**Bivalvia %**	**Gastropoda %**	**Malacostraca %**	**Polychaeta %**	**Other %**
TUA1	Control	10.32	4.92	0.55	1.22	81.05	1.94
TUA2	Control	0.00	18.38	1.13	0.68	77.61	2.20
TUA1	Exclusion	4.17	12.44	3.34	1.13	77.92	1.00
TUA2	Exclusion	2.74	12.07	4.50	2.67	75.82	2.19
ONG1	Control	6.09	7.85	2.33	2.73	80.59	0.40
ONG2	Control	6.77	14.81	4.06	1.53	72.28	0.54
ONG1	Exclusion	2.70	10.09	2.16	1.24	82.98	0.83
ONG2	Exclusion	7.83	10.72	2.80	2.97	74.45	1.24
ONG3	Control	13.24	16.22	9.74	3.42	56.15	1.23
ONG4	Control	7.81	20.31	13.63	3.08	53.29	1.88
ONG3	Exclusion	5.57	16.37	7.51	1.67	66.37	2.50
ONG4	Exclusion	4.43	38.33	4.80	5.75	45.60	1.10
ORE1	Control	0.30	67.82	10.55	11.31	10.02	0.00
ORE2	Control	3.80	65.09	6.44	8.00	13.31	3.35
ORE1	Exclusion	0.00	76.89	2.08	4.17	12.69	4.17
ORE2	Exclusion	5.09	36.19	6.45	1.44	50.82	0.00
ORE3	Control	12.81	52.75	9.32	8.22	16.71	0.18
ORE4	Control	3.19	59.21	8.12	10.31	19.16	0.00
ORE3	Exclusion	6.20	78.62	7.82	2.68	0.39	4.29
ORE4	Exclusion	4.83	53.99	6.80	12.15	18.53	3.70
ORE5	Control	5.40	65.46	11.93	9.29	7.92	0.00
ORE6	Control	3.51	69.55	2.32	6.69	17.92	0.00
ORE5	Exclusion	8.12	53.36	11.97	3.67	22.88	0.00
ORE6	Exclusion	3.96	79.09	4.34	5.36	7.25	0.00
ORE7	Control	6.95	80.52	4.00	2.51	5.76	0.27
ORE8	Control	5.31	86.36	0.89	2.57	2.57	2.30
ORE7	Exclusion	6.95	80.52	4.00	2.51	5.76	0.27
ORE8	Exclusion	4.55	73.34	4.80	4.01	11.23	2.07
WAI1	Control	1.06	74.95	8.82	4.21	10.78	0.20
WAI1	Exclusion	0.00	87.57	1.85	2.55	8.04	0.00
WAI2	Control	0.00	88.34	0.25	3.60	7.81	0.00
WAI2	Exclusion	2.00	88.52	3.78	4.59	1.11	0.00
WAI3	Control	0.24	88.96	2.66	5.97	1.93	0.24
WAI3	Exclusion	8.35	67.19	3.24	12.96	1.47	6.78

WHA1	Control	16.11	25.83	10.64	24.22	8.78	14.42
WHA2	Control	3.81	6.32	5.93	61.55	7.30	15.08
WHA1	Exclusion	1.83	17.26	11.13	46.95	4.56	18.27
WHA2	Exclusion	11.36	11.24	3.49	56.94	10.51	6.44
WHA3	Control	24.14	22.33	8.08	9.91	34.87	0.67
WHA4	Control	17.96	34.20	7.18	6.39	32.95	1.32
WHA3	Exclusion	2.47	25.22	21.13	10.52	38.32	2.35
WHA4	Exclusion	6.24	40.06	7.26	8.85	34.54	3.05

Appendix 2 – Community diversity, abundance, and cockle juvenile-adult proportions.

Table 4: Table displaying the raw data for community diversity and abundance with varying cockle density.

Site name	Treatment	Ambient cockle	average diversity	Average total abundance
ONG1	Control	208.00	21.33	300.00
ONG1	Exclusion	208.00	21.33	255.33
ONG2	Control	215.00	21.33	264.67
ONG2	Exclusion	215.00	17.33	240.33
ONG3	Control	526.00	21.33	264.00
ONG3	Exclusion	526.00	18.33	212.33
ONG4	Control	210.00	20.33	208.67
ONG4	Exclusion	210.00	19.00	216.33
ORE1	Control	640.00	8.67	104.33
ORE1	Exclusion	640.00	4.33	26.67
ORE2	Control	395.00	11.33	61.67
ORE2	Exclusion	395.00	5.33	30.00
ORE3	Control	565.00	12.33	131.67
ORE3	Exclusion	565.00	6.67	61.67
ORE4	Control	340.00	7.67	90.00
ORE4	Exclusion	340.00	5.00	18.67
ORE5	Control	273.00	10.33	93.67
ORE5	Exclusion	273.00	8.33	69.67
ORE6	Control	272.00	6.67	55.00
ORE6	Exclusion	272.00	6.00	30.67
ORE7	Control	481.00	10.67	146.00
ORE7	Exclusion	481.00	10.67	146.00
ORE8	Control	462.00	5.00	79.00
ORE8	Exclusion	462.00	7.25	48.50
TUA1	Control	171.00	15.00	180.00
TUA1	Exclusion	171.00	13.67	110.00
TUA2	Control	183.00	10.00	106.67
TUA2	Exclusion	183.00	10.00	86.00
WAI1	Control	501.00	13.00	161.00
WAI1	Exclusion	501.00	5.67	28.33

WAI2	Control	641.00	10.00	109.67
WAI3	Exclusion	641.00	3.67	14.33
WAI3	Control	671.00	13.67	126.00
WAI4	Exclusion	671.00	3.33	11.00
WHA1	Control	186.00	16.00	107.67
WHA1	Exclusion	186.00	15.67	92.33
WHA2	Control	158.00	16.00	185.33
WHA2	Exclusion	158.00	10.67	139.67
WHA3	Control	331.00	20.67	166.00
WHA3	Exclusion	331.00	21.00	203.33
WHA4	Control	393.00	16.67	99.67
WHA4	Exclusion	393.00	18.67	88.00

Table 5: Table displaying the juvenile and adult proportions with varying ambient cockle density.

Site name	Treatment	Ambient adult cockle density	Average juvenile count	Average adult count
WHA2	C	158.00	8.00	8.00
WHA2	E	158.00	6.00	0.67
TUA1	C	171.00	4.33	0.00
TUA1	E	171.00	4.00	1.00
TUA2	C	183.00	4.00	0.00
TUA2	E	183.00	4.33	0.33
WHA1	C	186.00	13.00	8.33
WHA1	E	186.00	8.33	1.00
ONG1	C	208.00	6.00	6.67
ONG1	E	208.00	9.67	4.67
ONG4	C	210.00	9.33	8.00
ONG4	E	210.00	8.33	2.00
ONG2	C	215.00	5.67	3.00
ONG2	E	215.00	4.33	2.67
ORE6	C	272.00	20.67	22.00
ORE6	E	272.00	19.33	1.00
ORE5	C	273.00	34.00	22.67
ORE5	E	273.00	18.00	3.67
WHA3	C	331.00	2.67	18.33
WHA3	E	331.00	18.33	2.67
ORE4	C	340.00	30.33	20.67
ORE4	E	340.00	6.33	2.00
WHA4	C	393.00	17.67	22.33
WHA4	E	393.00	13.67	6.33
ORE2	C	395.00	12.00	17.67
ORE2	E	395.00	4.00	3.33
ORE8	C	462.00	12.67	28.00
ORE8	E	462.00	40.25	7.00
ORE7	C	481.00	65.33	32.00

ORE7	E	481.00	115.33	6.00
WAI1	C	501.00	85.33	15.33
WAI1	E	501.00	19.67	1.00
ONG3	C	526.00	18.67	6.00
ONG3	E	526.00	15.00	10.67
ORE3	C	565.00	40.00	28.00
ORE3	E	565.00	26.00	11.00
ORE1	C	640.00	43.67	36.33
ORE1	E	640.00	20.00	4.67
WAI2	C	641.00	57.00	31.33
WAI2	E	641.00	7.67	1.67
WAI3	C	671.00	88.33	25.00
WAI3	E	671.00	7.67	0.33

Appendix 3 – SIMPER analysis outputs

Table 6: SIMPER output Tuapiro 1.

Species name	average	sd	cumsum	p
Pronispio.aucklandia	0.2071	0.1415	0.51	0.301
Anthopleura aureoradiata	0.0468	0.0291	0.62	0.001 ***
Magelona.dakini	0.0272	0.0163	0.69	0.501
Nereids.Cera	0.0239	0.016	0.75	0.301
Heteromastus.filiformis	0.0224	0.0116	0.81	0.601
Macomona.liliana	0.0199	0.013	0.86	0.101
Capitella.spp	0.007	0.0085	0.87	0.901
Phoxocephalidae	0.0052	0.0045	0.88	0.301
Nemertea	0.0045	0.0035	0.9	0.301
Notoacmea.sapha	0.0041	0.0063	0.91	0.801
Nuculidae	0.004	0.0046	0.92	0.301
Orbinia.papilosa	0.0036	0.0035	0.92	0.801
Oligochaeta	0.0036	0.0028	0.93	0.201
Scolecolepedes.benhami	0.0028	0.0032	0.94	0.501
Cominella.ganiformis	0.0028	0.0033	0.95	0.401
Colorostylis.lemurum	0.0025	0.002	0.95	0.201
Z..subcarinatus	0.0025	0.002	0.96	0.201
Aonides.trifida	0.0025	0.0038	0.97	0.101
Aricidea.sp	0.0025	0.0038	0.97	0.101
Z..lutulentus	0.0015	0.0018	0.98	0.801
Diloma.ubrostrate	0.0014	0.0021	0.98	0.801
Micrelenchus.huttonii	0.0014	0.0021	0.98	0.801
Arcualuta.senhousia	0.0013	0.002	0.99	0.001 ***
Halicarcinus.whitei	0.0012	0.0019	0.99	0.101
Scoloplos.cylindrifer	0.0012	0.0019	0.99	0.101
Boccardio.syrtis	0.0011	0.0017	1	0.801

Table 7: SIMPER output Tuapiro 2.

Species name	average	sd	cumsum	p
Pronispio.aucklandia	0.1109	0.0632	0.44	0.042*
Nuculidae	0.0225	0.0069	0.53	0.042*
Magelona.dakini	0.0223	0.0059	0.62	0.042*
Heteromastus.filiformis	0.013	0.0044	0.68	0.042*
Cominella.ganiformis	0.0096	0.0081	0.71	0.708
Macomona.liliana	0.0092	0.0058	0.75	0.708
Oligochaeta	0.0074	0.0063	0.78	0.375
Nereids.Cera	0.0074	0.0027	0.81	0.708
Paradoneis.lyra	0.0039	0.0045	0.83	0.708
Scolecolepedes.benhami	0.0039	0.0045	0.84	0.708
Paracalliope.novizealandiae	0.0038	0.0044	0.86	0.042*
Colorostylis.lemurum	0.0038	0.0031	0.87	0.375
Z..subcarinatus	0.0038	0.0033	0.89	0.375
Capitella.spp	0.0038	0.0044	0.9	0.708
Nemertea	0.0037	0.0002	0.92	0.708
Orbinia.papilosa	0.0037	0.0042	0.93	0.042*
Boccardio.syrtis	0.0037	0.0029	0.95	0.708
Alpheus.sp.	0.002	0.0023	0.96	0.708
Aonides.trifida	0.002	0.0023	0.96	0.708
Z..lutulentus	0.002	0.0023	0.97	0.708
Nereid.nicon	0.0019	0.0022	0.98	0.042*
Pisinna.zostereophila	0.0019	0.0022	0.99	0.042*
Anthopleura	0.0018	0.0021	0.99	0.708
Diloma.ubrostrate	0.0018	0.0021	1	0.708

Table 8: SIMPER output for Ongare 1.

Species name	average	sd	cumsum	p
Pronispio.aucklandia	1.02E-01	3.15E-02	0.35	0.301
Magelona.dakini	3.43E-02	2.67E-02	0.47	0.901
Anthopleura	2.11E-02	1.97E-02	0.54	0.601
Nuculidae	1.82E-02	1.43E-02	0.6	0.701
Pseudopolydora.corniculata	1.63E-02	1.32E-02	0.66	0.701
Heteromastus.filiformis	1.42E-02	1.07E-02	0.7	0.201
Phoxocephalidae	8.80E-03	3.04E-03	0.73	0.001 ***
Sphaerosyllis.semiverrucosa	8.70E-03	5.36E-03	0.76	0.101
Z..subcarinatus	7.20E-03	5.33E-03	0.79	0.701
Macomona.liliana	7.10E-03	7.76E-03	0.81	0.901
Eatoniella.sp	5.10E-03	2.01E-03	0.83	0.401
Cominella.ganiformis	4.60E-03	3.43E-03	0.85	0.601
Aricidea.sp	4.60E-03	3.02E-03	0.86	0.301
Z..lutulentus	3.80E-03	3.45E-03	0.88	0.901
Pseudopolydora.paucibranciata	3.50E-03	3.97E-03	0.89	0.101

Nereid.perinereid	3.10E-03	9.80E-04	0.9	0.001 ***
Oligochaeta	2.60E-03	2.65E-03	0.91	0.301
Halicarcinus.whitei	2.60E-03	2.17E-03	0.92	0.401
Notoacmea.sapha	2.50E-03	2.50E-03	0.92	0.101
Capitella.spp	2.30E-03	2.12E-03	0.93	0.501
Boccardio.syrtis	2.10E-03	1.49E-03	0.94	0.401
Nemertea	1.90E-03	1.20E-04	0.94	0.001 ***
Cyclaspis.thomsoni	1.50E-03	1.62E-03	0.95	0.401
Paracalliope.novizealandiae	1.50E-03	1.61E-03	0.96	0.801
Austrominius.modestus	1.30E-03	1.88E-03	0.96	0.101
Colorostylis.lemurum	1.20E-03	9.20E-04	0.96	0.301
Neoguraleus.sinclairi	1.00E-03	9.80E-04	0.97	0.801
Torridoharpinia.hurleyi	8.00E-04	1.01E-03	0.97	0.801
Diloma.ubrostrate	8.00E-04	1.00E-03	0.97	0.801
Nereids.Cera	8.00E-04	1.00E-03	0.98	0.801
Hyalidae.spp	7.00E-04	9.90E-04	0.98	0.801
Nebaliacea	7.00E-04	9.90E-04	0.98	0.801
Paradoneis.lyra	7.00E-04	9.90E-04	0.98	0.801
Austrohelice.crassa	7.00E-04	9.80E-04	0.98	0.001 ***
Heterosquilla.sp	6.00E-04	9.60E-04	0.99	0.801
Nereid.nicon	6.00E-04	9.60E-04	0.99	0.801
Perinereis.vallata	6.00E-04	9.60E-04	0.99	0.801
Platynereis.australis	6.00E-04	9.60E-04	0.99	0.801
Squilla.sp	6.00E-04	9.60E-04	1	0.801

Table 9: SIMPER output for Ongare 2.

Species name	Average	sd	cummsum	p
Pronispio.aucklandia	0.1056	0.0815	0.31	0.801
Magelona.dakini	0.0435	0.0386	0.44	0.101
Heteromastus.filiformis	0.0427	0.0309	0.56	0.501
Pseudopolydora.corniculata	0.0414	0.0529	0.68	0.601
Anthopleura	0.0164	0.0112	0.73	0.401
Nereids.Cera	0.0139	0.0101	0.77	0.001 ***
Nuculidae	0.0126	0.006	0.8	0.501
Macomona.liliana	0.011	0.0072	0.84	0.401
Sphaerosyllis.semiverrucosa	0.0101	0.0015	0.87	0.001 ***
Cominella.ganiformis	0.0042	0.002	0.88	0.201
Arthritica.bifurca	0.0032	0.0049	0.89	0.201
Boccardio.syrtis	0.0032	0.003	0.9	0.701
Colorostylis.lemurum	0.003	0.0033	0.91	0.201
Halicarcinus.whitei	0.003	0.0023	0.92	0.101
Pseudopolydora.paucibranciata	0.0027	0.0017	0.92	0.201
Nereid.perinereid	0.0025	0.0025	0.93	0.501
Aricidea.sp	0.0023	0.0019	0.94	0.001 ***
Neoguraleus.sinclairi	0.002	0.0019	0.94	0.201

Torridoharpinia.hurleyi	0.0019	0.0015	0.95	0.601
Z..lutulentus	0.0019	0.0016	0.95	0.901
Capitella.spp	0.0018	0.0016	0.96	0.801
Nemertea	0.0017	0.0014	0.96	0.701
Nereid.nicon	0.0015	0.0016	0.97	0.801
Z..subcarinatus	0.0015	0.0016	0.97	0.801
Paracalliope.novizealandiae	0.0014	0.0011	0.98	0.101
Oligochaeta	0.001	0.0012	0.98	0.401
Phoxocephalidae	0.0008	0.0012	0.98	0.301
Scolecolepedes.benhami	0.0008	0.0012	0.98	0.201
Austrominius.modestus	0.0007	0.0011	0.99	0.301
Diloma.ubrostrate	0.0007	0.0011	0.99	0.301
Eatoniella.sp	0.0007	0.0011	0.99	0.301
Exoginae	0.0007	0.0011	0.99	0.301
Macrolymenella.stewartensis	0.0007	0.0011	1	0.301

Table 10: SIMPER output Ongare 3.

Species name	average	sd	cumsum	p
Anthopleura	7.19E-02	1.74E-02	0.26	0.001 ***
Pronispio.aucklandia	5.02E-02	2.52E-02	0.43	0.001 ***
Z..subcarinatus	2.83E-02	2.30E-02	0.53	0.901
Nuculidae	1.90E-02	1.77E-02	0.6	0.601
Heteromastus.filiformis	1.62E-02	1.15E-02	0.66	0.301
Phoxocephalidae	1.34E-02	4.10E-03	0.7	0.001 ***
Aricidea.sp	8.70E-03	5.11E-03	0.74	0.301
Magelona.dakini	6.90E-03	4.37E-03	0.76	0.901
Nemertea	6.30E-03	2.69E-03	0.78	0.001 ***
Oligochaeta	4.80E-03	3.66E-03	0.8	0.801
Cominella.ganiformis	4.50E-03	1.49E-03	0.81	0.101
Macomona.liliana	4.20E-03	3.70E-03	0.83	0.901
Austrominius.modestus	4.10E-03	2.64E-03	0.84	0.901
Sphaerosyllis.semiverrucosa	3.90E-03	2.32E-03	0.86	0.001 ***
Aonides.trifida	3.80E-03	4.12E-03	0.87	0.101
Pseudopolydora.corniculata	3.80E-03	2.83E-03	0.88	0.201
Nereids.Cera	3.70E-03	3.13E-03	0.9	0.901
Eatoniella.sp	3.20E-03	4.84E-03	0.91	0.801
Boccardio.syrtis	3.20E-03	1.33E-03	0.92	0.301
Z..lutulentus	2.60E-03	2.47E-03	0.93	0.301
Scolecolepedes.benhami	2.10E-03	3.22E-03	0.94	0.901
Chiton.glaucus	2.10E-03	1.88E-03	0.94	0.201
Diloma.ubrostrate	2.10E-03	1.82E-03	0.95	0.101
Isocldadus.spp	1.50E-03	2.32E-03	0.96	0.101
Halicarcinus.whitei	1.00E-03	1.19E-03	0.96	0.901
Cyclaspis.thomsoni	8.00E-04	1.24E-03	0.96	0.001 ***
Exoginae	8.00E-04	1.24E-03	0.97	0.001 ***

Colorostylis.lemurum	8.00E-04	1.23E-03	0.97	0.801
Orbinia.papilosa	8.00E-04	1.23E-03	0.97	0.801
Torridoharpinia.hurleyi	8.00E-04	1.23E-03	0.98	0.801
Nereid.nicon	8.00E-04	1.21E-03	0.98	0.801
Notoacmea.sapha	8.00E-04	1.16E-03	0.98	0.101
Paradeneis.lyra	8.00E-04	1.16E-03	0.98	0.101
Hemigrapas.sexdentatus	7.00E-04	1.12E-03	0.99	0.101
Owenia.petersenae	7.00E-04	1.12E-03	0.99	0.101
Pseudopolydora.paucibranciata	7.00E-04	1.12E-03	0.99	0.101
Xymene.pleibeius	7.00E-04	1.12E-03	1	0.101

Table 11: SIMPER outpu for Ongare 4.

Species name	average	sd	cumsum	p
Pronispio.aucklandia	0.1102	0.0764	0.31	0.408
Magelona.dakini	0.0501	0.0168	0.45	0.708
Z..subcarinatus	0.0255	0.0101	0.52	0.108
Anthopleura	0.0154	0.0098	0.56	0.608
Nereids.Cera	0.0139	0.0112	0.6	0.208
Diloma.ubrostrate	0.0131	0.0096	0.64	0.108
Oligochaeta	0.013	0.0125	0.68	0.508
Heteromastus.filiformis	0.0128	0.0086	0.71	0.608
Notoacmea.sapha	0.0105	0.0077	0.74	0.208
Macomona.liliana	0.0093	0.006	0.77	0.408
Nuculidae	0.009	0.0066	0.79	0.508
Phoxocephalidae	0.0067	0.0041	0.81	0.108
Micrelenchus.huttonii	0.0066	0.0103	0.83	0.408
Cominella.ganiformis	0.0052	0.0038	0.84	0.708
Capitella.spp	0.0051	0.005	0.86	0.208
Paradoneis.lyra	0.0047	0.0052	0.87	0.708
Austrominius.modestus	0.0044	0.0049	0.88	0.208
Nemertea	0.0037	0.0035	0.9	0.208
Colorostylis.lemurum	0.0029	0.0033	0.9	0.208
Orbinia.papilosa	0.0029	0.0033	0.91	0.208
Boccardio.syrtis	0.0027	0.0005	0.92	0.308
Nereid.perinereid	0.0027	0.0005	0.93	0.308
Scolecolepedes.benhami	0.0027	0.0022	0.93	0.108
Aricidea.sp	0.0027	0.0025	0.94	0.808
Isocldadus.spp	0.0025	0.0028	0.95	0.208
Hemigrapas.sexdentatus	0.0024	0.0037	0.96	0.708
Z..lutulentus	0.0022	0.0019	0.96	0.808
Austrohelice.crassa	0.0022	0.0034	0.97	0.408
Chiton.glaucus	0.0019	0.0015	0.97	0.108
Aonides.trifida	0.0015	0.0016	0.98	0.208
Neoguraleus.sinclairi	0.0013	0.0014	0.98	0.208
Tritia.burchardi	0.0013	0.0014	0.98	0.208

Halicarcinus.whitei	0.0008	0.0013	0.99	0.708
Sphaerosyllis.semiverrucosa	0.0008	0.0013	0.99	0.708
Squilla.sp	0.0008	0.0013	0.99	0.708
Torridoharpinia.hurleyi	0.0008	0.0013	0.99	0.708
Pseudopolydora.corniculata	0.0008	0.0012	1	0.708

Table 12: SIMPER output Orewa 1.

Species name	average	sd	cumsum	p
Austrominius.modestus	0.3004	0.0378	0.33	0.001 ***
Notoacmea.sapha	0.1616	0.0941	0.51	0.001 ***
Diloma.subrostrate	0.0981	0.0418	0.62	0.001 ***
Lasaea.parengaensis	0.0626	0.0392	0.69	0.901
Cominella.ganiformis	0.0615	0.0419	0.75	0.501
Hemigrapas.sexdentatus	0.052	0.0416	0.81	0.001 ***
Macomona.liliana	0.03	0.0272	0.84	0.901
Phoxocephalidae	0.026	0.039	0.87	0.001 ***
Nuculidae	0.023	0.0348	0.9	0.901
Scoloplos.cylindrifer	0.019	0.0183	0.92	0.901
Austrohelice.crassa	0.0156	0.0187	0.94	0.901
Hemiplax hirtipes	0.013	0.0195	0.95	0.001 ***
Sphaerosyllis.semiverrucosa	0.013	0.0195	0.96	0.001 ***
Capitella.spp	0.0111	0.0168	0.98	0.901
Anthopleura aureoradiata	0.0105	0.0158	0.99	0.001 ***
Neoguraleus.sinclairi	0.0102	0.0153	1	0.001 ***

Table 13: SIMPER output Orewa 2.

Species name	average	sd	cumsum	p
Austrominius.modestus	0.3004	0.0378	0.33	0.001 ***
Notoacmea.sapha	0.1616	0.0941	0.51	0.001 ***
Diloma.subrostrate	0.0981	0.0418	0.62	0.001 ***
Lasaea.parengaensis	0.0626	0.0392	0.69	0.901
Cominella.ganiformis	0.0615	0.0419	0.75	0.501
Hemigrapas.sexdentatus	0.052	0.0416	0.81	0.001 ***
Macomona.liliana	0.03	0.0272	0.84	0.901
Phoxocephalidae	0.026	0.039	0.87	0.001 ***
Nuculidae	0.023	0.0348	0.9	0.901
Scoloplos.cylindrifer	0.019	0.0183	0.92	0.901
Austrohelice.crassa	0.0156	0.0187	0.94	0.901
Hemiplax.Hirtipes	0.013	0.0195	0.95	0.001 ***
Sphaerosyllis.semiverrucosa	0.013	0.0195	0.96	0.001 ***
Capitella.spp	0.0111	0.0168	0.98	0.901
Anthopleura aureoradiata	0.0105	0.0158	0.99	0.001 ***
Neoguraleus.sinclairi	0.0102	0.0153	1	0.001 ***

Table 14: SIMPER output Orewa 3.

Species name	average	sd	cumsum	p
Anthopleura aureoradiata	0.1918	0.1171	0.3	0.301
Pronispio.aucklandia	0.1278	0.1283	0.5	0.101
Notoacmea.sapha	0.0752	0.0738	0.62	0.901
Austrominius.modestus	0.0724	0.0766	0.73	0.901
Scoloplos.cylindrifer	0.0521	0.0724	0.81	0.001 ***
Diloma.ubrostrate	0.0166	0.0135	0.84	0.901
Macomona.liliana	0.0142	0.0102	0.86	0.601
Nuculidae	0.014	0.0055	0.88	0.601
Austrohelice.crassa	0.0121	0.0187	0.9	0.901
Magelona.dakini	0.0087	0.0137	0.92	0.001 ***
Cominella.ganiformis	0.0084	0.0068	0.93	0.001 ***
Hemigrapas crenulatus	0.0081	0.0125	0.94	0.001 ***
Hemigrapas sexdentatus	0.0074	0.0112	0.95	0.001 ***
Lasaea.parengaensis	0.0068	0.0072	0.96	0.501
Oligochaeta	0.0052	0.0071	0.97	0.901
Edwardia.sp	0.0044	0.0068	0.98	0.001 ***
Halicarcinus.whitei	0.004	0.0063	0.99	0.001 ***
Paracalliope.novizealandiae	0.004	0.0049	0.99	0.901
Scalibregmatidae	0.0025	0.0037	1	0.001 ***

Table 15: SIMPER output Orewa 4.

Species name	average	sd	cumsum	p
Scoloplos.cylindrifer	0.322	0.2498	0.41	0.154
Pronispio.aucklandia	0.092	0.1573	0.53	0.964
Macomona.liliana	0.059	0.0343	0.6	0.022 *
Anthopleura aureoradiata	0.058	0.0224	0.68	0.076
Notoacmea.sapha	0.048	0.0584	0.74	0.399
Magelona.dakini	0.045	0.0807	0.8	0.964
Austrominius.modestus	0.033	0.0238	0.84	0.628
Lasaea.parengaensis	0.032	0.0417	0.88	0.694
Nereids.Cera	0.019	0.0343	0.9	0.964
Heteromastus.filiformis	0.01	0.0189	0.92	0.964
Nuculidae	0.01	0.0112	0.93	0.226
Hemigrapas.sexdentatus	0.01	0.0162	0.94	0.145
Cominella.ganiformis	0.009	0.0113	0.95	0.844
Diloma.ubrostrate	0.009	0.0109	0.96	0.226
Oligochaeta	0.008	0.0098	0.97	0.846
Nemertea	0.007	0.0108	0.98	0.765
Torridoharpinia.hurleyi	0.003	0.0052	0.99	0.964
Z..subcarinatus	0.003	0.0052	0.99	0.964
Neoguraleus.sinclairi	0.002	0.0034	0.99	0.964
Z..lutulentus	0.002	0.0034	0.99	0.964

Aonides.trifida	0.001	0.0017	1	0.964
Boccardio.syrtis	0.001	0.0017	1	0.964
Micrelenchus.huttonii	0.001	0.0017	1	0.964
Paradoneis.lyra	0.001	0.0017	1	0.964
Phoxocephalidae	0.001	0.0017	1	0.964

Table 16: SIMPER output Orewa 5.

Species name	average	sd	cumsum	p
Scoloplos.cylindrifer	0.1886	0.0517	0.28	0.001 ***
Notoacmea.sapha	0.0873	0.0655	0.41	0.601
Anthopleura aureoradiata	0.0731	0.079	0.52	0.401
Austrominius.modestus	0.0683	0.0501	0.62	0.101
Nereid.perinereid	0.0532	0.0803	0.7	0.701
Macomona.liliana	0.0302	0.0203	0.75	0.501
Pronispio.aucklandia	0.0275	0.0287	0.79	0.701
Diloma.ubrostrate	0.0247	0.0107	0.83	0.101
Lasaea.parengaensis	0.0232	0.0206	0.86	0.301
Nuculidae	0.0211	0.0114	0.9	0.001 ***
Cominella.ganiformis	0.0185	0.0185	0.92	0.101
Austrohelice.crassa	0.016	0.0241	0.95	0.701
Paramoera.chevreuxi	0.013	0.0137	0.97	0.201
Nereid.nicon	0.0127	0.0111	0.98	0.201
Aonides.trifida	0.0036	0.0057	0.99	0.601
Orbinia.papilosa	0.0036	0.0057	1	0.601
Hemigrapas.crenulatus	0.0027	0.004	1	0.701

Table 17: SIMPER output Orewa 6.

Species name	average	sd	cumsum	p
Scoloplos.cylindrifer	0.2488	0.1597	0.33	0.201
Austrominius.modestus	0.1219	0.0601	0.49	0.001 ***
Lasaea.parengaensis	0.0779	0.0635	0.59	0.601
Anthopleura aureoradiata	0.075	0.039	0.69	0.101
Macomona.liliana	0.0563	0.0631	0.76	0.301
Colorostylis.lemurum	0.0492	0.0656	0.83	0.701
Notoacmea.sapha	0.029	0.0443	0.87	0.701
Nereid.nicon	0.0224	0.0259	0.9	0.701
Cominella.ganiformis	0.0161	0.0242	0.92	0.601
Diloma.ubrostrate	0.0155	0.0228	0.94	0.701
Capitella.spp	0.0099	0.0151	0.95	0.201
Hemigrapas.sexdentatus	0.0099	0.0151	0.96	0.201
Scolecolepedes.benhami	0.0099	0.0151	0.98	0.201
Exosphaeroma.waitemata	0.0089	0.0144	0.99	0.701
Magelona.dakini	0.0089	0.0144	1	0.701

Table 18: SIMPER output Orewa 7.

Species name	average	sd	cumsum	p
Nuculidae	0.1889	0.0418	0.32	0.001 ***
Anthopleura aureoradiata	0.1267	0.0828	0.53	0.101
Pronispio.aucklandia	0.0685	0.0706	0.64	0.501
Macomona.liliana	0.0442	0.0304	0.71	0.701
Lasaea.parengaensis	0.0325	0.0267	0.77	0.901
Notoacmea.sapha	0.0289	0.0227	0.81	0.101
Austrominius.modestus	0.0198	0.0157	0.85	0.101
Cominella.ganiformis	0.0165	0.0198	0.88	0.901
Orbinia.papilosa	0.0093	0.0105	0.89	0.501
Glycera.ovigera	0.0081	0.0065	0.9	0.001 ***
Nereids.Cera	0.0069	0.0104	0.92	0.901
Diloma.ubrostrate	0.0068	0.0104	0.93	0.001 ***
Magelona.dakini	0.0068	0.0104	0.94	0.001 ***
Heteromastus.filiformis	0.0064	0.0065	0.95	0.901
Hemiplax.Hirtipes	0.0056	0.0071	0.96	0.901
Nereid.nicon	0.0049	0.0058	0.97	0.901
Nemertea	0.0046	0.0071	0.98	0.001 ***
Neoguraleus.sinclairi	0.0046	0.0071	0.98	0.001 ***
Z..lutulentus	0.0038	0.0057	0.99	0.901
Boccardio.syrtis	0.0034	0.0052	0.99	0.901
Colorostylis.lemurum	0.0034	0.0052	1	0.001 ***

Table 19: SIMPER output Orewa 8.

Species name	average	sd	cumsum	p
Macomona.liliana	0.1454	0.1597	0.21	0.001 ***
Anthopleura aureoradiata	0.1305	0.0601	0.41	0.301
Scoloplos.cylindrifer	0.0866	0.0635	0.53	0.201
Pronispio.aucklandia	0.0842	0.039	0.66	0.101
Oligochaeta	0.0503	0.0631	0.73	0.701
Austrominius.modestus	0.0489	0.0656	0.8	0.601
Notoacmea.sapha	0.0355	0.0443	0.86	0.701
Austrohelice.crassa	0.0346	0.0259	0.91	0.401
Nemertea	0.024	0.0242	0.94	0.201
Cominella.ganiformis	0.0237	0.0228	0.98	0.701
Arthritica.bifurca	0.0145	0.0151	1	0.601

Table 20: SIMPER output for Waiwera 1.

Species name	average	sd	cumsum	p
Pronispio.aucklandia	0.2859	0.0861	0.34	0.001 ***
Notoacmea.sapha	0.1357	0.0561	0.5	0.001 ***
Nuculidae	0.0988	0.0339	0.61	0.001 ***

Anthopleura aureoradiata	0.0654	0.0328	0.69	0.001 ***
Lasaea.parengaensis	0.0452	0.0315	0.74	0.901
Macomona.liliana	0.0411	0.0237	0.79	0.901
Diloma.ubrostrate	0.0291	0.0181	0.83	0.001 ***
Scoloplos.cylindrifer	0.0289	0.0285	0.86	0.901
Austrominius.modestus	0.0205	0.012	0.88	0.001 ***
Cominella.ganiformis	0.0142	0.0111	0.9	0.001 ***
Nereid.perinereid	0.0138	0.0207	0.92	0.001 ***
Nereid.nicon	0.0118	0.0122	0.93	0.901
Nereids.Cera	0.0068	0.0086	0.94	0.901
Colorostylis.lemurum	0.0059	0.0089	0.95	0.001 ***
Hemiplax.Hirtipes	0.0059	0.0089	0.95	0.001 ***
Nemertea	0.0059	0.0089	0.96	0.001 ***
Z..subcarinatus	0.0059	0.0089	0.97	0.001 ***
Austrohelice.crassa	0.0051	0.0081	0.97	0.901
Eatoniella.sp	0.0051	0.0081	0.98	0.901
Paracorophium.excavatum	0.0051	0.0081	0.99	0.901
Paphies.australis	0.0045	0.0072	0.99	0.901
Z..lutulentus	0.0045	0.0072	1	0.901
Hemigrapas.sexdentatus	0.0028	0.0041	1	0.001 ***

Table 21: SIMPER output for Waiwera 2.

Species name	average	sd	cumsum	p
Lasaea.parengaensis	0.2128	0.0603	0.26	0.001 ***
Austrominius.modestus	0.1192	0.0951	0.4	0.101
Nuculidae	0.0965	0.1302	0.52	0.901
Paphies.australis	0.0636	0.0162	0.6	0.001 ***
Exosphaeroma planulum	0.0549	0.0838	0.66	0.001 ***
Nereid.nicon	0.0448	0.0407	0.72	0.301
Diloma.ubrostrate	0.0315	0.0245	0.76	0.001 ***
Scoloplos.cylindrifer	0.0315	0.0245	0.8	0.001 ***
Microspio	0.0274	0.0416	0.83	0.001 ***
Macomona.liliana	0.0272	0.0244	0.86	0.001 ***
Notoacmea.sapha	0.0178	0.0268	0.88	0.001 ***
Cominella.ganiformis	0.0152	0.0243	0.9	0.901
Nereid.perinereid	0.0145	0.023	0.92	0.901
Arthritica.bifurca	0.0137	0.0208	0.94	0.001 ***
Hemigrapas.sexdentatus	0.0137	0.0208	0.95	0.001 ***
Paracorophium.excavatum	0.0113	0.0177	0.97	0.901
Austrohelice.crassa	0.0089	0.0134	0.98	0.001 ***
Halicarcinus.whitei	0.0089	0.0134	0.99	0.001 ***
Z..lutulentus	0.0089	0.0134	1	0.001 ***

Table 22: SIMPER output for Waiwera 3.

Species name	average	sd	cumsum	p
Lasaea.parengaensis	0.219	0.0921	0.27	0.008 **
Anthopleura	0.0829	0.1036	0.38	0.608
Notoacmea.sapha	0.0597	0.0248	0.45	0.008 **
Austrominius.modestus	0.0496	0.0107	0.51	0.008 **
Macomona.liliana	0.0439	0.0256	0.57	0.008 **
Scoloplos.cylindrifer	0.0412	0.0161	0.62	0.008 **
Diloma.ubrostrate	0.0354	0.0345	0.66	0.108
Nereid.nicon	0.0339	0.035	0.71	0.108
Cominella.ganiformis	0.0327	0.0274	0.75	0.108
Paphies.australis	0.0327	0.0274	0.79	0.108
Z..lutulentus	0.0312	0.0064	0.83	0.008 **
Glycera.ovigera	0.0185	0.0146	0.85	0.108
Nereid.perinereid	0.0185	0.0146	0.87	0.108
Z..subcarinatus	0.0185	0.0146	0.9	0.108
Paracorophium.excavatum	0.0161	0.0184	0.92	0.708
Austrohelice.crassa	0.0151	0.0169	0.94	0.708
Colorostylis.lemurum	0.0143	0.0161	0.95	0.608
Boccardio.syrtis	0.01	0.0156	0.97	0.408
Oligochaeta	0.01	0.0156	0.98	0.408
Hemiplax.Hirtipes	0.0085	0.0132	0.99	0.408
Pseudopolydora.paucibranciata	0.0085	0.0132	1	0.408

Table 23: SIMPER output for Whangateau 1.

Species name	average	sd	cumsum	p
Paracorophium.excavatum	0.1675	0.1213	0.28	0.501
Anthopleura	0.0996	0.0429	0.44	0.001 ***
Oligochaeta	0.0449	0.0263	0.52	0.401
Colorostylis.lemurum	0.0421	0.0315	0.59	0.101
Pisinna.zostereophila	0.038	0.0472	0.65	0.401
Nuculidae	0.0298	0.0208	0.7	0.001 ***
Z..subcarinatus	0.0288	0.0221	0.75	0.501
Paraviveria.sp	0.0169	0.0161	0.78	0.401
Syllinae	0.0127	0.0106	0.8	0.701
Exosphaeroma.waitemata	0.0104	0.0079	0.82	0.001 ***
Isocldadus.spp	0.0103	0.0057	0.84	0.701
Pronispio.aucklandia	0.0093	0.0059	0.85	0.301
Halicarcinus.whitei	0.0084	0.0089	0.86	0.301
Nemertea	0.0077	0.0064	0.88	0.001 ***
Phoxocephalidae	0.0073	0.0069	0.89	0.601
Sipuncula	0.0071	0.0073	0.9	0.901
Nereid.perinereid	0.006	0.0055	0.91	0.601
Capitella.spp	0.0052	0.0065	0.92	0.601

Nereids.Cera	0.0052	0.0046	0.93	0.301
Pseudopolydora.paucibranciata	0.0051	0.0062	0.94	0.601
Paramoera.chevreuxi	0.0049	0.0074	0.95	0.601
Boccardio.syrtis	0.004	0.0032	0.95	0.201
Cominella.ganiformis	0.0036	0.0037	0.96	0.201
Macrolymenella.stewartensis	0.0033	0.0049	0.96	0.601
Magelona.dakini	0.0027	0.0041	0.97	0.001 ***
Scoloplos.cylindrifer	0.0027	0.0041	0.97	0.001 ***
Exosphaero.planulum	0.0022	0.0034	0.98	0.501
Aonides.trifida	0.002	0.0032	0.98	0.501
Austrominius.modestus	0.002	0.0032	0.98	0.501
Macomona.liliana	0.002	0.0032	0.99	0.501
Torridoharpinia.hurleyi	0.002	0.0032	0.99	0.501
Hemigrapas.sexdentatus	0.0019	0.003	0.99	0.501
Melita.awa	0.0019	0.003	1	0.501
Micormaldane	0.0016	0.0025	1	0.601

Table 24: SIMPER output for Whangateau 2.

Species name	average	sd	cumsum	p
Paracorophium.excavatum	0.215	0.1262	0.47	0.201
Oligochaeta	0.0628	0.0466	0.6	0.301
Anthopleura aureoradiata	0.0464	0.0264	0.7	0.001 ***
Z..subcarinatus	0.0202	0.0165	0.75	0.001 ***
Boccardio.syrtis	0.0143	0.0156	0.78	0.101
Pseudopolydora.paucibranciata	0.0142	0.0083	0.81	0.301
Colorostylis.lemurum	0.0106	0.0085	0.83	0.101
Pisinna.zostereophila	0.0089	0.0097	0.85	0.101
Nereid.perinereid	0.0073	0.0058	0.87	0.801
Lasaea.parengaensis	0.0067	0.0039	0.88	0.801
Nemertea	0.0063	0.0044	0.89	0.801
Pronispio.aucklandia	0.0061	0.0046	0.91	0.001 ***
Microspio	0.0055	0.0062	0.92	0.001 ***
Nuculidae	0.0046	0.0035	0.93	0.501
Sipuncula	0.0037	0.0058	0.94	0.601
Halicarcinus.whitei	0.0036	0.0028	0.94	0.001
Macomona.liliana	0.0031	0.0036	0.95	0.401
Capitella.spp	0.003	0.0045	0.96	0.001 ***
Cominella.ganiformis	0.003	0.0045	0.96	0.001 ***
Lysianassidae	0.003	0.0045	0.97	0.001 ***
Lumbrineridae	0.0021	0.0033	0.98	0.701
Hemiplax.Hirtipes	0.0018	0.0027	0.98	0.401
Sphaerosyllis.semiverrucosa	0.0015	0.0018	0.98	0.601
Arcualuta.senhousia	0.0012	0.0019	0.99	0.601
Macrolymenella.stewartensis	0.0012	0.0019	0.99	0.601
Neoguraleus.sinclairi	0.0012	0.0018	0.99	0.701

Nereid.nicon	0.001	0.0016	0.99	0.301
Paphies.australis	0.001	0.0016	1	0.301
Phoxocephalidae	0.001	0.0016	1	0.301
Z..lutulentus	0.0009	0.0014	1	0.401

Table 25: SIMPER output for Whangateau 3.

Species name	average	sd	cumsum	p
Anthopleura aureoradiata	0.1249	0.0063	0.24	0.001 ***
Pronispio.aucklandia	0.1181	0.0894	0.47	0.201
Notoacmea.sapha	0.0632	0.0367	0.59	0.001
Nuculidae	0.0358	0.0101	0.66	0.001 ***
Pisinna.zostereophila	0.023	0.0136	0.71	0.001 ***
Paramoera.chevreuxi	0.022	0.0193	0.75	0.001 ***
Phoxocephalidae	0.0109	0.0077	0.77	0.401
Isocldadus.spp	0.01	0.0023	0.79	0.301
Torridoharpinia.hurleyi	0.01	0.0068	0.81	0.001 ***
Diloma.ubrostrate	0.009	0.006	0.83	0.201
Halicarcinus.whitei	0.0084	0.0058	0.84	0.201
Heteromastus.filiformis	0.0079	0.0071	0.86	0.901
Lasaea.parengaensis	0.0075	0.0059	0.87	0.201
Paracorophium.excavatum	0.0073	0.007	0.89	0.901
Macomona.liliana	0.006	0.005	0.9	0.001 ***
Paravireia sp	0.0048	0.0028	0.91	0.001 ***
Lyssionassiae	0.0047	0.0061	0.92	0.401
Oligochaeta	0.0045	0.0051	0.93	0.101
Microspio	0.0045	0.0048	0.94	0.101
Pseudopolydora.paucibranciata	0.0033	0.0019	0.94	0.201
Z..subcarinatus	0.0033	0.0019	0.95	0.201
Cominella.ganiformis	0.003	0.0025	0.95	0.101
Colorostylis.lemurum	0.0024	0.0021	0.96	0.901
Nereid.perinereid	0.0022	0.0017	0.96	0.401
Austrohelice.crassa	0.0021	0.0016	0.97	0.101
Nereid.nicon	0.0019	0.0015	0.97	0.301
Neoguraleus.sinclairi	0.0018	0.0014	0.97	0.301
Aonides.trifida	0.0013	0.0016	0.98	0.801
Hemigrapas.crenulatus	0.0011	0.0017	0.98	0.701
Armandia.maculata	0.001	0.0016	0.98	0.101
Macrolymenella.stewartensis	0.001	0.0016	0.98	0.101
Z..lutulentus	0.001	0.0016	0.98	0.101
Chiton.glaucus	0.001	0.0015	0.99	0.101
Cyclaspis.thomsoni	0.001	0.0015	0.99	0.101
Paphies.australis	0.001	0.0015	0.99	0.101
Boccardio.syrtis	0.0009	0.0013	0.99	0.201
Exosphaero.planulum	0.0008	0.0013	0.99	0.901
Hemigrapas.sexdentatus	0.0008	0.0013	1	0.901

Lagis.australis	0.0008	0.0013	1	0.901
Sipuncula	0.0008	0.0013	1	0.901
Syllinae	0.0008	0.0013	1	0.901

Table 26: SIMPER output for Whangateau 4.

Species name	average	sd	cumsum	p
Anthopleura aureoradiata	0.1438	0.0445	0.23	0.001
Pronispio.aucklandia	0.1226	0.0188	0.43	0.001
Microspio	0.0748	0.0203	0.54	0.001
Lasaea.parengaensis	0.0623	0.0389	0.64	0.201
Nereids.Cera	0.0272	0.0235	0.69	0.901
Nereid.nicon	0.0219	0.02	0.72	0.901
Nereid.perinereid	0.0215	0.0158	0.76	0.901
Lyssionassiae	0.0205	0.0146	0.79	0.401
Z..subcarinatus	0.0108	0.0075	0.81	0.801
Nuculidae	0.0106	0.0087	0.82	0.101
Cominella.ganiformis	0.0099	0.0098	0.84	0.801
Heteromastus.filiformis	0.0093	0.0073	0.86	0.001
Notoacmea.sapha	0.0089	0.0064	0.87	0.101
Paracorophium.excavatum	0.0089	0.0097	0.88	0.401
Colorostylis.lemurum	0.0089	0.0076	0.9	0.901
Lumbrineridae	0.0069	0.0068	0.91	0.801
Macrolymenella.stewartensis	0.0055	0.0082	0.92	0.101
Nemertea	0.0054	0.0037	0.93	0.101
Z..lutulentus	0.0054	0.0044	0.94	0.301
Oligochaeta	0.0045	0.0041	0.94	0.401
Paphies.australis	0.0039	0.0029	0.95	0.201
Macomona.liliana	0.0038	0.0028	0.95	0.001
Sipuncula	0.0036	0.0055	0.96	0.101
Exosphaeroma.waitemata	0.0034	0.0051	0.96	0.901
Halicarcinus.whitei	0.0025	0.003	0.97	0.901
Orbinia.papilosa	0.0025	0.0029	0.97	0.401
Aonides.trifida	0.0019	0.0029	0.98	0.001
Capitella.spp	0.0019	0.0029	0.98	0.001
Diloma.ubrostrate	0.0019	0.0029	0.98	0.001
Pisinna.zostereophila	0.0019	0.0028	0.99	0.801
Arcualuta.senhousia	0.0018	0.0027	0.99	0.101
Wiatangi.brevirostris	0.0018	0.0027	0.99	0.101
Edwardia.sp	0.0018	0.0027	0.99	0.101
Phoxocephalidae	0.0018	0.0027	1	0.101
Neoguraleus.sinclairi	0.0017	0.0025	1	0.901

Appendix 4 – Raw macrofauna data metasheet

https://docs.google.com/spreadsheets/d/1qoXIcNNYor9kPn_-G3XCj5RSzZsg0TTxDtVKl35JeB4/edit?usp=sharing – Link to google spreadsheet, access by permission.