Ahumoana tawhito (ancient aquaculture): the translocation of toheroa (*Paphies ventricosa*) and other marine species by Māori

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Tutaki ki rungato kete toheroa, ka wehe Toronge ki raro.

“since the basket of toheroa was closed at the top, Toronge separated it from below”.

If one solution to a problem is effectively blocked, try another way. Furthermore, the obvious solution is not always the most effective.

Nga Pepeha a nga Tīpuna. Mead and Grove, 2004

The special gift that each of us possess was not given to us for ourselves, it was given to share with mankind. Imagine how rich we would be, if we all shared.

John Aramete Wairehu Steedman, 1996

Abstract

Throughout time, humans have cultivated and translocated plants and animals. Ancient mariculture (the cultivation of marine species) often leaves little trace of human agency. Consequently, the extent to which mariculture was used in the distant past largely remains a mystery. In Aotearoa (New Zealand), Māori have a long history of translocating and cultivating terrestrial and freshwater species. Increasingly, it is becoming apparent that the translocation of marine species is a resource management tool that has been utilized by Māori for hundreds of years. Research into the population genetic structure of a large surf clam endemic to Aotearoa, the toheroa (*Paphies ventricosa*), has led to the hypothesis that Māori have undertaken long-distance transport and translocation of this shellfish during the earlier phases of Māori occupation within Aotearoa. Specifically, this "translocation hypothesis" suggests that Māori successfully transported toheroa from the West Coast of Te ika-a-Māui (the North Island) to the South Coast of Te Waipounamu (the South Island) thereby explaining the unique and disjunct distribution pattern of this taonga (treasured) species. This thesis weaves together knowledge from multiple disciplines to test the toheroa translocation hypothesis, explore technologies used by Māori and reclaim traditional knowledge regarding resource management.

An examination of archaeological databases revealed a record that was not consistent with toheroa being endemic to Murihiku (southern South Island). On the west coast of Te Ika-a-Māui, 968 midden records were identified of which 40% either contained or consisted entirely of toheroa. In contrast, along the South Coast of Murihiku (Southland, Te Waipounamu), 122 midden records were examined, of which only 6.5% contained toheroa. Toheroa were not a major component of any of these middens. Toheroa were also absent from a natural shell deposit within Murihiku that pre-dates human arrival to Aotearoa. The general absences of toheroa in all but a few southern middens lends itself to the notion that toheroa did not occur there naturally, but were introduced by Māori at a later date.

An examination of anthropological, historical and traditional knowledge was conducted to explore the human elements of toheroa translocation. Specifically, I wanted to better understand the reasons why early-Māori might have wanted to translocate toheroa, as well as the capacity and opportunities they would have had to undertake such long-distance transport of live bivalves. The movement of iwi from the north to the south is a concept steeped in kōrero tuku iho (oral history) and is referred to many times in ethnohistorical and contemporary literature. This included the very first movements of Polynesian explorers north to south, as well as multiple accounts of expeditions and southward migrations by Māori originating from the north. Toheroa were an important resource for the earliest occupants of northern regions in Aotearoa and this is evident in the prominence of toheroa in northern Māori culture. Interestingly, while they are a taonga of southern Māori today, toheroa are conspicuously absent in the narratives, whakataukī (proverbs) and whakapapa (genealogy) of Murihiku (Southland). This could be explained by a later introduction of toheroa to the area, leading to less time and opportunity of the resource to shape southern Māori identity. While toheroa may not have been endemic to the south, there was ample opportunity for them to be relocated, either through trade, or as part of a southward migration. Archaeological records of industrial stone, such as obsidian, provide evidence for trade between northern and southern Māori as early as the 14th century. It is clear that people who had come from or were closely connected to northern Māori have occupied the southern most areas of Aotearoa, in the earliest phases of the prehistoric sequence.

While it is apparent that the opportunity for shellfish translocation existed, the suitability of toheroa for relocation was unknown. This would depend on their ability to cope with and combat stressors (such as hypoxia, bacterial proliferation, starvation and desiccation) associated with such a journey. Respiration rates, morphometric indices, behavioural responses and physiological responses to these stressors were measured in a series of *in situ* experiments. Toheroa displayed an overall physiological robustness to lack of oxygen and food and, when held in seawater and treated with antibiotics, toheroa were able to switch to anaerobiosis and survive for extended periods of time (more than two weeks). The primary causes of health deterioration were found to be bacterial proliferation (of particular prevalence when held in anoxic water) and desiccation. These are risks that could easily have been mitigated during a translocation journey.

The pōhā, a natural kelp bag fashioned from the large brown alga *Durvillaea* spp., is a southern Māori technology said to have been used in the translocation and re-seeding of toheroa and other shellfish species, prehistorically. An important first step in understanding this technology was to review the traditional knowledge associated with pōhā and of rimurapa (southern Bull Kelp) from which pōhā are constructed. The literature contained a variety of information covering prehistoric practices to contemporary management of this natural resource as well as details of its wide and varied uses. Interestingly, contemporary use of pōhā and rimurapa has included translocation and restoration of seagrass in Te Waipounamu.

While there are many historical references to pōhā being used for translocating shellfish, the details of exactly how they were used are missing, both in the literature and in the memories of traditional practitioners of pōhā with whom I have been lucky enough to speak with. Consequently, the final component of this thesis explored the biochemical and bacterial implications of holding live toheroa in pōhā. I found that the photosynthetic blades of the algae were able to replenish dissolved oxygen consumed by the toheroa during respiration. Furthermore, it was clear that the microbiome associated with pōhā, or the secondary metabolites released by pōhā, influenced the bacterial community to which toheroa were exposed when held within the algal bags. From these experiments, it appears unlikely that pōhā were used in the manner employed in this experiment (filled with seawater and left to stagnate) as this resulted in the rapid deterioration of the pōhā bags. However, the biochemical and bacterial results that were found, have direct implications for the functionality of pōhā and the toheroa held within. While possibly not the main vessel in which toheroa were translocated, kōrero tuku iho about the use of pōhā in shellfish re-seeding, suggest that raw pōhā may have been the last link in the chain of shellfish translocation by providing protection while acclimating to a new area.

The research I have undertaken for this thesis is novel and it contributes to our growing understanding of indigenous resource management in Aotearoa. While I have not been able to determine definitively whether toheroa in the south are solely a consequence of Māori translocation, the evidence presented here is consistent with that hypothesis. The experiments undertaken here are the first of their kind for toheroa, and they highlight how the complex nature of surf clam physiology and behaviour would play into their cultivation, either in ancient or contemporary contexts. This thesis reclaims traditional knowledge regarding the management of two taonga species (toheroa and rimurapa) and highlights several possible avenues for future research. Furthermore, this research demonstrates how academic knowledge and indigenous knowledge can be interwoven, to attempt to unravel the mysteries of the past and to pave the way for the future.

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A foreword on dialect, nomenclature and terms

Southern Māori dialect differs from Northern Māori in that a “k” replaces the more commonly used “nga”, for example *mahi**k**a kai*/*mahi**nga** kai* (resource gathering grounds). These are often used interchangeably in modern times and within sections of this thesis, the southern dialect will be used where deemed appropriate.

From a Te Ao Māori (the Māori world) perspective, whakapapa (genealogy/ancestry) is fundamental to the nomenclature of a species. In this way, nomenclature can provide information regarding the ecological connections that different Māori communities have with local environments (Rainforth, 2008). Documentation of the “Southernmost Māori” undertaken by Herries Beattie (1954) provides insight into the ethnohistory and nomenclature of Māori within Te Waipounamu (South Island), with relation to kaimoana (food from the sea) and other environmental resources, intrinsic to Māori way of life. Beattie writes;

> *It has long been my opinion that there are more dialectal differences over the nomenclature of shellfish than any other branch of natural history in Māoridom. The Māoris recognise this themselves and make comparisons of the names in various parts of New Zealand. They know the names vary a bit even in the South Island at such places as Kaikōura, Akaroa, Moeraki and Foveaux Straight. Some Aucklanders claim that the toheroa is to be found only on the long beach in Northland, but my Māoris tell me it is found on many beaches throughout the Dominion under eight or more different Māori names, some noticeably good specimens being found on the beaches in Southland.*

Quotes and excerpts such as the one above have been relayed exactly as they were found in the texts, although macrons have been added to Māori terms where appropriate.

Evidence provided by historians suggests toheroa have had several names, particularly within the southern regions of Te Ika-a-Māui (the North Island) and in Te Waipounamu. These include; hoemoana (‘oar of the ocean’), tohemaunga, roroa-nui, tupehokura (in Otago), whakai-a-tama (in Nelson, Canterbury/Moeraki, meaning ‘feed the son’) and tohemanga (in Ōtaki (North Island, Horowhenua/Kāpiti)).

It is, however, unlikely all of these refer directly to the species known today as *Paphies ventricosa* (previously *Mesodesma ventricosum*). The most accurate identification by western ethnographers of toheroa in the south has been documented as the Murihiku roroa-nui (big roroa) (Beattie and Anderson, 1994). Classifications of bivalves by Beattie and other researchers (dated between 1793 and 1926) are at the Otago Museum. On inspection (pers.

obs.), the specimen roroa appears to be what is now known as tuatua or pipi (*Paphies subtriangulata* and *Paphies australis*), both being closely related bivalves. The intertidal surf clam *P. subtriangulata* is often misidentified for toheroa, although *P. subtriangulata* grow to a much smaller adult size than toheroa in northern areas, at least, and are easily distinguishable to those who are familiar with the species.

Throughout this document, the term prehistoric will be used. Prehistoric and historic refers to before and after written accounts of Aotearoa existed. This term is used because much of the research here refers to Māori occupation and activities before Europeans first made contact in the 1800s. The use of this is not intended to separate modern Māori from their tīpuna (ancestors), nor does it subscribe to the notion that European arrival to Aotearoa (and consequently their written accounts) dictates the narrative of Māori and their cultural history. Rather it is used to place occupancy and events in the context of time. Prehistoric refers to earlier occupants of Aotearoa in which the Māori culture was still developing and evolving, as people adapted to (and shaped) the new land.

Kuputaka (Glossary)

ahi-kā-roa	keeping the fires of occupation burning
ahumoana tawhito	ancient aquaculture
Atua	god
Hapū	Subtribe
Harakeke	Native flax (*Phormium tenax*)
ipu	wooden bowl
iwi	tribe
karakia	prayer used to invoke spiritual guidance and protection
kai	food
Kai-hau-kai	exchange, trade or gifting of food resources
kaimoana	seafood
Kāinga/ papa kaika	village or settlement
kai rangtitira	food of chiefs
kaitiaki	guardian
kaitiakitanga	stewardship, guardianship
kaupapa	topic, policy, purpose
Kete	basket woven from harakeke
kete whiri	harakeke basket specifically for shellfish
kōhanga	nursery
koorero	conversation, discussion
kōrero tuku iho	oral history and traditions
kotawa	juvenile fruit of a gourd (*Lagenaria* sp)
mahinga kai/ mahika kai	traditional food, natural resources and the places they are obtained
mana	respect, spiritual power
manaakitanga	hospitality, kindness, generosity, support - the process of showing respect, generosity and care for others
mātaitai	saltwater reserve
Matariki	cluster of stars which signify the Māori new year
mātauranga	knowledge
mauri	spiritual essence, life force
moana	ocean
Murihiku	Southland
Pātua	Watertight basket made from tōtora (*Podocarpus totara*) bark
Pingao	sand sedge endemic to New Zealand (*Ficinia spiralis*)
pōhā	bag made of kelp (Durvillaea poha)
pōhā-tītī	muttonbird (*Puffinus griseus*) preserved in poha
poua	Grandfather (southern)
rangatiratanga	Chieftainship
rimuheria	seagrass (*Zostera novazelandica*)
rimurapa/rimupuka	southern bull-kelp (*Durvillaea* spp.)
rohe	territory or boundaries of an area
rokiroki kai	food preservation
rua	storage pit
Tangaroa	god of the sea
Tangata Tiaki	Customary Fisheries Appointee

tangata whenua	people of the land
taonga	something to be treasured, of great value
Te Ao Māori	Māori world view
Te Oneroa-a-Tōhē	Ninety Mile Beach
Te Taitokerau	Northland
tikanga	custom
tiwha	wooden plug
tohe roa	to persist
tohunga whakatere waka	traditional Māori navigator
wai	water
waiata	song
waka-hourua	double-hulled voyaging canoe
Whakaaiai	hand fertilisation of flowering plants
whakapapa	genealogy
whakaputu	food storage
Whakataukī	proverb
whakatīpu mātaitai	seeding shellfish
whakawhiti kaimoana	propagation of seafood
wharenui	large meeting house

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Chapter One

General Introduction

1.1 Background

Substantial evidence exists of how hunter-gatherer, pastoral and agricultural peoples have profoundly altered marine ecosystems for millennia. Translocations of organisms is one of the ways in which humans have had long lasting impacts on coastal ecosystems and these activities have been conducted by countless cultures and at many points in time. The ecological consequences of translocations have affected our understanding of species distribution substantially, with human-mediated translocation of species dating back to the Late Pleistocene (Boivin et al., 2016). One example is the transport of a tree dwelling marsupial, the northern common cuscus (*Phalanger orientalis*), from New Guinea to eastern Indonesia, the Solomon Islands and the Bismarck Archipelago approximately 20–23,000 y ago.

People of Polynesia have transported and introduced many different plant and animal species throughout the pacific since approximately 3,500 y B.P. (Boivin et al., 2016). These were the result of either purposeful movement by humans, or an accidental by-product of their movement, for example, as stowaways (Summerhayes, 2007). Within the early Holocene, evidence suggests that translocations mirrored the movement patterns of maritime obsidian exchange in Melanesia, which suggests that purposeful movement of both stone and animal has taken place concurrently, even in the earliest of times (Summerhayes, 2007; Boivin et al., 2016).

Archaeological, paleo-ecological and genetic research across the globe suggests that by the Late Pleistocene, niche constructing behaviours exhibited by *homo sapiens* have, through time, culminated in advanced transformation of global biodiversity. The activities humans have engaged in have altered the distributions of many species across almost all taxonomic groups (Boivin et al. 2016). While our understanding of translocations of terrestrial and freshwater species is broad, we know very little about how humans from early prehistoric ages have modified marine ecosystems. Evidence of mariculture occurring in the deep past exists, such as the ancestral clam gardens off the Northwest Coast of North America (see below) but we only have a limited view of the true extent to which ancient mariculture activities may have occurred. Due to the oceanic influence in shaping and changing coastal environments, much of the physical evidence of these activities, and their impacts, have likely been erased.

Research into phenomena such as prehistoric translocations may help us understand how humans interacted with their environments long ago, while also providing possible tools and insights that can be directly applicable to modern conservation, restoration and environmental management (Erlandson and Rick, 2010; Rick et al., 2013; Bull and Maron, 2016). Where translocations may have occurred in the distant past, a multidisciplinary research approach is highly beneficial. Researchers who restrict themselves to the bounds of one discipline (academic silo) can sometimes develop a narrow outlook to their research. Because of this disconnection which is common in academia, many researchers have dismissed or fail to accept that indigenous communities from eras past would have the inclination and capacity to undertake mariculture activities. Particularly those which have led to the modification of a species ecology or distribution.

Indigenous knowledge and archaeology have often been neglected in conservation and ecology, including in studies of shellfish species (Reeder-Myers et al., 2022). Reeder-Myers et al. (2022) explores this concept, focusing on a case study of oysters (Ostreidae) spanning Australia, the Pacific Coast of North America and the Atlantic and Gulf of Mexico coast of North America. Oysters are indicator species of environmental health, while also holding cultural and economic significance globally. Despite contributions from several archaeological disciplines to research surrounding oysters, conservation strategies rely primarily on data collected within the last 200 years, in which many fisheries are known to have collapsed due to over-fishing, disease and other factors. In contrast to this, indigenous fisheries are known to have survived for a millennia. The abundance of oyster middens identified across archaeological sites was reflective of the breadth and scale of Indigenous oyster fisheries across the study regions. Although it is difficult to identify oyster farming and cultivation from archaeological records, Reeder-Myers et al. state it is highly likely to have occurred. Further to this, midden records demonstrate the sustainable nature of oyster harvesting undertaken over thousands of years and that people had powerful ecological knowledge related to oyster harvest and ecology.

It is becoming increasingly more recognised that an open mind and a more holistic approach can be valuable when tackling ecological questions. Within a contemporary environmental management context, the knowledge of Indigenous peoples is invaluable. Indigenous approaches to the environment, both historically and today, are holistic in nature, with knowledge derived by practitioners working in both a community and the environment. Bringing together the knowledge of indigenous practitioners, historians, archaeologists, anthropologists, ecologists, biologists (and many other disciplines) may reveal the mysteries of ancient societies and how they have utilized, modified and managed marine resources.

1.2 Human-mediated marine translocations and enhancement

Shellfish have always been an important resource for coastal communities, both today and in ancient times. Being nutritious, abundant, easily harvested, easily preserved, and often available year round, shellfish tended to be important as both a source of food and an item for trade prehistorically (Mannino and Thomas, 2002; Lepofsky et al., 2015). In addition to harvesting of wild stocks, people in the distant past engaged in marine farming, also known as aquaculture. For example, farming of oysters (*Crassostrea gigas*) in the Neolithic era involved the introduction and the cultivation of brood stock to new areas in Far East Asia (Rakov and Brodianski, 2010).

The American soft-shell clam (*Mya arenaria*) is known to have been translocated from America to Europe by man, with radiocarbon dating of *M. arenaria* shell from the coast of the Skagen Ode in Northern Jutland (Denmark) falling between the calibrated age range of 1245-1295 AD (Peterson et al., 1992). Petersen et al. (1992) hypothesised that the species was transferred from North America to Europe by the Viking (Norse) settlers, 200 years before the discovery of America by Columbus. Dated shell was found to predate Columbus's voyage in 1942. The clam became extinct in Europe but remains present in North America (Essink et al., 2017). Radiocarbon dating of shells from several areas in the Netherlands was undertaken, to further explore this hypothesis. Essink et al. (2017) found that the shells from four locations within the Netherlands clearly dated as pre-Columbian and supported the hypothesis of Viking-mediated dispersal of this species from northeast America across the northern Atlantic Ocean.

Indigenous peoples of the Northwest Coast of North America (British Columbia) have up until recently been considered “hunter-gatherers”. Research into ancient traditional resource management of the Northwest Coast has generated a movement away from this school of thought, leading to a broader understanding of this indigenous group in eras past as active resource managers (Deur et al., 2015). Research efforts have focused on the human mediated enhancement of clam beds (given the term “clam gardens”) in coastal British Columbia. The clam gardens provide evidence for intertidal shellfish management, enhancement and conservation of a shellfish resource by indigenous peoples, with clam garden structures on Northern Qaudra Island, BC, determined to be approximately 3500 years old (Smith et al., 2019).

These ancestral clam gardens were clearly anthropogenic in nature, constructed and developed to extend and support favourable habitats for several species of clams. These species were suggested to have contributed substantially as a food resource to the Kwakwaka'wakw communities and other nations up and down the coast of British Columbia. In the indigenous language, the gardens were termed *loxiwey* (to roll), a reference to the rolling of rocks out of clam beds and into the lower intertidal. Gardens were developed over hundreds of years, with existing clam habitats improved through the act of moving large stones, thereby increasing the availability of sandy substrate by widening and levelling the beach (Deur et al., 2015). Through site survey and excavations, three different types of clam garden structures have been recognized, each depending on the pre-existing geology and ecology of specific beaches (Smith et al., 2019). The clam gardens provide evidence for ancient shellfish mariculture by indigenous communities, with the construction and maintenance of these directly enhancing the distribution, abundance and productivity of clam species, along with shaping the intertidal ecology of these coastlines.

Translocations of marine species in Aotearoa (New Zealand)

Māori and their Polynesian ancestors have a long history of translocating plants and animals. A terrestrial example of this includes the translocation of rengarenga, an endemic Aotearoa rock lily (*Arthropodium cirratum*). Outside of its natural distribution, rengarenga is found to be associated with archaeological sites and is considered to have been transported and cultivated within these areas prehistorically by Māori (Shepherd et al., 2016).

Many documents and cultural narratives indicate that Māori put great efforts into the transfer of fish around Aotearoa, with much study centred on understanding the habits and movements of fish species (Strickland, 1993). Within freshwater systems, Māori are known to have translocated freshwater species, particularly eels, to bodies of water which did not contain fish (Best, 1929). The common smelt (*Retropinna retropinna*; pōrohe/paraki), is a freshwater fish indigenous to Aotearoa. The generally accepted view was that smelt was introduced to two lakes within Te Ika-a-Māui (the North Island); Rotorua and Rotoiti by Europeans as trout food, in the early 1900s. However, research into traditional knowledge and European documents referring to these species led Strickland (1993) to hypothesise that smelt were actually translocated by Māori in prehistoric times. Strickland (1993) provides evidence from kaitiaki and Māori researchers from the early 1900s regarding traditional freshwater fisheries. One researcher had listed smelt as a species present in Lake Rotorua, which pre-dated the introduction of trout (1888), indicating their presence before the proposed introduction by Europeans (early 1900s) and that it was a fishery known to Māori.

Within Lake Rotorua (Te Rotorua-nui-ā Kahumatamomoe; Figure 1.2), evidence suggests that several types of freshwater fish, including the native species kaoro (*Galaxias brevipinnis*), became established in the area due to transfers by Māori. Oral tradition tells of moving fish within “huge” pātua (watertight vessel made of tōtora bark; Figure 1.1). Inanga (whitebait species) and smelt are suggested to have been transferred to Maketū and Rotorua (Figure 1.2) from areas further north, transporting them in hue (gourds; Figure 1.1) filled with seawater. Kōura (freshwater crayfish) is also said to have been transferred to new areas in the same manner (Strickland, 1993 and references therein). Accounts such as these demonstrate the interests of Māori in mediating translocation of species around the country.

Strickland (1993) comments that Māori had up to a thousand years to enhance natural stocks of fish with favoured species. The purpose of such activities stemmed from the urgent need to provide a sustainable food resource, comparative to European introductions of exotic species, which was for commercial reasons or for sport. The intimate knowledge held by Māori of important fisheries within Aotearoa far exceeded that of Europeans, as Māori had much more time to formulate methods and develop understandings key to the success of fish translocations. The introduction of trout was at the expense of traditional Māori fisheries, with little acknowledgement or remorse by European fishery managers, with this extending through to the modern day. Fisheries managers have gone so far as to prohibit the taking of species established by Māori, with the reason being that these species were not for human consumption but were food for trout.

Figure 1.1 Examples of hue (gourd) bottles in kete (harakeke/flax woven baskets)[1] (left) and pātua (vessel made of totora bark)[2] (right).

Details surrounding aquaculture and marine farming of various iwi claimants was collated in a Waitangi Tribunal report (Wai 953), prepared by Legislative Direct in 2002. The claimants stated in broad terms that the reforms surrounding marine farming practices failed to provide adequately for their interests in aquaculture. Detailed examples of traditional aquaculture and conservation practices undertaken in the past were presented. Northern iwi Ngāti Kahunguna and Ngāti Whātua provided evidence for traditional conservation, resource enhancement and kaitiakitanga of coastal spaces, along with customary interest in marine aquaculture, within their rohe (territory or boundaries). Examples of this included the collection and cultivation of mussel spat and the transplanting of different shellfish species to new sites, viewing contemporary aquaculture as an extension of traditional management practices. Another

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[1] Image from https://www.rnz.co.nz/news/te-manu-korihi/243691/hue-exhibition-in-whanganui

[2] Image from https://collections.tepapa.govt.nz/object/124751

account detailed historical participation of the iwi Te Atiawa in marine farming. Evidence was provided for the active farming in which "boulders were placed in circles about two feet high with smaller boulders with mussels attached to them being place in the middle to breed"[3]. Another management tool was the translocation of juvenile pāua, to new areas associated with kelp.

Transplantation or translocation was a prevalent management strategy that appeared throughout the Waitangi Tribunal report (Legislative Direct, 2002), with many iwi from different areas citing this activity as an important customary practice. Sowing and maintaining shellfish beds promoted the growth and establishment of new populations closer to areas in which Māori communities where living, while ensuring the survival of stocks further afield and in areas of significance.

Evidence provided by David Higgins of Ngāi Tahu relayed customary practices employed by southern Māori. This included the restorative practice of transferring toheroa (*Paphies ventricosa*), the largest endemic surf calm endemic to Aotearoa, from one bed to another to enhance stocks. The report states:

> *Specifically, it was said that toheroa were transferred from Ōreti Beach in Murihiku to Moeraki pursuant to 'kaihaukai agreements' between particular whānau, who would collect rimurapa for pōhā at Moeraki.*[4]

Kaihaukai acknowledges the exchange, trade or gifting of food resources between iwi. Moeraki appeared to have many reseeding and translocating activities associated with that area, including reseeding of cockles (tuaki/tuangi, *Austrovenus stutchburyi*) and juvenile pāua.

Translocation of toheroa (*Paphies ventricosa*)

Toheroa (*Paphies ventricosa*) are the largest endemic surf clams within Aotearoa, belonging to the endemic genus, *Paphies* (family: *Mesodesmatidae*). This genus includes the estuarine *Paphies australis* (pipi) and two open coast species, *P. subtriangulata* (tuatua, sometimes referred to as pipi) and *P. donacina* (deep water tuatua) (Cook, 2010). Toheroa (*Paphies ventricosa*) are long neck clams, with exhalant and inhalant siphons able to extend great lengths to the surface of the sediment. The foot is large, muscular and triangular, with the animal being highly active and capable of rapid burial, to a depth of 300 mm (Akroyd et al., 2002; Redfearn, 1974). This characteristic enables them to survive in a high energy environment and within the dynamic nature of fine clean sediments (Heasman et al., 2012). Toheroa are intertidal, found between the mean high tide and low tide (Akroyd et al., 2002).

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[3] Legislation Direct (2002) for the Waitangi Tribunal (Wai 953) Pg. 30

[4] Legislation Direct (2002) for the Waitangi Tribunal (Wai 953) Pg. 31

Historically, toheroa are known to exceed 100mm, while ancient midden and pre-human shells have been found to measure up to 180mm (Ross, pers. comm.).

In the early nineteenth century, toheroa flourished in healthy and sizable numbers at a number of exposed surf beaches, along the west coast of Te ika-a-Māui and at beaches in the South Coast of Te Waipounamu (Williams et al., 2013) (Figure 1.2). Historical evidence and oral tradition (kōrero tuku iho) indicate Māori (estimated to have arrived in Aotearoa between 1250 and 1350 AD (Beattie and Anderson 1994)) undertook traditional management and harvest of toheroa beds, with harvesting efforts particularly prevalent in Te Ika-a-Māui. The toheroa was a staple and a taonga for many hapū, with the whakapapa (genealogy) of toheroa intrinsically linked to several northern iwi.

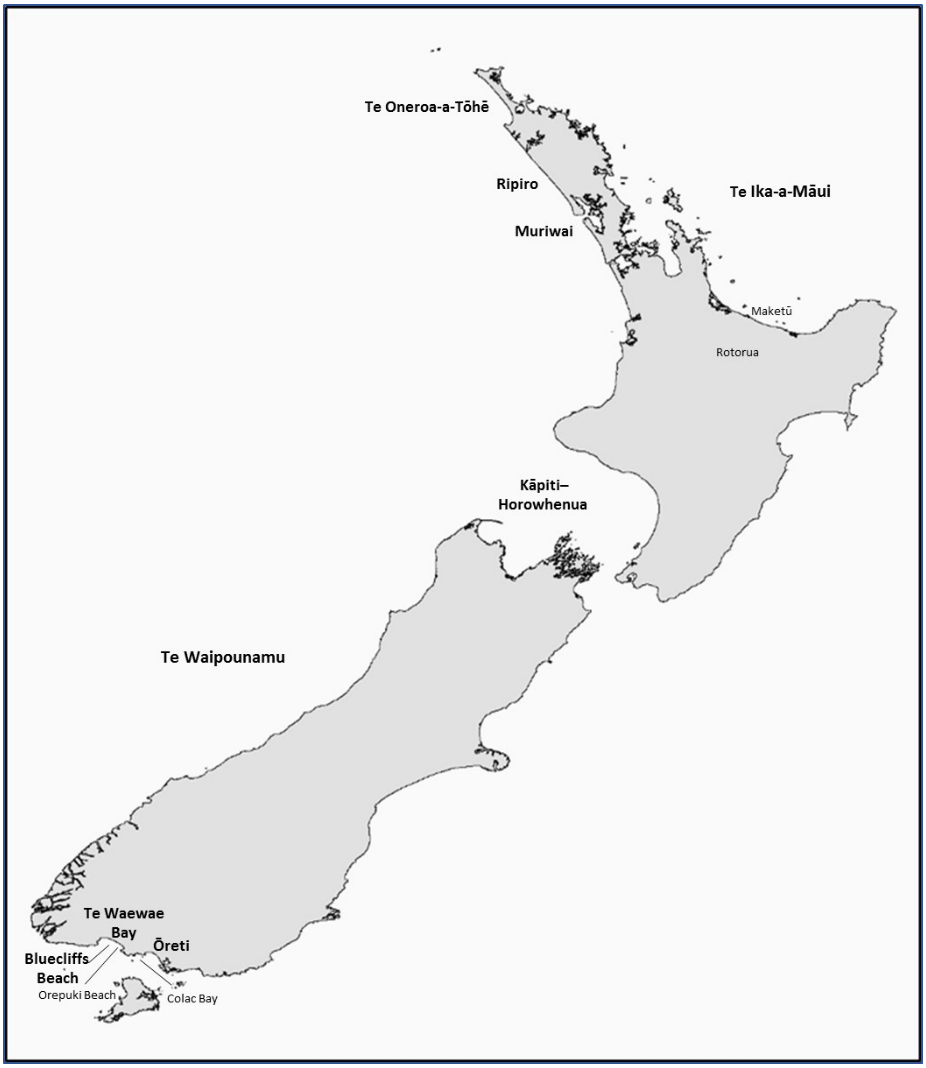

Figure 1.2 Locations of beaches with toheroa present historically. Rotorua and Maketū also labelled for reference.

Major populations of toheroa exist today along Te Oneroa-a-Tōhē and Ripiro beach in Te Taitokerau (Williams et al., 2013) and at Ōreti Beach in Murihiku (Beentjes, 2010). Historically, they were also present at Muriwai (west of Tāmaki Makaurau (Auckland)) and on the Kāpiti-Horowhenua Coast, although they have largely disappeared from these locations. This disjointed distribution is unique among marine invertebrates in Aotearoa. It is highly unlikely that these populations are connected through larval dispersal (Ross et al., 2018).

Oceanic currents surrounding Aotearoa are suggested to be hydrological barriers, limiting gene flow between water masses. Northern coasts are influenced by the East Auckland, East Cape and Tasman currents, the central coast is influenced by the D'Urville current and the southern coast is influenced by the Southland current (Smith et al., 1989). Smith et al. (1989) suggests that these currents may explain the genetic divergence found between northern and southern green-lipped mussel (kuku, kutai; *Perna canaliculus*) off the east coast and between the east and west coast populations of snapper (tāmure*; Chrysophrys auratus*) around Te Ika-a-Māui. It is likely that these currents also effect gene flow and recruitment in tuatua and toheroa populations. It is likely that there is limited genetic connectivity between the southern and northern toheroa populations; indicating they are likely to be reproductively isolated. There is currently no evidence for extant or extinct populations that could connect southern and northern populations.

Research into the distribution of toheroa (*Paphies ventricosa*), incorporating genetic, archaeological and historical data sources support the notion that the contemporary distribution of toheroa across Aotearoa has been modified by human mediated transportation and translocation (Ross et al., 2017; 2018). This hypothesis can explain the unusual geographic distribution of toheroa in Aotearoa.

Traditional management methods of toheroa have included the thinning of numbers at healthy beds, re-seeding to depleted beds and the introduction of toheroa to entirely new areas. Te Kaitiaki toheroa, James Te Tuhi and Barry Searle of the Taitokerau region, have been translocating toheroa to beaches along the West Coast of Te Ika-a-Māui since the 1960s. Redfearn (1974) stated that there was popular belief that toheroa populations on the east coast were translocated there from the west coast, though this was speculative. Translocations to Wakapatu Beach and Colac Bay, in Murihiku, have also been suggested to have taken place in the recent past (Futter, 2011).

Historical documents and kōrero tuku iho indicate that Māori used kelp bags, also known as pōhā, as a vessel for toheroa, and other kaimoana species (Williams, 2016). Pōhā have been manufactured by southern iwi for hundreds of years and are made from the southern bull-kelp species *Durvillaea spp.*, a large brown algal species endemic to Aotearoa.

The importance of toheroa to both Māori and Pākehā has resulted in considerable public attention for toheroa in earlier years, specifically in geographical areas where toheroa once grew in abundance. The history of toheroa is a complex one, having cultural, ecological and biological implications spanning generations and to this day. Toheroa is a taonga species of many northern iwi and a smaller group of hapū in Murihiku. It is not only an important resource but has shaped the identity of many Māori and several Pākehā communities. Ongoing research management and education is now key to the bivalves' survival both from ecological and resource perspectives. There is considerable scope to broaden our understanding of traditional resource management of shellfish and this includes species translocations. In this thesis a multi-disciplinary approach incorporating archaeology, anthropology, traditional knowledge, ecology and biology will be used to examine the "translocation hypothesis".

1.3 Thesis structure, aims and objectives

This research has incorporated multiple disciplines as discussed above, to understand contemporary, historic and prehistoric distribution and translocation of toheroa (*Paphies ventricosa*). Archaeological evidence was used to test hypotheses around the human-modified distribution of toheroa. Following this, through several experiments and reviews, this study examined the tools and methods used by early Māori to translocate toheroa and other kaimoana. This research aimed to determine how the mātauranga (knowledge) of kaimoana translocation has been employed and how it may contribute to contemporary restoration and management of depleted shellfish resources. Further to this, I aimed to explore the mechanisms behind the unusual distribution of toheroa. The specific aims and objectives for each research chapter is described below.

In **Chapter Two** I review Māori prehistory, with the aims to better understand when, why and by whom long-distance toheroa translocation may have been undertaken. In this review, concepts surrounding the incentive, capacity and opportunity of such a journey are discussed. Archaeological reports of significance found within the Heritage NZ Digital Library were retained and critically analysed. Sites that have been radio carbon dated are identified and discussed. Papers, books and reports that comprised literature pertaining to anthropological, archaeological or kōrero tuku iho (oral tradition) of Māori migration, subsistence patterns, southern Māori prehistory and toheroa were collated and integrated within this review.

In **Chapter Three** I examine archaeological evidence for the "toheroa translocation hypothesis", in which it is hypothesised that toheroa are only present in Murihiku (Southland) because they were translocated there from northern Aotearoa. Specifically, I identify areas that have supported toheroa populations in deep history. Evidence for the prevalence of toheroa between northern and southern areas will be examined by analysing toheroa middens (ancient shell refuse heap). If toheroa were always present in southern Aotearoa (alongside northern populations), we would expect toheroa shell to be present throughout the midden record in all locations. Further to this, if toheroa existed in the south, we would expect this to be represented in pre-human natural beach deposits.

A critical analysis of archival resources across Aotearoa that refer to the historical distribution of toheroa was conducted. The primary information sources were the Archaeological Site Recording Scheme (ArchSite NZ), archaeological site investigation reports held by Heritage New Zealand and the field notes of archaeologists who have worked in locations of interest. Investigations of middens across Aotearoa was undertaken, with a focus on areas of interest to historical contemporary toheroa populations. Following an extensive search of all archival reports, data was collated and a broad scale midden analysis was undertaken.

In **Chapter Four** I conduct a series of experiments to better understand toheroa physiology and in particular, toheroa tolerance to the stressors that might be associated with translocation. The aim of this chapter was to elucidate the responses of the bivalves when removed from their environment and exposed to different stressors. In understanding the leading causes of deterioration in bivalve health, we may determine their ability to withstand long-distance travel under differing conditions.

Traditional practices have often involved the use of the brown algal species rimurapa (Southern Bull Kelp; *Durvillaea* spp.) in many novel ways, including as pōhā for transportation. In **Chapter Five** I review southern Māori novel technologies developed from the algal species. This chapter aims to integrate traditional knowledge surrounding rimurapa and pōhā, weaving this together with a western science perspective. This chapter aims to determine the use of pōhā in traditional and prehistorical maritime practices.

In **Chapter Six** I utilise the knowledge obtained in the above chapters to undertake a novel experiment, in which raw pōhā were used as a form of receptacle, to hold live toheroa. This chapter aimed to assess the chemico-physical, biological and microbiological outcomes, when rimurapa is used as pōhā to hold live toheroa.

In **Chapter Seven** I synthesize the findings of the above research chapters and develop new concepts and hypotheses, regarding ancient translocations and traditional resource management tools. Aspects of the thesis which may inform future research are presented here.

Chapter Two

Exploring Māori culture and archaeological evidence to inform the "toheroa translocation hypothesis"

[5]

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[5] Hoturoa Barclay-Kerr's Haunui waka hourua (https://www.stuff.co.nz/pou-tiaki/300317018/learning-how-maori-ancestors-got-around-the-world-by-waka-hourua)

2.1 Introduction

Recent research into population genetics of the large surf clam toheroa (*Paphies ventricosa*), endemic to Aotearoa (New Zealand), has led to the hypothesis that prehistorically, Māori have undertaken long-distance transport and translocation of the species (Ross et al., 2018). This may have occurred, via migratory, trade or exploratory routes, from parent populations located on the West Coast of Te Ika-a-Māui (North Island), to the southern-most beaches of Te Waipounamu (South Island), giving rise to an altered population distribution that has up until recently been considered endemic within the south. Long-distance transport and translocation of toheroa would have been contingent on three main concepts co-occurring prehistorically. These include having an *incentive*, the *opportunity* and the *capacity*, to undertake such a feat.

Translocating species is a long-standing traditional practice of Polynesians and consequently, of Māori. Polynesian people are known to have transported and introduced many different plant and animal species throughout the pacific since around ~3,500 y B.P. (Boivin et al., 2016). One example of this occurring within Aotearoa was the translocation by Māori of the common smelt (*Retropinna retropinna*; pōrohe/paraki) into new water bodies, leading to the establishment of an important fishery to local iwi (tribes) (Strickland, 1993). Other marine animals suggested to have been transported around Aotearoa prehistorically are kōura (freshwater crayfish; *Paranephrops* spp.), kākahi (fresh water mussels; *Echyridella* spp.), tio (native rock oysters; *Saccostrea cucullata*) and pāua (*Haliotis* spp.) (Strickland, 1993; Garven, 1997; Rainforth, 2008; McEwan et al., 2020).

In a contemporary setting, traditional translocation practices have been used for bivalve species such as toheroa by many kaitiaki (guardians). The philosophies behind this practice were born from sustainability and resource management concerns, and a desire to spread the fishery so more people had access to it (ensuring manaakitanga by extending the resource availability to different areas and for different communities). There is much evidence for the use of translocation and reseeding of toheroa (whakatīpu mātaitai) as a customary practice, within the past 100 years (Garven et al., 1997; Walker and Wakefield, 2005; Newcombe et al., 2015; Williams, 2016) and it is evident that Māori would have had the inclination to translocate toheroa prehistorically. The limited distribution of toheroa would have encouraged Māori to translocate the taonga (treasured) resource further afield, bringing the mana (prestige, strength) of toheroa with them and seeding the resource close to new areas of occupation. A question of great importance is, what would the incentives have been behind translocating the bivalves so far away from their parent populations? Here we can explore the push and/or pull of iwi or smaller groups to travel or migrate southward with resources such as toheroa in tow.

It is known that southern iwi maintained specific long-distance seafaring practices long after northern Māori. This was to facilitate movement around the island and to take advantage of seasonal abundance of different marine and coastal resources (Tau and Anderson, 2008). The capacity of Māori to undertake this journey would rely on the modes of transport (by waka or land), the use of vessels for transport and the ability of the toheroa to survive prolonged periods of time out of their habitat. The underlying mātauranga (knowledge) of the species by Māori would be instrumental in facilitating prolonged survival.

Archaeological evidence can give insights into the capacity of early Māori to undertake such an expedition, in particular, analysing the movement of industrial rock from their source regions. Analysing lithic and artefact material may also contribute to our understanding of the opportunities available to undertake long-distance transport of toheroa. Investigating migration and trade routes, together with dated archaeological sites and kōrero tuku iho, provides evidence of when such a journey or journeys may have taken place in the prehistoric sequence and potentially, by whom.

The following review examines archaeological and anthropological evidence, along with exploring kōrero tuku iho (oral tradition), to critically analyse the "toheroa translocation hypothesis" occurring in Aotearoa. Within this chapter, evidence for Māori movement is gathered from a variety of sources, including evidence of the movement of lithic material around Aotearoa to inform occupancy, migration and trade, based on the origins of different lithic material from the north and south. The ability to undertake long distance travel and the means by which transport would have been facilitated is explored from an archaeological, anthropological and kōrero tuku iho perspective. Key cultural concepts are explored and the fundamentals behind these which have inspired Māori movement and occupancy and shaped cultural identity between northern and southern iwi. This is integral to understanding how, when and why long distance transport of taonga marine resources such as toheroa may have occurred in the deep past.

2.2 Inclination of Māori to translocate marine species

The settlement of Aotearoa was the last phase of the Austronesian expansion, with Polynesian migrants estimated to have arrived in Aotearoa by the thirteenth century AD (Walter et al., 2010). The temperate and sub-Antarctic climate of Aotearoa differed considerably from the migrants' place of origin, with them previously bearing a tropically-adapted lifestyle (Walter et al., 2017). The Southland region (Murihiku) and the waters and shores of Te Ara-a-Kiwa (Foveaux Straight) (see Figure 2.1) are the coldest and windiest environments in Aotearoa, a stark difference from the tropical environments of Polynesian homelands, yet archaeological evidence suggests Polynesian settlers occupied these areas as early as any other areas within

Aotearoa (Walter et al., 2010). Within Murihiku, water-sourced foods were of particular importance because of the harsh climate, which made it very difficult, if not impossible, to grow extensive horticultural crops (Tau et al., 1992).

Five broad time periods have been established for Polynesian colonisation of Aotearoa: pre 1250 (pre Māori settlement), 1250-1500 (early settlement), 1500-1650 (occupation and interaction between tribes), 1650-1800 (settlement marked by inter-tribal fighting) and 1800 onward (after the arrival of the first European settlers) (Wehi et al., 2013). Previous literature ascertain that the colonisation of Aotearoa was rapid, with settlements of humans on the landscape establishing across the full range of climatic zones within decades (Walter et al., 2017).

Iwi of the north

The Far North (Te Taitokerau, which stretches from Auckland to Cape Reinga; see Figure 2.1 for locations) of the Te Ika-a-Māui has been intensely occupied by Māori prehistorically and is an area of great significance to Northern Māori, both spiritually and traditionally. Toheroa is a taonga[6] of many northern iwi, the species having supported Māori communities for generations, before the fishery became overwhelmed by commercial harvesting and export. The Muriwhenua are a group of northern Māori iwi: Ngāti Kuri, Ngāti Takoto, Te Pātuu, Ngāti Kahu, Te Aupōuri and Te Rarawa, of the Far North. The Aupōuri Peninsula encompasses all areas within the long stretch of the tip of Te Ika-a-Māui. Along the West Coast, this includes Te Oneroa a Tōhē, which has extensive toheroa middens throughout its beach and dune systems, evidence of the utilization of toheroa for hundreds of years within this area.

Ripiro Beach, known for supporting dense toheroa populations in the past, lies between Waipoua and Pouto, with the beach itself approximately 72.4km in length from Maunganui Bluff to the Kaipara North Head (Akroyd et al., 2002). Te Roroa is the iwi from the Hokianga Harbour and the Kaipara Harbour, including Ripiro Beach. Te Roroa is an iwi interconnected with other iwi, under Ngāti Whātua and these iwi may act together or independently. Ngāti Whātua are iwi of the lower Northland Peninsula.

Southern Māori

Since the “great migration” of prehistoric Māori to Aotearoa, the order in which ancestral iwi colonised Te Waipounamu (the South Island), agreed upon by many, was Te Rapuwai-Waitaha-Kāti Māmoe (Ngāti Māmoe)-Kāi Tahu (Ngāi Tahu). Little is known of the iwi Te Rapuwai, other than it was absorbed by Waitaha (Beattie and Anderson, 1994).

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[6] Although there is no direct translation in English for taonga, in this context it may be translated as a treasured and culturally valued resource

The two principal iwi within Te Waipounamu, prior to Kāi Tahu, were Kāti Māmoe and Waitaha. Waitaha was an older tribe suggested to have arrived from Hawaiki. One kōrero tuku iho tells that the Waitaha people arrived from Hawaiki on the Uruaokapuarangi (Uruao) waka, captained by Rākaihautū. The Uruao is believed by many to have settled in Te Waipounamu, landing in Nelson (Whakatū) and continuing to sail along the east coast of Te Waipounamu. Their descendants, the Waitaha peoples, were to eventually make their homeland in the Canterbury region (Garven et al., 1997).

Towards the end of the sixteenth century, Waitaha were superseded by Kāti Māmoe, an iwi originating from Te Matau-a-Māui (Hawkes Bay), along the East Coast of Te Ika-a-Māui, who themselves were expelled from their homeland in the north and forced (or pushed) south. Kāti Māmoe were linked to the ancient hapū Kāti Rakai, descendant from Rākaihautū, a figure that is also recognised within Taitokerau (Northland) traditions.

When Kāti Māmoe reached Te Waipounamu they began to dispossess and integrate with Waitaha through conquest and marriage between iwi (Williams, 2010). Both ancient tribes Waitaha and Kāti Māmoe have recognised historical connections with older iwi identities in the Muriwhenua region of the far north of Te Ika-a-Māui, such as Kāti Kuri and Te Aupōuri. A few other northern tribes are also connected to the Uruao waka and the same ancestors of the Waitaha and Kāti Māmoe peoples (Garven et al, 1997; Tau et al, 1992).

Through warfare, marriage and political alliances, Kāti Māmoe was eventually subsumed with Kāi Tahu, who themselves were migrants from the North (Williams, 2010). Kāi Tahu were to migrate south due to pressure from conflicting iwi, along with the pull of Te Waipounamu's increasingly attractive and abundant resources. A hapū of Kāi Tahu, Ngāti Kuri, successfully took control of Kāti Māmoe peoples in the Kaikōura district. Other communities of Kāi Tahu went further south, taking control of eastern Te Waipounamu.

From the time of the great migration, it is estimated that 300 years had passed by the time Te Rapuwai, Waitaha and Kāti Māmoe had integrated and become one people, with the arrival of Kāti Māmoe at the end of the sixteenth century (McIntyre, 2007). The invasion of Kāi Tahu into Te Waipounamu is suggested by Beattie (1915), based on his informants in Te Waipounamu regions, to have occurred around 1650 AD. James Stack has suggested that Kāi Tahu migration began in about 1677. Another account suggests that the entire migration sequence, up to the truce between Kāi Tahu and Kāti Māmoe around 1790, occurred between 1710 and 1790 (Tau and Anderson, 2008).

Figure 2.1 Map of Aotearoa (New Zealand) identifying locations of significance.

Subsistence strategies in prehistoric Aotearoa

> *He aha te kai a te rangatira? He kōrero, he kōrero, he kōrero. What is the food of the leader? It is knowledge, it is communication.*[7]

The diverse climate and resources across Te ika-a-Māui and Te Waipounamu have made it impossible for there to be a single subsistence economy prehistorically. It is suggested that regional variation was as prevalent during early Polynesian settlement as it was in the 18th and 19th centuries. Polynesian settlers where proficient gardeners, fisherman and when game was available, hunters, able to quickly adapt and utilise the abundant and highly variable resources across Aotearoa (Davidson, 1983).

The gourd (*Lagenaria siceraria*; hue) was, along with kūmara (*Ipomea batatas*), one of the first crops to be introduced and successfully grown by Polynesian settlers in Te Ika-a-Māui. Such successes were not able to occur in the colder, harsher climates of Te Waipounamu, leading to wholly different subsistence regimes by southern communities, who were unable to utilize staples bought with them from their homeland (Davidson, 1983). In some regions subsistence changed very little from early settlement and throughout the prehistoric sequence, while within other areas, economy changed considerably. Many regions within Te Ika-a-Māui, prehistorically and historically, were able to support a long-standing sedentary lifestyle, based on natural environments which supported gardening and utilization of estuarine and coastal resources (Davidson, 1983).

Mahika kai (mahinga kai) and subsistence patterns in the south

> *Long-distance travel allowed Ngai Tahu to trade amongst themselves and to keep their rights to distant resources alive*[8]

Mahika kai (mahinga kai) is a body of knowledge pertaining to harvesting areas, harvesting practices, preparation and utilisation of natural resources (Futter, 2011). Geographically diverse takiwā (district, area) of mahika kai were travelled to, and utilized, seasonally. A hapū or group would have a proprietorial right to differing mahika kai, through ancestral inheritance and a workable knowledge of that resource, also being actively responsible for the upkeep and protection of it. This principal is known as *ahi kā roa* (the long burning fires of occupation) (McIntyre, 2007; Dacker, 1994). Once a resource was acquired, it had to be secured by ahi kā roa, the continued occupation of a mahika kai, so as to be recognised by other hapū or groups (Tau et al., 1992).

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[7] Māori whakataukī

[8] (Legislation Direct, 1992) Pg. 191

The phrase mahika kai can be misleading, inferring that it incorporates areas only harvested for food. Williams (2010) examines the meaning more closely and maintains that perhaps the best definition is “places where the husbandry of faunal, floral and even lithic resources were carried out” (Pg. 151).

There are multiple interpretations of mahika kai. The literal definition is described in Phillips et al. (2016) paper, which critically analyses the inception of mahika kai in creation narratives:

> *Mahinga” [Mahika] meaning “sites denoting work” and “kai” meaning “food”. “Mahinga” incorporates the verb “mahi”, meaning “to work”; “ngā” is a suffix that converts a verb into a noun and thus “mahinga” literally means “the work.*[9]

Although this is a literal translation, Phillips (2016) goes on to state that the importance of mahika kai to iwi, hapū and whānau transcends any cursory definition and “it was a livelihood, an identity, a part of the people” (Pg. 64).

The life cycles of animals and plants where closely monitored, as they were depended upon for survival and cultural continuation (Dacker, 1990). An advanced understanding of the habitats and breeding cycles of fish, birds and plants of value was obtained from careful observations made over years. It was with this understanding that Māori were able to harvest these resources at their seasonal optimum, while maintaining the resource for future use (Tau et al., 1992). Marine mahika kai was of fundamental importance to southern iwi, as the climate precluded many horticultural practices (Rout and Reid, 2020).

Within the harsher environments of Te Waipounamu, complex systems were established, with a shift in focus on different resources throughout the year. Mahika kai activities were sophisticated, expertly executed and involved travel over long-distances, and through geographically and environmentally diverse conditions. These expeditions dictated much of the social and work activities throughout the year and thus shaped the lives of southern Māori (Tau et al., 1992).

In Murihiku, a seasonal calendar was adhered to for gathering different resources in different areas, this creating a regimen of subsistence patterns necessary for survival (Garven et al., 1997). Subsistence in the south was reliant upon five groups of native resources: marine mammals, marine fish and shellfish, riverine fish, birds and vegetable foods. Within each of the five groups, abundance, access and dependability favoured one type over others. These are suggested to be fur seals, barracoota, eels, tītī (muttonbirds) and kauru (cabbage tree root) (Anderson, 1998). From evidence given by southern informants to ethnologist Herries Beattie

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[9] (Phillips et al., 2016) Pg. 64

(Beattie and Anderson, 1994) in 1915, no mention of toheroa (or variant name of the species) is recorded as a mahika kai resource or subsistence species, nor is toheroa mentioned in mahika kai lists which have been recorded and analysed historically.

Along the West Coast of Te Ika-a-Māui, within iwi such as Ngāti Whātua, certain whanau, following the mahika kai of toheroa formed and worked by their tīpuna (ancestors), continue to be appointed ahi-ka-roa over toheroa. This is important in maintaining the intergenerational occupation and kaitiakitanga of the taonga species. Their ability to continue mahika kai husbandry of toheroa populations has however been greatly hindered by the regulations and prohibitions issued, since the toheroa cannery works of the mid 1950s led to the subsequent depletion of toheroa populations. Northern iwi have been subjected to constant struggles to claim rights to the toheroa and to practice traditional species management (Murton, 2006; Trego-Hall, 2020).

2.3 Whakataukī and whakapapa; indication for the lack of toheroa in the south in the deep past

Within Beattie's notes on ethnology, several mentions of toheroa allude to its lack of presence within Te Waipounamu prehistorically. One informant mentioned that toheroa and tohemango were names in different parts of Te Ika-a-Māui which referred to the same shellfish but could not give a Te Waipounamu equivalent. In another example, Beattie (Beattie, 1915) writes very briefly of toheroa, simply stating; "An old man said there was no such shellfish as toheroa in the South Island".

Although in more recent times, toheroa have become an important shellfish to the people of Ngāi Tahu, in historical times, there is little mention of toheroa being utilized as a significant resource by southern Māori prehistorically. This is of particular significance comparative to the Northland regions, in which it was a central kaimoana species in shaping the ancestry and identity of local iwi, this being evident in whakataukī and whakapapa. In a collection of whakataukī from the Taitokerau region a small excerpt by Edward Shortland, an explorer, scholar and interpreter, is noted;

> *He toheroa te kai o taua whenua [Ripiro]; nā Kupe I whakatō hei kai mā tama tamāhine, mā Te Tai-tuauru-o-te-marowhara, waiho hei ingoa mō te ngaru nui, ā, e mau nei anō ngā whakataukī…*

> *Toheroa are the food from that land [Ripiro]; Kupe put them there as food for his daughter, for Te Tuauru [or hauauru] –o-te-marowhara, and this remained the name for the surf there, and is continued in sayings…*[10]

Kupe is suggested to be involved in the first Polynesian colonisation of Aotearoa. This excerpt refers to the history of toheroa being seeded in Taitokerau (Northland) areas with the first arrivals of Polynesians' to Aotearoa but of more importance in this context, emphasises the link between toheroa and very early Māori in the Northern areas.

This has again been documented by Colleen Sheffield and relayed in a brief history of Muriwai Regional Park by Murdoch (1994)

> *Some say that it was Kupe who left the shellfish delicacy the toheroa, on the western coastline. In Ngāti Whātua tradition the placement of this taonga or treasure on 'Te One Rangitira' [the chiefly beach] is however credited to Mareao one of the crew of the Tākitimu canoe that visited the area over six centuries ago.*[11]

There are several legends pertaining to the whakapapa of toheroa, as described by northern iwi. Jim Te Tuhi, a noted toheroa kaitiaki of the north writes;

> *The first legends speak of the dune grass Pingao, the seeds resemble toheroa spat and it is said that the seeds are blown from the dunes to the sand, take seed and become toheroa. In another iteration, Pingao was placed in the dunes by her father Tangaroa, to nurture her whanau, the toheroa.*[12]

One version tells of the High Chief Mareao who bought toheroa from Hawaiki and planted them on the west coast of Te Ika-a-Māui, as was mentioned earlier. The final narrative tells of a pursued chief and his people who utter a karakia asking their atua to save them. His men, not soon after, found small slits in the sand on the beach and assuming kaimoana lived beneath, they dug but found nothing. A voice gave them a message "tohe-roa, tohe-roa" which meant "persist a long time" and so his men continued to dig and finally found the toheroa, which fed and saved them (Heasman et al., 2012).

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[10] (Kawharu, 2008)

[11] (Sheffield 1963:24) Pg. 2

[12] (Te Tuhi and Te Awa, 2008)

The intrinsic nature of toheroa within northern iwi communities is summarised by Murton (2006). They state;

> *Part of the identity of Māori living along the Kaihū and Wairoa [Northern] river valleys was bound up with toheroa. The shellfish was not only an important food source but was symbolic of their existence.*[13]

From critical analysis of ethnological texts, books, literature and archival reports, along with interviews with kaitiaki in Murihiku, none such narratives, whakataukī or whakapapa could be found within the current study for toheroa along the southern coastline.

2.4 Capacity and opportunity to transport toheroa south; analysis of waka voyaging, migration and trade

Kōrero tuku iho; oral traditions of Māori exploration south

There are many waka hourua (double hulled voyaging waka) suggested to have been involved in the Polynesian migration to Aotearoa from Hawaiki. Of these, seven prominent waka hourua are referred to as the 'great fleet' and include Tainui, Te Arawa, Mātaatua, Aotea, Kurahaupō, Tokomaru and Tākitimu.

The Tākitimu migration to Aotearoa is generally agreed upon to have occurred about the year 1250 AD and was said to have explored the length of Aotearoa from North to South (Tau and Anderson, 2008). Tākitimu has been linked to the Chief Mareao, who it has been claimed by Ngāti Whātua sources, brought toheroa to Aotearoa and seeded the shellfish on the west coast of Te Ika-a-Māui, before traversing the two islands to eventuate in Murihiku (Evans, 2009). The concept of long-distance transport is embedded within this narrative, where translocation, toheroa seeding and long-distance travel from the north to the south are represented.

There are several accounts pertaining to the Tākitimu voyage, most variants tending to have many similarities. The following is one such narrative taken from several sources. From the initial landing at Awanui, at the southern end of Te Oneroa a Tōhē (Figure 2.1), the Tākitimu is said to have proceeded north, around the North Cape (Muriwhenua), voyaging down the eastern side of the Island. It is suggested that these pioneers may have been instructed by earlier voyagers to take this route, if they had travelled the West Coast, they would have encountered less resource-laden and sheltered harbours and more dangerous river mouths (Mitchell, 2014; Evans, 2009). During this journey, one account states that live eels were

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[13] (Murton, 2006) Pg. 35

transported aboard the Tākitimu and these were subsequently released in the Whakatāne River (Evans, 2009).

When Tākitimu reached Murihiku, it was said to have sailed through Te Ara-a-Kiwa (Foveaux Straight) into the Southern Ocean and on to Te Waewae Bay (see Figure 2.1 for locations). Tākitimu was then directed towards the mouth of a river which flowed into the bay and due to its strong currents, was named Waiau. One account tells that while approaching the Waiau River (Figure 2.2), the Tākitimu went aground but was saved when the waves were called upon to lift the waka up, where it was taken ashore and turned to stone in Murihiku (Evans, 2009). Slight variants to this account, suggests that the Tākitimu was shipwrecked at Te Waewae Bay or at the entrance to Waiau River (Mitchell, 2014; Tau and Anderson, 2008; Evans, 2009). Although many accounts appear to exist regarding the resting place of the ancestral waka, most agree that the fate of the waka was to land or be shipwrecked along the Southern coastline of Murihiku, particularly in association with Te Waewae Bay and the Waiau River (Mitchell, 2014; Tau and Anderson, 2008; Evans, 2009)

In one legend, Tamatea-ariki-nui, the captain of Tākitimu who explored Aotearoa from Muriwhenua (Far North) to Murihiku (deep south), upon wrecking his canoe was said to have spent some time in Murihiku, before returning North, with the captains final resting place being in Hokianga (Garven et al., 1997, Beattie and Anderson, 2004). Important in this narrative is the idea of long-distance travel from northern areas (associated to toheroa), to the deep south, only to return again to the north.

The earliest written Te Waipounamu account of the Tākitimu is given by Edward Shortland in 1851, where the waka is referred to as a mountain inland of Aparima, Riverton (Figure 2.1), the mountain described by the locals as originally being a canoe (Prendergast-Tarena, 2008). A thesis centred on the change in southern Māori oral traditions by Prendergast-Tarena (2008) suggested that this is the only early account that was not published in the twentieth century, and may be indicative of authentic, pre-contact tradition.

The journey of Tākitimu is one example of kōrero tuku iho (oral history and tradition) of long-distance transport from north to south, by prehistoric explorers. All documented interpretations of the Tākitimu may be the result of interwoven accounts, serving, in an historical and contemporary context, as a device for differing iwi of their tribal origins. It is suggested by Prendergast-Tarena (2008) that the shipwrecking of a waka is a common metaphor and may be used as a means to claim descent of an ancestral canoe when wrecked within a groups territory.

Interpretations of the Tākitimu tradition may provide theŌretical evidence for a migration or voyage, which begins on the West Coast, purposefully traversing the coastlines of both islands and eventually arriving in Murihiku. During this voyage, knowledge of both environments and marine resources would have been accumulated and communicated to others. Knowledge of toheroa and their habitats may have travelled via these lines of communication.

Transport by waka-hourua

Prehistorical water transport in Murihiku involved the continued use of the ancestral voyaging waka hourua, while this type of waka was quickly phased out in the north. The waka hourua had one hull larger than the other with an interlinking deck which held sails, these waka being robust and difficult to capsize (Coutts, 1970). Contemporary long-distance voyages, utilizing ancestral waka hourua and traditional navigation practices, have been undertaken by Māori navigators in the recent past. It is said that the waka would sail 24 hours a day, with a crew working 6-hour watches. On such journey, the average speed of a waka hourua was 9.26 km/h (5 knots), though they are capable of speeds up to 22.22 km/h (12 knots).[14] If hypothesising that the route taken from the west coast of Te Ika-a-Māui (Te oneroa a Tohe; Figure 2.1) was first around the northern tip of the island and then down along the East Coast of Aotearoa to Muruhiku, this distance would be roughly 1700-1800 km via water. Considering the speeds calculated by contemporary waka voyages, it would take approximately 7-8 days to journey from the West Coast to the southernmost beaches of Murihiku.

The use of archaeology in determining the capacity of long-distance transport

Analyses of early Māori mobility and migration patterns have contributed greatly to our understanding of adaptation and cultural evolution. This may be monitored by archaeological means, through the identification and sourcing of lithic material from non-local sources and where possible, placing them within the context of time (Brooks et al., 2010). Brooks et al. (2010) states that within Murihiku (Southland, Te Waipounamu) this form of monitoring is particularly powerful, as it is the furthest distance south to have received and provided lithic resources to northern distribution networks. Studies of the geographic distribution of stone artefacts across Aotearoa can give researchers an indication of shifts in human mobility, behaviour and trade in prehistoric times (McCoy and Carpenter, 2014). The term artefact includes any items used by a human and left at an archaeological site, often not found within the area naturally.

Archaic cultural material and artefact types are generally dated between ca. 1300AD and ca. 1500AD, while classic Māori artefacts are considered to be from the 1500 AD to the arrival of cook around 1769. A small transitional period (intermediate period) overlaps the two (Davidson,

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[14] https://www.sciencelearn.org.nz/resources/633-waka-hourua?fbclid=IwAR15IJbzhc787fXcSfkRwXR77QQDwrpU3D8iqVmxjVsAoKdNFGI75o_lEds

1987). Anderson (2016) suggests that the transitional period from Polynesian colonisation to classic Māori culture is dated at about AD 1450 -1650.

It has been suggested that widespread exchange systems were more prevalent in earlier time periods, before intense warfare of the later prehistoric period caused these networks to collapse (Davidson, 1987). Many pathways within these networks would have been blocked following abrupt halts in communication, even if only for a period of time. Davidson (1987) states that evidence of the exploitation and distribution of greenstone in Te Ika-a-Māui, which took place during the period of universal pa warfare, indicates that warfare did not completely disrupt the general flow of goods through Aotearoa. It could be postulated that transport of live animals such as toheroa may have occurred before pa warfare, when widespread exchange systems were not disrupted by disputes.

An important skill of Polynesian settlers was their ability to identify the technological characteristics of rocks. Rocks, such as obsidian and pounamu, have traversed the length of Aotearoa, identifying the breadth to which trade and transport of useful lithic material by Māori was achieved and the implications of this in the early development of complex social networks (Davidson, 1983). The geological knowledge of Māori prehistorically was incredibly detailed. Māori are suggested to have known and utilized lithic materials from sources which may have yet to be found by modern researchers and scientists (Davidson, 1987). Within Aotearoa, there is evidence for widespread early transport of industrial stone across the entire country (Irwin et al., 2017).

Archaeological investigations of Palliser Bay (central Aotearoa, see Figure 2.1 for location), on the South Coast of Te Ika-a-Māui, has been undertaken extensively in the past. Archaeological sites within Palliser Bay have contributed greatly to our understanding of movement, settlement and trade during earlier periods in the prehistoric sequence, particularly due to its central location within the country (Leach, 1981). Evidence suggests its inhabitants had been utilizing lithic resources from as many as 15 different places throughout the country, from both Te Ika-a-Māui and Te Waipounamu (Davidson, 1983).

Lithic material found at Palliser Bay included obsidian from the Coromandel Peninsula, Tūhua (Mayor Island) and the central North Island, chert from the Wairarapa and argillite from D'Urville Island. Small amounts of nephrite jade (Pounamu) were also present at the site, this sourced from the West Coast of Te Waipounamu and silcrete, potentially from Central Otago. The rocks and artefacts that have been found in Palliser Bay provide evidence for the movement of natural materials, utilized by prehistoric people, for several hundred kilometres both north and south across Aotearoa (Leach, 1981; Davidson, 1987). The northern extremities of Te Ika-a-Māui are separated from the South Coast of Murihiku by more than

1500 km, yet lithic material has managed to be transported down the country during the earliest periods of Polynesian settlement (Reeves and Ward, 1976).

Ideas such as the concept of toheroa transport to new areas may have spread from group to group, down the length of Aotearoa; much like the change in artefact styles (such as fishing hooks) in different areas. Ideas which prompted change in behaviour spread along the same lines of communication and trade routes in which tangible goods, raw materials and lithic material travelled, from one kin group to another (Davidson, 1983). Further to this, knowledge of local landscapes, both coastal and inland would have been disseminated through these channels.

Southern iwi developed hooks with a range of barbs, while Northern iwi used simpler one piece hooks and lures, much like styles introduced from Polynesia, for much longer (Davidson, 1983). Difference in hooks may have implications in dating archaeological sites and hooks from northern iwi found in southern areas may indicate their migration and presence.

Obsidian/Tūhua

Of all the lithic materials in Aotearoa, obsidian has been the most studied, as it has been identified in many sites spanning all prehistoric phases. Obsidian (volcanic glass; Tūhua) source deposits are restricted to the northern and central parts of Te Ika-a-Māui, yet obsidian is ubiquitous across Aotearoa archaeological sites, reflective of the wide spread settlement of Polynesians throughout the country (Reeves and Ward, 1976). Being the subject of detailed research, obsidian is at present considered the best indicator of prehistoric communication and strongest material indicator of travel in Aotearoa. Tūhua (Mayor Island, see Figure 2.1) obsidian is the most common obsidian present across all Early Period sites, with the most extensive deposits of obsidian within Aotearoa being found here (Davidson, 1987; McCoy and Robles, 2016). There has been no source of flake-quality obsidian found within Te Waipounamu, although poor quality obsidian (of no archaeological or workable value) has been found at Banks Peninsula (Figure 2.1) (Armitage, 1971). Identifying obsidian in southern archaeological sites may provide evidence for the presence of northern Māori in southernmost areas at the earliest stages of the prehistoric sequence.

Most communities across Aotearoa have utilized obsidian prehistorically, with the potential to come into possession of this resource a number of ways, via trade, transport or communication routes across the country. Tūhua obsidian was the earliest to be widely transported and utilized and has continued to be a large proportion of the obsidian found within archaeological sites. Tūhua obsidian is distinctive in appearance, ranging from black to dark green in reflected light and green to yellow-green in transmitted light. Due to its distinct characteristics, it has been recognised and differentiated from mainland obsidian since the earliest archaeological studies undertaken in Aotearoa (Armitage, 1971; Reeves and Ward, 1976). Obsidian from Taupō and Tūhua is known to have reached Murihiku prehistorically (Reeves and Ward, 1976).

Tūhua obsidian in Murihiku archaeological sites

Archaeological sites identified in Murihiku (Figure 3.2) are rich in lithic and cultural material. Six of the eight sites were found to have stone tools, seven with adze or adze chips, eight sites were found to have obsidian and three with nephrite jade. One site was found to have moa bone. Cultural material within these sites offer insights into the types of occupation, and the periods in which the South Coast was occupied.

A salvage excavation of a Murihiku archaeological site was undertaken in 2009, with the site being considered a top priority on the South Coast, due to its rapid deterioration and its contents having a rich array of archaeological information. The location of the site was at Kahukura, near Waikawa (G47/128) (see Figure 2.2 for archaeological sites with obsidian and pounamu present along the South Coast of Murihiku). In the southern margins of the site, a small oven was found along with a single flake of Mayor Island obsidian and the butt end of a Duff Type 1A adze. This adze type is found only with very early occupation and is likely to represent one of the earliest settlement phases in this area, being suggested to be in the 14th to early 15th century (Brooks et al, 2010). Another inland part of the site was found to have a flake of obsidian "green in transmitted light, which suggests Mayor Island origin" (Brooks et al., 2010; Pg. 8).

Another archaeological area of interest along the South Coast has been found at Tiwai Point. Tiwai Point is located at the end of a peninsula, east of Bluff, sitting between Awarua Bay and Te Ara-a-Kiwa (Figure 2.1, Figure 2.2). Tiwai Point is the largest habitation and adze manufacture site of the area, and it is considered an important site for investigating how the earliest Polynesian settlers targeted new lithic material for tool production (Jennings and Weisler, 2020).

Within this site, small middens, pits, large ovens and stone working areas with high concentrations of flake material, were found. A wide variety of rock had been worked at this site, including local argillites, quartzite, chalcedony, obsidian and sandstone. Argillite, a sedimentary rock formed from consolidated clay, is the most famous of the rocks used for adze tool manufacture, due to its robust qualities. It is naturally sourced from Te Waipounamu, including from the Nelson/Malborough area and in Murihiku (Riverton, Tiwai Point, see Figure 3.2) (Petersen and Barr, 2009; Leach and Leach 1980).

Work undertaken by Reeves and Ward (1976) have identified obsidian found at the Tiwai Point as coming from both Tūhua and Taupō, along with placing the site within the "early phase' period of Aotearoa occupancy. The source-site distances, calculated by Reeves and Ward (1976) were 1220km from Tūhua to the site and 1080km from Taupō.

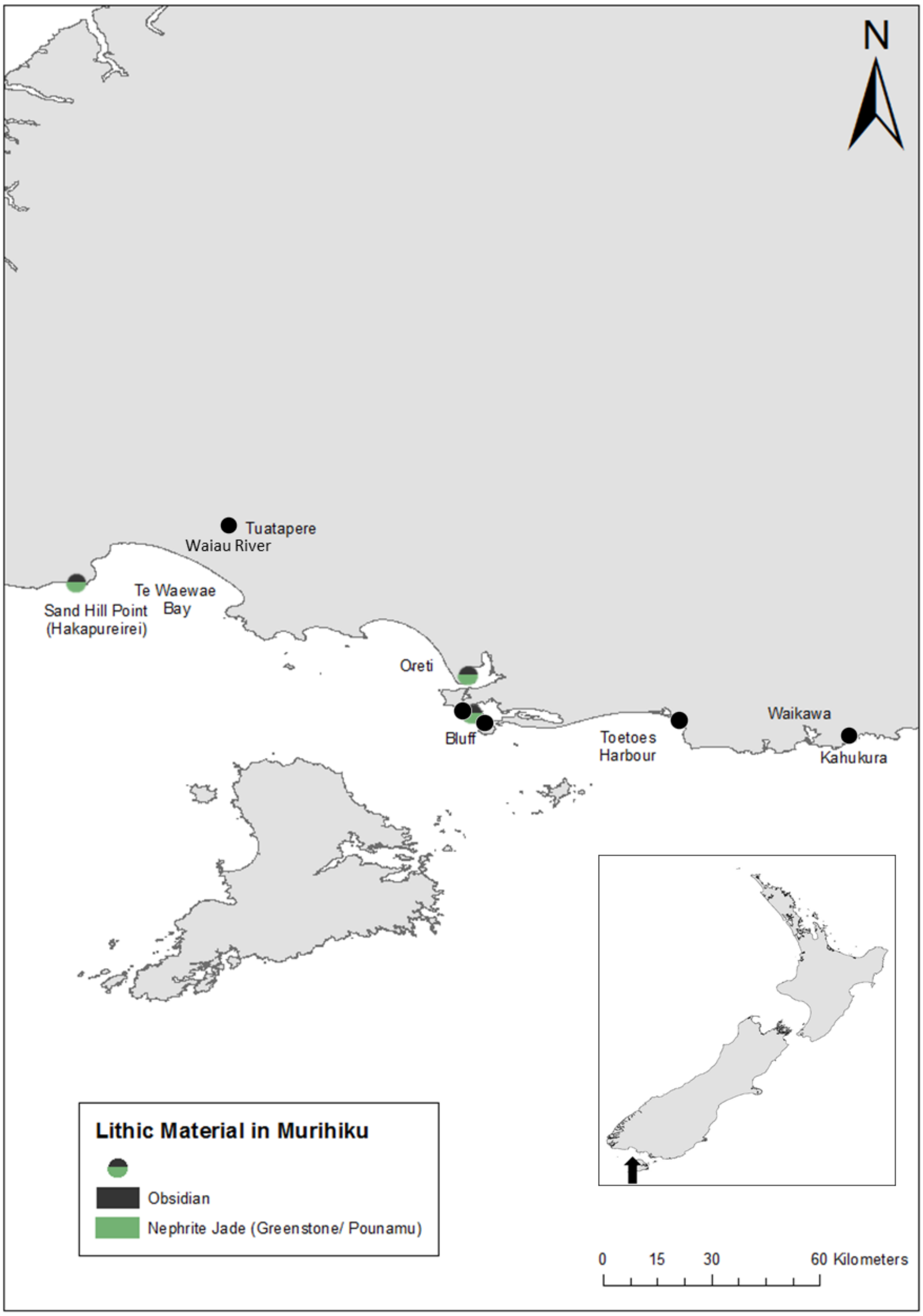

Figure 2.2 Archaeological sites on the coast of Murihiku, Te Waipounamu identified in ArchSite NZ which have pounamu and/or obsidian present. Sites were imported into ArcMAP Version 10.4.1 and overlaid on a geographic shapefile (New Zealand coastlines and islands polygons topography; LINZ Data Service (https://data.linz.govt.nz/license/attribution-3-0-new-zealand/)). The co-ordinate system was set to a NZ traverse Mercator (NZTM 2000) projection.

One Site (D45/6) located approximately 9 km inland from the centre of Te Waewae Bay near Tuatapere (Figure 2.2), was found in ArchSite NZ, with no corresponding report. The lithic material and artefacts of this site, along with the location of the site so close to Bluecliffs Beach, makes it of interest to the current study. This site has been described as archaic, with artefacts dating back to early prehistoric colonisation. The descriptions of the site were given by D. R. Simmons and L. J. Scott (owner of property) in 1967, with cultural material being found accidentally when ploughing. The description reads;

> *8 artefacts, consisting of a large obsidian core, 4 unfinished adzes, 3 complete adzes and a broken adze butt were found in a cache at the above map ref. by Mr L. J. Scott, who presented them to the Southland Museum. They are all of 'Archaic' style, and with the exception of 2 adzes of greywacke, all the rest are southern argillite's.*[15]

The obsidian core was described as large, which may give indication that it was relatively new or unused. Smaller cores are reflective of having been flaked multiple times on their journey, while larger cores indicate relatively new material that is being transported and worked (Coster and Johnston, 1976). This may provide evidence for the occupants having made a long-distance journey from northern areas, early in the prehistoric sequence.

Further evidence of northern occupancy of the South Coast, coupled with no evidence of toheroa present, is represented in the Hakapureirei archaeological site (Sandhill Point, C46/31), located in Te Waewae Bay. Within this site nine midden features were found, all dominated by shell, though none containing toheroa (Coutts et al., 1970; Walter and Jacomb, 2005). Work undertaken by Reeves and Ward (1976) identified samples of obsidian from Sandhill Point to derive from Tūhua, Taupō and Huriuki (Northland) deposits. The source site distances calculated by Reeves and Ward (1976), being an approximate straight line distance in kilometres, was 1245 km from Tūhua, 1110 km from Taupō and 1345 km from Huriuki. To consider the distance this obsidian has travelled prehistorically and through some of the harshest environments within Aotearoa, is staggering.

One-piece bait hook fragments made of moa bone were recovered from the site and these are largely restricted to the earliest part of the Aotearoa prehistory, with the authors suggesting the duration of occupation was no more than a century or two (Walter and Jacomb, 2005). This site, along with site D45/6 of Tuatapere, indicates that the southernmost areas of Aotearoa were occupied during archaic periods. Furthermore, the presence of Tūhua obsidian in sites such as this provides direct evidence for the migration, communication and trade from

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[15] (Archsite NZ, 1967)

northern regions which was undertaken by Murihiku occupants, during the earliest phases of Aotearoa colonisation.

Nephrite Jade/Pounamu

Along with obsidian, greenstone/pounamu is a stone used famously by Māori. This stone appears to have become prominent later than obsidian, being found much less in archaeological sites. Due to the absence of pounamu relative to obsidian throughout sites, and there being not as much geological work done regarding natural sources of nephrite jade, less is known about the prehistoric distribution of pounamu (Davidson, 1987). Although obsidian is no longer utilized, pounamu is still used and is valued to this day. Pounamu occurs in several limited geographic ‘fields’, with a shared geological ancestry. It is naturally sourced only in the Te Waipounamu, as far north as D’Urville Island and Nelson, within Westland, Otago and Murihiku. Pounamu sources, well known to prehistoric Māori, include Westland and West Otago (Adams et al., 2007).

Pounamu has been identified in several archaeological sites in the Far North, Aupōuri Peninsula, including at one of the northern most beaches of Aotearoa (Figure 2.3). This provides further evidence for the connectivity of Māori prehistorically between the north and the south.

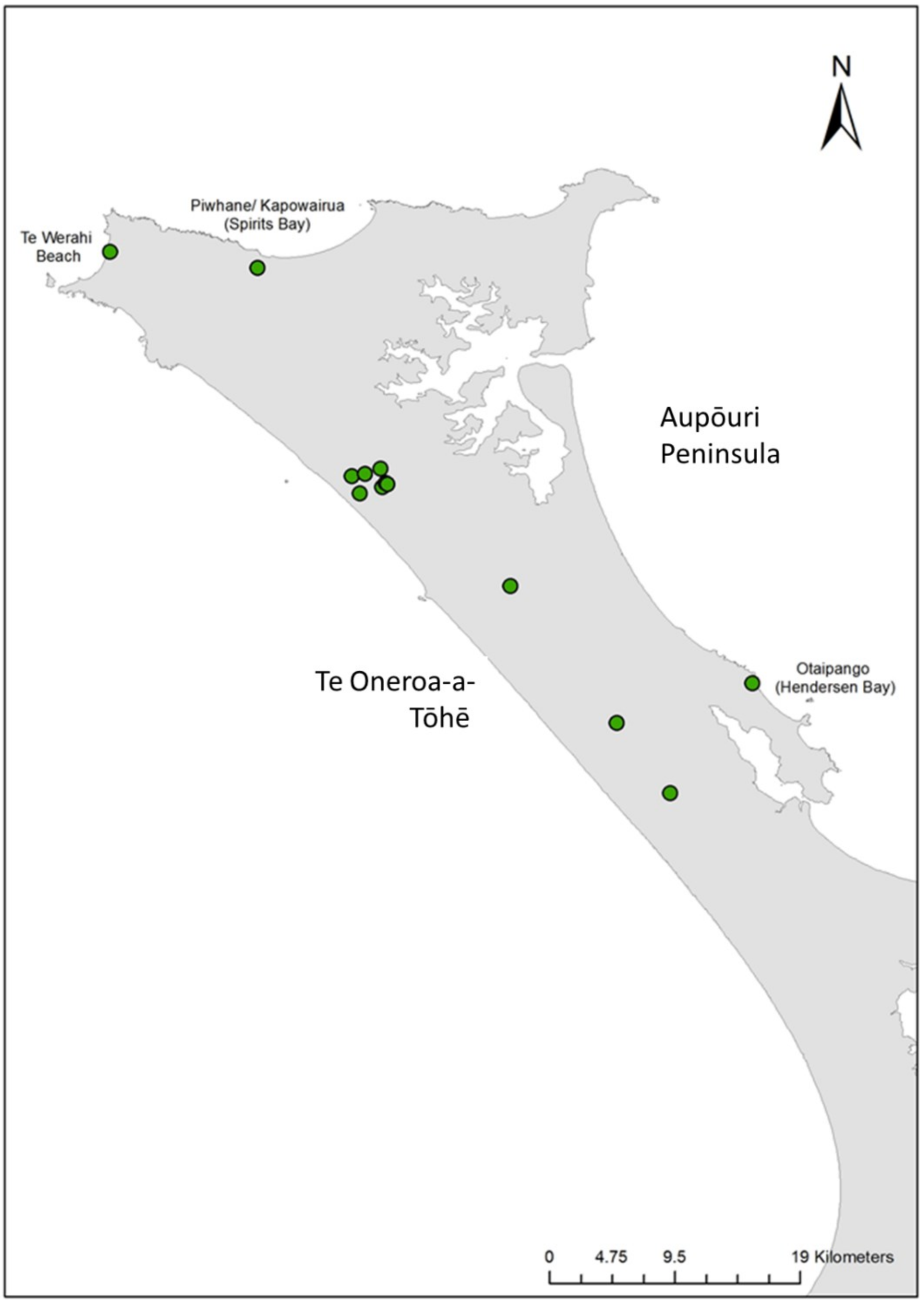


Figure 2.3 Archaeological sites in the Aupōuri Peninsula identified in ArchSite NZ which have pounamu present. Pounamu sites imported into ArcMAP Version 10.4.1 and overlaid on a geographic shapefile (New Zealand coastlines and islands polygons topography; LINZ Data Service (https://data.linz.govt.nz/license/attribution-3-0-new-zealand/)). The co-ordinate system was set to a NZ traverse Mercator (NZTM 2000) projection.

Navigation and trade routes

Important in the history of migration, is the navigation routes by which iwi moved across the islands and in particular, the importance of these routes for resource allocation and resource trading. Trails that traversed the high country of Te Waipounamu provided important economic and social links. Māori retained a detailed knowledge of different trails and were able to relay, in accurate detail, the sequence of place names along a complex river system (McIntyre, 2007).

As resource management culture became developed, hierarchal frameworks evolved, with allocation and management of resources through specialisation. This allowed for more of an emphasis on knowledge and skills of leaders, rather than an emphasis on whakapapa alone (Tau et al., 1992). Each hapū had an area of their own, defined by natural boundaries or landmarks, such as mountains and rivers. These were named by iwi, identifying that this was their rohe (territory) and signifying their distinct identities. Whanau groups became specialized in the production of resources from their areas. These were then traded or exchanged with people from different areas, who were specialized in different products. This was termed kai-hau-kai and occurred on a scale ranging from local to national. Southern Māori possessed unique resources, such as pounamu and pōhā-tītī (a natural bag made from the brown algal species *Durvillaea* sp., filled with preserved mutton bird), these being among many highly prized goods that were traded with northern iwi (Tau et al., 1992).

Within Te Waipounamu it is suggested that pounamu was of most significance in the system of gift exchange. Likely modes of transport in earliest times were along the coast by waka, and after a time, carried over the alpine passes, when the strong waka hourua, which could withstand the rough conditions along the West Coast were no longer being built. Kaiapoi (see Figure 2.1) or Kaiapohia pa is suggested to have become the centre of pounamu trade to the north, this occurring when Kāi Tahu built a pa and subsequently took control of the area, its trails and the surrounding resources in the 17th century. From Golden Bay, the resource would be placed in waka to continue its journey north (McIntyre, 2007).

Pōhā was developed into an important adaptation to facilitate storage and exchange specific to the needs and resources of Te Waipounamu (Williams, 2016). The traditional system of exchange was sustained by porterage and waka and was a mechanism not only for dispensing resources beyond their source locality, but as an important social and economic institution (Anderson, 1998). This system resulted in frequent and seasonal long-range movement, as resources were collected directly or moved around via trade networks. One such trail extends over half the length of the East Coast of the south, from Kaiapoi through to Te Ara-a-Kiwa with intermittent stops (Anderson, 1998).

Stories of migration, at many points, refer to the importance in trading, ritual and personal adornment. Most foods were preserved in some form for later feasting and exchanges. Many animals were preserved inside pōhā in their own fats, these being decorated with feathers and other embellishments, to signify importance (this has been called kai rangitira; the food of chiefs). These were prized items in the system of trade that occurred across the length of Te

Waipounamu, with links even across Te Moana-O-Raukawa (Cook Straight) (Tau and Anderson, 2008).

McIntryre (2007) writes that kaimoana and birds were preserved and carried in rimu (seaweed) since before the 'pounamu wars', which may have begun to occur around 1500 AD. This suggests that rimurapa or pōhā has been utilized in the south for many hundreds of years. Pōhā and rimurapa have been used as a restorative tool in the planting or seeding of kaimoana prehistorically and historically (Williams, 2016). The pōhā may have provided a way in which toheroa could be held or translocated by Māori, particularly in southern regions.

2.5 Concluding remarks

The northern most areas of Te Ika-a-Māui are separated from the southern coast of Te Waipounamu by more than 1600 km, yet industrial stone has managed to be transported down the country during the earliest periods of Polynesian settlement (Reeves and Ward, 1976). Not only physical goods, but important ideas around resource management, geography and environmental knowledge may have travelled along trade routes and migratory paths via these lines of communication. Coastal beach habitats in which toheroa reside have highly specific topographical features and this information may have been easily remembered and potentially disseminated via communicatory pathways from the north to the south.

A study undertaken by Walter et al., (2017) found that there are a higher proportion of archaic archaeological sites (14th century), which are assigned to the early settlement phase within Te Waipounamu comparative to the north. This could indicate that many communities colonised the south first, followed by different triggers prompting a widespread movement north. The rapid and effective widespread exploration of Aotearoa in the earliest phases is evident in the archaeological records of lithic resource exploitation (Walter et al., 2017).

The Murihiku sites critically analysed above provide evidence for occupancy in the southern most parts of Aotearoa, in the earliest phases of the prehistoric sequence, by humans who had either come from northern areas or were closely connected to northern communities. Furthermore, toheroa middens have not been found within these sites (see Chapter Three), even in sites such as Sandhill Point (C46/31) which is dominated by midden and located in an area known to support toheroa populations historically.

The presence of one toheroa shell in the "Riverton site" (detailed in Chapter Three) does not provide evidence for toheroa populations being present in the surrounding environment during these periods of occupation. The toheroa shell may have been used as a tool or was of symbolic importance (see Figure 2.4) and was transported to the area from the north. It could be postulated that the presence of one shell infers that occupants of the site were explorers from northern regions.

Figure 2.4 Ancient toheroa shell from Muriwai area. The shell is not only large but the shell depth is much thicker than extant species, making for a useful tool.

Occupancy along the South Coast in some areas is suggested to be for short periods of time, specifically to collect resources for transport elsewhere. This provides evidence for capacity, opportunity and incentive to journey to the South Coast in the earliest periods of Polynesian settlement via waka, to collect resources, explore the environments and then depart. During this time a rapid period of discovery and adaptation would have been occurring.

Midden analysis, along with evidence of adze and flakes in the Riverton site has led to the conclusion that the area was a specialist camp, whose occupants engaged in argillite adze manufacture, while utilizing surrounding coastal and forest resources. The area is suggested to be primarily used for the extraction and preparation of raw material for export and the site was likely accessed by waka, suggested to have been occupied for no longer than a few days per visit (Leach and Leach, 1980: Jennings, 2009). The Riverton site provides evidence of the earliest Polynesian settlers short term occupancy in the area.

The presence of an obsidian core found at the archaic site inland of Te Waewae Bay may provide evidence that the occupants had undergone long-distance transport on a short time scale, from its source location in the north. Analysis of obsidian from the South Coast undertaken by McCoy and Robles (2016), found a surprising amount of interaction between

Murihiku and communities in Te Ika-a-Māui during the earliest periods of Aotearoa's prehistory. They state: "**People certainly had the logistical capacity to travel the length of the country**".

Toheroa have the most demanding and specific habitat requirements of the surf clams in Aotearoa and this contributes to the difficult nature of toheroa conservation. There are stark commonalities shared between the beach environments along the West Coast in Te Taitokerau and South Coast in Murihiku which provide favourable habitats and have supported or still support toheroa beds. This is particularly true of West Coast beaches along the Aupōuri Peninsula, the North and South Kaipara peninsulas and the coastline of Ōreti Beach in Murihiku, which are all west coast facing, are 'dissipative', flat and wide, are exposed to prevailing winds and are among the largest remaining active dune complexes within Aotearoa (Beentjes, 2010). Further commonalities shared between most beach habitats which support toheroa include: highly exposed coastal areas with high energy surf zones, fine grained sand, protective onshore dune systems and a distinctive feature of small seeps or streams entering the coastal beach zone (Cassie, 1955). The distinctiveness of these environments would have been identifiable by early-Māori.

Walter et al. (2017) suggests that the range of lithic resources found in the earliest archaeological sites are indicative of a systematic exploration programme by Polynesian settlers, leading to the rapid acquisition of geographical knowledge and establishment of networks across the country. Communities across Aotearoa may have quickly developed topographical, coastal and riverine knowledge allowing for planned re-colonisation from the north to the south repeatedly throughout the prehistoric sequence. Temporary occupants to the South Coast of Murihiku would have gained intimate knowledge of the coastal environments and the corresponding resources, such as the wide stretching beaches known today to support toheroa beds.

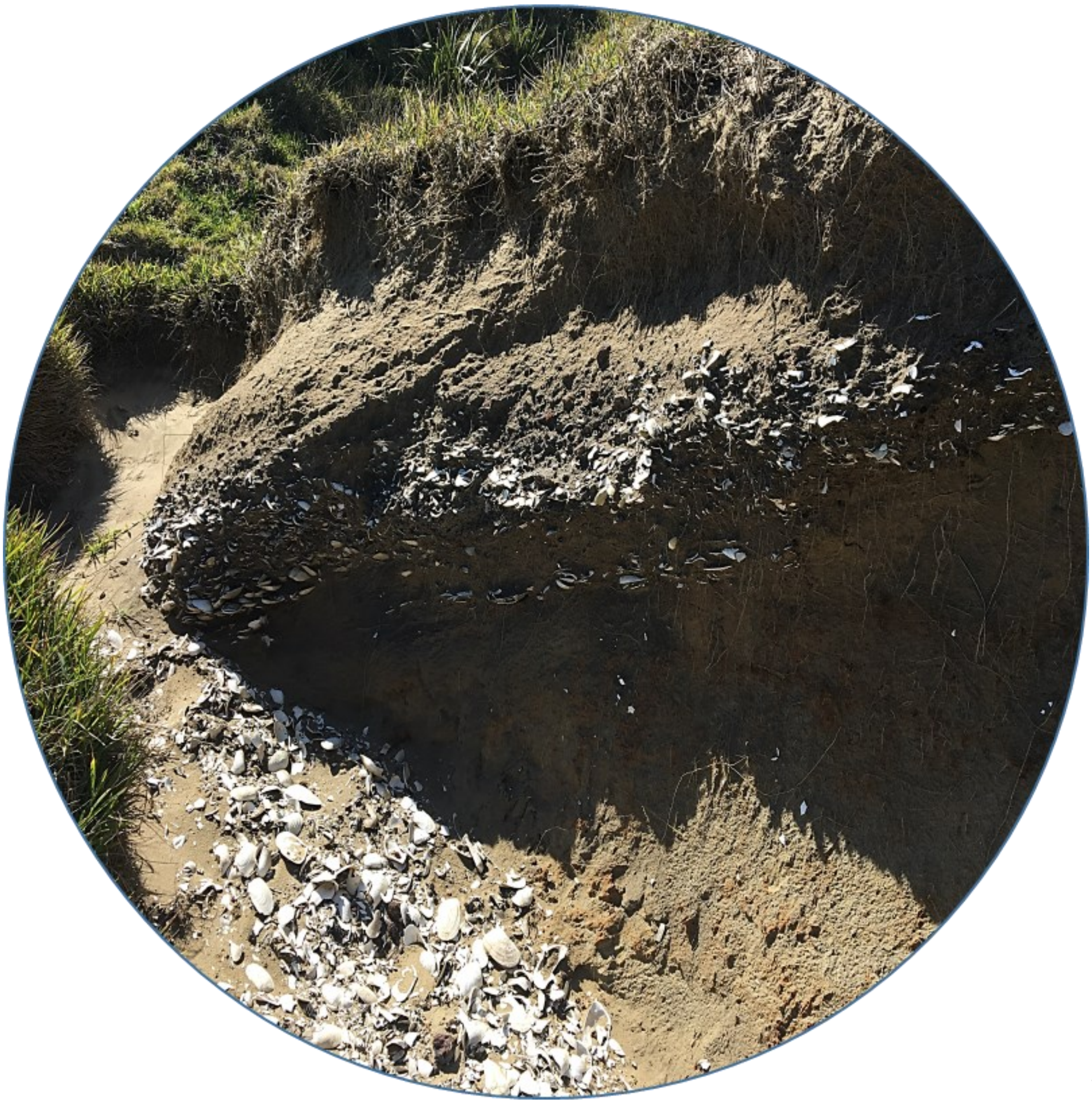
These exploratory and resource driven expeditions to the south may have allowed visitors to recognise habitat similarities, leading to the transmission of environmental knowledge, either by travel back north or via routes of communication. This may have seeded the idea of toheroa translocation to southern beaches, creating an incentive for long-distance whakatīpu mataitai of toheroa. Subsequent journeys of northern groups to obtain lithic resources, such as argillite, from the Riverton site, may have provided the opportunity to transport kaimonana during these expeditions. It is clear from contemporary voyages of waka hourua, that these journeys would be not only feasible, but would have occurred in relatively short periods of time. Transport of toheroa may have been undertaken by ancestors of, or early communities from, Kāti Māmoe, earlier on in the prehistoric sequence (1400s). Kāti Māmoe have links with ancient hapū in

Taitokerau and Muriwhenua and were also likely to have intimate knowledge of toheroa as an important mahika kai species.

Kōrero tuku iho, like that of the two waka; Tākitimu and Uruaokapuarangi (Uruao), suggests that voyages such as these where often prompted, in part, by insights from previous navigators. This may have made way for pre-emptive decision making, based on environments and resources likely to be encountered, while also providing opportunity to consider resources which would be advantageous to bring on such a journey. Evidence provided here suggests that such a voyage was indeed plausible, and probably occurred on multiple occasions during the early phases of Polynesian colonisation and throughout the prehistoric sequence.

Chapter Three

Kia whakatomuri, te haere ki mua[16]: an archaeological perspective to inform toheroa distributions in the deep past



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[16] *I walk backwards into the future with my eyes fixed on the past* Māori whakataukī (proverb)

[17] Toheroa midden along the coastline of Ripiro Beach

3.1 Introduction

Gaining an understanding of the lives and behaviours of humans from eras with no written records can prove challenging. Indigenous oral histories can provide cultural and ecological narration of human practices in prehistory. However, over many generations, ancestral knowledge can become fragmented and lost, particularly post colonisation. Where this is the case, the archaeological record can play a role in piecing together our understanding of the ancient past. Archaeological tools, such as shell midden, may provide insight into human movements, resource utilization and community and societal structure (Clune and Harrison, 2009); all of which can contribute to our understanding of a peoples way of life in the deep past (Balbo et al., 2011).

Archaeological evidence of an artefactual nature (structures or tools clearly constructed by humans) is much less prevalent in coastal regions than in inland areas (Coster, 1983). This may be due to the lack of long term domesticity of people along the coast, with inland areas more likely to be camping sites and larger settlements. One example of this is evident in large, single species (*Anadara granosa*) shell middens found along the Abydos coastal plain of Western Australia. These are suggested to be remnants left by large indigenous groups living a semi-sedentary lifestyle after the wet season, occupying an area and taking advantage of specific coastal species on an annual basis (Clune and Harrison, 2009). Coastal areas may serve an important function in large scale processing of marine resources (Coster, 1983). Further to this, coastal archaeological sites are often damaged or erased by the dynamic nature of the coast and ocean, from changes in sea level, erosion and historical or recent human activities (for example, human fossicking, off-road vehicle use, land use works etc.) (Brooks et al., 2008). Together, these factors increase the challenge of trying to understand the history and deep past of a coastal region and people.

Middens, which are formations containing biological remains such as shell and bones, are archaeological features that are ubiquitous in coastal regions (Waselkov, 1987). Shell middens have been described as refuse heaps, but they are much more complex than this. They can range from small and seasonal sites, to massive intricately deposited mounds enveloping entire landforms, these symbolising an indigenous groups intrinsic connection to the resource that has been utilized, the area which has been occupied and the subsequent remains left behind. In this way, middens may be deeply significant to indigenous both past and present (Reeder-Myers et al., 2022).

Some of the oldest known shell middens are the Danish '*køkkenmøddingers',* these large shell middens representing the most prominent archives of information on the lifeways of the last hunter gatherers in Scandinavia (Balbo et al., 2011; Larsen et al., 2018). Middens generally lack artefacts within their deposits, yet they are often informative in constructing a picture of human behaviours in prehistory and their relationships to coastal resources. Because of the lack of artefacts, the first discovery of Danish middens gave rise to the discussion as to whether these sites were natural phenomenon or were created my humans. To solve this question, scientists from several disciplines came together, including an archaeologist, zoologist, a botanist and an expert on molluscs and in 1851 the *køkkenmøddingers* were placed in their correct context, as settlement remains from early human activities (Gutiérrez-Zugasti et al., 2011). The development in Danish shell midden research has oriented towards understanding ecological and economic aspects of a site and middens are investigated as a whole, in order to expose and understand habitation of an area from its cultural layers (Gutiérrez-Zugasti et al., 2011).

Globally, shell midden analysis has helped understand key topics in human history, such as human dispersal, resource management, human impacts on intertidal environments and the development of complex societies. Further to this, shell middens can reveal human mediated changes in species distribution patterns and ecology. It is suggested that human impact on coastal environments may have modified Pacific Island mollusc communities as early as 4 ka (Balbo et al., 2011). Middens can tell us about a species availability, size and abundance as a food source, where that food source may have been collected, how species have been harvested, the diet preferences of differing species to people and how all of these may have changed through time within an area. To determine the time period in which a midden was created by people (and therefore the era in which a coastal location was inhabited), midden material such as shell and bone is often dated using radiocarbon methods (Enright and Anderson, 1988; Gutiérrez-Zugasti et al., 2011).

Over several decades, shell midden archaeology in Japan has made significant advances in both theory and method. Japanese midden studies have contributed significantly to understandings in various subfields including environmental anthropology, historical, cultural and evolutionary ecology and palaeontology (Habu et al., 2011). Extensive data exists of regional variability in shell middens across north-eastern Japan. A comparative analysis of shell middens from four regions was undertaken by Habu et al. in 2011. The information extracted from such analyses provided evidence for subsistence strategies spanning thousands of years.

Research problems surrounding comparative analysis of shell midden include the vast variability of shell midden sites and trying to define a midden area for quantitative analysis. It is necessary to direct research efforts to exposing as large an area of midden as possible to extract useful data regarding site layout and function. Choices such as these should be informed by ethnographic information and indigenous knowledge (Gutiérrez-Zugasti et al., 2011). The effect of changing coastlines and sea-level rise on the preservation of coastal sites is also a confounding issue, with systematic methods of quantifying these effects still largely missing from shell midden methodological approaches (Balbo et al., 2011).

Midden formation

Large mounds of curated shell stand today as monuments to long-term sustainability.[18]

Along the coast, midden formation is reflective of the forms of harvesting that has been undertaken in an area and the temporal scale to which this harvesting has taken place. Low, long shell mounds can often be found, these orientated parallel to shorelines and closely distributed to associated molluscan resources. Gatherers may return to the same general area for many years, creating shell debris which may completely cover an area of ground and create an seemingly continuous, undulating midden, though in reality it would be many individual shell heaps built up through time (accretion midden) (Waselkov, 1987). Blanket middens, which are a result of a single large deposition event, are much less documented than accretion middens. They are considered the result, from rapid processing and disposal of a large amount of shells dumped either near a permanent camp or at a site purely for shellfish preparation for storage or trade (Waselkov, 1987; Habu et al., 2011). There is ample evidence that shellfish resources were smoked, dried and preserved prehistorically and animals collected and prepared may have been eaten months later, far away from the place they were harvested (Coster, 1983).

'*In situ*' middens are a preserved remnant of a former age, remaining almost exactly as they were at the time of deposition. The constant movement of sand by wind and water can deflate '*in situ*' deposits leading them to collapse and scatter, often across vast areas. (Slocombe, 1991). Deflated middens can often be difficult to interpret or be of lesser archaeological value. They are a series of deposits through time which have collapsed down upon each other, leaving a mixture of both natural and cultural remains (Slocombe, 1991).

Natural beach deposits and shell banks may also provide insights into both prehistoric and prehuman species distributions in an area. Natural shell beach deposits appear via a process of natural accumulation and can often develop on sand bars in the mouths of river estuaries, over long periods of time, forming natural shell banks with horizontally layered stratigraphy (Bailey, 1977).

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[18] Reeder-Myers et al. (2022) Pg. 10.

Midden analyses in Aotearoa

Within Aotearoa, archaeologists did not turn their attentions to the analysis of non-artefactual remains (such as middens) in archaeological sites until the mid to late 1960s. Prior to this, shell midden deposits were largely neglected during archaeological digs and as a consequence, there is a lack of recording of valuable midden data, particularly of shell midden, before the 1960s. However, Davidson (1967) suggests that several pre-1960s archaeologists did give some attention to midden deposits, usually when excavating sites for artefacts, and so, even if unwittingly, have contributed to the growing body of knowledge surrounding shell and bone middens. Archaeologists began to become interested in middens with the discovery of moa bones in archaeological sites, this prompting a new era of archaeology in Aotearoa. Researchers were becoming aware of the ability to make inferences of man's relationship to his environment through the analysis of middens (Davidson, 1967). The first systematic attempts at midden analysis and classification had only begun around 1958 (Davidson, 1967). Once attention had turned to cultural midden deposits, analysis of these have led to a much greater understanding of early Māori subsistence patterns from a western perspective.

The value and cultural significance of midden sites to Māori is deeply rooted in cultural identity, with ancient middens a direct reflection of a peoples connection to their environment and their livelihood. Many midden sites would be associated to areas of mahika kai husbandry, and reflect ancestral inheritance, a workable knowledge of the resource and a responsibility to that resource; a principal known as ahi ka roa (McIntyre, 2007; Dacker, 1994). These concepts have been explored in depth in Chapter Two.

Long-distance translocation of toheroa

Aotearoa (New Zealand) is unique in that it has a very young prehistory. It was one of the last major land masses occupied by humans, and as such, oral traditions/histories can provide a window into the lives of the earliest occupants. Although much oral tradition (kōrero tuku iho) has been lost following colonisation, many oral traditions still remain and are of great cultural, ecological and historical value. Midden analyses may contribute significantly to concepts or hypotheses about prehistory which have derived from oral history or other fields of research. One such hypothesis which may be interrogated using archaeological means, is the long-distance transport and translocation of an endemic bivalve species, toheroa, by Māori.

Ross et al. (2018) have suggested that, based on genetic analysis, the unusual distribution of toheroa within Aotearoa is a consequence of prehistoric translocation. They hypothesised that toheroa are not endemic to Te Waipounamu (the South Island) but were translocated there, prior to the 1800s. Oral tradition and history surrounding shellfish enhancement and restoration practices indicate that, prehistorically, Māori transported and transplanted shellfish, such as the large endemic surf clam, toheroa, to different areas around Aotearoa. It is suggested that such activities were undertaken many times prehistorically, as part of traditional resource management practices (Futter, 2011, see also Chapter 2). The oral record of putative long-distance translocations is however, particularly fragmented and incomplete. Combining information gathered from midden analyses with oral tradition may generate a more complete understanding of the traditional practices of toheroa translocation.

Archaeological research into Māori shellfish middens have identified that toheroa were a significant resource prehistorically and have been collected and consumed for many hundreds of years. This is specifically true of the coastal dune middens along the West Coast of Te Ika-a-Māui (North Island) (Akroyd et al., 2002, 2008). Shellfish middens with stratigraphic layers of toheroa (often in their hundreds) are a prevalent fixture of coastal areas spanning several areas along the West Coast of Te Ika-a-Māui. If toheroa were present within southern areas for the entirety of Māori occupation, they would also be a major component of coastal middens within these dune systems.

Aims and objectives

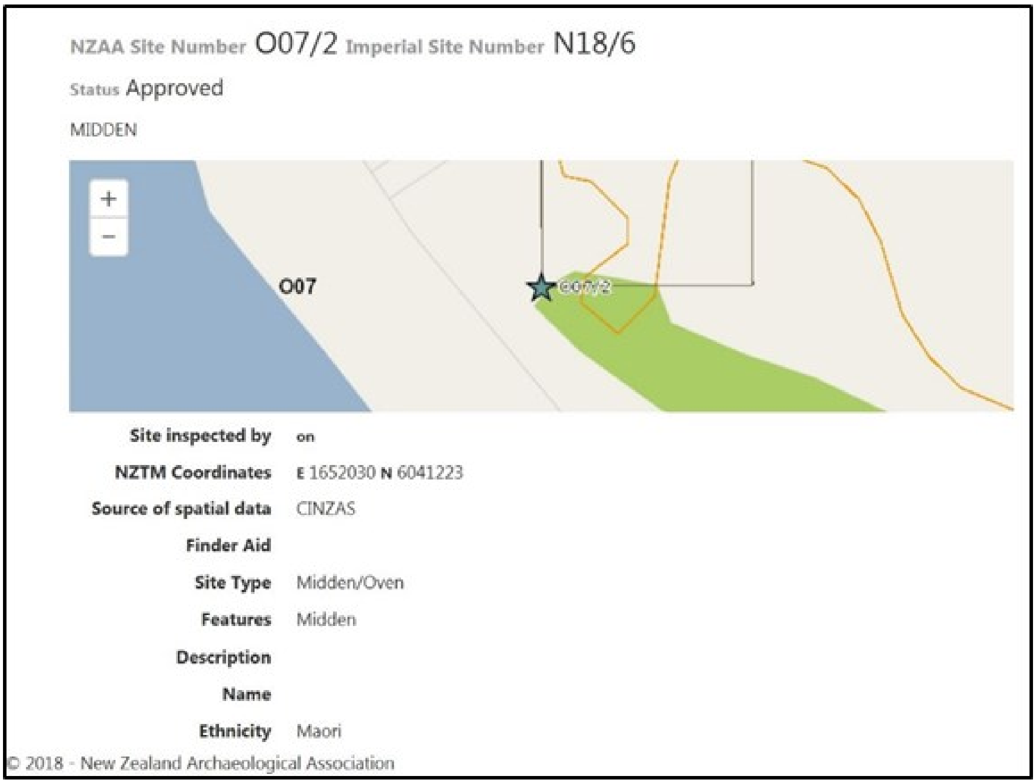
The principle objective of this chapter was to identify midden sites across Aotearoa with toheroa shell present and if possible, to date the sites. A nationwide review and analysis of midden data from all areas associated to toheroa populations (see Figure 3.2 for all locations) was employed to challenge the "translocation hypothesis". A particular focus is given to middens along the South Coast of Te Waipounamu and along the northern west coast of Te Ika-a-Māui. Ross et al., (2018) has hypothesised that toheroa were translocated from northern populations to southern populations. We suggest that if toheroa populations were present at southern and northern locations concurrently through time, we would expect to find similar proportions of toheroa middens adjacent to these populations. If toheroa were introduced to Murihiku, they would be absent in archaeological records prior to this time and reflective of this, be absent in many middens. If this is the case, the current study may provide an indication of if and when toheroa were introduced to Murihiku.

3.2 Methods

Comparative analysis of coastal middens allow us to make inferences about the geographical differences in subsistence strategies of Māori prehistorically. These analyses are important for a number of reasons, including informing researchers about biological resources that were available or present in different regions in the past. They can also provide supplementary evidence in support of traditional narratives (Reeder-Myers et al. 2022). The current study is in alignment with this and has utilized archaeological tools to investigate the hypothesis of long-distance translocation of toheroa by Māori prehistorically, from the upper west coast of Te Ika-a-Māui, to the southernmost beaches of Murihiku (Te Waipounamu).

Primary resources for toheroa midden search

A meta-analysis of pre-recorded shellfish midden sites was conducted, utilizing the Heritage New Zealand (HNZ) Digital Library and ArchSite NZ (www.archsite.eaglegis.co.nz/NZAA/), an interactive map and database. The HNZ Digital Library, as of March 2018, comprised a total of 6750 archaeological reports scanned and/or converted to PDF format, the oldest dating back to 1958. The digital library was obtained from Heritage New Zealand in Wellington, courtesy of the Archaeological Manager. ArchSite NZ is an online database which incorporates information from the New Zealand Archaeological Association (NZAA) Site Recording Scheme, a recording system for information regarding archaeological sites within Aotearoa/New Zealand. ArchSite NZ has over 60,000 sites held within its database, using ArcGIS (Geographic Information System) mapping technology to manage and display information, with the user being able to obtain information by navigating through an interactive map (Figure 3.1).



NZAA Site Number O07/2 Imperial Site Number N18/6

Status Approved

MIDDEN

Site inspected by	on
NZTM Coordinates	E 1652030 N 6041223
Source of spatial data	CINZAS
Finder Aid	
Site Type	Midden/Oven
Features	Midden
Description	
Name	
Ethnicity	Maori

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Figure 3.1 Example of ArchSite NZ site and basic description.[19]

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[19] Taken from https://archsite.eaglegis.co.nz/NZAA/Map

Sites within ArchSite NZ often have a corresponding HNZ report. Within ArchSite NZ an "authority number" and a "site number" is given. The authority number is based on grid references within a 100m^2 area using co-ordinates as a baseline. These sites were recorded in the 1960s and 70s, and many HNZ reports correspond with and were written during these years. Attempts to find middens which are referenced with an "authority number" is often not achievable, as the area in which it is mapped is too wide spread. Sites recorded in this era usually comprised only brief aids to relocation, with grid references derived from old inch to the mile series maps (Johnson, 2014). In contrast, the "site numbers" are GPS co-ordinated, with GPS only coming into use around the year 2000.

Different site labels and disparity of recording between sites in HNZ reports and sites in ArchSite NZ made it necessary to search for each resource (HNZ Digital Library and ArchSite NZ) independently. This was done by searching through the digital library catalogue for reports of significance and later searching through ArchSite NZ sites. Following this, the next step involved re-calibrating information from reports back to their ArchSite NZ counterpart in an Excel database. New sites of significance, which had not been found previously in a report, were also identified while searching through ArchSite NZ manually (on a site by site basis).

Study areas

Pre-recorded archaeological sites across Aotearoa are in the order of tens of thousands, therefore a locational analysis was undertaken, focusing only on areas of significance to toheroa. Coastal locations in any way significant to toheroa distribution, historically and presently, were included in this study (see Appendix A (Table A 1) for all locations). These areas were chosen based on information from a variety of sources including suggestions from kaitiaki, ecologists, archaeologists and community members across Aotearoa, and through literature reviews of ethnographic and ecological studies pertaining to toheroa.

Within Te Ika-a-Māui, extensive toheroa populations have been documented on exposed surf beaches; along the West Coast of Te Taitokerau (Northland); Te Oneroa-a-Tōhē (Ninety Mile Beach), Ripiro (Baylys Beach, Glinks Gully, Omamiri), Muriwai (Te Oneone Rangitira) and beaches on the Kāpiti-Horowhenua Coast beaches; such as Tangimoana, Waitārere, Hokio Beach, Ōtaki Beach, Te Horo Beach and Peka Peka (Williams et al., 2013 and references therein). Other areas known to have had smaller populations of toheroa within Te Ika-a-Māui, either historically or currently, can be seen in Figure 3.2 (Cassie, 1995, Redfearn 1971, Morrison and Parkinson, 2008, Williams et al., 2013).

Toheroa have a more restricted distribution in Te Waipounamu. Prominent populations grow along the South Coast of Murihiku (Southland) including at Ōreti Beach and at Bluecliffs and Orepuki Beach in Te Waewae Bay. Smaller populations have been documented and/or observed along the East Coast including at Kaikōura, Hampden, Moeraki, Waikouiti and Long Beach (Figure 3.2) (Redfearn, 1974; Ross et al., 2017 and references therein). A list of all locations which were included in the search can be found in Appendix A.

Figure 3.2 displays the current and historic locations of toheroa (*Paphies ventricosa*) within Te Ika-a-Māui (the North Island) and Te Waipounamu (the South Island) in Aotearoa (New Zealand). Extensive populations (historic and/or current) are in bold. Locations along the east coast of Te Waipounamu are anecdotal and locations which are italicized are suggested areas of translocation activities.

Site search parameters

To begin, the HNZ digital library catalogue was searched using the term midden*. Reports were noted, extracted from the library and stored by location, for future investigation. This process was then repeated, using locations of significance to toheroa as search terms (Appendix A). Place names, both Māori and European, Territorial Local Authorities and all other iterations of location titles were searched for in the catalogue.

Following the search of the HNZ digital library, sites within ArchSite NZ, in areas of interest (see Figure 3.2) were searched on a site by site basis. This process involved selecting each site to determine its site classification (midden, midden/pit, terrace, pa etc.). Records of all sites classified as midden were then opened and examined. Each site record includes a site description which has been provided by the investigator at the time it was examined. Most areas tend to be covered by a particular archaeologist, or team of investigators, who were at one point working on a certain project in an area.

Additional ArchSite NZ midden searches of the Kāpiti-Horowhenua and the Murihiku coastline were undertaken, to insure that middens within these areas were represented accurately. Sites within these areas appear to lack corresponding reports, which is usual for many archaeological sites identified in ArchSite NZ. Reports are generally only produced when archaeological monitoring of an area is undertaken prior to earthworks (e.g. roading of forestry), often as part of the consents process, or as part of a broad scale archaeological monitoring programme (Coster, pers comms; pers. obs.).

Midden assemblage data

A count of all midden sites which were examined for toheroa was retained, these being found from both HNZ archaeological reports and ArchSite NZ. Site numbers, location, author/investigator and co-ordinates were retained only for sites which had toheroa present, excluding Murihiku sites in which all midden site details were retained for further analysis. Archaeological sites which were searched through in ArchSite NZ were, whenever possible, limited to between 5 and 10km from the coast.

All of the information available for a midden site in which toheroa were present was recorded. These details were taken either from reports, ArchSite NZ or a combination of the two. Descriptions available for any particular site could range from very detailed (number of middens, midden type, size etc.) and quantitatively measured (lengths and minimum number of individuals; MNI), to only a few words describing contents of the midden. A midden that was found to have no account of species present was omitted from the search, as were sites considered to be historic (post-colonial).

Archaeological sites along the South Coast of Murihiku, a coastal area beginning at Hakapureirei (Sandhill Point) and ending at Tiwai Point, (Figure 3.5) were further analysed to better visualise total middens within these areas. The site co-ordinates for every midden site was entered into ArcGIS and a map was produced.

ArcGIS mapping analysis

Presence-absence locational data for toheroa middens were imported into ArcMAP Version 10.4.1 and overlaid on an existing geographic shapefile (New Zealand coastlines and islands polygons topography[20]). The co-ordinate system was set to a NZ traverse Mercator (NZTM 2000) projection. NZTM is used for small-scale mapping, and is based on the NZGD 2000 datum using the Geodetic Reference System 1980 (GRS80) reference ellipsoid.

Within ArcMap Version 10.4.1, the following maps were produced; midden sites identified with toheroa present, sites described with abundant toheroa, toheroa size classes in sites with larger individuals, toheroa sites with low abundance and all midden sites along the South Coast of Murihiku. Toheroa abundance and size class maps can be found in Appendix A.

Investigation of a sub-fossil beach deposit in Murihiku

In 2018, a sub fossil beach deposit located at Sandy Point (New River Estuary) 1.7 km inland of Ōreti Beach (Figure 3.5 for location), of Waihōpai was investigated. The deposit was photographed and key species were recorded. The beach deposit was considered of interest as it is estimated to be around 4000 years old (Chandler, 1977) and the shell deposits are from areas in which contemporary toheroa beds now reside.

3.3 Results

From the top of Te Ika-a-Māui, down to Pouto Point (North Kaipara Peninsula), covering an area of approximately 330km of coastline, 968 middens were identified and searched for toheroa. Of these middens 40% were found to have toheroa present. This is only a partial representation of middens within the area, hundreds more are recorded in ArchSite NZ along this coastline, but not all could be incorporated due to time restraints. Further to this, along less easily accessible West Coast beaches, there are many more middens that have not been formally documented by any researcher to date. This is particularly true of Ripiro Beach (approximately 72.4 km stretch of coast, Figure 3.8) and its complex, stabilised dune systems. From personal inspection, there are many large middens within these foredunes that are not recorded within the ArchSite NZ database. These middens are large, containing thousands of

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[20] LINZ Data Service (https://data.linz.govt.nz/license/attribution-3-0-new-zealand/)

shells, are almost exclusively toheroa and can be seen in situ and spilling down the sides of eroding dunes (see Figure 3.3 for examples).

Toheroa shells are not similarly abundant in middens on the southern coast of Murihiku. Along the South Coast, approximately 140km of coastline (Sandhill Point to Tiwai Point) was searched in Archsite NZ and the Heritage New Zealand Digital Library for middens. Of the 122 midden sites recorded, only 6.5% (8) contained toheroa (see Table 3.1). An exhaustive search of reports relating to these areas confirmed the scarcity of toheroa in Murihiku middens. Undocumented shellfish middens are most likely to exist, though the prevalence of toheroa within them is unknown. From personal inspection of some areas and communications with kaitiaki at Te Rūnaka o Waihōpai (Invercargill) and with local historian Lloyd Esler, ancient toheroa midden deposits do not appear to be a feature of these areas.

Toheroa middens within the Kāpiti-Horowhenua coastline are also sparse. The coastline from Tangimoana to Waikanae, an area approximately 80 km along the coastline, was searched for middens. From ArchSite NZ, 340 middens in total were counted, of which 4% (14) had toheroa present. Northern West Coast beaches which extend South from Dargaville were found to have extensive toheroa middens. From the South Kaipara Head, down through to South Manukau Head, an area of coastline covering approximately 100km, 247 middens were investigated, of which 31% contained toheroa. Further to this, it is likely that middens are highly underrepresented within the current study, in these areas as well. A breakdown of middens searched, toheroa presence and percentages by location can be found in Table 3.1, while midden proportions are presented in Figure 3.4.

Other areas where small amounts of toheroa midden were found include; Doubtless Bay (Northland East Coast) and Whakatāne (East Coast, Bay of Plenty). Overall, a total of 486 sites with toheroa were identified from Te Ika-a-Māui and in Murihiku of Te Waipounamu within the current study. Of these 486 toheroa midden sites, 310 sites (64%) were recorded as deflated, eroded or exposed in some way, while 255 (52%) were identified as *in situ* deposits. 159 sites (33%) were found to be exposed or eroding, while also having *in situ* components. Many sites had several midden, all at varying degrees of erosion.

Table 3.1 Locations and number of middens (toheroa present vs absent) identified within the current study.

Location	*Middens identified*	toheroa absent (total number/%)	toheroa present (total number/%)
Te Aupōuri Peninsula	586	365 (62%)	221 (37.7%)
Mitimiti-North Kaipara Head	382	215 (56%)	167 (43.7%)
South Kaipara Head- South Manukau	247	171 (69%)	76 (30.7%)
Kāpiti-Horowhenua Coast	340	326 (95%)	14 (4.1%)
South Coast, Murihiku	122	114 (93%)	8 (6.5%)

Figure 3.3 images of several undocumented *in situ* and eroded toheroa midden identified at Mahuta Gap, Ripiro Beach, on the West Coast of Te Ika-a-Māui, in 2018.

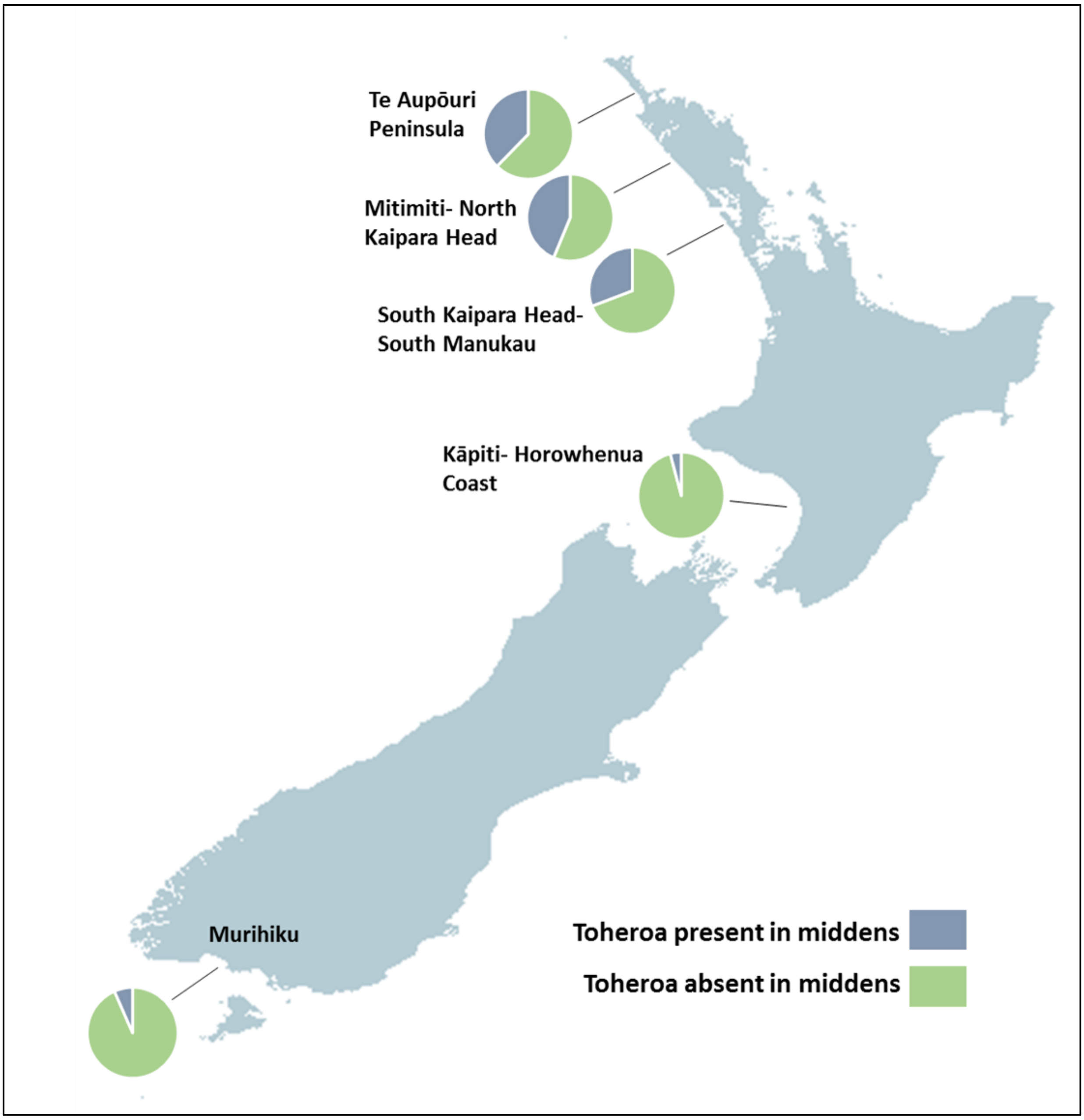

Figure 3.4 Map of Aotearoa (New Zealand) with pie charts indicating the proportions of coastal middens in which toheroa (*Paphies ventricosa*) were identified as being present and absent.

Recordings of sites/midden did not always provide information about species abundance. Of the middens containing toheroa, where abundance was recorded, 98 described toheroa as being either abundant, the predominant species, or the only species present. These sites were found to cluster in areas along Te Oneroa-a-Tōhē, several were found between Ahipara and North Kaipara and a large portion were found within the North and South Kaipara Peninsulas. The southernmost middens in which toheroa were abundant were located at South Manukau Head. Conversely, in 179 of the middens identified in this study, toheroa were found to be rare or were not the predominant species. On occasion, only a single toheroa was found in a midden or at a site.

Several sites were found to have both abundant toheroa and occasional toheroa. In these instances, the site had several midden components. Low abundance, or lack of predominance appears to be a feature of all locations where toheroa midden has been found, including all areas along the upper West Coast where abundant toheroa have also been located. However, unlike the upper West Coast of Te Ika-a-Māui, middens along both the Kāpiti-Horowhenua Coast and South Coast of Murihiku were found to have low abundances, or only single individuals present if the recording of a site made mention of abundance. It is important to note that not all sites had descriptive or measurement data available. Maps displaying sites with high abundance and low abundance can be found in Appendix A (Figure A 1 and A 2).

Reports which recorded the size class of an individual were collated and a map was produced, which can be found in Appendix A (Figure A 3). Of these sites, 68 middens were described as containing large toheroa. These sites were concentrated in the far north (Te Oneroa-a-Tōhē), in the North Kaipara Head and extending as far South as Muriwai Beach. There are many middens for which size data was not recorded and this is a reflection of the varied quantitative approaches employed by archaeologists during surveys.

Further analysis of the South Coast of Murihiku

Archaeological sites along the South Coast of Murihiku were further explored. A length of the coast relating to historical and contemporary toheroa distribution was chosen (Sandhill Point to Tiwai Point) and all midden sites which exist within Archsite NZ were identified and mapped (Figure 3.5). There are comparatively few midden sites recorded along this coast and toheroa midden sites are rare.

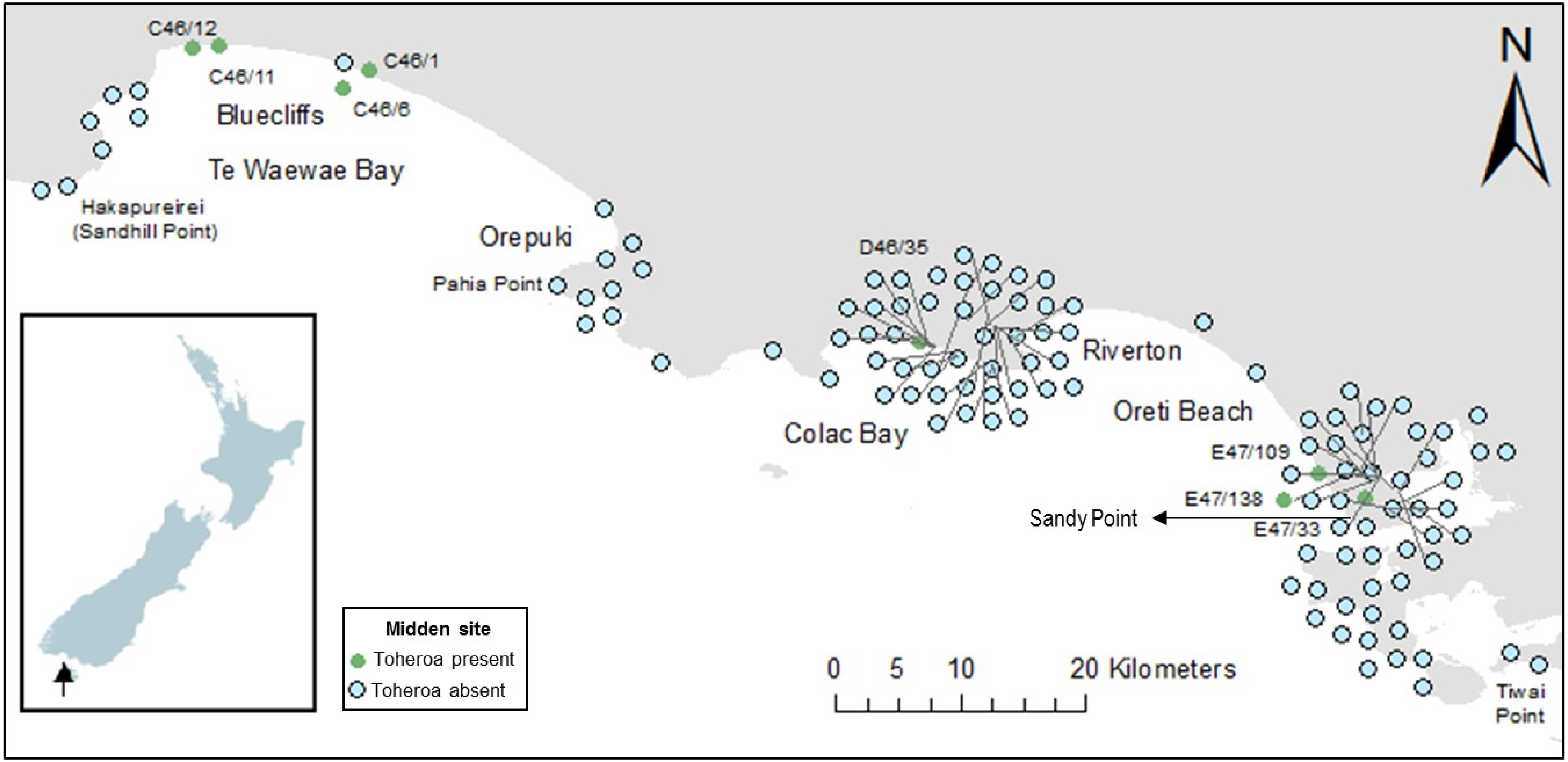

Figure 3.5 displays a map of all middens found between Hakapureirei (Sandhill Point) and Tiwai Point, South Coast of Te Waipounamu (the South Island). Midden with toheroa (*Paphies ventricosa*) present are labelled. Toheroa site names are the closest label to its corresponding toheroa midden point

Sub fossil beach deposit

A c. 4000 year old sub fossil beach deposit located near Ōreti beach, was found to span several metres along the shoreline adjacent to the New River Estuary. This deposit has been undergoing many years of erosion (Figure 3.6). Several different shellfish species from a range of habitats were present within the deposit (Table 3.2). These included *Tawera spissa, Zethalia zelandica, Crassula aequilatera, Paphies subtriangulata, Mactra discors, Ruditapes largillierti, paphies australis, Mactra ovata* and *Ostrea chilensis*. *Crassula aequilatera* (Triangle shell) and *Mactra discors* (ocean cockle, known as a Southwesterner to local Southlanders) are large surf clams which often wash up along Ōreti Beach. The oyster *Ostrea chilensis* (tio) was also present and are found around the southern coastline growing on muddy bottoms, or sand gravel, attached to rocks and forming dense beds (Cook, 2010). *Paphies subtriangulata* beds are often found growing intermingled with toheroa beds.

Figure 3.6 shows a sub fossil shell deposit located at Water Ski Club Sandy Point, Ōreti River, Waihōpai (Invercargill). Taken May 2018.

Table 3.2 Shell present in sub-fossil beach deposit located at Sandy Point, Waihopai (Invercargill). Samples of the shells are held at the Coastal Marine Field Station, University of Waikato, Tauranga.

Species	**Habitat**	**Tidal height found**	**Class**	**Image**
Tawera spissa	Open coastal beach	Subtidal	Bivalvia	
Zethalia zelandica	Open coastal beach	Subtidal	Gastropoda	
Crassula aequilatera	Open coastal beach	Subtidal	Bivalvia	
Paphies subtriangulata	Open coastal beach	Intertidal	Bivalvia	
Mactra discors	Open coastal beach	Subtidal	Bivalvia	
Ruditapes largillierti	Sheltered harbours/ estuaries	Intertidal	Bivalvia	
Paphies australis	Sheltered harbours/ estuaries	Intertidal	Bivalvia	
Mactra ovata	Sheltered harbours/ estuaries	Intertidal	Bivalvia	
Ostrea chilensis	Sheltered harbour with muddy bottoms/ on rocks/ course sand gravel	Intertidal/ subtidal	Bivalvia	

3.4 Discussion (critical analyses of toheroa midden by location)

To better understand archaeological midden sites across Aotearoa in which toheroa are prevalent, in depth analyses of corresponding reports of interest was undertaken and are discussed below.

Te Aupōuri Peninsula

Te Oneroa-a-Tōhē lies on the West Coast of Te Aupōuri Peninsula and has extensive middens throughout and along its beach and dune systems (see Figure 3.7 for toheroa midden). Between 1976 and 1986 archaeological field work was undertaken along the Aupōuri Sand Dunes of Te Oneroa a Tōhē (covering approximately 120 km), by John Coster and his team. This resulted in the recording of approximately 400 archaeological sites within these areas (Coster, 1988). One of the aims of Costers' broad scale study was to establish a sequence of dates for human occupation sites on the West Coast dunes, through surveying and radiocarbon dating.

Samples of marine shell including *Paphies subtriangulata* and *P. ventricosa* were taken for radiocarbon dating from several sites during surveys of the Aupōuri Dunes. Radiocarbon dates appear to fall into early, middle and late categories. The earliest dated site in Northland was found at Paengarēhia (Twilight Beach) one of the northern most beaches of Aotearoa, where culturally archaic occupations occurred 600-700 years ago (Coster, 1982).

Carpenter (2014) identified several sites, including N02/1137 (ArchSite NZ), near Te Paki Stream in Aupōuri (Carpenter, 2014), where middens were dominated by tuatua (62.1% of midden contents) and toheroa (36.8%). Toheroa were small to average for their species size, with no individual exceeding 70.48mm (Carpenter, 2014). Carpenter suggested that none of the toheroa were over 2 years old, and that these results indicated that toheroa were collected from beds of younger individuals. It is possible these age classes of toheroa were purposefully targeted as a preferred size for transporting, eating or processing. Te Oneroa-a-Tōhē was utilized extensively as a route for travellers and was a major source of kaimoana, such as toheroa, providing marine resources for tangata whenua, prehistorically and through to the present day (Coster, 1988).

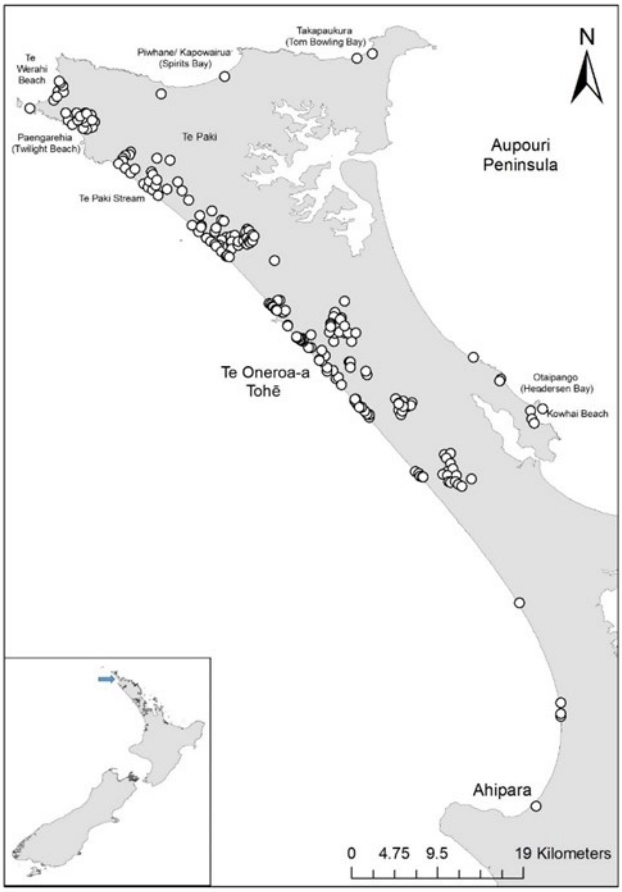

Figure 3.7 Map of the Aupōuri Peninsula displaying 221 toheroa midden sites identified from survey

Mitimiti, Hokianga

Mitimiti is a small township along the West Coast of Te Ika-a-Māui, located North of the Hokianga Harbour. Its beaches are known to have supported toheroa populations, with anecdotal evidence suggesting recent translocation of toheroa has been undertaken by kaitiaki both into and within this area. The limited archaeological attention that the northern Hokianga has received over the past 30 years has been due to the areas remote isolation (Bruce, 2002). Of the archaeological sites that have been identified in the Northern Hokianga, shell midden were found to make up 42% (Bruce, 2002). A survey of the area undertaken in 1977 stated; “sites are generally concentrated around streams (where the best toheroa beds occur at the present time [1977]) and rocky reefs which provide a greater variety of seafoods than the sandy beach” (Wright and Court, 1977; Pg. 23).

Maunganui Bluff to Pouto (North Kaipara Peninsula)

Ripiro Beach, known for supporting dense toheroa populations in the past, lies between Maunganui Bluff to the Kaipara North Head and is approximately 72 km in length (Akroyd et al., 2002). Ripiro beach is backed by stabilised dune systems and sandstone cliffs. Toheroa middens identified in this area are represented in Figure 3.8.

Formal identification and reporting of midden sites along the West Coast in the past have primarily been produced due to mandated archaeological surveys of areas which were to be affected by forestry operations (Waipoua Forest and Pouto Forest). Surveys largely occurred adjacent to the southern end of Ripiro beach within the Northern Head of the Kaipara Peninsula (Johnson, 2000; 2014). Outside of these areas, few archaeological surveys have been undertaken, particularly along the stretch of Ripiro Beach and its surrounding dune complexes. Consequently, many middens adjacent to toheroa beds remain undocumented and are therefore severely unrepresented in the current study.

Archaeological investigations on the Kaipara North Head area suggest that occupation has spanned the entire period of Aotearoa prehistory. Settlement of the area is suggested to have reached its peak in the 16th and 17th centuries but dropped dramatically in the late 18th century after initial contact with Europeans and outbreak of infectious diseases (Johnson, 1996).

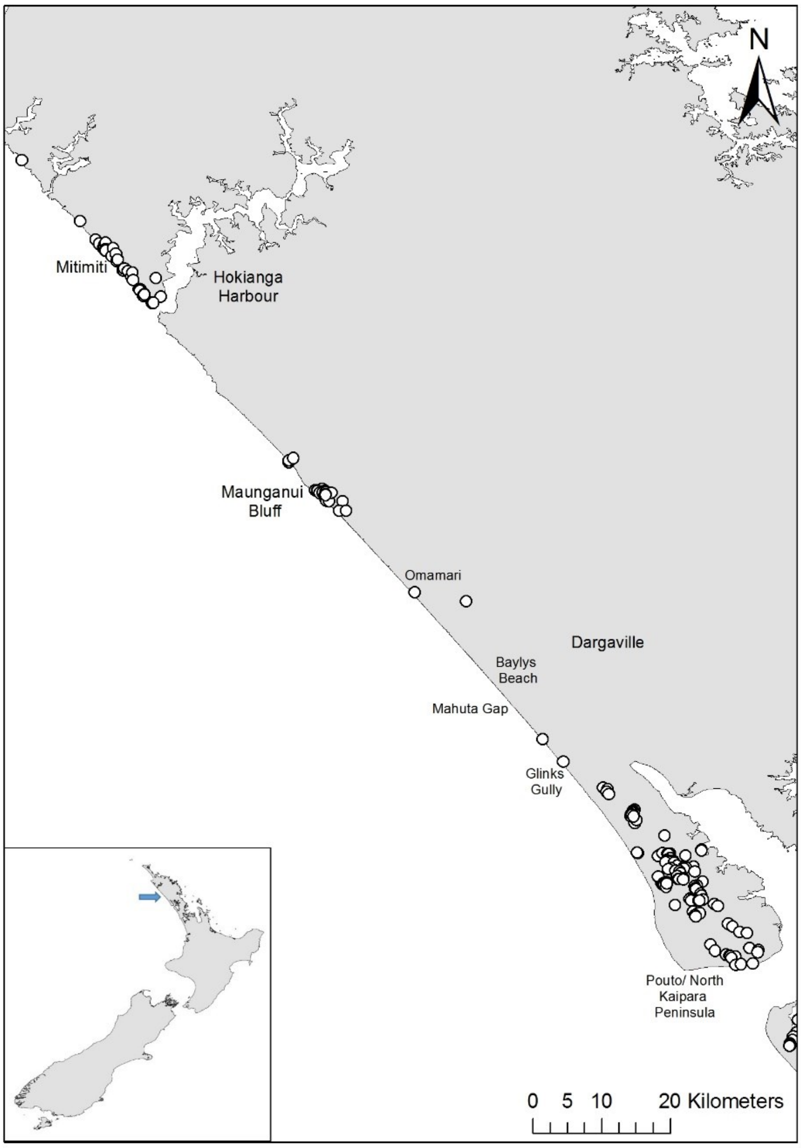

Figure 3.8 Mitimiti, Dargaville beaches and North Kaipara Head/Pouto displaying 167 toheroa midden sites.

Tāmaki Makaurau (Auckland) West Coast

Muriwai beach runs from South Kaipara Peninsula to Otakamiro Point (Figure 3.10). Several toheroa middens were found in these areas (see Figure 3.9), this a reflection of toheroa beds which have grown on the sandy beaches of Muriwai in the past.

Figure 3.9 Midden found at Muriwai. Photo by the infamous and soon to be councillor Dr Phil M Ross.

A midden site (Q11/36) reported by Hayward and Diamond (1968) inland of Bethells Beach (Te Henga), was of interest due to having species stratification amoung the midden layers and a variety of shellfish species, which is unusual for middens along this coast. One of the investigators stated;

> *Toheroa shells are found only in the very old sites. I arrived at this conclusion from sites I have located over the last 20 years. In every instance the layers in these few middens have followed the same pattern of shell deposits. The first layer is pure or almost pure toheroa shells, some measuring 7 inches, then working upwards the layers show other local shell-fish, then complete absences first of toheroa then tuatua while the top layer consists only of mussel and white rock shell or in many instances just mussel shells*.[21]

This may be an indication of fluctuations in the abundance of toheroa, followed by a decline in populations in the area through time. Alternatively, it may be a consequence of change in species preference by Māori in different time periods. Whatever the case, these middens, and

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[21] ArchSite NZ site report. Hayward and Diamond (1968)

others through northern Aotearoa indicate toheroa were present in this area during early periods of the prehistoric sequence.

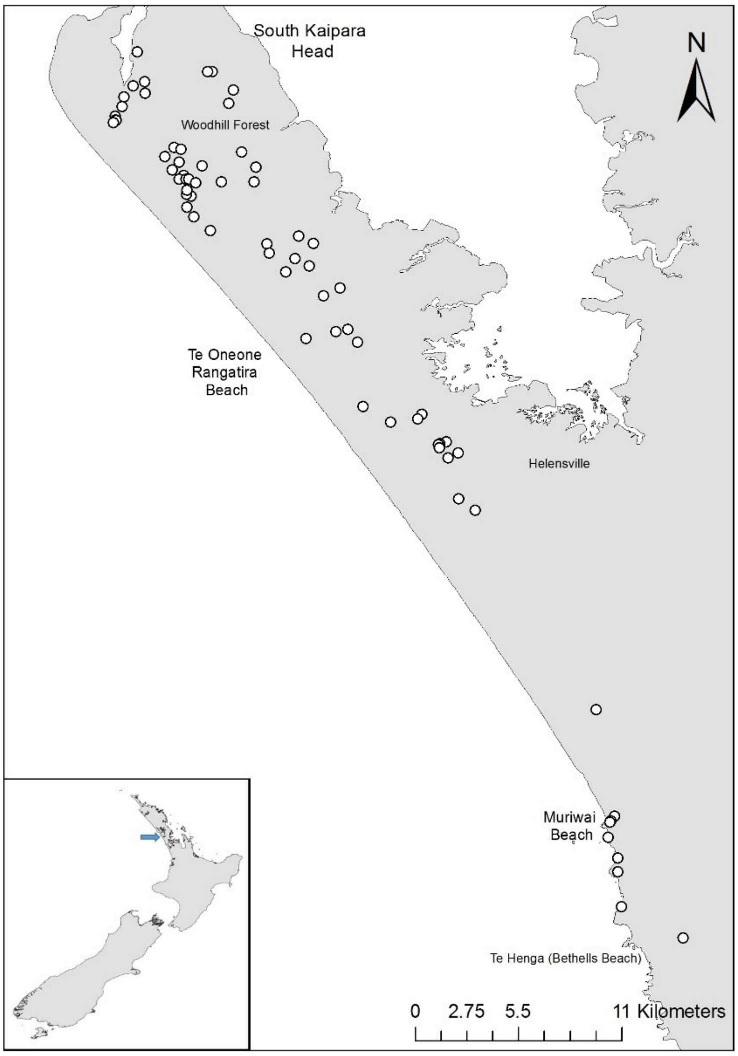

Figure 3.10 South Kaipara Head to Muriwai displaying 76 toheroa midden sites.

Kāpiti-Horowhenua Coast

Due to the dynamic action within the complex dune systems of the Kāpiti-Horowhenua Coast, archaeological sites in sand dunes of the area are suggested to have been periodically exposed and buried throughout time (O'Keefe 2002). O'keeffe (2002) suggests there are many midden sites located along the dune sequences, though there is little systematic recording undertaken along the coast, so it is likely there are many sites which are unidentified, unrecorded, difficult to locate or lost (McFadgen, 1997). Although this may be the case, O'keeffe (2017) maintains that enough sites have been recorded to give a clear indication of the types of occupation which occurred in the region prehistorically.

Most archaeological sites along the coastal dunes are middens (O'Keeffe, 2017). Midden content within the Kāpiti-Horowhenua Coast sites varies, with shell deposit and occasionally bone, providing evidence for both temporary resting places of people or occasionally permanent settlements. Middens along the coast are sometimes comprised almost entirely of tuatua (O'Keeffe, 2005). From radiocarbon dating of archaeologist deposits, the earliest dates on the Kāpiti-Howowhenua Coast fall in the fifteenth century AD. Māori are suggested to have had settlements along the Kāpiti-Horowhenua Coast for several hundred years (Dodd, 2016).

A survey was undertaken in 1984 by Bailey and Kozyniak, to identify archaeological sites along the coastal strip between Rangitikei River and the Manawatu River mouth (see Figure 3.11 for location of river inlets along the coast). Seventeen sites were found within the survey area, with the majority of sites presumed to be between 100-400 years old and tuatua were predominant to a large degree across all middens. Toheroa however, were not found within this survey. Bailey and Kozyniak (1984) comment on this, stating; "*The complete lack of toheroa (*Paphies ventricosa*) is surprising, but suggests that this highly-prized food species was not present on the coast at the time of the Māori occupation*" (Bailey and Kozyniak, 1984; Pg. 15).

A midden located north of Tangimoana (Figure 3.11), investigated in 1986, was found on a low lying sandy soil, presumably deposited on the edge of a swamp. The midden was dominated by fresh water mussels and tuatua, with several other marine species present in lower numbers, including toheroa. Cassells (1986) suggests the midden may represent a seasonal camp site of a small family group, with the occupants taking trips to different habitats nearby for kaimoana. The site is estimated to be anywhere from 200 to 400 years old (Cassels, 1986). Of the three samples taken, toheroa is present in only one, where it had an MNI of one and a composition percentage of 2%. Cassels (1986) states; "*The presence of toheroa is significant, as it shows that this species was present in the pre-European period, although apparently quite rare*" (Pg. 3).

Another site in Peka Peka was investigated and toheroa fragments (MNI of one) where found in one midden. This was considered notable "*because of the relative scarcity of toheroa in modern beach deposits*" (Dodd, 2017; Pg. 3), in the Kapiti-Horowhenua coastal area. Shell samples of *Dosinia anus* and *P. subtriangulata* from the site were dated and placed they ranged between the late fifteen and late sixteenth centuries, this considered to be later in the prehistoric sequence. Again, the presence of one shell makes it difficult to infer any information regarding a species population or abundance prehistorically.

Figure 3.11 Kāpiti-Horowhenua Coast displaying 14 toheroa midden sites identified from survey.

Waikanae

An archaeological site in Waikanae (see Figure 3.11) was found to have densely packed midden, with tuatua being dominant (88%) but toheroa also being present (12%) (Greig, 2003). Greig (2003) remarks that the presence of toheroa in this site was ‘very unusual’. The taxonomic identification was confirmed by Bruce Marshall (Te Papa Tongarewa Museum of New Zealand). Greig stated:

> *Although naturally occurring on the Kāpiti Coast, it is absent from the vast majority of the numerous shell middens recorded there. Further research is required to understand the possible reasons for this absence. The presence of toheroa in this midden makes it an unusual site of high scientific value.*[22]

In 2016, archaeologist Mary O'Keeffe was advised of a midden being revealed in the Ferndale Subdivision, located in Waikanae. The midden was identified as an untouched *in situ* deposit. Nine species were present, with the dominant species being tuatua (MNI of 1184). Toheroa were also present, although where very rare (MNI of two). O'Keeffe (2016) reflects that far fewer toheroa specimens have been found in surrounding middens in Peka Peka (Figure 3.11) than might be expected, given the available extent of coastline and that they are considered a delicacy today. She notes "*Specific further research on the historical prevalence and extent of toheroa is necessary*" (O'Keeffe, 2016; Pg. 26).

From the sites found along the Kāpiti-Horowhenua Coast and Waikanae, it appears toheroa middens were seldom a feature, which brings into question when or if toheroa populations were prolific along this coastline. Radiocarbon dating of shell material from archaeological sites in these areas indicate toheroa were, at the very least, present later in the prehistoric sequence (Peterson, 2007, 2008; Dodd, 2017). Prehistoric translocations to the area after the 1500s from toheroa populations further north may explain the sparsity of toheroa in middens of these areas. Random transportation events of small amounts of toheroa for food, or transport of shell for use as a tool, may also explain why some middens only had one or two toheroa shells.

Murihiku

The South Coast of Te Waipounamu lies within what is broadly termed Murihiku (Southland). The current study has focused on areas that fall within or near Te Waewae Bay, Colac Bay, Bluecliffs, Ōreti and Bluff (Figure 3.5). Ōreti beach, much like the west coast beaches along Te Ika-a-Māui, is a south-west facing coast, exposed to the prevailing wind and swell direction. This coastal area, along with Aupōuri Peninsula and the North and South Kaipara peninsulas is among the largest remaining active dune complexes in Aotearoa.

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[22] (Greig, 2003) Pg. 3

Te Waewae Bay

Te Waewae Bay is a large embayment adjacent to Te Ara-a-Kiwa (Foveaux Straight), which extends for approximately 45kms. The coastline of Te Waewae Bay is bound by 5 to 45 metre high cliffs, with historical changes in sea level promoting the formation of the cliffs. The Waiau River, a major tributary of western-central Southland is a prominent feature entering the bay and is suggested to have shifted back and forth from east to west through the historic period. The main sweep of Te Waewae Bay begins to the west stretching approximately 32 km to Bluecliffs Beach (Ritchie and Cave, 1977). This beach faces southwest and is a wide and formerly sandy[23], gently sloping beach, which backs on to coastal cliffs. The beach has been a recognized source of toheroa (Beentjes, 2006). Two rivers drain into Bluecliffs Beach, the Rowallan Burn and the Waikoau River (Ritchie and cave, 1977).

An archaeological survey of the Te Waewae Bay–Waiau catchment was undertaken by Ritchie and Cave in 1977, in which prehistoric and historic sites were systematically identified and recorded. Seventeen midden sites were identified with the investigators noting that very few of the middens found were undisturbed by either humans or the elements. Four sites were identified with toheroa in them. One site (C46/12, *see* Figure 3.3) found at the mouth of the Waikoau River was described as an interesting and ecotonal midden collection of species from varying sources; predominantly mussel, with small pockets of other species, including cockles, toheroa and catseyes (small gastropod) (Ritchie and Cave, 1977).

A sister site to this (C46/11), also located at the Waikoau River was found to have an in situ section of *Perna* sp. and *Mytilus* sp. (both mussel species), charcoal and bottle glass running for 26m towards the sea. Bottle glass indicates that this section of the midden at least, is from the European era. Below this layer, a second layer of a few *Perna* sp. and toheroa shells were identified. Within the same site an exposed area containing “finely communited and often burnt decayed shell” (Ritchie and Cave, 1977) is described, consisting of *Perna* sp., toheroa and small catseye/pūpū (*Lunella smaragda*). This layer varied in depth (up to 10cm) and bottle glass and .303 shells from firearms were found to lie at the surface. The descriptions of this site makes it difficult to place the site in time, though due to the presence of European artefacts and decayed shell, this site is likely to have been occupied in the late prehistoric, proto historic and/or historic periods.

Another two middens sites (C46/1 and C46/6) found at the mouth of the Groveburn River also had toheroa present, though abundances were not mentioned in the report. Midden within C46/1 was somewhat destroyed, with one *in situ* area remaining, consisting of *Perna* sp.,

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[23] A site visit in 2018 revealed the beach is slowly transitioning to rock and gravel and toheroa habitat has been lost.

Spisula sp. (surf clam), toheroa and Cooks turban (*Cookia sulcata*) shells (large gastropod), with a small description stating the "shell is very rotten", suggesting it is not an old midden, as evidence of tissue decomposition would indicate the shells have been discarded in the recent past. Midden within C46/6 was described as some broken and some whole small toheroa shells, measuring 7cm in length.

An archaeological site of importance within Murihiku is located in Te Waewae Bay is the Hakapureirei site (Sandhill Point, C46/31) and has been investigated several times in the past (Coutts et al., 1970; Walter and Jacomb, 2005). Nine midden features were found, all dominated by shell, though none containing toheroa. Many artefacts were found across this site, often in isolation, though there were several zones with higher densities of artefacts. One-piece bait hook fragments made of moa bone were recovered from the site and these are largely restricted to the earliest phase of the prehistoric sequence (Walter and Jacomb, 2005). The lack of any toheroa within middens adjacent to beaches known for contemporary toheroa beds is notable for this site.

Riverton and Colac Bay

Colac Bay lies between Te Waewae Bay and Riverton, along the South Coast (Figure 3.5). Located to the west of Riverton, it is characterised by a sweeping sandy bay backed by dunes. Within a small cove at the eastern end of Colac Bay, a large site (Site D46/35) called "the Riverton Site" was surveyed by Leach and Leach in 1980. Due to the large area covered by the Riverton site, midden and faunal analyses (including MNI) were calculated from three different areas in the survey. Of the shell species found across the site, mussels were found to form the bulk of the midden, followed by paua and catseye/pūpū. In one area studied, an MNI for toheroa of one was found. When remarking briefly on this find, the authors write;

> *The food status of the sandy shore individuals is in even greater doubt. Except in the case of the medium sized* Struthiolaria *which occurred in three areas, the others are so few in number that they may have been picked up on the beach for industrial purposes. A deliberate trip to the long sandy beach of Colac Bay for toheroa or other large edible bivalves would surely have been rewarded with a greater quantity.*[24]

The authors discuss other perplexities surrounding the presence of certain shellfish. A mud snail, from an estuarine environment was also found, in low numbers in the site. Of this they write;

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[24] Leach and Leach, 1980; Pg. 111

> *It is unlikely that either the four mud snails of the* Māori colpus *could have been thrown up on the beach in front of the site and there collected by the prehistoric occupants. They must therefore constitute evidence of transportation, presumably by man from an estuary. Once again the question arises: why so few? They are small enough to have been missed by the excavators but this argument does not hold for the heavy-shelled southern toheroa, which is also a rare component.*[25]

One feature of this site, that distinguishes it from other archaic beach middens, is the thousands of flakes which were, in places, piled several layers deep. Most of the rocks present were termed “Riverton argillite” and are suggested to be of local origin. Leach and Leach (1980) concluded that “*the occupants prime objective was the manufacture of a wide range of Archaic adzes from the local argillite*” Pg. 139.

Midden analysis, along with evidence of adze and flakes, has led to the conclusion that the area was a specialist camp whose occupants engaged in adze manufacture while utilizing surrounding coastal and forest resources. The area is suggested to be primarily used for the extraction and preparation of raw material for export and may not have been occupied for more than a few days at a time, during times of settled weather and over years (Leach and Leach, 1980). The presence of only one toheroa shell in the area gives little indication of toheroa distribution. The toheroa shell may have been used as a tool and transported to the area. Its presence within the site does not provide evidence for toheroa populations being present in the surrounding environment at the time of occupation. Further to this, the presence of one toheroa shell may indicate that the occupants had travelled from northern areas, with the knowledge of the South Coast and its stone resources incentivising the long-distance travel.

An archaeological survey from Riverton to Bluff (Tiwai Point) was undertaken by Cave et al. in 1978, covering a distance of 176km of coastline (see Figure 3.5). From archaeological investigations, it is clear that the Jacobs River Estuary (located in Riverton) was used extensively by Māori (James-Lee, 2010). Eleven sites were identified on the Bluff Peninsula, seventeen located around the New River Estuary (located between Ōreti Beach and Bluff), one at Ōreti Beach and twenty three along the Jacobs River Estuary. Of the sites found, 32 were identified as midden or oven/midden. Within the report, one midden site (E47/33, Figure 3.5) located at the Ōreti River mouth is described as a midden/oven with *Amphibola* (tītīko, mud snail), a predominance of cockles and “some toheroa”. This site was cross checked with site details in the ArchSite NZ Database, with the resulting ArchSite NZ descriptions of E47/33

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[25] Leach and Leach, 1980; Pg. 111

having minimal detail and no mention of toheroa. From the authors discussion, only two toheroa shells were found. Cave et al., (1978) write;

> *Few sites were found along the section of Ōreti Beach between the mouths of the New River and Jacobs River Estuaries. When the limited number of resources, the lack of shelter and water (only one stream enters this area) is considered the paucity of sites is not surprising. However the absence of toheroa (for which Ōreti Beach is famous) in middens except for two found in the New River Estuary area is worth noting*.[26]

Of the sites identified within Murihiku, none are described as having extensive toheroa middens, large toheroa or toheroa being the main or predominant species. This may be a reflection of inadequate midden reporting in some cases, or is an indication that abundant toheroa midden are not a feature of these areas. Prehistoric middens are a common characteristic found across Aotearoa, though archaeological investigations of middens in Murihiku, along with the knowledge surrounding the prehistory of Riverton and Murihiku, is suggested to be limited (James-Lee, 2010).

Further notes on Murihiku (Southland)

Lloyd Esler is an author, guide, educator and a notable historian of Southland, particularly of Waihopai and the surrounding coastal environments of the South Coast. A magazine article which featured Esler was written in 2017, by Phil McCarthy, focusing on the southern coastline of Te Waipounamu and in particular, Ōreti Beach, the Sandy Point peninsula and Omaui. The article speaks briefly of the erosion occurring at the beaches southern end, the transformations of the dune systems as a product of currents, storms and the natural instability of a soft shoreline. The article also speaks briefly of toheroa in the area. McCarthy writes;

> *One of Esler's more intriguing ideas is that the prized and scarce Southland delicacy toheroa are not native inhabitants of the area: the shifting sands show no signs of the shellfish beyond the past 100 years. "I've got a theory that toheroa were brought here and seeded, because they're not showing up in midden and the old dunes"*.[27]

Esler formed this hypothesis independently and has been an active observer of the southern coastline for 28 years (McCarthy, 2017). Having found this article, Esler was sought out for an interview. When asked about his theory that toheroa were not endemic to the area he suggests that;

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[26] (Cave et al., 1978) Pg. 9

[27] https://www.noted.co.nz/life/life-in-nz/southlands-oreti-beach-and-beachcombing-discoveries/

> *the lack of mention of them in any reference, the lack of any sign of them in old beach deposits suggests that they are a recent arrival and may not have been a traditional Māori food, until 100 years ago or when they first appeared*.[28]

Esler had undertaken a desk top search of all archival documents that pertained to toheroa in Murihiku. The earliest mention of toheroa was from a newspaper segment, The Otago Daily Times, published in Dunedin in 1906. The small excerpt simply states; "A novelty so far as southerners are concerned will be exhibits of canned toheroa, a very large species of clam, cockle-shaped, which is found on the Kaipara- beach" (Adams, 1906; Pg. 7).

The excerpt indicates that, to the European population of Murihiku at least, the presence of toheroa was unknown in the early 1900s. The Southland Fisheries Department became aware of the existence of toheroa populations near Riverton and at Te Waewae Bay around 1913 (Ayson, 1913). Toheroa was a novelty to the Southerners, with existing toheroa populations most likely being known and undoubtedly protected by Māori of each of the areas in the late 19th and early 20th centuries.

Esler maintains that he has never found toheroa in the older midden deposits of Ōreti or Te Waewae Bay. Erosion plays a key factor in the landscape of Ōreti Beach and Esler maintains that although erosion means the loss of many archaeological or midden sites, it also leads to the exposure of many more. This is not the case in the area.

Ritchie and Cave (1977) suggest that the distribution and somewhat limited variety of prehistoric sites surrounding Te Waewae Bay are a good reflection of the resources available in the area, but also suggest that early occupants were in some areas strongly limited by localised environmental factors. As an example, Richie and Cave state;

> *The heavy forest cover formerly over most of the survey area appears to have effectively precluded sustained occupation and human movement* ***other than along the coast and up the Waiau Valley***.[29]

Ritchie and Cave (1977) continue that middens of the area generally suggest a "*predominant utilization of hard-shore shellfish species located adjacent to these areas*" Pg. 11

It is unlikely that toheroa would not be collected and utilized as a resource, if they were present in the area, particularly given the prolific nature with which they have been utilized in the north prehistorically. The large bivalves would have been an easily collected resource for people travelling along the coast. Any Māori occupying areas near these populations, assuming they

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[28] Esler, Pers. Comms., 2018

[29] Ritchie and Cave (1977) Pg. 11

were aware of their existence, would opportunistically seek sustenance in these shellfish. It is of particular significance that the lack of toheroa middens along the coastline has been noted by previous archaeologists as a point of interest. This has not been investigated further until now.

Sandy Point sub-fossil deposit

When considering the sub-fossil beach deposit located at Sandy Point (Figure 3.5 for location) species from open coastal and beach environments present within this deposit would have grown in the same environment, at varying depths, as toheroa. Toheroa shells however are absent from this sub-fossil deposit. One would expect toheroa shells to have swept around the bay, along with other surf clam species present in the deposit, such as *Paphies subtriangulata* and washing up in the area if they were present in abundance at Ōreti Beach at the time of deposition.

Alternate explanations

The dynamic nature of coastal regions and anthropogenic influences of them has sometimes led to severe damage of archaeological sites and subsequent loss of information. A comprehensive survey of the South Coast of Murihiku called the Southland Coastal Heritage Inventory Project (SCHIP) was founded in 2003. The SCHIP was created and undertaken to address this information gap through an intensive and systematic site survey of the Southland coastal marine environment (Jacomb, 2008). Field work for the programme was undertaken in two stages between 2004 and 2006.

During the SCHIP survey, over half of the previously recorded sites in the NZAA Site Recording Scheme were not found, while conversely many new sites were identified. This highlighted that the landscape was and is rapidly changing and indicated that it was likely that many more sites may have been lost over the past century and will continue, given the increase in developmental pressures along the coast (Jacomb, 2008). Along with the loss of sites, many new sites were and are being continuously exposed. One alternate hypothesis, contrary to the concept that toheroa middens are largely absent along the South Coast of Murihiku, is that there has been a systematic loss of toheroa middens spanning years.

The dynamic and complex dune systems would mean the South Coast has seen a loss of midden and archaeological sites through time. However, this is also true of the West Coast of Te Ika-a-Māui as well. With the erosion, accretion and general movement of dunes systems over time, it is likely that archaeological sites have been lost through time in both areas. What is more difficult to ascertain is the loss and exposure of middens along the West Coast comparative to the South Coast. The effect of changing coastlines and sea-level rise on the preservation of coastal sites is a confounding issue, with systematic methods of quantifying these effects still largely missing from shell midden methodological approaches (Balbo et al., 2011).

Within Murihiku and along the Kāpiti-Horowhenua coast, toheroa are a novel characteristic of middens and are therefore usually identified and remarked upon if they are present (McFadgen; Brooks, pers. comms.). Archaeologist Emma Brooks, a researcher for the Southland Coastal Heritage Inventory Project (SCHIP), has stated that the contents of middens along the South Coast of Te Waipounamu generally reflected resources from the local environments in which they were located. From personal observation, Brooks could not recall finding toheroa within middens while undertaking surveys of the South Coast sites (Brooks, pers. comms.).

Large scale fluctuations in toheroa populations through time is a well-documented occurrence (Redfearn, 1974). Abundance and distribution of the toheroa populations at Ōreti and Bluecliffs may have fluctuated over several hundred years, potentially being scarce during periods of early occupation, thus leading to the lack of utilization as a resource by early Māori. Further to this, cultural or social restrictions may have been in place over the populations, if they were known to the southern Māori and were endemic to the area. Of the resources available within coastal regions of the South Coast, toheroa may not have been the favoured species. Other marine or freshwater species may have been preferred over toheroa, leading to a lack of representations in middens.

Ritchie and Cave (1977) suggest that the distribution and somewhat limited variety of prehistoric sites surrounding Te Waewae Bay are a good reflection of the resources available in the area, but also suggest that early occupants were in some areas strongly limited by localised environmental factors. As an example, Richie and Cave state;

> *The heavy forest cover formerly over most of the survey area appears to have effectively precluded sustained occupation and human movement other than along the coast and up the Waiau Valley*. Pg. 11

Ritchie and Cave (1977) continue that middens of the area generally suggest a “predominant utilization of hardshore shellfish species located adjacent to these areas” Pg. 11

With this in mind, it is difficult to assume that toheroa were not collected and utilized as a resource if they were present in the area, given the prolific nature with which they have been utilized in the North Island prehistorically, from all known populations. The large intertidal bivalves would have been an easily collected resource for people travelling along the coast. Any Māori occupying areas near these populations, assuming they were aware of their existence, would opportunistically seek sustenance in these shellfish. It is of particular significance that the lack of toheroa middens along the coastline has been noted by previous archaeologists as a point of interest. This has not been investigated further until now.

3.5 Concluding remarks

The presence of only a few middens containing toheroa along the coast of Murihiku suggests that toheroa were in the south at some stage prehistorically and that if the resource was there, Māori would utilize it. However, the overall lack of toheroa in middens across Murihiku brings about several questions, including the periods of time when toheroa were present, in what areas and by whom they were exploited. One could postulate that the general absence of toheroa in all but a few middens, indicates that toheroa were not present in Murihiku for as long as Māori were occupying these areas. Evidence presented in the current study does not disprove the notion that human-mediated translocation of toheroa to the southern coast has occurred prehistorically.

Reeder-Myers et al. (2022) undertook a “historical ecology” analysis of oyster fisheries (Ostreidae) spanning Australia, the Pacific Coast of North America and the Atlantic and Gulf of Mexico coast of North America. This study integrated sea level histories, quantitative archaeological oyster abundance data, descriptions of the size function and distribution of archaeological sites and ethnographic accounts of oyster harvest, management and farming. Much of the data generated within the study had come from analysing oyster bearing middens and other archaeological sites for comparative analysis.

The scale of indigenous oyster fisheries was reflected in the abundance of oyster middens across archaeological sites. Although it is difficult to identify oyster farming and cultivation from archaeological records, it is highly likely to have occurred. Further to this, midden records demonstrate the sustainable nature of oyster harvesting undertaken over thousands of years and that people had powerful ecological knowledge related to oyster harvest and ecology.

Archaeological data analysed by Reeder-Myers et al. (2022) demonstrated that Indigenous oyster fisheries were immense, providing a crucial food source spanning millennia. The fisheries were largely sustainable and reflective of indigenous worldviews and traditional practices. These fisheries were successfully woven into traditional marine resource management and cultural systems, this being a part of the longevity of the fisheries and producing the abundance that was later exploited by settler, colonial enterprises. Data of oyster harvest suggests that after European settlement, environmental impacts devastated oyster fisheries in ways that sustained, intensive Indigenous harvests did not. This may be an international example of what has occurred to toheroa populations within Aotearoa.

Reeder-Myers et al. (2022) comments:

> *Although there are instances of predation pressure at some localities, our data suggest long term-term sustainability of Indigenous oyster fisheries. These Indigenous fisheries were complex, with some focused on local consumption of shellfish combined with hunting, farming fishing and exchange, while in others (e.g., the Pacific Northwest) people were producing food for surplus, exchange and accumulation of wealth. They were sustained by social relationships, cultural expectations, foodways and conservation ethics, within societies that treated entire watersheds as interconnected systems rather than separate economic niches (i.e. logging, fishing, farming).* Pg.10

As discussed previously, many middens across Aotearoa have not been surveyed and remain undocumented. The number of middens which are documented however, give an ample representation of midden composition and distribution across the country. From this desktop analysis, it was found that an adequate amount of archaeological monitoring has been undertaken along the coastline of Murihiku, to present an acceptable representation of middens in the areas of interest (Brooks et al., 2008).

As the current study is primarily desktop, it has several limitations. The most obvious is the inability to access each site and undertake field investigations personally and this study is therefore reliant on previous researchers work. Sites which were recorded in the 1960s and 70s are often unable to be relocated and are therefore unable to be cross-checked if needed. Along with this, many sites which have been investigated in the early years of archaeological investigation, often have meagre descriptions and/or have been relayed by amateur archaeologists. In this case, the accuracy of descriptions is unknown. The current study has taken all site descriptions and reports at face value.

Misidentification of species in some midden samples may also cause some discrepancies within the data. There is a degree of uncertainty regarding some investigator’s taxonomic capabilities, particularly in the earliest site investigations undertaken by amateur archaeologists. Tuatua and toheroa may sometimes be mistaken for one another, although mature toheroa are generally larger, and the younger specimens have a much thinner shell comparative to tuatua. To the eye of an expert the differences in species can be identified relatively quickly. Several midden descriptions do not state what species are present at all, and these have been omitted from the results.

To support the current desktop analysis, further study could incorporate field work, monitoring and analysis, combining an examination of the geological history of the south, to better date the dune systems. Undertaking archaeological surveys of coastal environments, adjacent to known southern toheroa populations, may result in identification of both unknown midden and the relocation of documented midden. Correct taxonomic identification of shell middens at sites within the current study, particularly along the South Coast of Murihiku, would be of great value to this research. Further to this, sampling of toheroa shells within stratified midden layers, for radiocarbon dating, may provide more conclusive results on the presence, distribution and utilization of toheroa throughout the prehistoric sequence within Murihiku.

Chapter Four

Robust and remarkable creatures: physiological tolerances and behavioural adaptations of tuatua (*Paphies subtriangulata*) and toheroa (*P. ventricosa*)

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[30] Toheroa siphons

4.1 Introduction

Translocation of shellfish species is a long known concept within Māori tradition and has been used as a restorative tool historically within Aotearoa (New Zealand) (Futter, 2011). Oral tradition and historical accounts suggest that early-Māori undertook transport and translocation of bivalve species, such as toheroa (Garven et al., 1997). Long-distance translocation of toheroa is hypothesised to have occurred from parent populations in the West Coast of Te Taitokerau (Northland) to the southern-most beaches of Te Waipounamu (the South Island) (Ross et al., 2018). As this is hypothesised to have occurred within the deep past, there are a lot of unknowns regarding the logistical capacity and methodology behind such practices.

Successful long-distance transport and translocation would be reliant on several key factors. This includes the robustness of the bivalve's physiology to combat stressors exposed to during this process, and the methods employed to undertake such a feat (Eissa and Wang, 2014). If long-distance transport of toheroa has occurred, we would also assume that the people who undertook these activities had comprehensive knowledge of toheroa physiology and ecology.

The physiological tolerances of marine organisms are shaped by interactions between their biology and the abiotic and biotic stressors associated to their natural habitat (Pörtner, 2010). As intertidal molluscs are exposed to extreme fluctuations in environmental condition, they have developed the ability to withstand periods of dissolved oxygen depletion, change in temperature gradients and salinity fluxes, starvation and desiccation (Barbarro and de Zwaan, 2008). When removing soft shore bivalves, such as toheroa (*Paphies ventricosa*) and tuatua (*Paphies subtriangulata*), from their natural habitat for transport, they are likely to experience most or all of these stressors. It is therefore important to understand the robustness of these species, when considering their ability to withstand short and long-distance transport, translocation and acclimation to a new environment. Understanding physiological and biological responses are also key when considering the suitability of these species for aquaculture (Eissa and Wang, 2014).

When monitoring the responses of organisms to environmental stress, biomarkers are an important tool, particularly in understanding physiological tolerances (Sokolova et al., 2012, Eissa and Wang, 2014). Such biomarkers may fall under one of two monitoring approaches; that of measuring whole animal function, or of measuring an organism's response at the cellular level (Joyner-Matos et al., 2009). Functional biomarkers in bivalves include metabolic responses, such as respiration rates (oxygen uptake) and clearance rates (Marsden, 1999); morphometric indices, such as Condition Index (CI) (Joyner-Matos et al., 2009) and Scope for Growth (SFG); behavioural responses such as burial rates (Hull et al., 1998), gaping and valves closure (Schade et al., 2019); and physiological responses such as mortality (Norkko et al., 2005).

Aerobic Respiration

Marine bivalves have several adaptive mechanisms to deal with fluctuations in oxygen availability, with physiological and molecular responses being specific to each species (Norkko et al., 2005). Prolonged exposure to oxygen concentrations below the tolerance threshold of a species will lead to irreversible physiological damage and eventual mortality. The effect of declining oxygen on respiration rates of bivalves has been studied comprehensively, with attempts to understand the mechanisms which control oxygen uptake (Tang and Riisgård, 2018).

Oxyconformer vs oxyregulator

Marine bivalves can attempt to maintain oxygen delivery a number of ways (Norkko et al., 2005; Stickle et al., 1989). Based on an animal's respiratory response to decreasing bio-available oxygen, they may be classified as an "oxyconformer" or an "oxyregulator". In oxyconformers, a decrease in environmental oxygen would generate a similar decrease in oxygen uptake by an animal and this response would continue with decreasing oxygen tension (Dung et al., 2016; Mueller and Seymour, 2011). An oxyregulator is suggested to regulate oxygen uptake independent of ambient oxygen concentrations until an oxygen threshold or critical oxygen concentration is reached (Tang and Riisgård, 2018). When this occurs, the organism can no longer regulate or maintain oxygen consumption and will switch to a "conformer". This threshold may also give indication of a change in metabolic processes from aerobic toward anaerobic pathways (Mueller and Seymour, 2011; Artigaud et al., 2014). Most animals will generally exhibit respiratory responses that fall somewhere between a regulator and a conformer, in relation to environmentally available oxygen concentration (Mueller and Seymour, 2011).

Anaerobiosis

Environmental hypoxia or anoxia can be experienced by marine animals with limited mobility, such as bivalves, as they are unable to actively escape environments during periods of low oxygen. As most marine bivalves are exposed to daily periods of emersion, they are adapted to cyclic interruptions of oxygen availability and during this time, they may close their valves and shift to anaerobic metabolism (Muller et al., 2012). Cellular hypoxia refers to low DO in the haemolymph or cytosol of an animal and this can be induced by environmental hypoxia, or by chemicals inhibiting oxygen fluxes from the surrounding water into an individual (Lee et al., 2008). Functional hypoxia occurs when an animal is active (e.g. burrowing deeper into sediment to avoid a predator), oxygen demand cannot keep up with energy demand and a brief hypoxia ensues (Carroll and Wells, 1995). In bivalves, tolerance to anoxia develops with growth of body size, the ability to reduce heat dissipation and conserve energy under anoxic conditions increasing with developmental stages (de Zwaan and Eertman, 1996).

When coping with hypoxia and anoxia, marine bivalves may employ several strategies. Studies that have compared anoxia tolerance and survival in bivalves have found that they possess several biochemical adaptations of anaerobiosis. These include the formation of alternative end-products to enhance ATP production, maintaining fermentable fuel reserves and metabolic depression (de Zwaan et al., 2002). The pathways of anaerobiosis are suggested to not only vary between species, but vary within species, dependent on the nature of the hypoxic stress (Carroll and Wells, 1995). Anaerobic metabolism is a significant energy saving strategy and can undoubtedly be attributed to the success of many inshore bivalves (Cockcroft, 1990: Laudien et al., 2002).

When oxygen is unavailable, a factor governing survival rate of a species is the scale in which energy expenditure can be reduced during these periods (de Zwaan and Eertman, 1996). Metabolic stress from environmental hypoxia/anoxia coupled with muscle work (e.g. burial), can contribute greatly to the decline of an animals health (Chiou et al., 1997), as it will more quickly use up its energy reserves during these times (Dung et al., 2016).

Although behaviour during oxygen deficiency can vary considerably, a common response includes the drastic reduction in movement and activity (Shumway et al., 1983). Many marine fauna have the ability to depress their metabolic rate and enter a dormant or hypometabolic state in response to exposure to unfavourable conditions. When oxygen is limiting, facultative metabolic rate depression is a mechanism utilized by some marine species who display extreme anoxia tolerance (also known as euryoxic invertebrates) (de Zwaan and Eertman, 1996). Intertidal marine invertebrates such as bivalves can depress metabolic rate in the presence of anoxia and ensure that energy demands are met by the ATP output from fermentative pathways alone (Storey and Storey, 1990; Brooks and Storey, 1997). It has been suggested that some species of bivalve may switch to air-breathing during times of exposure, therefore escaping total anaerobiosis (de Zwaan and Wijsman, 1976).

In general, bivalves have substantial tolerances to hypoxic conditions, however these are highly interdependent with exogenous conditions, such as temperature and tidal emersion regime, along with endogenous conditions (e.g. nutritional state) (Artigaud et al., 2014; Dung et al., 2016). Under hypoxia, the thermal window of tolerance for bivalves can be greatly reduced, along with associated aerobic performance (Artigaud et al., 2014; Portner and Lannig, 2009).

The metabolic rate of poikilothermic species, such as toheroa, is dependent on environmental temperature. Metabolic processes rely on enzymes which show increased catalytic responses with increasing temperature. This can be expressed by the temperature coefficient (Q10 ºC) of 2 to 3 for poikilotherms, which indicates that metabolic functioning can increase 2 to 3 fold with an increase of 10 ºC, until the tolerance range of a species is reached (de Zwaan and Eertman, 1996).

Increased temperatures during exposure to acute anoxia may greatly increase a bivalves mortality rate. Poikilotherms have compensation mechanisms for change in temperature on a seasonal scale, although acute change in temperature, particularly below or above a species tolerance range, would block such mechanisms, particularly under anoxic conditions (de Zwaan and Eertman, 1996).

Aims and objectives

In order to determine the biological feasibility of undertaking long-distance transport of toheroa and tuatua, several experiments were undertaken within a laboratory setting. These aimed to assess the suitability and robustness of the bivalves to withstand long-distance transport. While these experiments aim to provide insight into the physiology of toheroa and tuatua, they may also contribute to our understanding of transportation techniques which are more or less likely to contribute to animal health and mortality. As toheroa are a threatened and well protected species, the species-specific respiratory responses of tuatua and toheroa were compared, to assess if tuatua would be a good proxy for toheroa in further physiological experiments.

The experiments within this chapter investigated bivalve responses to various stressors. These stressors included; anoxia, hypoxia, aerial induced hypoxia, desiccation, sulphide toxicity and bacterial infection. The aims of these experiments were as follows:

1. To examine respiration rates of toheroa and tuatua under normoxic conditions
2. To examine respiration of toheroa and tuatua under hypoxic conditions, in which the animals are likely to be exposed to if transported in seawater
3. To investigate the physiological responses and survival of toheroa when held under different conditions, reflective of different modes of transport (e.g., in or out of seawater)
4. To assess the impacts of anoxia with and without the presence of pathogenic bacteria proliferation
5. To examine the behavioural responses of toheroa when held under different conditions.

It was hypothesised that animals would survive indefinitely under normoxic conditions, but would have shorter survivability when held under anoxia and aerial exposure. In previous research, anoxic and survival-in-air responses have been used as an early indicator of environmental contaminant induced stress (de Zwaan and Eertman, 1996). This study presents new data on the physiological responses and tolerances of *Paphies subtriangulata* and *Paphies ventricosa*. The information accrued within this study provides useful insight which can contribute to unravelling the mysteries of prehistoric long-distance translocations. Further to this, this study will contribute to our understanding of toheroa and tuatua, in future aquaculture practices and in restoration efforts by way of translocations.

4.2 Methods

Respiration experiments

Respiration rates of toheroa and tuatua were investigated, by measuring oxygen consumption under self-induced hypoxic conditions and under normoxic conditions, at a temperature of 14 ºC ± 0.5 ºC. A series of short, closed system (static) respirometry experiments were undertaken *ex situ*, over five days in October 2019. Taylor and Eggleston (2000) have suggested normoxic conditions in a saltwater environment are above a dissolved oxygen concentration of 6 O_2 mg/L, moderate hypoxia falls between 4- 3 O_2 mg/L, severe hypoxia falls between 3- 1.5 O_2 mg/L and anoxia falls under 1.5 O_2 mg/L. These will be considered as approximate levels of each category in the following experiments.

Animal collection

Nine toheroa (70 - 90 mm shell length) were collected from the intertidal zone of Ripiro Beach, on the West Coast of Te Taitokerau (Northland) in October of 2019. Sixteen tuatua (50 +mm) were collected from the subtidal zone of Omanu Beach, on the East Coast of Te Ika-a-Māui (the North Island). All bivalves were held in natural seawater, under aeration and transported to the Coastal Marine Field Station, Sulphur Point, Tauranga (approx. 6 hours transit from Ripiro and 20 minute transit from Omanu). Upon arrival, the bivalves were cleaned of all epibionts and transferred to temperature controlled (14 ºC ± 0.5 ºC), aerated, UV sterilised and filtered seawater for an acclimation period of 2-3 days. The salinity and temperatures were ambient to that of the bivalves natural environments and filtered seawater was changed daily.

Bivalves were starved during the acclimation period to measure basal levels of respiration. Previous experiments on *Paphies donacina* undertaken by Marsden (1999) measured the period of time required for bivalves to void their gut contents. This was found to be temperature dependant, however 90% of gut contents were expelled within 24 hours, this being considered a standard period of starvation.

Experimental set up

Closed system respirometry can be a relatively simple experimental set up, in which an animal is placed in a closed, sealed chamber and as the animal respires, the decline in oxygen concentration is measured through time (Svendsen, 2016). This system was incorporated in the following experiments.

Sixteen tuatua and nine toheroa respirometry replicate trials were run over the course of five days. For each replicate, one animal was placed within a 1 L glass jar with lid, previously filled with 750 ml of UV filtered seawater. This was then placed in a 14 °C temperature controlled water bath. Once the bivalves were placed in their replicate jar with seawater, the seawater was aerated for 30 minutes, to allow animals to acclimate and recover from handling, while maintaining oxygen saturation. Animals were then held under static conditions (no water exchanges) between 300–500 minutes, dependant on oxygen decline within an individual replicate. Lids of each jar were drilled with two holes large enough to fit oxygen and temperature probes and these were sealed, ensuring jars were kept airtight, except when needed to briefly insert and remove the probes when measuring oxygen and temperature (see Figure 4.1 for schematic diagram of set up).

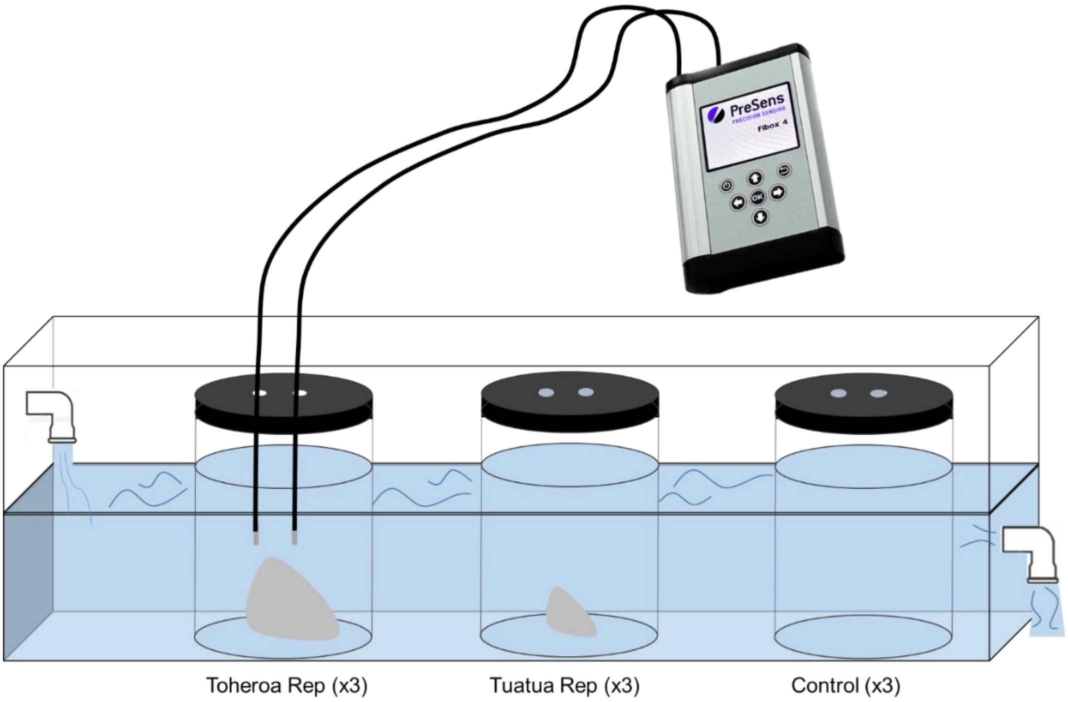

Figure 4.1 Schematic representation of experimental set up. Temperature controlled water bath was set at 14ºC. Fibox 4 (PreSens GmbH, Germany) was attached to oxygen and temperature probes. Lids were sealed shut if not being measured.

Three controls (glass jars with filtered 750 ml of filtered seawater and no animals), were run alongside animal replicates each day, amounting to a total of 15 control replicates. UV filtered seawater previously temperature acclimated and oxygen saturated were used within all replicates, with experiments being undertaken under natural light.

Respiration rates of tuatua and toheroa were measured using a stand alone Fibox 4 (PreSens GmbH, Germany), with attached and calibrated oxygen and temperature probes. Readings were taken at 20 and 30-minute intervals in each replicate until anoxia was reached (< 1 O_2 mg/L). Jars were occasionally agitated throughout the experiments to insure mixing.

Further respirometry trials were undertaken to assess oxygen consumption when kept under normoxic conditions. Intermittent-flow respirometry allows for measuring of oxygen consumption in a closed (no-flow) system, while also maintaining normoxic conditions, due to periods of intermittent flushing (Svendsen et al., 2016). For these trials, methods were the same as above, except when oxygen dipped below normoxic levels (approximately 5 O_2 mg/L), jars were flushed, and newly aerated seawater was added. Three replicate trials were undertaken for each species, however one trial for tuatua was not able to be used in the analysis due to the complete lack of oxygen consumption by the individual.

After respiration trials ceased, bivalves were stored in a -80^{o}C freezer for freeze drying and further analysis. All animals were weighed, measured and dry weight Condition Index % was calculated.

Analyses

Condition Index %

The *dry flesh weight: dry shell weight ratio* is a condition index used widely, with the measurements involved making it easy to standardize and more universally applicable than other indices. The use of dry tissue weight eliminates the bias of water content fluctuation within tissues. The index can give meaningful indications about the physiological state of a bivalve, with a low value inferring that major energetic effort has been expended. As such this can be a good biological indicator of stress placed on an animal, from exposure to poor environmental conditions or disease, or from production and release of gametes (Lucas and Beninger, 1985; Marsden, 2000).

CI values were calculated using the following equation (Matozzo et al., 2012):

$$CI\% = \frac{dry\ tissue\ weight}{dry\ shell\ weight}\ x\ 100$$

Respiration rate

Many tuatua individuals displayed periods of inactivity, where no oxygen consumption occurred. To account for this, several more tuatua replicates comparative to toheroa were undertaken for a more robust data set. Toheroa behaviour was uniform, in that all individuals were found to consume oxygen throughout respiratory trials. If replicates were found to be inactive for part or all of a trial, and this was reflected in no change of oxygen between readings, these measurements were excluded from the data set. The data set of respiration rates included in analyses can be found in Appendix B (Table B 2, B 3 and B 6).

Individual respiration rates (mg O_2 g DW $^{-1}$h^{-1}) were calculated using the following equation:

$$RR = \frac{\left(O_2\ Ctrl^{start} - O_2Ctrl^{end} \times 60/t^{min}\right) - \left(O_2^{start} - O_2^{end} \times 60/t^{min}\right)}{\left(DW^{total}\right) \times V}$$

Where O_2Ctrl^{start} denotes the oxygen concentration (O_2 mg/L) at the beginning of the measurement period in the control (an average measurement of three control replicates), O_2Ctrl^{end} denotes the average control measurements at the end of a measurement period, t^{min} is the time period between each measurement which is divided by 60, to calculate the change in O_2 concentration per hour. Controls are incorporated to account for difference due to electrode drift of the oxygen probe and any microbial activity that may be occurring within the water or containers (Beets, 2017; Gatti et al., 2002). O_2^{start} denotes the oxygen concentration of a replicate at the start of the measurement period and O_2^{end} at the end, in concurrence with control calculations. DW^{total} represents the total dry weight of the animal within a replicate and V is the total volume of water in a replicate. Respiration rate calculations are taken partially from Beets (2017).

As animals for each species have slight differences in weight, individual respiration rates were standardised to 1g for comparative analysis, using the following equation taken from Dung et al. (2016), Bayne and Newell (1983), Artigaud et al. (2014) and Savina and Pouvreau (2004);

$$RR_s = \left(\frac{W_s}{W_m}\right)^{b} \times RR_m$$

Where RR_s is the weight-standardised respiration rate, W_s is the standard (1g), W_m is the measured weight of the experimental animal, RR_m is the uncorrected (measured) respiration rate and b is the allometric exponent for the respiration rate function (Artigaud et al., 2014). Marsden (1999) found that the weight exponent of *P. donacina* was close to 0.8 at seawater temperature in both summer and winter. Savina and Pouvreau (2004) undertook a review of allometric exponents for several bivalves and found that the average weight exponents for respiration was around 0.75. This value has been used in several comparative studies and will be used here (Artigaud et al., 2014; Savina and Pouvreau, 2004).

Respiration rates were placed in intervals reflective of oxygen concentration at time of measurement (eg. 8-7 O2 mg/L) and by time elapsed (minutes) for each species, for further comparison and statistical analysis. Respiration rates were plotted to visualise change in respiration rate over time and under different oxygen concentrations. Respiration data can be found in Appendix B (Tables B 2, B 3 and B 4).

Due to different behavioural responses between species, the number of measurements for each grouping were often uneven. To assess differences within and between species respiration rates, based on either O_2 concentration or time elapsed, several non-parametric Kruskal-Wallis Rank Sum tests were undertaken in RStudio (R Core Team, 2020). Post-hoc Dunn tests (Dinno, 2017) were undertaken to tease out key differences within the data. Output tables can be found in Appendix B (Tables B 6 and B 7).

Intermittent-flow respirometry

Respiration rates calculated from intermittent-flow respiration trials which fell within normoxic ranges <6 mg/L, were pooled by species (tuatua and toheroa), for comparison. A Kruskal-Wallis Rank Sum test was undertaken in Minitab 18® to determine if respiration rates were statistically different and a box plot was produced to visualise the two sets of data.

Mortality experiment

Mortality experiments of wild and cultured bivalves have been undertaken extensively in previous studies to investigate and understand physiological tolerances to abiotic stressors, such as anoxia. A commonly used measure of tolerance to stressors such as anoxia is assessing anoxic survival time when held under static conditions (no water changes or water flow) (de Zwaan and Eertman, 1996; de Zwaan et al., 2002; Babarro and de Zwaan, 2008). Further to this, antibiotics have been introduced to these traditional incubation experiments, to control for anaerobic bacterial proliferation. Survival in air is also a simple, feasible and sensitive monitoring response to evaluate aerial exposure in bivalves (de Zwaan and Eertman, 1996). The current study has incorporated these methods to assess abiotic and biotic stressors on toheroa.

Animal collection

Twenty–four toheroa (70-90 mm shell length), were collected from Ripiro Beach in January of 2020 and transported via the same methodology as above, to the Coastal Marine Field Station, Tauranga. Animals were acclimated within temperature controlled, aerated and filtered seawater at 19 ºC (ambient sea surface temperature) for three days prior to the experiment. Animals were not fed and water changes occurred daily.

Experimental conditions

Individual toheroa were held under different conditions and behavioural responses and survival rate were monitored. The experiment incorporated four treatments (see Table 4.1), each with six replicates. The experiment was undertaken in a temperature controlled unit (set at 18 ºC) with each replicate held in a 1L glass jar and housing one toheroa. The experiment was run for 12 days.

Table 4.1 displays four treatments, codes and associated factors within the experiment. Code descriptions are as follows; seawater + self induced anoxia (SW-A), seawater with daily antibiotics + self induced anoxia (SW-A-AB), aerial exposure (AE), aerated + water changed daily (CTRL).

Treatment	Code	Seawater	Antibiotic	Aeration + Water change
1	SW-A	Y	-	-
2	SW-AB-A	Y	Y	-
3	AE	-	-	-
Control	CTRL	-	-	Y

Treatment descriptions

Seawater treatments (SW-A and SW-AB-A) were filled with 1L of filtered and aerated seawater at the beginning of the experiment. One toheroa was placed within each glass jar and the seawater was left to reach self-induced anoxic levels. Aerial Exposure (AE) treatments were lined with a soaked and folded paper towel, to maintain moisture and one toheroa per replicate was placed within. Lids were fitted loosely on all treatments. The control treatment involved glass jar replicates filled with 1L of filtered seawater. These were held under constant aeration and seawater exchanges were undertaken daily.

To supress bacterial growth under anoxic conditions, the pharmaceutical grade, broad scale antibiotic Chloramphenicol was used. This antibiotic has been used in previous mortality experiments (de Zwaan et al., 2002, Babarro and de Zwaan, 2008) and is suggested to be a broad-spectrum antibiotic as it can act on both gram-positive and gram-negative bacteria, by inhibiting protein synthesis (de Zwaan et al, 2002).

SW-AB-A replicates were administered a liquid concentration of Chloramphenicol (5%w/v), with a daily dose of 2 mg/L (0.4ml). Unfortunately, there was only a limited amount of antibiotic available during the experiment and antibiotic intervention ceased after four days. The full effect of correct dosing across the entire experiment would have likely produced different mortality results and extended survivability in antibiotic replicates.

Temperature and oxygen (mg/L) was measured using a stand alone Fibox 4 (PreSens GmbH, Germany), with attached and calibrated oxygen and temperature probes, twice daily until anoxia was reached in anoxic treatments. Control treatments were measured until the end of the experiment, with oxygen levels never dipping below 6 mg/L. Although the room was temperature controlled (set at 18˚C), temperature was found to fluctuate up and down by several degrees (Ave = 20.21 ºC, Min = 18 ºC, Max = 22.4 ºC), corresponding with natural night/day cycles.

Behavioural observations such as siphon and foot activity, valve closures and pseudofaece expulsion were documented twice daily (morning and evening) to produce presence/absence behavioural data. Mortality assessment of bivalves was based on a failure to respond (siphon contraction or valve closure) when the gaping individuals were probed with a metal rod (Laudien et al., 2002). After the experiment was finished, toheroa were frozen, freeze dried, weighed, measured and Condition Index% (CI%) was calculated.

Analyses

Survival rates of the bivalves were plotted and described. CI% data was found to be normally distributed and therefore compared, by treatment, using a one-way ANOVA in Minitab. A suite of behavioural data was catalogued based on presence or absence at each sampling period, for further analysis. Number of different behaviours observed for each treatment across the entire experiment were summed and can be found in Appendix B (Table B 8). Behaviours that were considered prevalent for each treatment were qualitatively described based on predictor variables dissolved oxygen concentration and time elapsed.

4.3 Results

Intermittent-flow respirometry

To investigate the respiration rates of tuatua and toheroa under normoxic conditions (>6 O2 mg/L), oxygen consumption of both species were measured under static conditions and compared. A non-parametric Kruskal-Wallis test did not identify a significant difference (X^2= 2.49, *p*=0.114) between the two groups. Figure 4.2 indicates toheroa had a larger spread of respiration rates, while tuatua rates appeared to be slightly lower, apart from an outlier from one tuatua observation. Toheroa respiration rates ranged from 0.41 to 1.46 mg O_2 g DW $^{-1}$h^{-1}, while tuatua respiration rates ranged from 0.42 to 1.45 mg O_2 g DW $^{-1}$h^{-1}. Although no statistical differences were identified between respiration rates, the behavioural responses of each species dictated much of the results and differences found between oxygen consumption of the animals. Bivalve measurements, respiration rates and dry weight CI% can be found in Appendix B (Table B 1).

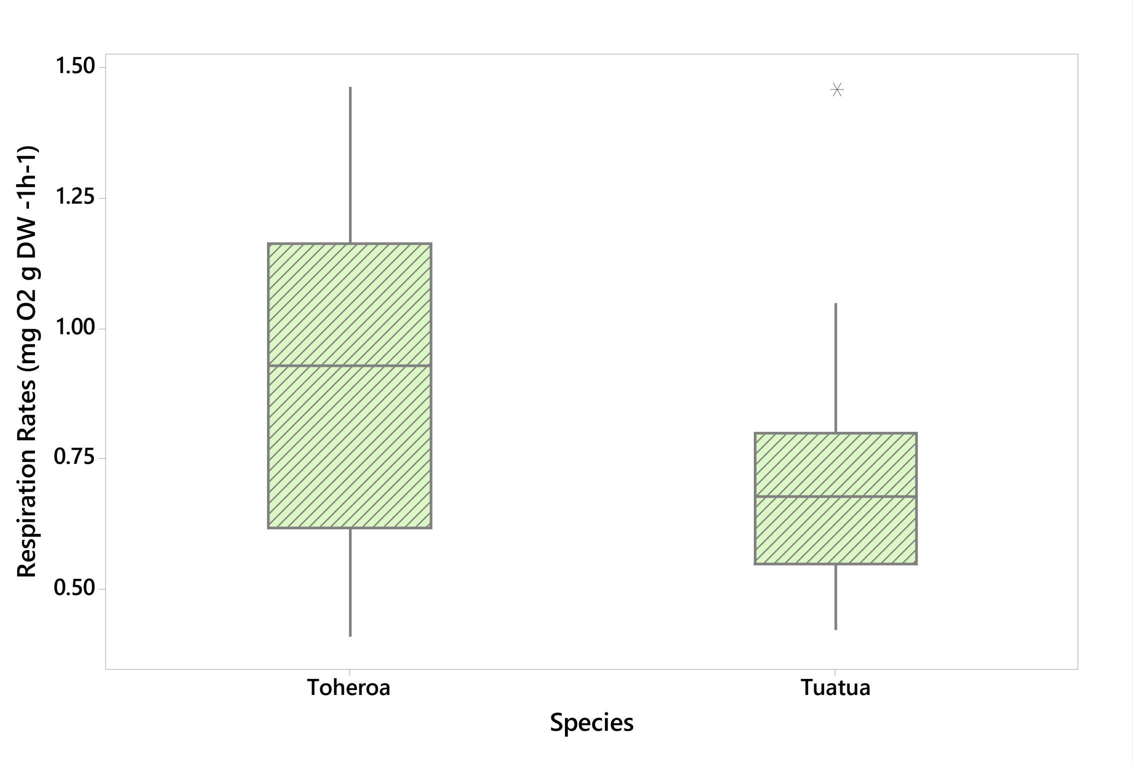

Figure 4.2 Respiration rates of tuatua (n=16) and toheroa (n=11) when held under normoxic and static conditions (>6 O2 mg/L) at 14°C ± 0.5°C. Line: median, box; interquartile range, whiskers: min/max, asterisk identifies outliers. No statistical differences were found between the two groups of data (Kruskal-Wallis X^2= 2.49, P = 0.114).

Respiration rates under self-induced hypoxia

Toheroa were found to consistently and rapidly enter into a self-induced state of hypoxia, reflective of an opportunistic aerobic response in the presence of oxygen saturated seawater. Significant differences found between oxygen intervals gave indication that rates of respiration began to slow when oxygen concentrations reached around 4-3 O_2 mg/L. No significant difference was found between intervals 8-7 and 3-2 (Figure 4.3), although the lack of sample data in these intervals may hamper the ability to identify significant differences if they were present.

Interestingly, tuatua were found to display opposite and counteractive respiratory behaviours to toheroa, with tuatua replicates (within the time frame of the respirometry trials) never entering into a state of anoxia. Figure 4.4 shows less differences in tuatua respiration rates between oxygen intervals comparative to toheroa, with the majority of observations being measured under self-maintained, normoxic conditions.

The patterns described above are evident when visualising respiration rates over time within a plot. Figure 4.5 indicates through time tuatua and toheroa forge their own patterns of respiratory responses. A steady decline in respiration rate and, by proxy, oxygen levels, within toheroa replicates is maintained. Respiration rates appear to be slightly higher in toheroa than tuatua, during the first half of the trials. At around 135 minutes, a crossover can be seen in the trend, where toheroa respiration rates begin to slow. Tuatua respiration rates appear to have a slight decrease from the beginning of the experiment to the end but, comparative to toheroa, maintain a relatively consistent trend over lowering oxygen tensions.

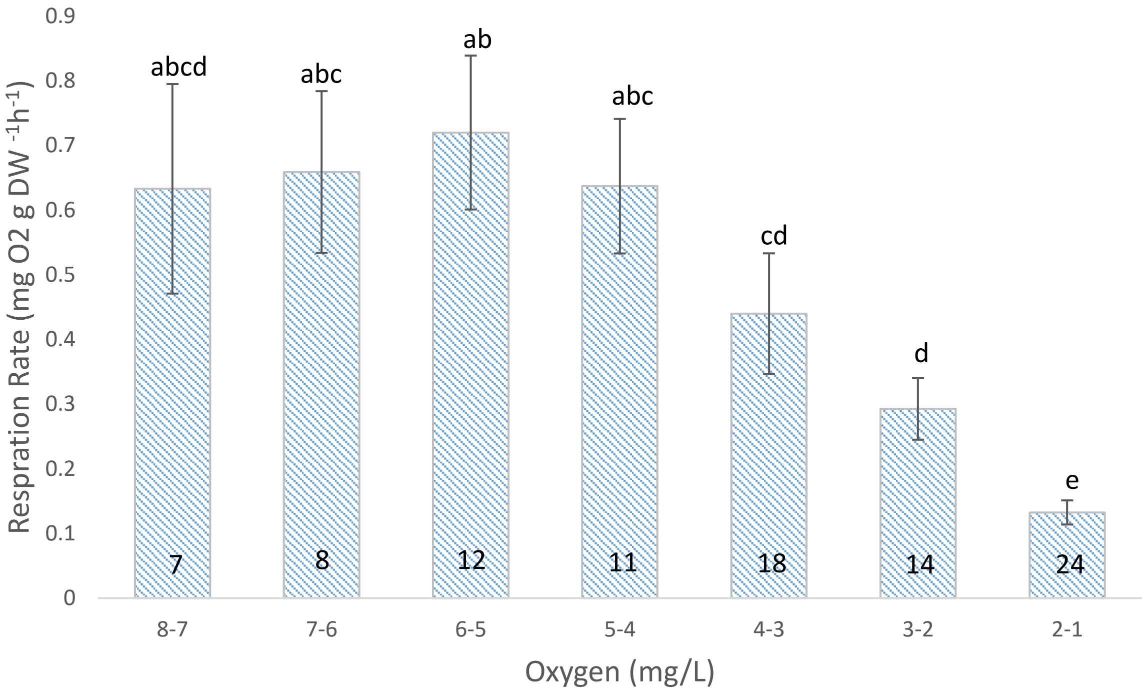

Figure 4.3 Mean respiration rates of toheroa across different oxygen (mg/L) intervals (±SE bars) held at 14°C ± 0.5°C. Superscripts (a,b,c,d and e) identifies RR mean between intervals which are significantly different from each other (bars that do not share the same letter are significantly different, post hoc Dunn Test, P<0.05). Number on bars represent the number of observations within each oxygen interval used for analysis. Experiment consisted of 9 toheroa replicates and 14 tuatua replicates.

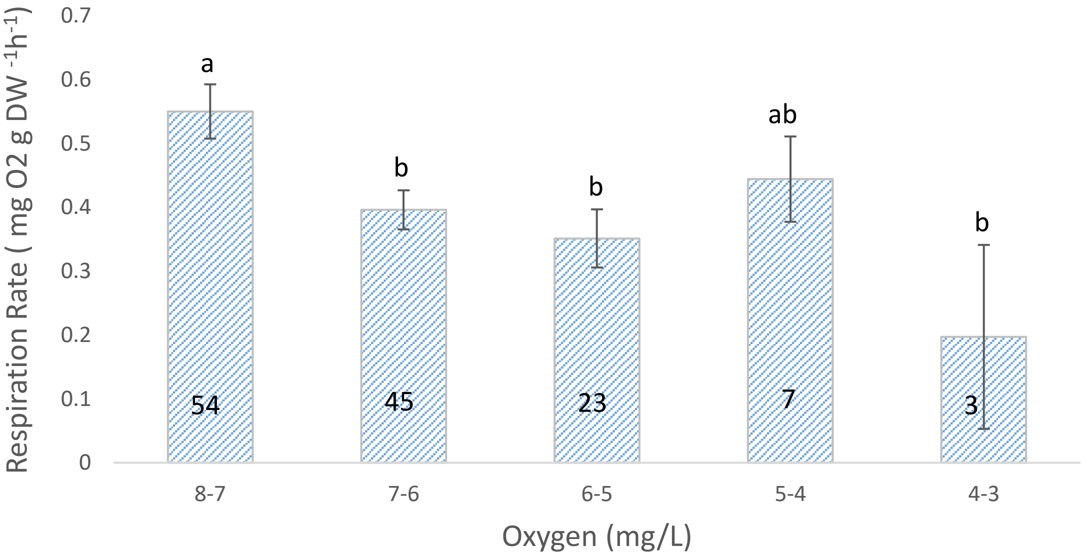

Figure 4.4 Mean respiration rates of tuatua across different oxygen (mg/L) intervals (±SE bars) held at 14°C ± 0.5°C. Superscripts (a,b,c,d and e) identifies RR mean between intervals which are significantly different from each other (post hoc Dunn Test, P<0.05). Bars that share the same letter are significantly different. Number on bars represent the number of observations within each oxygen interval used for analysis. Experiment consisted of 9 toheroa replicates and 14 tuatua replicates.

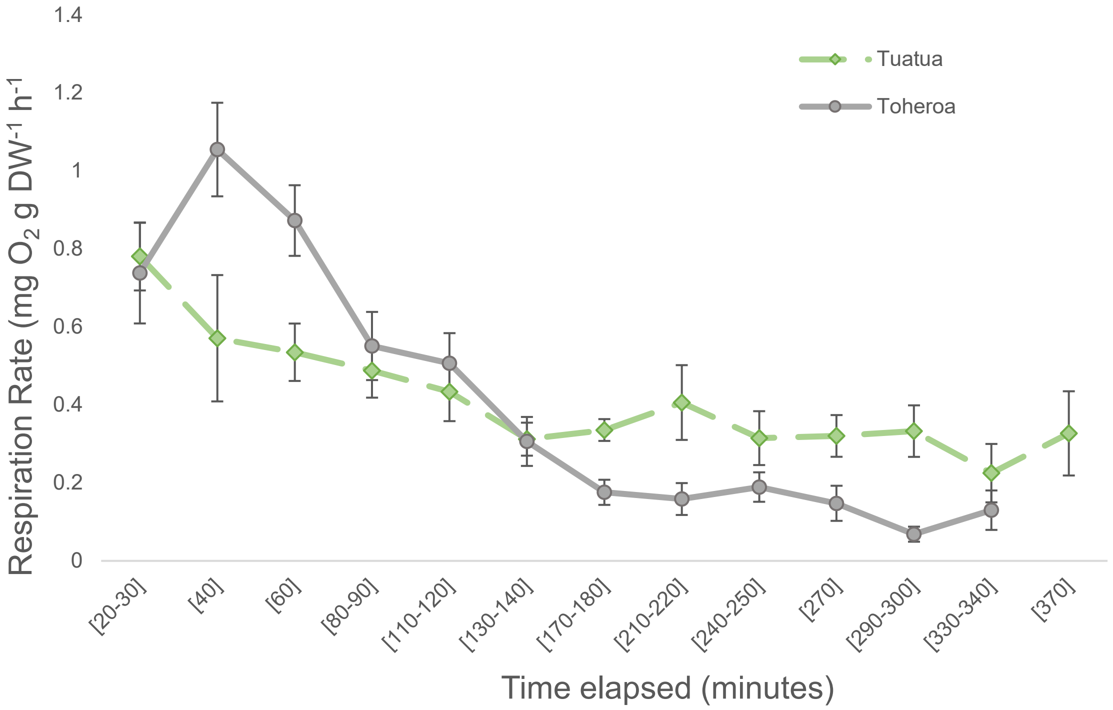

Figure 4.5 Mean respiration rates of tuatua (green) and toheroa (grey) ± SE bars over time when held in static seawater conditions. Experiment consisted of 9 toheroa replicates and 14 tuatua replicates.

Grouping respiration responses by oxygen integers may allow us to define the rate at which respiration occurs, and changes, along a spectrum of normoxia to hypoxia. As can be seen from Figure 4.4, tuatua respiration trials rarely reached truly hypoxic conditions, with only three observations collected at oxygen levels under 4 O_2 mg/L. Because of this, comparisons of respiration rates under anoxic conditions between toheroa and tuatua were not able to be done. Toheroa however appeared to display the opposite results, with the most observations being found at hypoxic/anoxic levels and more of a spread of observations collected across all oxygen levels.

The respiration responses of tuatua were found to be sporadic, with periods of no oxygen consumption even under normoxic conditions, this behaviour also signified by a complete valve closure. Toheroa responses were much more uniform, with all individuals found to consume oxygen consistently throughout respirometry trials, quickly dropping to hypoxic levels. The siphons, mantle and foot of toheroa individuals were observed to be much more visible and active than tuatua.

Physiological responses and survival of toheroa

Rate and timing of survivability of toheroa varied between treatments. Mortalities began at 4 days and continued until 12 days when the experiment was ended. The first mortality occurred in Seawater-Anoxia treatments, while toheroa survivability was most prevalent in controls. An unexplained mortality was recorded for one animal in the control group (at 4-5 days), with all other control replicates surviving the entirety of the experiment, as was predicted. The ST_{50} (median survival time) of SW-A treatments was 3-4 days and the ST_{50} of aerial exposure and seawater antibiotic anoxia treatments was 6 days (Figure 4.6). These two treatments followed similar trends, with extended survivability for some individuals. The last remaining animal, aside from controls, was from the AE treatment. SW-A replicates displayed the most uniform response, with mortalities occurring closer together and more rapidly than other treatments. No relationship between bivalve size and survival time was found.

Condition Index Percentage

The dry weight CI% and corresponding bivalve measurements can be found in Appendix B (Table B 5). No significant differences were found for mean CI%. Within the control group the only animal to expire, at an early stage in the experiment, had the second lowest CI% across all treatments (CTRL5; CI%=14.88, Survival time=105 hrs). The lowest CI% was also found for an individual in the AE treatment (AE1; CI%=14.5, Survival time=144 hrs), the first individual lost, of this treatment.

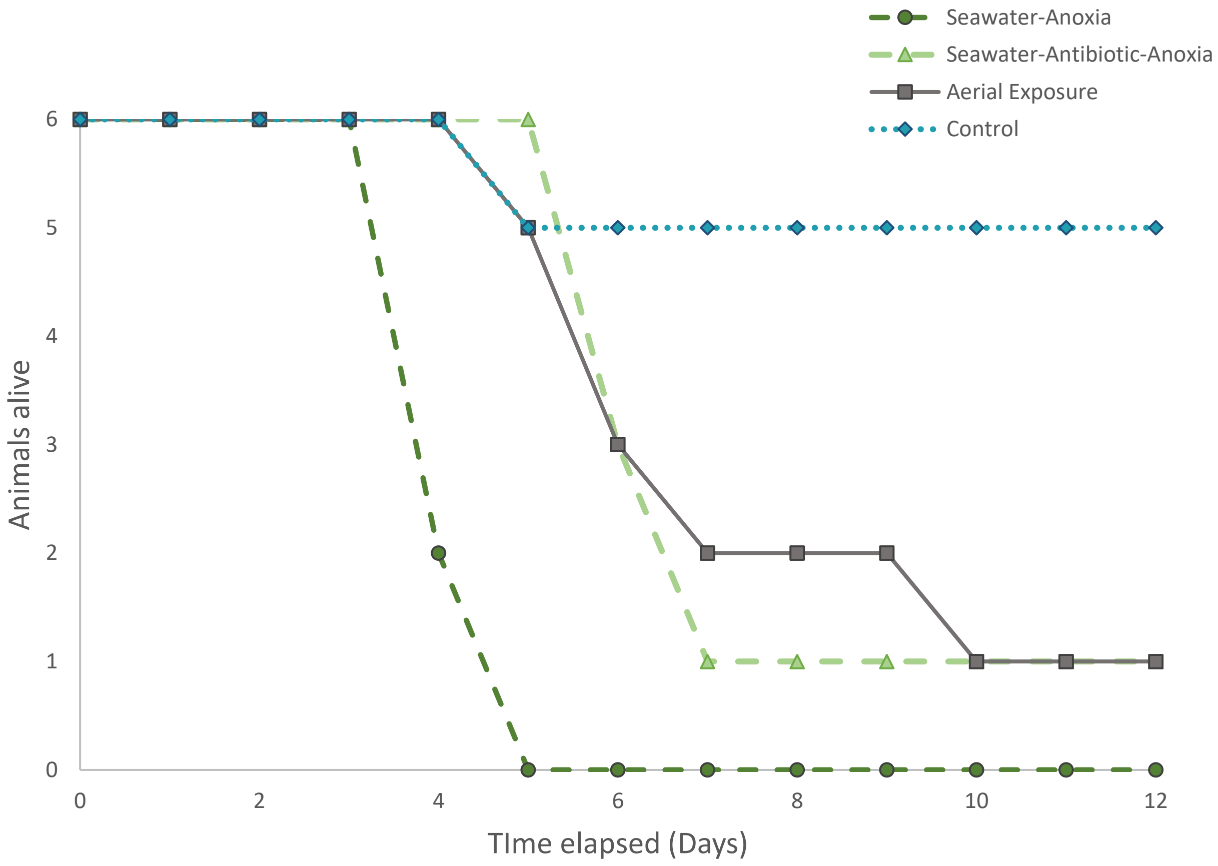

Figure 4.6 Survival rates of toheroa under differing treatments (n = 3)

Behavioural responses when held under differing conditions

Behavioural data was recorded twice daily to give insight into toheroa responses when held under different conditions. Both seawater treatments quickly moved toward anoxic conditions as was expected. Consideration of the position in which the toheroa are held (on their side) must be taken into account when considering behavioural responses. Toheroa held upright, or in the natural position they sit when buried, may have produced different responses. Positions of the bivalves within the current study would be reflective, in its natural habitat, of toheroa unburied, sitting above the sediment profile and exposed to the swash zone or to air.

Table 4.2 Prominent behaviours of toheroa observed during the experiment when held under different conditions. See Figure 4.7 and 4.8 for examples of some of the behaviours.

Prominent behaviours observed	**Control (in water under normoxic conditions)**	**Seawater - Antibiotic - Anoxia**	**Seawater - Anoxia**	**Aerial Exposure**
Foot fully retracted (Image E)	Yes	No	No	Yes
Siphons retracted	Yes	No	No	Yes
Foot visible (but retracted)	Yes	No	No	Occasionally
Siphons visible (but retracted) (Image B)	Yes	No	No	Yes
Siphons extended (Image G)	No	Yes	Yes	No
Foot extended (Image I2)	Occasionally	Yes	Yes	No
Siphons flaccid (Image L)	No	No	No	Yes
Outer mantle swelling (mantle retaining water) (Image E)	Yes	No	No	Yes
Outer mantle (or valves) gaping (Image K)	No	No	No	Yes
Valves seen contracting or clapping	No	No	No	Occasionally
Siphons open (Image C2)	Yes	Occasionally	No	Yes

Control – held in aerated seawater

When held under normoxic conditions and with minor temperature fluctuations much of the bivalves behaviour was uniform. The average oxygen concentration found across all control replicates was 6.7 mg/L. While being continuously submerged in aerated seawater, the siphons and foot were either fully retracted or just visible throughout the experiment (see Figure 4.7 A and B), with the toheroa favouring either one of these siphon behaviours over any form of elongation.

Both siphons were visibly open intermittently throughout the experiment, although this was more prevalent within earlier stages (3 - 152 hours). The observation that both siphons are open can be considered as representative of the bivalves actively pumping seawater (Thorin et al., 2008). The outer mantle of many replicates within the control were found to be swollen, particularly from 19 hours onward (Figure 4.7 E). Large amounts of pseudo-faeces were expelled from the exhalant siphons of the control replicates throughout the experiment (Figure 4.7 F) and this behaviour was not observed in individuals from any other treatments. Apart from this occurring, toheroa within the control experiment appeared to employ behaviours which may aid in energy conservation, such as limited movement and siphon withdrawal.

Seawater- Antibiotic - Anoxia

Within anoxic replicates treated with antibiotics, patterns in behaviour clearly changed with differing oxygen levels through time. Siphon extension and foot extension (Figure 4.7 G, Figure 4.8 H, I1 and I2) were associated with oxygen levels lower than 0.5 mg/L and this behaviour was observed the majority of the experiment. Sporadic suspension of siphons within the water were found to occur occasionally between 19 and 144 hours, with the siphons being active and occasionally swaying (Figure 4.8 I1 and I2). Inhalant siphons were noted as open for several replicates occasionally throughout the experiment. This was most prevalent for the longest surviving replicate (SW-AB-A2) towards the end of the experiment.

Seawater- Anoxia

Behavioural responses observed in anoxic (stagnant) treatments were similar for individuals in the SW-AB-A treatment, with siphon and foot extension prevalent under low oxygen concentrations. Foot probing was observed in some replicates when oxygen was still at normoxic levels.

A general pattern was detected in which siphons were retracted or just visible in most replicates in the first hours of the experiment and then begin to elongate between 3 and 19 hours, where they generally remained extended. This showed a considerable and relatively quick shift in behaviour, which coincided with decrease in oxygen concentrations.

Extension and suspension of siphons within the water was also observed within one replicate of this treatment, this response occurring near the end of individuals survivability and interestingly, one of the last replicates of this treatment to perish.

Aerial Exposure

Time elapsed when held in air was the main driver for change in behaviours and physiological responses of the bivalves in this treatment. The inhalant and exhalant siphons of all replicates generally never extended past 1-3 cm. Siphons could sometimes be seen sitting inside the mantle cavity (Figure 4.8 K). A behavioural response exclusive to this treatment was the animal’s siphons becoming flaccid, particularly the exhalant (see Figure 4.8 L), this was observed later in the experiment (8-11 days).

The foot of replicates in this treatment were found to be fully retracted the majority of the experiment (x= 86%). Siphons were found to be perceptibly open much more in this treatment than others, with the inhalant open an average of 38% of the time, a behaviour prevalent across the entire experiment for this treatment. This may be reflective of animals attempting to draw air into the mantle, resulting in the siphons becoming increasingly desiccated (see Figure 4.8 L and M). Bivalves were also observed to gape, with one individual seen clapping or contracting their valves in a repetitive motion.

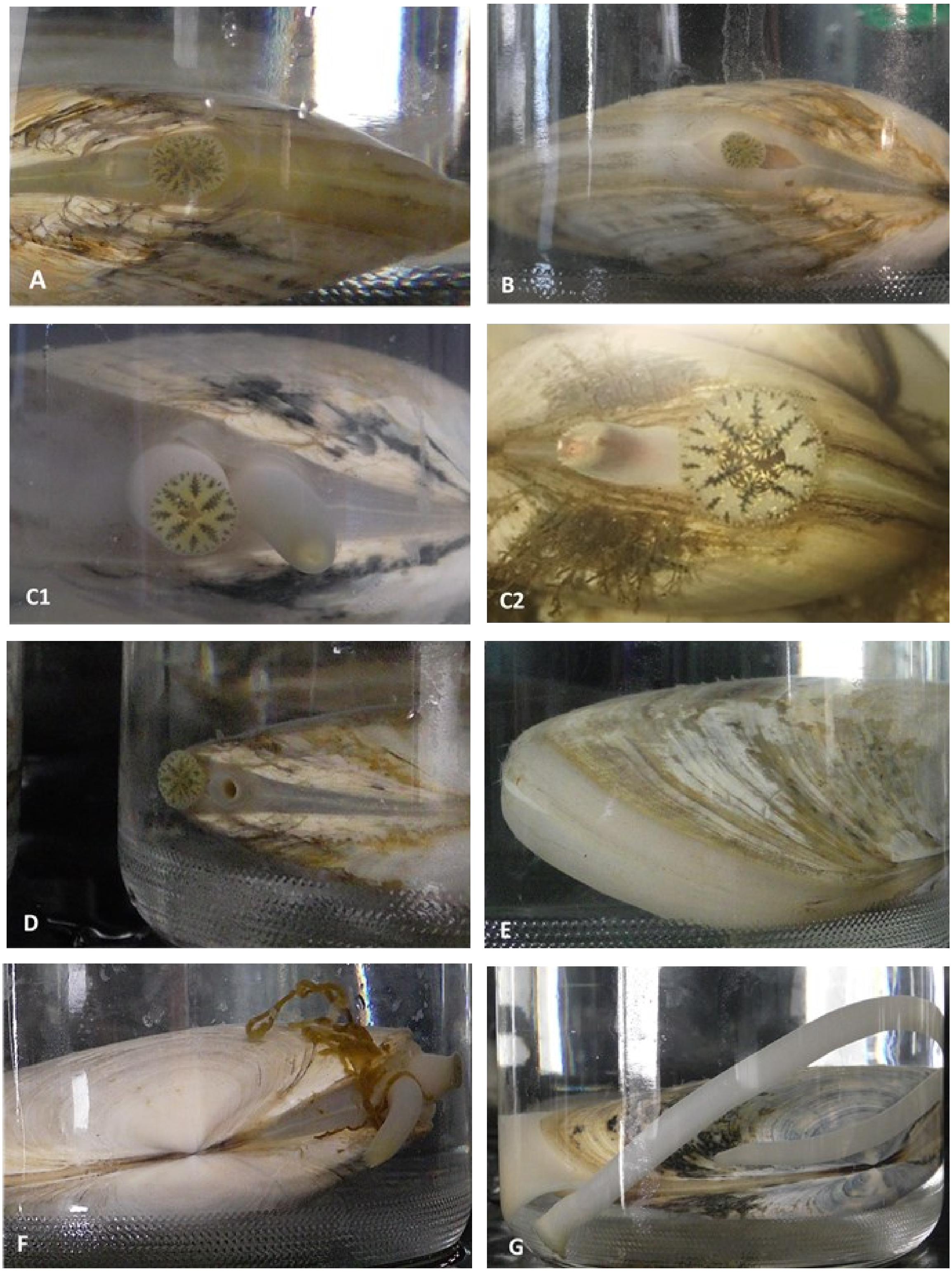

Figure 4.7 Examples of different behavioural responses of toheroa (*Paphies ventricosa*) (held in seawater treatments). A: Siphon visible, B; Inhalant visible, exhalant fully retracted, C1: Inhalant siphon open (Anoxic treatment), C2: Example of open siphon (*Paphies subtriangulata*), D: Inhalant open, E: Mantle swollen, F: Pseudofaeces expelled from open Inhalant siphon, G: Siphons extended.

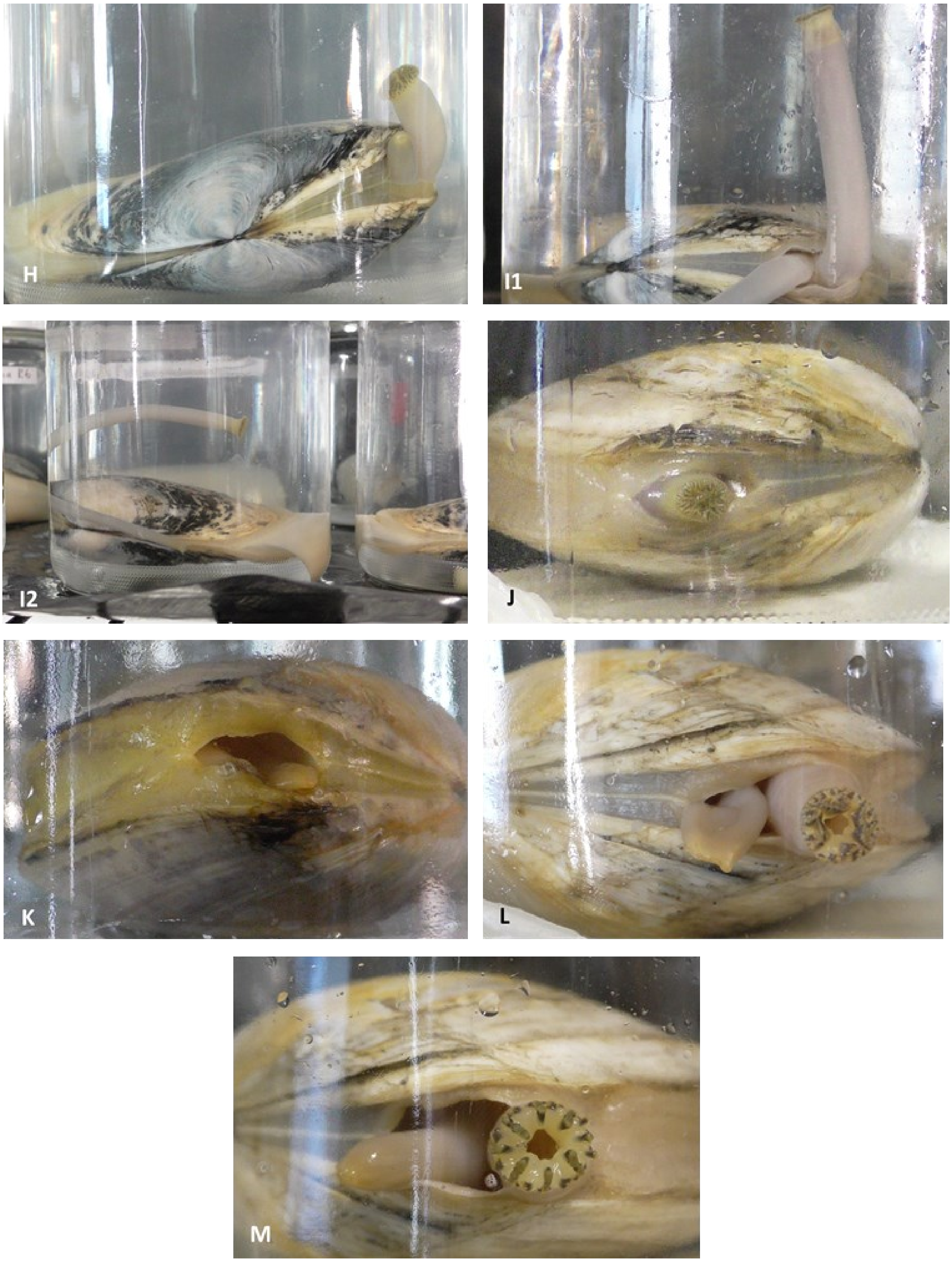

Figure 4.8 Examples of behavioural responses of toheroa (*Paphies ventricosa*) continued (J-M are held under aerial exposure). H:Siphon partially extended, II and 2: Siphon extended and suspended in water, J; Siphon visible in air, K, Siphons retracted and sitting in open mantle, L: Inhalant siphon flaccid, M: Desiccated siphon aperture.

4.4 Discussion

Bivalve respiration

An animals ability to respire is a key function of their physiology and therefore important to understand when trying to keep them alive. Toheroa and tuatua were found to have similar rates of oxygen uptake when actively respiring under normoxic conditions. However, static respirometry of tuatua and toheroa indicated that each species had differing respiration responses under decreasing oxygen tension. A study of the respirations rates of the manila clam (*Ruditapes philippinarum)*, the second most important bivalve worldwide to be grown in aquaculture, was undertaken by Nie et al. in 2017. They found that at a temperature of 15 °C oxygen consumption rate of the clams ranged from 0.275 to 0.767 mg g^{-1} h^{-1} and 0.603 to 1.906 mg g^{-1} h^{-1}, for a white strain of the clam and a zebra strain, respectively. Toheroa and tuatua respiration rates were found to be comparable to these values, deviating somewhat from Marsden's (1999) findings. Marsden (1999) found that the respiration rates of a deeper dwelling tuatua, (*Paphies donacina*) under normoxic conditions, were low compared with many other temperate bivalves.

Surf clams have been suggested to be mild oxyregulators (Tang and Riisgård, 2018) in which oxygen consumption will be maintained at a steady rate, or increase, independent of changes in external oxygen concentration. Regulation of respiration may occur as oxygen concentration decreases, until a threshold of oxygen is reached and regulated oxygen consumption can no longer be maintained (Davenport and Wong, 1986; Artigaud et al., 2014; Dung et al., 2016). Toheroa respiration was consistent with this, with the bivalves opportunistically respiring in the presence of decreasing levels of oxygen.

This behaviour was not found within tuatua. Tuatua appeared to conform to change in ambient oxygen, thereby avoiding hypoxic conditions, with the animals displaying an effective overall response to the onset of self-induced hypoxia. The level of conformity was somewhat confounded by the animals ability to sporadically cease aerobic respiration, regardless of oxygen concentration.

Toheroa appear to oxyregulate until a threshold or critical oxygen concentration of around 4-3 O2mg/L is reached, where a switch to conforming can be seen with significantly lowered respiration rates. Observations of tuatua were starkly different and were found to decrease or even halt oxygen uptake under slight decreases in oxygen concentration, and interestingly, when still held under normoxic conditions. This behaviour was so prevalent that very rarely during the experimental periods did oxygen levels reach a state of hypoxia in tuatua replicates.

A critical threshold in oxygen concentration was never reached for tuatua over the course of the respiration trials, giving further indication of the species oxyconformity.

Respiratory behaviour observed within toheroa and tuatua is in alignment with each species ecology. Toheroa habitats are highly specific. Characteristics of these habitats include exposed coastal areas with high energy surf zones, fine grained sand, protective onshore dune systems and a distinctive feature of small seeps or streams entering the coastal beach zone (Ross et al., 2017). They are likely to experience long periods of emersion, while buried within the sand each tidal cycle and when exposed to highly oxygenated seawater during high tide, they are likely to opportunistically respire and filter feed.

Tuatua distribution throughout Aotearoa is much wider. They are not restricted to coastal beaches, with many populations of tuatua found in sub tidal areas, where they are less likely to be exposed to prolonged anoxia. Marsden (1999) suggests that, although it would be expected that a high metabolic rate would be consistent with a high energy habitat, like that of tuatua, the animals also need to maintain their position within the substrate and during times of stress, these bivalves are more likely to be using anaerobic metabolism (Carrol and Wells, 1995). When considering transport in water for each of these species, it is likely that tuatua would withstand longer periods being held in unoxygenated water, tightly closing their valves and anaerobically respiring, while toheroa would quickly strip the water of oxygen and then continue with behaviours that attempted in seeking any available oxygen that may remain. Tuatua would likely conserve energy more efficiently when held under hypoxic conditions such as this.

Condition Index – impacts on survivability during transport

Temporal variations in physiological condition is influenced by numerous interacting factors, including food/nutrient availability and type, temperature/salinity fluxes and stage in the gametogenic cycle (Marsden, 2000; Boscolo et al., 2003). Previous research by Redfearn (1974) and Bennion (unpublished) found CI% values of toheroa from Ripiro Beach were consistently low over summer and high over winter.

The lower CI% values found for toheroa which were lost earlier in the experiment may suggest that these animals had lower energy reserves, were less robust and were therefore physically compromised. This could explain the loss of the control individual, an early mortality that was not anticipated but was found to have a low CI%. The poor conditions in which the bivalves were held in the mortality experiments would have contributed to lower CI% of all of the animals.

Considering individuals with lower CI% have a lower survival rate, and toheroa in general have higher CI% in winter months, it may be advantageous to transport toheroa in months between June and October. Animal condition and the added benefit of cooler temperatures may aid in prolonging the bivalves survival by increasing physiological tolerances (Stickle et al., 1989; Norkko et al., 2005).

Physiological and behavioural responses of toheroa

Exposure to air

Toheroa will be exposed to air on multiple occasions when removed from their habitat for transport. It is important to understand the physiological responses of toheroa during this process and how they may contribute to the animals decline or ability to survive under such conditions. Bivalve molluscs may respond to aerial exposure a number of ways, including closing the shell valves completely, maintaining only a narrow gape for gas exchange, while minimizing water loss, or gaping widely. Some bivalves have the potential to undertake aerial, aerobic respiration (Davenport and Wong, 1986).

Lee et al. (2008) suggests that clams may emerge from the sediment and become aerially exposed if they are experiencing cellular hypoxic stress and a loss in digging ability. Davenport and Wong (1986) found that the blood cockle, *Anadara granosa* displayed active responses to emersion, including widely gaping and a persistent rocking backward and forward, along with a periodic and sharp contract of the valves, followed by a slow parting, this referred to as “flapping”. This unusual behaviour is suggested to allow stranded animals the ability to utilize the rich oxygen available in air, while permitting access to water in or on the sediment surface. The blood cockles ability to aerial respire was suggested to be highly effective over short periods of time

When aerial exposed, toheroa individuals were observed several times to contract their valves, as if trying to draw in air, similar to the sharp contractions and slow parting found in the blood cockle. This behaviour was not overly prevalent but was present enough to consider the implications of such behaviour in the animals attempts or ability to assimilate oxygen from the atmosphere. Siphons of toheroa under held under aerial exposure were also found to be open much more than any other treatment.

A study by Babarro and Zwaan (2008) found that when an intertidal clam, *Macoma balthica*, was held under aerial exposure, animals survived for 24.8 days (LT_{50}). The intertidal species were found to survive significantly longer when held in air as appose to incubation in anoxic water and under nitrogen. Intertidal animals such as these have enormous potential to survive aerial exposure and Babarro and Zwaan (2008) highlight the substantial benefits that these bivalves appeared to receive from atmospheric oxygen availability.

Responses observed of the toheroa under prolonged exposure to air may indicate some ability of the animal to modify its behaviour, with the potential capacity for aerial respiration. Toheroa may attempt to draw oxygen from the atmosphere into the mantle cavity via contractions and gaping, although this is unlikely to be a usual occurrence for the deeply burrowing intertidal bivalve.

Filtration responses when held in seawater

During transport, if toheroa are held in seawater for all or part of the journey, they will consume oxygen quickly. Oxygen consumption is directly associated with filtration activity and feeding. When held under aerated seawater (the controls), toheroa were found to expel pseudofaeces from the exhalant siphons consistently throughout the experiment, this being an indication of active filtering. Starved animals will likely display reduced filtration activity and in the presence of environmental stressors, feeding rate is the first bioenergetic component to change. Under stressful conditions, individuals may simply cease feeding and marine bivalves such as tuatua and toheroa are able to withstand several weeks, potentially months, without food (Stickle et al., 1989; Norkko et al., 2005, pers. obs.).

The lack of pseudofaeces found in SW-A and SW-AB-A treatments inferred that filtering had ceased, or that filtration was occurring at a minimal rate after anoxic conditions had become established, and that the toheroa were retaining waste. Measurements of ammonia and nitrates (Ammonia-N, Ammonia-nitrogen production) would have been beneficial in confirming amount of soluble waste expelled between these treatments and the controls. Retention of solid wastes may be a mechanism to reserve remaining nutrients within the pseudofaeces, this behaviour being promoted by limited water flow and low oxygen tensions. Oxygen demand has been found to be lowered within marine invertebrates such as bivalves, by reducing filtering, feeding and movement (Long et al., 2008; Sagasti et al., 2001). The physiological responses and abilities described above are highly intuitive to long distance transport.

Bivalve siphons are neuromuscular appendages critical for nutrition, defence and reproduction. The current study found that when held under anoxic conditions, toheroa fully extended their siphons in the water column. The inhalant and exhalant siphons showed an impressive extension range, able to extend at the very least, beyond the length of their own valves. Siphon extension is a behaviour adapted not only to reach the sediment surface for feeding, but to extract oxygen, via diffusion, from the surrounding surficial sediment, while buried, and from the water column when submerged. This behaviour increases surface area of the tissue to the immediate environment (Sparks and Strayer, 1998; Taylor and Eggleston, 2000; Long et al., 2008). When immerged in seawater the extension of siphons and foot aid in animal migration, allowing toheroa to "swash ride", moving to more favourable areas along the shoreline in the surf zone (Ross, pers. comm.). Behaviours such as the extension and retraction of siphons show toheroas ability to respond to a range of less then favourable conditions and adapt to them to the best of their ability.

Anaerobic Pathways – differences in energy generation

The metabolic functioning of toheroa under anoxic and normoxic conditions is a bioindicator of the animals tolerances to lack of oxygen or food. Understanding these mechanisms will help inform methodologies surrounding transportation and aquaculture of toheroa, and other bivalves. During ATP synthesis, anaerobic metabolism in eukaryotes generally involves the generation of a terminal electron acceptor (in place of oxygen) endogenously via fermentation. Fermentations involve the donation of electrons onto terminal acceptors, such as fumarate (which produces succinate) and pyruvate (which produces lactate or opines). These are generated endogenously during metabolism, along mitochondrial energy pathways. In many free living marine invertebrates, succinate, acetate, alanine, lactate and opines are the end products of anaerobic metabolism (Müller et al., 2012).

The main anaerobic pathway available to vertebrates, arthropods and echinoderms, animals that are considered to have a low tolerance to anoxic conditions, is "classical glycolysis" (the glycogen-lactate pathway in which lactate is usually the sole end product) (de Zwaan and Putzer, 1985). Bivalves have evolved highly specialised adaptations for surviving hypoxic episodes, including alternate anaerobic pathways (Laudien et al., 2002). These pathways are efficient in energy production as well as reducing accumulations of toxic end products (Carroll and Wells, 1995).

The blue mussel (*Mytilus edulis*) is a rocky intertidal bivalve in which anaerobic metabolism and the response mechanisms of hypoxia has been studied extensively. The bivalves are able to withstand periodic environmental hypoxia by shutting their valves and switching to anaerobic metabolism (de Zwaan and Wijsman, 1976; Müller et al., 2012). Generally speaking, anaerobic metabolism of the blue mussel results in the accumulation of opines, involving a fermentation pathway, stated above, in which pyruvate is the terminal electron acceptor. Physiological responses from the current study suggests that the anaerobic metabolism of toheroa may also occur via opine pathways, this having implications for cell water regulation and overall animal health, which will be explored below.

During early stages of hypoxia, the amount of ATP generated by opine pathways is equivalent to that of the lactate pathway. An advantage of the former is that these pathways may reduce the osmotic stress present when lactate accumulates, and that end products are less acidic.

The free amino acids maintained in bivalves are involved in sustaining that osmotic process (Müller et al., 2012, Kube et al., 2007). Rather than being excreted as end products, opines remain in the tissue walls of an animal and are reoxidised when normoxic conditions return. This is suggested to be a general strategy for animals using an opine pathway (Müller et al., 2012).

A study by Carrol and Wells (1995) investigated the energetic pathways of tuatua (*Paphies subtriangulata*), pipi (*Paphies australis*), toheroa and several other bivalves under both environmental and functional hypoxia. Differences in pyruvate reductase between species were strongly correlated with the ability to tolerate environmental hypoxia and perform muscle work. When exposed to hypoxic conditions, tuatua and toheroa were found to have similar pyruvate reductases, with activities of D-LDH (lactate dehydrogenase) and ODH (Octopine dehydrogenase; the end point of an opine pathway). In contrast, pipi and other animals which inhabit sheltered embayments and estuaries, had differing pyruvate reductase activity and enzyme types. ODH activity has been linked with more active species and is suggested to release a high rate of energy production.

Swelling of the foot and mantle was prevalent in Control replicates (see Figure 4.7 E and Appendix B; Table B 8), and this may be attributed to change in osmotic pressure and cell water regulation. Although salinity fluxes were not measured throughout the experiment, it could be postulated that toheroa are poor at sustaining osmotic gradients between tissues and the external environment over prolonged periods of immersion in oxygenated seawater (Davenport and Wong, 1986). The lack of effective cell volume regulation, that is often found in estuarine bivalves, may serve to avoid energetic costs associated with consistent volume regulation, due to being exposed to frequent short term changes in salinity (Kube et al., 2007 and references therein).

As toheroa beds are often found near or in freshwater outputs (Williams et al., 2013), they are frequently exposed to lowered salinity. When exposed to lowered salinity, toheroa are also likely to be anaerobically respiring, while buried deep within de-oxygenated sediment. Toheroa are likely to be utilizing an opine pathway as one form of anaerobiosis, an adaptation to efficiently produce energy while also maintaining osmotic balance within tissues during periods of tidal emersion.

This could have implications when considering transport and aquaculture of toheroa, as constant submergence in seawater in an artificial setting may lead to increased cell turgor within tissues (as was observed in the aerated control of this study). When buried within sediments, periodic anaerobiosis and the energy provided by alternate metabolic pathways is a natural component of the bivalves temporal physiology. Removing environmental cues which enable this may have further consequences beyond what is currently understood of the animals metabolism, growth and energy requirements. The ability to switch to alternate energetic pathways is an advantageous mechanism if the animals are exposed to oxygen and food limiting conditions during transport.

Hypoxia/anoxia, bacterial proliferation and sulphide (H_2S) formation

If bivalves are held under stagnant, oxygen limiting conditions during transport, this can lead to detrimental bacterial growth and associated hydrogen sulphide accumulation. The formation of black sulphide (H_2S) precipitates (Coleman et al., 1993; Windoffer et al. 1999) were observed on the periostracum of toheroa valves, close to the mantle, in both Seawater-Anoxia and Seawater-Antibiotic-Anoxia treatments (Figure 4.9). Anaerobic degradation of organic matter, facilitated by sulphate-reducing bacteria (SRB), results in the production and accumulation of hydrogen sulphide (Laudien et al., 2002). The development of black deposits indicates high levels of anaerobic SRB and this was found to be most prevalent in Seawater-Anoxia replicates. Control and aerial exposed toheroa did not have these precipitates. Black sulphide compounds had also accumulated within the tissue of anoxic treatments (Figure 4.10). Babarro and Zwaan (2001) suggest that tissue necrosis may stimulate sulphide formation, whereby heterotrophic microorganisms breakdown the organic matter of the bivalves.

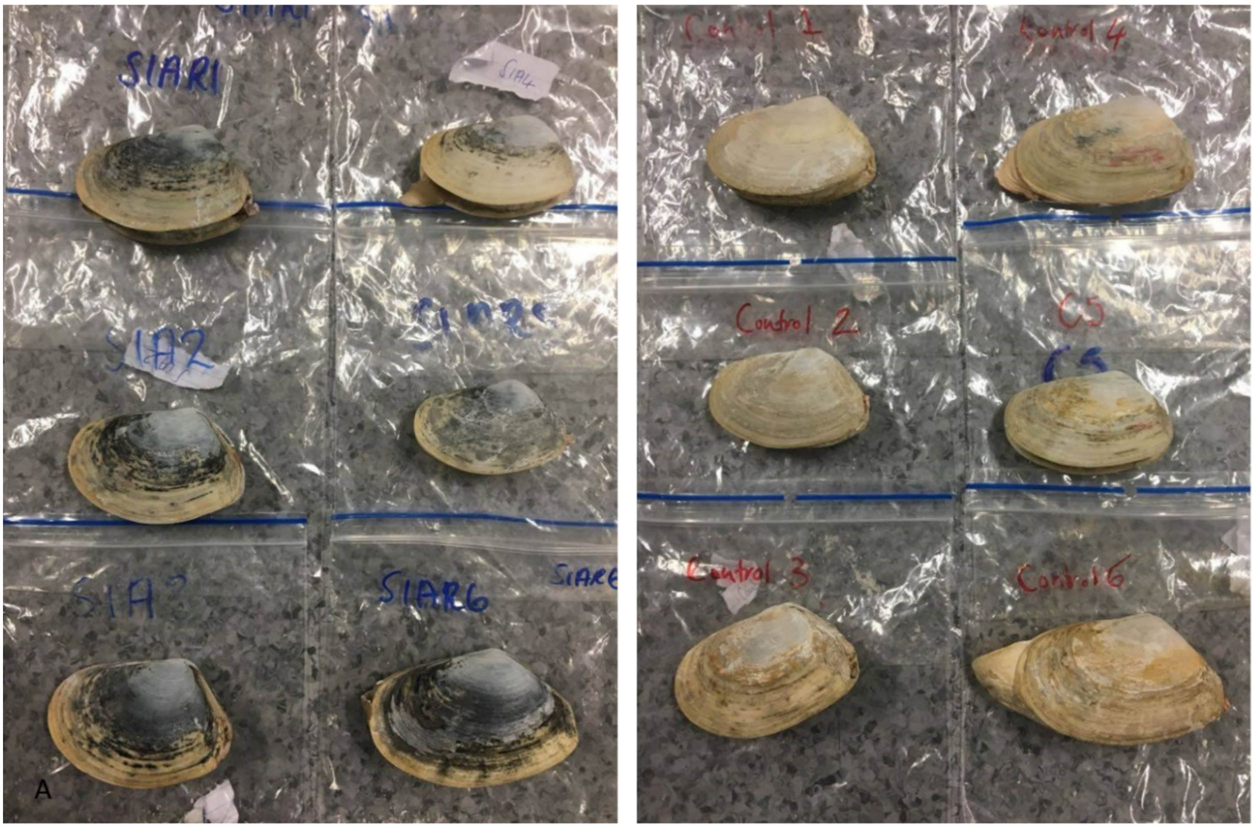

Figure 4.9 Freeze dried replicates of Seawater-Anoxia treatments displaying black sulphide deposits, next to Control replicates for comparison.

Figure 4.10 Black sulphide accumulation on gills and foot of Seawater-Anoxic replicates

A significant factor negatively effecting the distribution and survival of marine animals is the presence of hydrogen sulphide under hypoxic and anoxic conditions (Oeschger and Pedersen, 1994). Initial discoveries of invertebrates constantly exposed to high sulphide levels at hydrothermal vents has stimulated a multitude of research, to understand the adaptations which enable macrofauna to survive exposure to such a toxic substance. Endosymbiont sulphide-oxidising bacteria are suggested to be the basis of survival in such an environment (Oeschger and Pedersen, 1994 and references therein).

The adaptations of intertidal bivalves experiencing exposure to toxic hydrogen sulphide has been investigated many times in the recent past (Shumway et al., 1983; de Zwaan and Babarro, 2001; Laudien et al., 2002). Toxicity of hydrogen sulphide is attributed to the blockage of cytochrome c oxidase in the respiration chain and interferences with other vital enzymes (Oeschger and Pedersen, 1994).

Several experiments analogous to the current experiment have investigated the survival potential of bivalves held under static, anoxic conditions for prolonged periods of time. When kept in such conditions, the proliferation of anaerobic sulphate-reducing bacteria (SRB) contributes greatly to the decline of bivalves, through the pathogenic effects of the bacteria and the production of hydrogen sulphide (Laudien et al., 2002; Babarro and de Zwaan, 2008). The use of chloramphenicol as an antibacterial agent can directly address the effects of SRB on mortality by use of the antibiotic as a control. Further to this, bacterial infection and the biotic formation of sulphide may cause mortality before the critical limits of anoxic tolerance are able to be evaluated. Antibiotics such as chloramphenicol will disrupt bacterial proliferation and allow such assessments to be made (Babarro and de Zwaan, 2001).

Toheroa bury deep within the sediment (up to 190mm) (Bennion, unpublished data) and as such may be exposed to anoxic conditions and concomitant accumulation of sulphide. This is evident in the black sulphide deposits regularly found on toheroa shells taken from certain beds along Ripiro beach on the West Coast (pers. obs.). The black sulphide (H_2S) precipitates found on the shells are known to be non-toxic, stable sulphur-metal compounds (such as iron sulphide; Fe (II)) (Coleman et al., 1993; Windoffer et al., 1999). A study by Windoffer et al. (1999) investigated the morphological and chemical nature of these precipitates on *Macoma Balthica*. It was found that the blackening of the basal layer of the mantle edge was accumulations of copper, iron, zinc and sulphur in granular precipitate form and these are suggested to undergo different forms of binding, as a temporary pathway of sulphide detoxification or compartmentalisation. Combined with other physiological and ecological detoxification methods, this enables the clams to effectively protect against penetrating toxic sulphide.

Oeschger and Pedersen (1994) evaluated the influence of anoxia and hydrogen sulphide on the energy metabolism of *Scrobicularia plana,* the peppery furrow shell, a soft sediment clam. They found that when exposed to anoxic conditions, clams extruded their siphons continuously and a blackening of the outer shell layers and the mantle edge was observed. Once exposed to normoxia, the blackish colour disappeared within 24 hours. Laudien et al. (2002) also suggests that the permanent siphon extrusion in the presence of sulphide may be a strategy to monitor the water column for better conditions and this behaviour, under these conditions, is unlikely to be coupled with filtration activity. This behaviour and shell blackening was observed in toheroa treatments held under anoxia and hypoxia. Toheroa siphon extension may also be a mechanism to enable “swash riding” away from an unfavourable habitat, by utilizing currents and wave action in active migration.

De Zwaan et al., (2002) analysed anoxic seawater containing the bivalve *Mytilus edulis,* using a PCR-based approach. It was found that Sulphate Reducing Bacteria (SRB) *Desulfobacteria* and *Desulfobulbus* spp. were the predominant groups, these able to metabolize fatty acids such as propionate, a product of anaerobic metabolism. In this way, SRB species may have the potential to be in symbiosis with bivalves (Bennion, in prep), particularly under anoxic conditions, while bivalves are anaerobically respiring. The study by de Zwaan et al., (2002) found that opportunistic bacteria which became pathogenic under prolonged anoxia were associated to and introduced by the bivalves themselves, as they were incubated in sterile seawater. That is also the case in the current study. Chloramphenicol may have maintained the balance of bacterial growth, inhibiting bacterial proliferation and a consequential shift from potential symbiont (or commensal) to opportunistic pathogen.

De Zwaan et al., (2002) found that water quality deterioration (strong changes in pH, ammonium and sulphide) in the incubation medium was not a determining factor of survival time in the presence of, or with, the pre-treatment of chloramphenicol. This led to the suggestion that the primary cause of mortality was the proliferation of pathogenic bacteria within the bivalves, rather than poor water quality and sulphide toxicity. This has likely been observed in the current study as well. De Zwaan et al., (2002) suggest that pathogenic bacteria are different from the SRB present, although once mortality is reached in bivalves due to pathogenic proliferation, this would stimulate excessive growth of SRB. The researchers suggest that pathogens may cause negative effects under anoxic conditions by interfering with metabolic rest of the bivalves.

Behavioural adaptations and physiological responses of toheroa, observed and discussed in the current study, may indicate that, in the absence of pathogens, adults have developed effective defences in avoiding sulphide toxicity. However, when toheroa are exposed to pathogenic proliferation and concomitant H_2S accumulation, the animals defences are likely to be severely weakened, leading to H_2S toxicity and accelerated mortalities. These findings indicate that the prevention of bacterial proliferation should be a key component of long distance transport of toheroa. Antibacterial agents may provide support and bolster health of toheroa during transportation. Such antibacterial properties could be provided by natural sources, such as from exposure of toheroa to antibacterial properties produced by brown algae. This idea will be explored below and in the following chapters.

4.5 Concluding remarks

The behavioural and respiratory responses of toheroa and tuatua appear to differ significantly, giving indication that during transport, the two species would behave and respond to changes in external abiotic factors differently and are not a good proxy for the other. This should be considered for any future experiments when considering the two. Tuatua used within this study (from the East Coast, Papamoa) are essentially sub-tidal species, experiencing only sporadic periods of tidal emersion, while toheroa from the West Coast experience emersion daily. This would have a great influence over each species respiratory responses. It has been observed that during neap tidal events, toheroa beds have been exposed for an entire tidal cycle or potentially longer (Williams et al., 2013). High filtration and oxygen uptake of toheroa which was observed in this study may be adaptive mechanisms to events such as this, an opportunistic response when exposed to highly oxygenated waters. The tuatua from this study may be more passive with when and how oxygen is consumed, as the environment in which they live is never oxygen limited.

Toheroa and tuatua exhibit a wide range of tolerances to changes in abiotic and biotic factors, these being instrumental when considering the ability of an animal to withstand long distance transport. From the current study, when exposed to anoxia and held under air exposure, a number of physiological and behavioural mechanisms are employed to prolong survivability under unfavourable conditions. Both species are able to withstand prolonged periods of starvation and lack of oxygen in the absence of other detrimental factors. The ability to switch to anaerobic metabolism, and utilize alternate pathways such as an opine pathway, may be beneficial in maintaining osmotic balance and energy production when considering transport of the bivalves. Further to this, anaerobiosis may be an important mechanism utilized by the toheroa as part of its natural cyclic functioning and in maintaining energetic reserves.

When held under anoxic conditions, it is clear that pathogenic bacterial proliferation and associated H_2S accumulation will affect toheroa health before all other environmental stressors. The current study has highlighted several adaptive mechanisms displayed by the toheroa which may aid in avoiding H_2S toxicity. These were found to be effective in the absence of bacterial proliferation, indicating H_2S itself was not a leading cause of mortality. Further to this, when bacterial growth is controlled, toheroa displayed a substantial durability under prolonged anoxic conditions. Introducing antibacterial agents during transport may be a key factor in prolonging survival. The following chapters will explore the notion of exposing toheroa to natural antibacterial agents from the brown algal kelp, *Durvillaea* spp. *Durvillaea* spp. (rimurapa) is a large brown algal species which has been utilized by southern Māori for hundreds of years and is known to have antibacterial properties (Cruces et al., 2012).

Toheroa were found to survive when held in air for a reasonable amount of time, although the longer the toheroa were held in air, visual cues indicated that recovery from prolonged desiccation was unlikely. Although toheroa were found to be very robust animals, able to withstand a great deal of environmental stress, observations comparing tuatua and toheroa could indicate that tuatua may be even better equipped to deal with desiccation and anoxia and could potentially be the more robust of the two species to undergo long distance transport. Further experiments would be needed to demonstrate the validity of this.

From this study it is clear that when toheroa are removed from their habitat, the leading causes of health deterioration, particularly when exposed to temperatures outside of their thermal window, is bacterial proliferation (of most prevalence when held in anoxic water) and desiccation. These stressors could be avoided by undertaking a variety of preventative actions, including routine water flushes, or periodic exposure to new seawater, being kept out of direct sunlight, intermittently cleaning toheroa in fresh seawater or introduction of a non-toxic/natural antibacterial agent, and being transported in colder months. The robustness of toheroa and tuatua found within this study indicates it is plausible they could survive long-distance journeys, provided they are transported appropriately and the stressors highlighted above are sufficiently mitigated.

Chapter Five

The wharenui of the rocky shore: the extraordinary brown algal species, rimurapa (*Durvillaea* spp.) and its uses by Māori

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[31] Rimurapa from Brighton Beach, Ōtepoti (Dunedin)

5.1 Introduction

This review aims to gather information regarding a southern Māori technology, the pōhā; a natural kelp bag fashioned from the brown algal species *Durvillaea* spp.. Pōhā is suggested to have been used for transporting, translocating and re-seeding marine species such as toheroa, by southern Māori prehistorically. Multiple sources have referenced the use of pōhā in translocation of shellfish (Garven et al., 1997; Futter, 2011), yet there is no complete account of the logistics regarding these practices and little understanding remains of the processes of using pōhā in this way. For hundreds of years, Māori have utilized *Durvillaea* spp., known by its Māori name as rimurapa, in a myriad of different and ingenious ways.

This chapter collates knowledge pertaining to the distribution, ecology, traditional manufacture, uses and cultural narratives of *Durvillaea* spp.. Understanding all aspects of rimurapa and pōhā is in alignment with a holistic Te Ao Māori approach, in which everything is interconnected and therefore significant to the utilization, protection and management of the resource (Garven et al., 1997; Williams, 2016). A central focus will discuss the use of pōhā to aid in transport or translocation of marine species, and in particular, toheroa, to build a better understanding of the mātauranga pertaining to translocation. Gathering this information may give insights on how the use of pōhā as a tool and taonga resource could be used in a contemporary setting, contributing to traditional marine species management. The Ngāi Tahu Claims Settlement Act 1998 protects *Durvillaea* spp. from being commercially harvested within traditional seaweed gathering grounds.

5.2 *Durvillaea* spp. distribution, nomenclature and whakapapa

Rimurapa (Southern Bull-kelp; *Durvillaea* spp.) is a brown-algal genus in the class Phaeophyceae, which grows along exposed rocky coastlines and is found only in the Southern hemisphere. The species' distributions are primarily restricted to the South-western Pacific, occurring extensively around Aotearoa (New Zealand), the sub Antarctic Islands and Chile (Taylor and Schiel, 2005; Fraser et al., 2010). Rimurapa species are not considered true 'kelps', belonging instead to the fucoid group (Order: Fucales) (Cruces et al., 2012).

The algae are characterised by large holdfasts, one stipe and a large, broad and distinct lamina. The blades are thick and leathery, are highly successful in harsh, wave-exposed rocky shore habitats and persist, in part, due to high reproductive capacity and rapid growth rates (Schiel et al., 2006; Huovinen et al., 2010 and references therein). Fronds can reach up to 10m in length (Taylor and Schiel, 2005).

Rimurapa are dioecious plants (male and female gametes form on separate individuals), with conceptacles being produced on mature fronds when the algae is several years old. Raised male and female conceptacles scattered over the blades identify reproductive plants, although these are not always easily visble (Taylor and Schiel, 2003). Like other fucoids, the gametophyte stage of rimurapa is produced and remains on the sporophyte (Fraser et al., 2010). Conceptacles are located on the entire blade surface, expect in areas of new growth (Moss & Naylor, 1954; Schiel et al., 2006). Conceptacles develop slowly (June to the following April) and when they are fully mature produce gametes (beginning around May) for a period of up to five months, in winter (Moss and Naylor, 1954). Eggs are released in sets of four and the sperm, coated in mucilage, is released at the same time, this occurring at low tide (Schiel et al., 2006). Previous research has found that the dispersal capacity of *Durvillaea antarctica* gametes is limited, with rapid fertilisation occurring, following the release of eggs and sperm between autumn and early spring. Zygotes that are formed generally tend to settle very close (within a few metres) from the parent population, with unfertilized eggs surviving only a few days in the water column (Schiel et al., 2006; Collins et al., 2010). *D. antarctica* zygotes have been found to attach immediately and firmly to almost any surface. It is also suggested that, due to the buoyant nature of the propagules of *D. antarctica*, they have potential for long range dispersal comparative to other fucoid species (Taylor and Schiel, 2003).

Durvillaea spp. currently has six recognised species, four being unbuoyant and restricted to the south western Pacific. These include unbuoyant species; *D. chathamensis*, D ‘sp.A.’ (a yet undescribed species from Antipodes Islands), *D. potatorum* and *D. williana* and two being buoyant; *D antarctica* and *D. poha* (Fraser et al., 2010). The distribution of *D. williana* has been known to occur on both coasts of the Te Waipounamu (South Island) and as far north as Rangiwhakaoma (Castle Point) on the east coast of Te Ika-a-Māui (North Island). *D. antarctica* is distributed widely in Te Waipounamu, while also growing sporadically in the northern extreme of Te Ika-a-Māui (Naylor, 1953. See Figure 5.1).

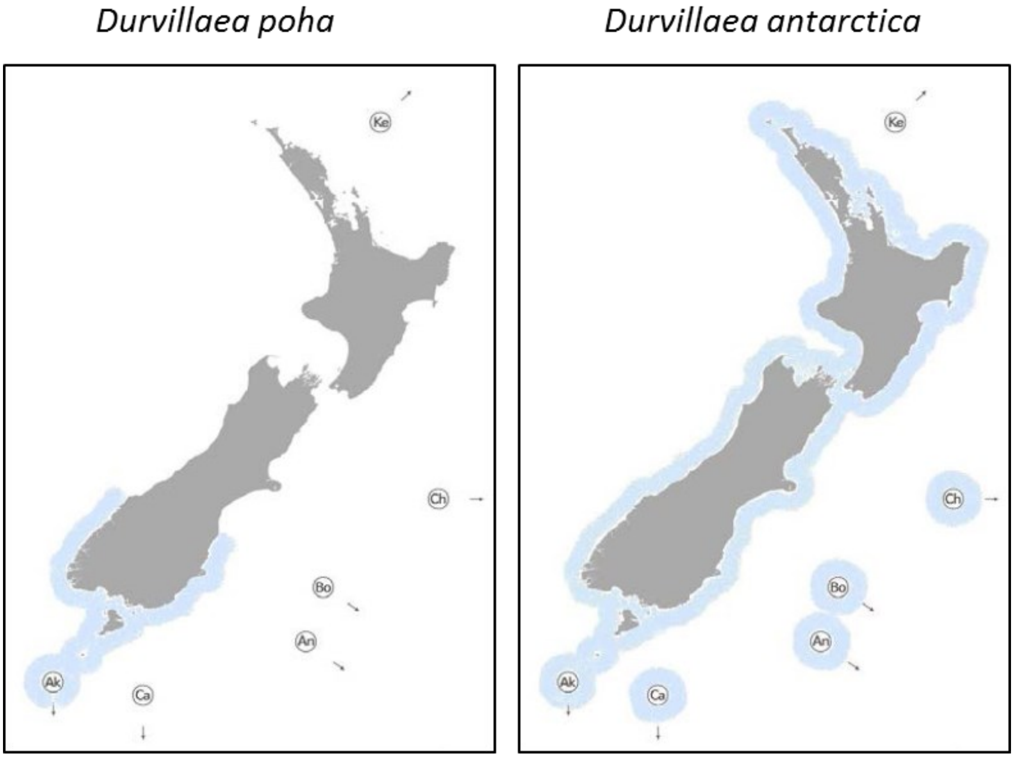

Figure 5.1 Distribution of *D. poha* on Te Waipounamu (South Island) and *D. antarctica*, across Aotearoa (New Zealand), taken from Neil and Nelson (2016). Two letter codes refer to outlying Island groups.

D. antarctica has previously been described to have five genetically diverse lineages. Within Aotearoa, phylogenetic analyses undertaken in recent years has demonstrated that two of the five lineages within the species *D. antarctica* are two separate species; *D. antarctica* and *D. poha*. Previously the two lineages within *D. antarctica* were theorised to be morphologically but not genetically different due to the “superficial” distinction of the blades (either ‘thonged’ or ‘caped’ blades) (Fraser et al., 2012). The amount of subdivision of the lamina in *D. antarctica* into strap like thongs was presumed to be related to the severity of exposure to wave action, although Naylor (1953) notes that morphological difference based on habitat may not be the case as the two forms were found to grow intermingled.

Phylogenetic research and nuclear genetic data analysis undertaken by Fraser et al. (2012) provides evidence for reproductive isolation of the “cape” lineage. *D. poha* was previously assumed to be a “cape” lineage due to the wider blades of the thalli correlating with individuals that occupied sheltered habitats, being less exposed to wave action. This was considered a function of morphological plasticity. The “thonged” lineage of *D. Antarctica* is more widespread then *D. poha* (Figure 5.1), with evidence suggesting that *D. poha* is endemic to Aotearoa. Its distribution is restricted to Te Waipounamu, Rakiura (Stewart Island), Tini Heke (the Snares Islands) and the Motu Maha (Auckland Islands). One theory for this species’ limited distribution, given that *D. poha* is highly buoyant, is that the blades are much less streamlined than the "thonged" blades of *D. antarctica* and may drift more slowly at sea (Fraser et al., 2010).

Fraser et al. (2012) describes *D. poha* as intertidal, growing commonly at mid-tide level on exposed rocky coasts, in a band above *D. Antarctica,* and on sheltered coasts across the intertidal zone. *D. Antarctica* are a deeper species and occur at the lowest limit of the midlittoral belt (subtidal boundary) in exposed, high energy, rocky coast environments and are often only exposed at the lowest of tides (Moss and Naylor, 1954; Taylor and Schiel, 2003).

D. antarctica and *D. poha* have lamina which are strongly inflated by honeycomb like structures of central air chambers (Figure 5.2), this characteristic distinguishing them from all other species of *Durvillaea* (Naylor, 1953). The honeycomb structure provides strength, is efficiently buoyant and offers protection from wave damage (Tala et al., 2013). The detached individuals are capable of continuing photosynthesis and surviving for extended periods, although the health of detached blades becomes somewhat diminished through time (Collins et al., 2010; Velásquez et al., 2019). Further to this, secondary metabolites produced within brown algae such as *Durvillaea* spp. are known to have antibacterial and antioxidant potential. These organic compounds may aid in defence against wounding, exposure to UV radiation, high temperatures and herbivory (Shannon and Abu-Ghannam, 2016).

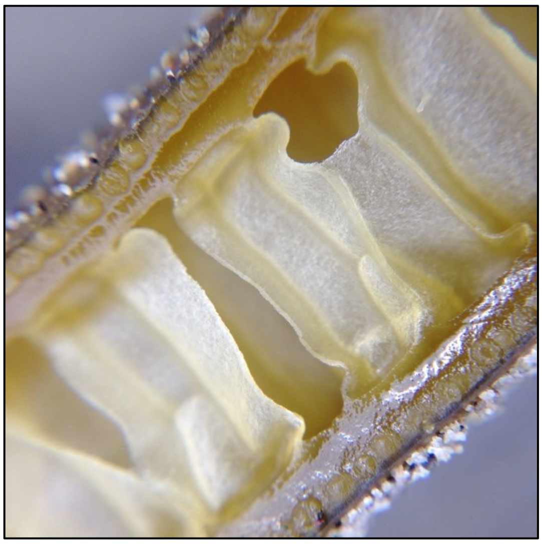

Figure 5.2 Internal honeycomb structure of *Durvillaea poha* and *Durvillaea antarctica*[32].

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[32] https://critterclubjournal.wordpress.com/2016/07/14/south-brighton-trip-13/

The whakapapa of rimurapa

The Māori name for *Durvillaea* spp. is either rimupuka or rimurapa. The nomenclature of rimupuka derives from the terms rimu (kelp) and puka, a name used to describe the 'membranous interior of the kelp', the honeycomb like structure found in the interior of the blades of *D. poha* and *D. antarctica*. Species within the genus *Durvillaea* are also named rimurapa (rapa having multiple meanings including, anything broad or flat and rubber) (Beattie and Anderson, 1994). Rimurapa is generally the term given to the Southern Bull-kelp, *Durvillaea* and has therefore been used within this review.

An origin story of rimu (seaweed) described by Elsdon Best (1929) tells of the many forms of seaweed and how they were created to provide a safe haven for shellfish. Within the whakapapa is important biological information which is retained in history through oral tradition. This origin story was collected from the Wellington region.

Best writes;

> *In the dawn of time, when trees, all forms of vegetation, and insects had been produced, then shell-fish were brought into being and were placed in the waters as denizens thereof for all time. In order to provide a safe haven for these shell-fish, they were taken to Whare-rimu and Whare-papa, where many forms of seaweed (rimu) cling to the rocks and shelter the offspring of Te Arawaru and Hine-moana. These seaweeds are the progeny of Hine-moana (sister of Rua-kawerau) and Kiwa, their names being-*
>
> *Te Rimu-rapa…..*[33]

The excerpt continues to name many forms of rimu. Relayed here is a symbolic reflection of rimu and its functions along the coastline, as observed by Māori; that of an ecosystem engineer important in providing shelter for many other species. Marine macroalgae have been recognised to play a critical role in habitat provision and are important species in structuring biodiversity within marine communities (Tait and Schiel, 2011). Implicit in the whakapapa of rimu is its ecological importance, an understanding derived from years of observation, utilization and management of different algae by Māori.

Elsdon continues;

> *These seaweed offspring of the ocean and its guardian were taken to Rakahore and Tumatua, and placed in their charge; theirs the task to tend and protect seaweed folk, even that those rock-clinging seaweeds might shelter the shell-fish folk who cling to Rakahore; for Rakahore and Tuamatua are the personified forms of rock and stones*

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[33] (Best, 1929) Pg. 73

> *in Māori myth. Thus we see, says the Māori, that Te Rimu-rapa and his younger brethren ever cling to their foster-parents.*[34]

5.3 Rimurapa and Pōhā

Pōhā is the Māori term given to rimurapa when it has been manufactured into a bag or bladder, primarily used for the storage of food. It is a storage technology developed by southern Māori to take advantage of flora and faunal resources, during their seasonal abundance (Garven et al. 1997). Pōhā and rimurapa has been used by Māori for hundreds of years, most commonly in Te Waipounamu (the South Island).

Pōhā were not only a useful tool, they were symbolic, often associated with knowledge, mana (respect, spiritual power) and rangatiratanga (chieftainship) of an area and its resources. In a report by Poharama et al. (1988), kōrero tuku iho (oral tradition) of the prehistorical occupancy of Kaikōura is relayed;

> *As far as can be determined, Ngāti Māmoe were the original occupants of the Takahanga Pa site at Kaikōura, but ceded mana to the warrior chief Maru Kaitatea of Ngāti Kuri and Ngāi Tahu, by presenting him with a pōhā or kelp bag of local food delicacies. The giving of the pōhā meant that the resources of the Kaikōura region were transferred peacefully according to Māori tradition and custom. Maru Kaitatea was the grandson of Kuri, the eponymous ancestor of Ngāti Kuri, and the hapū to which many Kaikōura Māori belong.*[35]

Resource laden pōhā were frequently traded among hapū and iwi, but in the context presented above, the transfer of pōhā symbolised a significant and respectful shift in power. The handing of the pōhā was a fundamental moment and is steeped in Ngāi Tahu history through karakia (prayer), whakataukī (proverbs), waiata (song) kōrero tuku iho and artworks of Ngāti Kūri and Ngāi Tahu.

Pōhā used in transport

Across Te Waipounamu, each major hapū had a wide range of resources (mahika kai, see Chapter Two) available to them, from a variety of locations. These would be accessed systematically throughout the year and resulted in frequent, long-distance movement of groups, as they moved between resources to manage and harvest. Beattie and Anderson (1994) writes of the use of pōhā for ‘porterage’, carrying goods from one place to another, often on long journeys;

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[34] (Best, 1929) Pg. 73

[35] (Poharama et al., 1998) Pg. 9

> *In the old days big pōhās (kelp bags) and potted foods were carried on men's backs long-distances to feasts. Three sticks or "legs" dangled from the load and were used when the porter required a rest. Many of the loads were so heavy that the carrier could not have hoisted them up unaided. My informant saw pōhā borne thus to the tangi for Hoani Korako at Otakou, but he never heard the name of the three sticks (which presumably form what Stack calls a "porter's stool"). It is said that it took the porters three weeks to bring their loads from Riverton to Otago Heads.*[36]

Beattie has documented further accounts, regarding porters and carrying/transporting receptacles such as full pōhā;

> *He [the "principal informant"] had heard of the kawe (shoulder straps) to which the kete was attached. The kauru was packed in kete, the weight being say forty pounds average. A strong person would carry two kete and a very strong man three = one hundred and twenty pounds roughly. Carrying = whakawaha. A staff was borne in the hand and for a rest the kawe would be slipped off. When carrying pōhā-titi a stool was carried behind and the load would rest on it at stops. He could not remember the name if these two sticks forming the stool as it was about one hundred years since it was used. He forgot the name of the "porters", but carrying food was "poi", hence the name Kaiapoi.*[37]

Kaiapoi (Figure 5.3) is a small district on the East Coast of Te Waipounamu near Ōtautahi (Christchurch) and was recognised prehistorically as a centre for trade routes (McIntyre, 2007). The excerpt highlights the prevalence of transporting food via trade routes through this area, so much so that it has informed the areas name.

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[36] (Beattie and Anderson, 1994) Pg. 98

[37] (Beattie and Anderson, 1994) Pg. 281

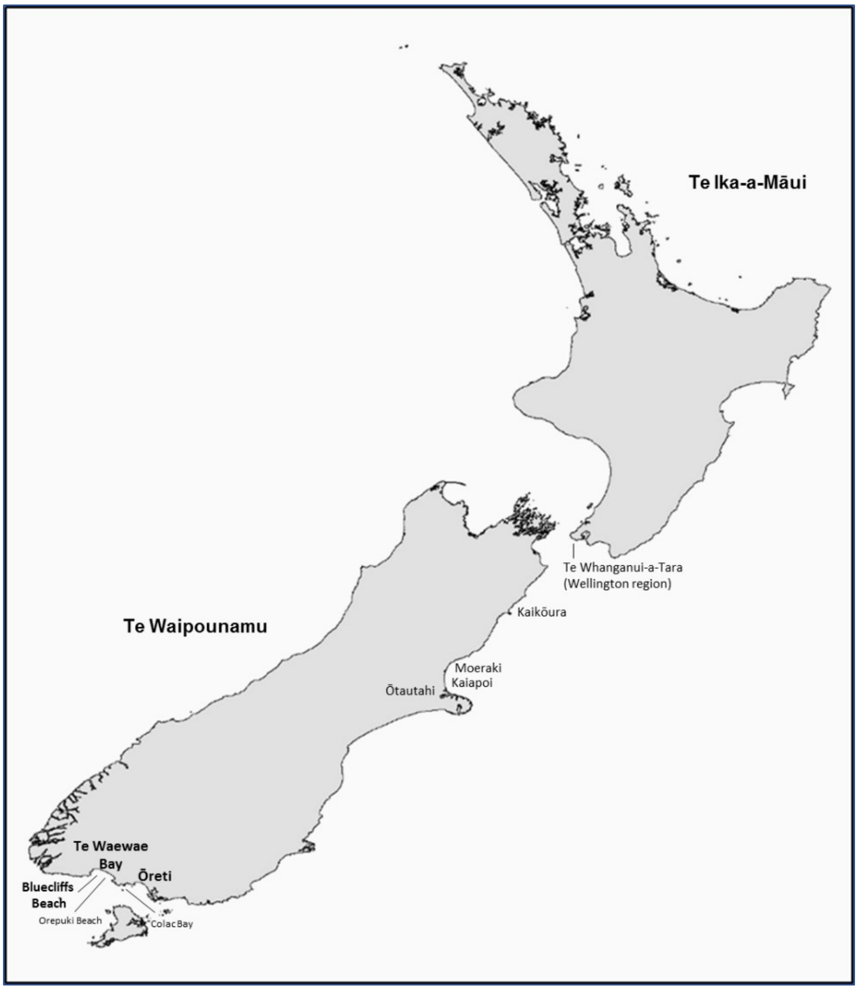

Figure 5.3 Locations of interest to pōhā and rimurapa

Evidence is given here about the robust quality of the pōhā as tools in transportation, as well as the technologies developed by Māori, who have enhanced natural resources to better preform difficult tasks. The pōhā would have been prepared quite specifically for use in travel, or for any of its other uses.

Rimurapa was also used as a receptacle for freshwater, a “he mau wai” or water carrier. Beattie writes of informants who spoke on the matter;

> *When near the beach fresh water used to be carried in rimu (kelp) say my Temuka friends. A piece of kelp was slit, the water poured in, the top tied, the kelp placed in a flax bag or basket and carried on the back. Although this was “green’ rimu it could be prepared the same as the dried rimu in the pōhā bags-by putting “tiwha” patches over*

> *the hole. The kelp used was just the ordinary rimupuka of which the pōhā-tītī ("muttonbird bladders") are manufactured.*[38]

Pōhā used in cooking and food preservation

Rimurapa was used in many different ways by Māori, each bearing a different name dependant on its function. Beattie (1915) states; "In its green state it was used to steam shellfish in – a process called murumuru te pōhā (singeing the kelp), and in its dried state it furnished fine receptacles for the preservation of food." One informant from Moeraki, described the use of pōhā as a cooking implement for shellfish;

> *At Moeraki the collector [this refers to the author, Beattie, himself] was told that the best way to cook kakihi (sea limpets) was to put them in a pōhā (kelp bag) and roll it over and over in the fire, this method being called murumuru te pōhā. Occasionally the bag bursts and then its contents have to be raked out of the fire as quickly as possible. There is a doubt if this method really is ancient as one of my informants saw some pakehas following this mode at Lyttelton and was assured by them it was a European way.*[39]

Harvesting large amounts of seasonal game was only viable if there were means of storage and preservation for exchange or later consumption. Preservation of food was done by a few methods, by either preserving in fat or drying. Drying was often the method used for fish and other kaimoana. Preservation using congealed fat required suitable containers, the most efficient being the supple pōhā (Beattie and Anderson, 1994; Tau and Anderson, 2008). Rimurapa individuals were cut from specific areas along the coast of Te Waipounamu in the summer. The blades were opened, creating a bag which was inflated and dried. These dried bags were worked into a supple leather-like material and were able to be used immediately or stored. Many instances of Māori utilizing pōhā for preservation of food has been found and evidence suggests that animals could last 8 months or longer within the pōhā, when prepared correctly (Anderson, 1998).

Animals said to have been preserved or stored in pōhā, after some form of preparation include; many species of fish such as barracouta (makaa in the south, manga elsewhere), tuna (kirirua; longfin eel), koura-waitai (salt water crayfish), stingrays, human flesh (kai-/kiko-tangata), rats (kiore, named pōhā-kiore, which kept a long time), varying species of birds including: tītī (muttonbird), ducks (maunu) (Beattie and Anderson, 1994). Pōhā is still used today in the preservation of tītī.

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[38] (Beattie and Anderson, 1994) Pg. 127

[39] (Beattie and Anderson, 1994) Pg. 112

One informant spoke to Beattie of the pōhā possessing special qualities in preservation (Beattie, 1915), prehistoric pōhā practitioners would have understood that the composition and characteristics of rimurapa allowed the development of pōhā as a technology for preserving food.

Mahika kai of rimurapa and the production of pōhā

The annual harvest (mahika kai) of rimurapa for pōhā-tītī is recorded by Beattie to have occurred in December or January, before the tītī season began (the beginning of April). A good shape, length and sized rimurapa blade would produce around 4 to 5 pōhā, though it is stated that at the time of recording, kelp blade condition was slowly declining and the lamina were not of such sizes as they were prehistorically. One reason is said to be due to the lack of harvesting of kelp beds in the late 1800s leading to poor quality of kelp, much like the continual pruning of a tree to produce better fruit (Williams, 2016).

Southern Māori were not only prominent subsistence farmers, but also worked a resource for trading purposes. An extension of resource management activities as they were continuously developed, was the active manipulation of the resources to maximise quality and quantity (Tau et al., 1992). This was also important for retaining a working knowledge of the resource, to continue mahika kai practices and conserve the resource and underlying mātauranga for future generations.

Pōhā practitioners interviewed by Beattie spoke of specific areas in which kelp was collected. The kelp on the coast from Riverton (Figure 5.3) (Murihiku, South Coast) was said to be “harder” (referring to the physical characteristics of the lamina) then kelp found round the Bluff, implying it was more robust to work with, while Bluff locals preferred their own kelp, indicating that it was more elastic, softer and more pliable.

Preparing poha

After the blades are collected, they are opened by pushing the hand through the honeycomb interior, careful to avoid the margins in case it splits. When making the pōhā, to push the hand through the interior of the blade is termed koko-pōhā. The kelp bladders were given different names dependant on whether they had been dried or remained hydrated (thus staying in their ‘green’ form). Pōhā which served as a hydrated kelp-bladder was called pōhā-mata (fresh or raw pōhā), while a pōhā that had been dried was called pōhā-maroke (dry pōhā) (Beattie and Anderson, 1994). Rimurapa bladders which have been inflated are called pōhā-hau, with the opening or lip of the bag which is tied being called te kutu. The opening of the pōhā has a cork like device, called a tiwha (Figure 5.4) which forms an airtight plug. If any holes are found or the pōhā bursts, a tiwha may be used to repair the damage, with the tiwha being inserted in the hole and tied. The pōhā could be inflated using a pupuhi-rimu, a hollow tube made from patete (seven finger (*Schefflera digitate*), a soft wood) with the pith removed. This was inserted into the opening next to the tiwha and when sufficiently inflated (Figure 5.5), it was removed and the opening tied tightly with harakeke.

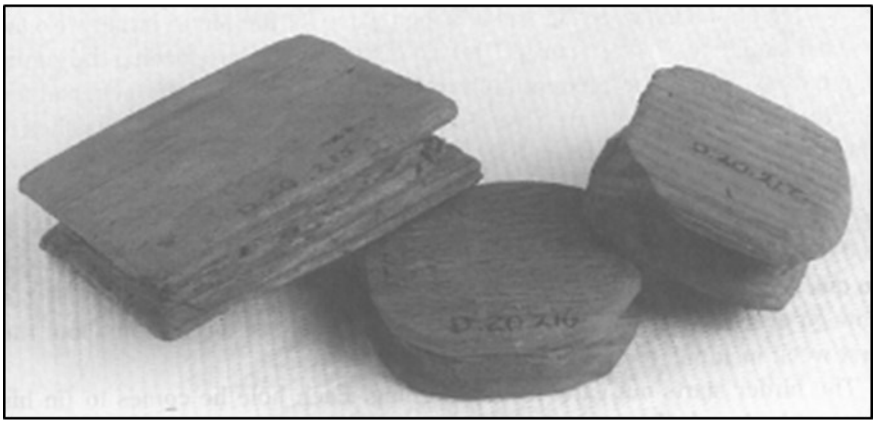

Figure 5.4 Three wooden tiwha given to Beattie at Moeraki, now in the Otago Museum. Taken from Beattie and Anderson (1994).

Figure 5.5 Kelp being inflated into bags. Taken from Beattie and Anderson (1994).

Beattie writes of an elder in Moeraki who spoke of patching up pōhā; “The kakahi is the saltwater limpet and the shells are used to make a quick tiwha (patch) on the pōhās (kelp bags) at the Tītī Islands. Always turn the open side of the shell to the inner side of the pōhā and it makes a better neater job." [40]

Once the pōhā has been inflated (pupuhi) they are hung to dry in the sun and wind, avoiding any contact with rain or wet. It is said to take around 3 days to dry, is then hung inside for one day to continue the drying process and then it may be deflated to soften (whakahau). It is processed further to remove any remaining hardness a number of ways. Usual practice involves lying the bags on the grass and covering with grass. If the bag is exposed to water whilst hard it is said to be ruined. Another method for softening, used more in historical times, involved placing the pōhā in earth (covering the bag with soil) and then later working the bag (much like leather) to produce an "elastic velvet" texture (Figure 5.6). When the bag is sufficiently pliable its edges are trimmed and then it is rolled up to be stored for future use.

To utilize the pōhā for tītī (muttonbirds; *Puffinus griseus*) preservation, the birds were captured and cooked in wooden basins with heated stones. Cooked birds were packed into the pōhā, and the reaming fat from the birds was poured in. The opening was tied tightly to exclude air. When the pōhā full of cooked tītī had cooled, the pōhā would be covered by totora bark (kiri-totora) and harakeke weaved tightly around it, with a basket attached to the foot of the bag (papa-pōhā) (Figure 5.7). Preservation was much more complex than the brief description given here, with one elder stating the tītī is handled in different ways up to sixteen times from its catching to its placement in pōhā (Beattie and Anderson, 1994).

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[40] (Beattie and Anderson, 1994) Pg. 178.

Figure 5.6 A pōhā from Bluff, now located at the Otago Museum. The kelp bag is said to now have the appearance of grey velvet. Taken from Anderson and Beattie (1994).

Figure 5.7 Figure Pōhā -tītī from the Riverton museum, Taken in 2018.

Mahika kai husbandry of rimurapa for pōhā-titi is still practiced today by southern Māori, such as kaitiaki Graham 'Tiny' Metzger and his whanau. This is an example of the practical application of mātauranga which has been passed down through generations and utilized today. The following information on the mahika kai of rimurapa and tītī was collected from personal communications with Tiny Metzger, in his Bluff home, in 2018.

Tiny Metzger and his whānau have been harvesting rimurapa to make pōhā for more than 70 years. His whānau are one of a few southern Māori who still undertake the annual mahika kai harvest of tītī from the offshore islands of Rakiura (Stewart Island). The Metzger family are in their fourth generation of tītī trading. Before their voyage to the Tītī islands, this whānau harvest and prepare pōhā from traditional mahika kai sites. If the rimurapa was regularly collected and 'pruned', it would not take long for the blades to grow in a way that was useful to make pōhā (Metzger, pers. comm.). The kelp would be pruned so the stipes would become elongated. Blades of rimurapa which have been growing for one year are suggested to be ideal, if the kelp has been maintained. If the kelp has been left to grow, without being managed, Metzger suggests that it may take blades 3 to 4 years to take a form useful for pōhā taonga mahi harvest.

Tiny and his whānau have had to travel farther afield over the years, to collect kelp that is healthy. Approximately 40 years ago, the harvest area was situated close to their home in Bluff, but Metzger attests that pollution to the area has deteriorated the quality so that it is unable to be curated into a pōhā bag without disintegrating. Tiny suggests that effluent pollution may be one of the causes of the deterioration of the kelp and fears this too may occur in other areas in which rimurapa is harvested.

Pōhā and toheroa translocation

Evidence pertaining to the enhancement of marine species by Māori has been documented by Williams (2004), with a particular focus on rimurapa and pōhā (*Durvillaea*). Williams (2004) relays a statement given by Ngāi Tahu kaumātua, Rikiihia Tau:

> *Rimurapa was, and still is, used in the planting or seeding of kaimoana around our coastline. Seafood did not just appear around our coastline waterways and lakes. In most cases these foods were planted there by our ancestors.*[41]

In a paper which discusses kaitiakitanga in Te Waipounamu, Williams (2016) gives an account of pōhā being used for the "transplantation" of shellfish to new areas. Evidence provided to

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[41] (Rikiihia Tau to the Waitangi Tribunal, Wai27) Pg. 135

the Waitangi Tribunal (a New Zealand commission of inquiry established under the Treaty of Waitangi Act 1975) is reiterated in Williams (2016) paper, with a Ngāi Tahu Kaumatua, Rakiihia Tau stating;

> *Toheroa have been seeded at South Brighton/Karorokaroro (Pegasus Bay). These root stocks came from Kahuraki point (North of Westport) and Waikawa (Picton); similarly, tuatua in Pegasus Bay; cockles in Ihutai (Heathcote Estuary) ex Ōtepoti (Otago harbour) and Kaikōura; scallop beds outside the North East bays of Akaroa*.[42]

The mātauranga pertaining to southern toheroa was investigated by Futter in 2011. Interviews were conducted with kaitiaki, local experts and scientists regarding toheroa populations in Te Waewae Bay and Ōreti (Figure 5.3). Information discussed included the historical and contemporary distributions and ecology of toheroa and traditional management practices undertaken in the areas. Many interviewees were aware of attempts in the past to translocate toheroa, being considered a customary practice and restorative tool, for the enhancement and management of southern toheroa. Translocation efforts relayed to Futter (2011) were from established populations within Murihiku, to beaches surrounding them, such as Colac Bay.

From the interviews undertaken, it was established that the main kaitiaki who initiated translocations in Murihiku in the recent past was Jack Te Au, who was working actively in toheroa conservation in the 1950s to the mid 1960s. Of particular importance was his role in seeding a new population of toheroa on Orepuki Beach (Figure 5.3) (Futter, 2011).

Futter (2011) writes briefly of the historical use of pōhā as a restorative tool used by kaitiaki;

> *Both Interviewee F and R alluded to the use of pōhā (bags of the lamina of bull kelp,* Durvillaea antarctica *to transplant toheroa spat in. The original source of this kōrero has passed away and unfortunately the finer details of his methodology were not captured in this present study. Pōhā may provide protection and nurture the toheroa spat in their new location in order to help them establish.*[43]

A Ngāi Tahu resource management strategy report, written by Garven et al. in 1997, refers to shellfish seeding as a traditional management tool. The text states; "*Shellfish beds were seeded with superior strains taken and transplanted from other areas, and established beds were both enhanced and depleted (culled) by biological methods*".[44]

The report refers to evidence given to the Waitangi Tribunal in support of Te kereme–the Ngāi Tahu claim. It offers that sophisticated traditional knowledge of management and

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[42] Williams (2016) Pg. 314

[43] (Futter, 2011) Pg. 27

[44] (Garven et al., 1997) Pg. 37

enhancement techniques were utilized in the south, including thinning or enhancing populations of shellfish to produce superior individuals. The most robust individuals were said to be recognised and thus used for transplanting to other areas. Seeding was an aquaculture practice utilized by Ngāi Tahu, which took two forms and was undertaken by people skilled in the management of the mahika kai (Chapter Two) of specific shellfish species.

The first form was seeding different types of shellfish to a new area, while the second involved the movement of shellfish out of their natural habitats to artificial environments such as rua (storage pits). In an excerpt from the text by Garven et al. (1997), methods surrounding shellfish management by seeding are offered;

> *Knowledgeable people would choose their kaimoana mātaitai (seafood) at a time when they were ready to seed and place them in pōhā rimurapa (a container made of seaweed). The pōhā would be placed along the shoreline near the kāinga where the pressure of the waves over the buried pōhā would trigger the release of the seeds from the kaimoana mātaitai. Alternatively, the pōhā would be gently kneaded by the cultivator so the seeds are pressured out.*[45]

The report expresses that this was an "oversimplification of a complex process". The viability of such practices from a biological and ecological perspective would involve consideration of many variables. Garven et al. (1997) writes about the recognition by the people of the importance of water and habitat quality. This is incorporated in the concept of mauri (spiritual essence, life force) and its life giving properties. Water quality must be suitable to allow regeneration of shellfish and "*the mauri of the river that enters the estuary or coastline where the kai mātaitai is planted should be compatible with the mauri of the waters from where the shellfish was originally taken*." [46] The tradition of seeding new wai mātaitai within southern regions has not been undertaken in recent years and much of the traditions around the cultural practices have been lost.

Further details for pōhā seeding is provided by Peter Ruka Korako to Waitangi Tribunal and relayed by Williams (2004). Ruka speaks of Rimurapa as "a gift", a taonga resource and important tool. Rimurapa was used by the elders to trap the spat and lay them in concentrated areas. He states:

> *At times the kai-moana-mataitai are ovid/gravid seeds being generally released along the beaches in a quite haphazard manner. It is at this time that our poua and taua use the gift of Rimurapa (sic) to trap the spat and lay them in concentrated areas close by*

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[45] (Garven et al., 1997) Pg. 37

[46] (Garven et al.,1997) Pg. 37, 38

> *the "papa kaika". The time sequence is critical and the preparation of the rimu is extremely painstakingly slow and sacred. The holes of dispersal are drilled using a special bone from the skeleton of the hāpuku [fish]. The numbers of holes are important as they must match up and duplicate the pattern of "matariki". When these sequences have been completed the karakia would then set apart all who will collect the gravid seafood and place them either on rocks or in the sand or mud.*
>
> *The old ones would collect their favourites and place them into pōhā, these pōhā would be punched with holes and buried in the 3rd and 4th wave line at low tide or placed carefully on the rocks or in crevices where the wave pressure would slowly disperse the eggs over a period of time . . .*[47]

The act of marking pōhā with the matariki design would have served several practical and symbolic functions (Williams, 2004). Holes drilled into the thick blade of the kelp would have a primary function of allowing spat to escape, while still receiving the benefits of protection within the pōhā. The design would also act as a label and a warning, telling others to not interfere with the re-seeding (whakatīpu mātaitai). Adherence to the rules of society would have been key to insure such investments were safe. Specifically, as mentioned previously, if root stocks were sourced from far afield.

Williams (2004) writes of the necessary knowledge base for importing seed stock of toheroa. He suggests that toheroa translocation would not have been accomplished by the first Māori colonists, as the knowledge base for toheroa would not have been acquired until a few generations after settlement to prevalent areas. Pōhā, which was a southern adaptation, would not have been utilized for translocation practices until the pōhā had been developed and used extensively (Williams, 2004).

The establishment of inter-regional relationships would have occurred over a period of time after settlement, along with the complex social structures and controls developed between iwi, these being required if pōhā was to be left in the surf zone untouched, to seed an area with shellfish. Williams observes that these conclusions are inferential, but the interpretation is consistent with all evidence available. Williams (2004) writes;

> *Although we do not know when the events mentioned in this paragraph began, it seems likely that the necessary mechanisms were not in place from the beginning of Māori occupation of Te Waipounamu. We do know, however, that all were in place by the time of European contact.*[48]

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[47] (Ruka to Waitangi Tribunal, Wai27) Pg. 135

[48] (Williams, 2004) Pg. 224

Contemporary use of pōhā in conservation (Wakefield, 2007)

In 2007, a restoration case study was undertaken by Wakefield which utilized traditional management practices of Ngāti Kurī, in response to the decline of rimurehia (seagrass; *Zostera novazelandica*) along the Kaikōura Peninsula. This case study was a small part of a larger PhD thesis, which was unique in its methodology, utilizing a Collaborative Kaupapa Māori Philosophy and framework. The thesis focused on traditional knowledge authentic to the hapū Ngāti Kurī and the application of this knowledge for conservation and restorative purposes.

Ngāti Kurī recognise the ecological importance of seagrass and its use as an indicator of the health of an ecosystem. A restorative plan was developed to translocate rimurehia using traditional methods of re-seeding, to assist the re-growth of healthy seagrass communities along the Kaikōura Peninsula coastline. The exercise aimed to translocate samples of seagrass to new areas using pōhā. Traditionally, Ngāti Kurī have used pōhā to translocate species, as a nurturing tool, to establish a kōhanga (nursery) and to replenish stocks (Wakefield, 2007). Several trials utilizing rimurapa were undertaken, which aimed to support and facilitate seagrass growth. Samples of seagrass with leaves and rhizomes intact were collected and inserted into fresh rimurapa blades. The role of pōhā in these trials was as a protective mechanism for juvenile seagrass against rough tidal and coastal conditions. The first trial utilized rimurapa blades still attached to rocks, creating a 'live pōhā'. Blades were selected and a slit was cut at the end of the blade, separating the tissue. The rhizomes and leaves of the seagrass were inserted into the live pōhā and holes were punctured in the bags for rhizomes to work their way out and settle in the sediments. The first trial found that some rhizomes did continue to grow in the pōhā, but overall there was limited or inconclusive success of seagrass settlement. However, the first trials were successful in informing changes for the methods of the second trials.

Small holes were made into the blade of the rimurapa (blades were not split to form a classic pōhā) and rhizomes were pushed through, resulting in the leaves of the seagrass on one side of the blade and rhizomes on the other. The rhizomes were then buried into the sediments and rimurapa blades were anchored to the sea floor using loose lime rocks. The rimurapa was essentially an incubating mechanism which anchored the rhizomes and supported their stabilization in the sediments. Monitoring of these trials took place over a year, with results indicating that rimurapa blades remained stable and that the seagrass rhizomes had grown, evidence that the kelp was an ideal incubator or kōhanga for the sea grass rhizomes.

5.4 Concluding remarks

The traditional knowledge of rimurapa and other algal species is rich within Aotearoa. The above experiments, utilizing pōhā to facilitate seagrass growth, are a successful example of utilizing mātauranga authentic to a hapū and the ability to adapt this knowledge to a new environment, through observation, trial and error. It appears that some of the mātauranga surrounding pōhā as a management tool may have already been lost, following European colonisation and historical and continuous devaluation of indigenous knowledge. However, Wakefield (2007) reclaims important ancestral knowledge and provides the opportunity for this mātauranga to be used in a contemporary setting. These experiments have provided an excellent example of how mātauranga can be adjusted to address new environmental challenges.

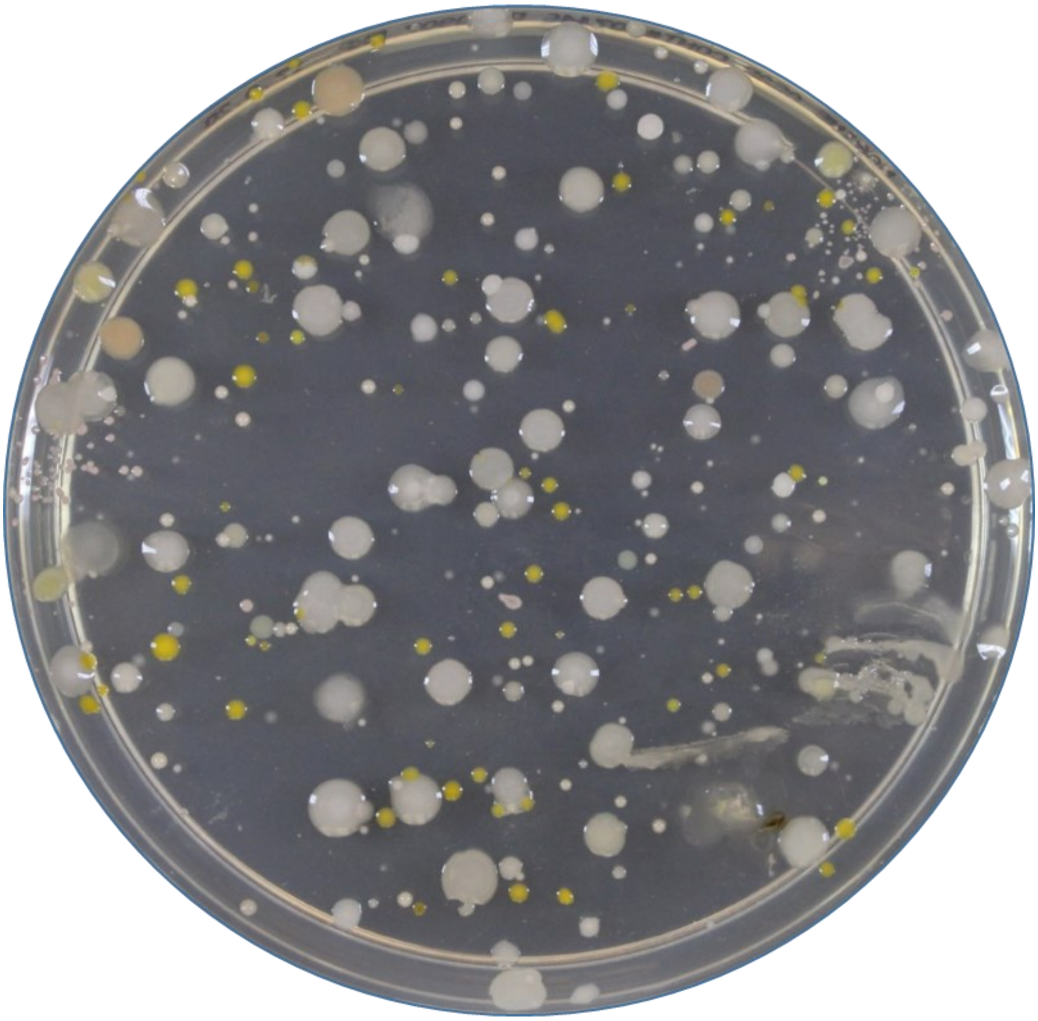
This review aimed to offer further opportunity for reclamation of such knowledge, by collating information regarding whakapapa, ecology and characteristics of rimurapa and to highlight its valuable and practical uses by Māori. Understanding the species physiology, life history, whakapapa and distribution is synonymous with the mātauranga of harvesting and utilizing a resource. Having this holistic knowledge is intrinsic to the success of intergenerational mahika kai husbandry.

Organic compounds within *Durvillaea* spp. are known to have antibacterial properties (Cruces et al., 2012) and pōhā could have great natural antibiotic potential. In this way, pōhā may act as a natural environmental control system when holding, transporting, or protecting other species such as toheroa. This will be explored further in the following chapter, along with the potential of live *Durvillaea* spp. tissue to provide oxygen via photosynthesis in otherwise oxygen limited environments.

Empirical evidence presented here details the use of rimurapa as pōhā, and how it may have been used to carry or hold live species when undertaking traditional management. Future, hapū-led, management exercises could incorporate the use of pōhā in whakatīpu mātaitai of taonga shellfish to new areas, including bivalve species that fall within the genus, *Paphies* (tuatua, pipi and toheroa).

Chapter Six

Pōhā into Practice: the bacterial and physiological implications of holding live toheroa (*Paphies ventricosa*) in pōhā (*Durvillaea* spp.)



[49]

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[49] Aerobic marine bacteria grown on marine agar. Bacteria are associated with rimurapa and toheroa

6.1 Introduction

The transportation, translocation and re-seeding (whakatipu mātaitai) of marine species is an approach to resource management that has been used extensively by Māori hundreds of years ago and continues to be used today (Chapters Two and Four). The endemic surf clam, toheroa (*Paphies ventricosa*) is a species with a long history of translocation, and it is hypothesised that toheroa were introduced to the southernmost beaches of Te Waipounamu (the South Island) from parent populations on the West Coast of Te Ika-a-Māui (the North Island) (Ross et al., 2018). If true, this hypothesis would explain the unusual and unique disjointed distribution of toheroa that until recently was considered to be entirely natural. Remedial management of toheroa has been a widely discussed topic in recent years (Williams et al., 2013) and restoration of the species by way of translocation and re-seeding of adult stocks (both within and between beaches), has been undertaken on numerous occasions by kaitiaki (guardian, conservator) in the recent past. Translocations have been documented within both Te Ika-a-Māui and Te Waipounamu (Futter, 2011; Williams, 2016; Wakefield, 2005).

Kōrero tuku iho (oral traditions) surrounding pre-historic transportation and whakatipu mātaitai of shellfish tell us that pōhā (a natural bag made from the brown algal species *Durvillaea* spp.), a southern Māori technology, were used in the transportation of toheroa and other shellfish (Garven et al., 1997; Futter, 2011; Williams, 2016). Pōhā were constructed from Southern Bull-kelp or rimurapa (*Durvillaea* spp.) which is a brown-algal genus in the class *Phaeophyceae*. Rimurapa are not true kelps (order Laminariales), but instead belong to the order Fucales (Cruces et al., 2012). *Durvillaea* spp. are found only in the Southern hemisphere, growing extensively along exposed rocky shores of Aotearoa, the subantarctic Islands and Chile (Taylor and Schiel, 2005; Collins et al., 2010). Rimurapa are known for their distinctive morphology, which consists of a large holdfast, single stipe and a large and broad lamina (blade) which is thick and leathery. Rimurapa inhabit harsh wave exposed, intertidal and subtidal habitats, along rocky shorelines (Schiel et al., 2006; Huovinen et al., 2010 and references therein). The fronds of *Durvillaea antarctica* have been found reach up to 10m in length (Taylor and Schiel, 2005).

Rimurapa or rimupuka are the Māori terms for the Southern bull-kelp species *Durvillaea antarctica* and *D. poha*, with rimurapa generally accepted as the broad term of the genus in Te Reo Māori. Pōhā is the Māori term given to rimurapa when it has been manufactured into a bag or bladder, primarily used for the storage of food. The pōhā is a storage technology that was developed by southern Māori, some time prior to European arrival in Aotearoa. Pōhā have been utilized in numerous ways, including transporting of drinkable freshwater and transporting and preserving food. Most famously, pōhā are used for the preservation of tītī (mutton birds; *Puffinus griseus*) with the potential to be be safely stored within poha eight months, if properly prepared (Chapter Five). The ability to preserve food in pōhā allowed Māori to take advantage of seasonal abundance, prehistorically (Garven et al., 1997; Chapter Five). The Ngāi Tahu Claims Settlement Act 1998 protects *Durvillaea* spp. from being commercially harvested within seaweed gathering grounds.

Durvillaea poha (Fraser at al., 2012) has only recently been split taxonomically from *D. antarctica*. The two species can be distinguished by the shape of their blades, with *D. antarctica* having thick thong like straps, previously labelled the "thonged" lineage and *Durvillaea poha* having large, broad flat cape-like blades, thus being previously named the "cape" lineage. *Durvillaea poha* is suggested to be endemic to Aotearoa (Fraser et al., 2012) and is named after the pōhā it is used to construct.

The lamina of both *D. antarctica* and *D. poha* are strongly inflated by medullar tissue, with well-developed central air chambers. This characteristic distinguishes them from all other species of *Durvillaea* (Naylor 1951; Tala et al., 2017) and provides strength, buoyancy and protection from wave damage (Tala et al., 2013). When the algae become detached from reefs or boulders by wave action, their blades act as rafts and when drifting, most of the blade will float at the sea surface. This exposes the blade to UV radiation and increased temperatures. The gas-filled sacs of the medulla allow the photosynthetically active area of the blade to be maximized as it floats on the surface, while also minimising self-shading (Harder et al., 2006). Drifting adults of *D. antarctica* have considerable potential for dispersal as they can continue photosynthesising and remain reproductively viable for extended periods after detachment (Collins et al., 2010). Tala et al. (2013) found that detached *D. antarctica* can survive for up to 30 days. The characteristics of *Durvillaea* spp. allow them to take the form of a natural airtight vessel.

Antibacterial potential of brown algae

Organic compounds within *Durvillaea* spp. may have antibacterial properties and, in this way, pōhā could have natural antibiotic potential. Brown algae often produce organic compounds with high biological activity and antibacterial properties (Shannon and Abu-Ghannam, 2016). This is particularly prevalent in species, like rimurapa, which occupy high-energy environments such as exposed coastal rocky reefs. Environmental stressors that rimurapa are exposed to include battering from wave action, osmotic stress, UV light exposure, changes in dissolved oxygen (DO) and salinity, herbivory and biofouling; all of which can lead to injury of the thallus (Schmitt et al., 1995; Taskin et al., 2007; Cruces et al., 2012).

Secondary metabolites with antibacterial properties have been identified in all classes of algae. Antibacterial activity has been found in numerous chemical functional groups within algae, these include phlorotannins, fatty acids, polysaccharides, peptides, terpens, polyacetylenes, sterols, indole alkaloids and aromatic organic acids. Secondary metabolites are not essential to physiological function of an organism, but are instead eco-physiological adaptations to specific biotic or abiotic conditions, such as listed above, within the marine environment (Mayer et al., 2013; Taskin et al., 2017; Shannon and Abu-Ghannam, 2016). Allelochemicals (secondary metabolites) can act as chemical inhibitors to competing organisms and can have high antibacterial or antibiotic potential. Such metabolites are more prevalent in sessile algae such as rimurapa, which are more prone to competition for space, biofilm formation and herbivory (Vieira et al., 2016; Shannon and Abu-Ghannam, 2016).

Phlorotannins are secondary metabolites currently only known to be produced in *Phaeophyceae* (brown algae). Phlorotannins, along with terpens, have allelochemical properties and can act as deterrents of herbivory, inhibit biofilm formation and act as antioxidants, protecting against UV damage and excess irradiation (Lüder and Clayton, 2004; Wei et al., 2016; Shannon and Abu-Ghannam, 2016; Generalić Mekinić et al., 2019). Brown algal phlorotannins can be synthesised rapidly during wound healing and sealing, after the thalli endure abrasions or amputations (Cruces et al., 2012), although biosynthetic pathways of Phlorotannins are largely unknown (Generalić Mekinić et al., 2019).

Existing research concerning phlorotannins is based primarily on its soluble forms, found in physodes, which are highly mobile organelles within the cytoplasm (Lüder and Clayton, 2004, Halm et al., 2011; Generalić Mekinić et al., 2019). Physodes are able to fuse with the membrane of the cell wall, allowing secretion of phlorotannin compounds which create complexes with alginic acid, thereby becoming constituents of the cell wall (Generalić Mekinić et al., 2019). Previous research has indicated that although physodes occur in most brown algal tissues (Verma et al., 2015), a higher abundance has been observed in outer tissues (such as epidermal, apical and meristematic), indicating these compounds may have key roles in thallus protection (Generalić Mekinić et al., 2019). These molecules are able to inhibit oxidative phosphorylation, along with binding to bacterial proteins and causing cell lysis, therefore reducing or preventing unwanted biofilm species from colonising the thallus (Shannon and Abu-Ghannam, 2016).

The synthesis of phlorotannins has been found to be operating in the free-floating blades of *D. Antarctica*, this contributing to physiological acclimation and protection (Tala et al., 2013). The production of phlorotannins in response to UV radiation and thermal stress is a protective mechanism which may minimize oxidative stress and aid in maintaining photochemical processes (Tala et al., 2013; Cruces et al., 2012). This adaptation supports the idea that these processes may continue when algal blades are detached and made into fresh pōhā or used as fresh rimurapa.

Algal Biofilms

To understand macro-algal functioning at an ecological level it is necessary to consider the interactions an alga has with its associated microbiota. Photosynthetic activity of a macro-algal host may provide a unique aerobic environment for epibiont colonizers, comparative to other marine surfaces where DO is a limiting factor (Egan et al., 2013). The algal thallus not only provides an aerobic substrate but produces many organic substances which can act as a nutrient supply for bacterial growth and biofilm formation (de Mesquita et al., 2019).

Consequently, the surfaces of macro-algae are particularly susceptible to colonization by microorganisms, with the position of algal blades in the water column and photic zone providing optimal conditions for biofilm growth. Within the marine environment, bacteria are the most prominent colonizers of exposed surfaces. However, despite the above characteristics which should make macro-algae prime hosts for colonising bacteria, bacterial growth is generally lower on macro-algal compared to non-biological surfaces (Steinberg et al., 1997; Dobretsov and Qian, 2002; Lam and Harder, 2007).

The absence of biofouling is explained by macro-algal secondary metabolites. These have a marked effect on bacterial colonisation and community composition. Different types of bacteria may be either harmful or beneficial for macro-algal hosts and it is likely algal species have evolved mechanisms which can selectively control bacterial growth. Further to this, secondary metabolites may extend beyond the thalli surface, with studies showing that macro-algal metabolites can affect bacterial communities in the adjacent water column (Sneed and Pohnert, 2011; Egan et al., 2013). Understanding the mechanisms by which the anti-bacterial properties of algae function can allow us to explore the implications of this in relation to the use of pōhā. If metabolites are able to extend beyond the thalli surface, they may influence the microbial growth directly associated with the contents of a raw pōhā, for example, toheroa in seawater.

Secondary metabolites, pōhā and shellfish translocation

It is unknown what role rimurapa secondary metabolites play in the utility of pōhā as instruments for preserving and transporting live or processed foods. Certainly, it is not inconceivable that the anti-microbial properties of rimurapa contribute to the longevity of processed foods stored in pōhā. Equally, it could be suggested that antimicrobial properties may contribute to the utility of pōhā as a tool for transporting live shellfish.

The physiological responses of toheroa when held under different environmental conditions have already been explored in this thesis (Chapter Four). They are remarkably resilient creatures, able to withstand low DO (dissolved oxygen) concentration and starvation for extended periods of time. When removed from their habitat, the leading causes of health deterioration is desiccation, bacterial proliferation and associated sulphide toxicity. All of these stressors are exacerbated by increases in temperature (Chapter Four). When transporting toheroa, any methods which may reduce these stressors will aid in successful translocation. Here we explore the notion that the use of raw (fresh tissue) rimurapa to construct pōhā, will have biochemical and bacterial effects when holding live bivalves. The anti-microbial properties and DO production of pōhā may provide health benefits for toheroa when used as a vessel for transport or translocation.

Aims

Two independent hypotheses were tested within the following experiment, which together assessed the chemico-physical, biological and microbiological outcomes when rimurapa is used as pōhā to hold live toheroa. The first stage of the experiment aimed to assess photosynthetic and respiratory activity that may have been occurring within pōhā, with toheroa present. It was hypothesised that, while the tissue of the alga was still alive and viable, it may continue to photosynthesis, thus replenishing DO within the pōhā, that the toheroa would quickly remove via respiration. This experimental stage occurred within twenty-four hours once the experiment began.

The second stage aimed to examine the microbial community associated with toheroa held under different conditions including with and without pōhā. It was hypothesised that antimicrobial metabolites produced by the algal thalli and the associated alga biofilm may effect bacterial growth, when incubating toheroa within pōhā. This could be manifested in the reduced abundance or altered diversity of bacteria, within or on the shellfish, in pōhā treatments. The use of the antibiotic Chloramphenicol in treatments for comparison, may allow us to further elucidate antibacterial effects of the pōhā. A pōhā treatment which involved turning the bags inside out (inverted) with the outer thalli exposed to the contents of the pōhā, was also included. This was to assess the effects of the algae’s biofilm and thallus to bacterial growth inside the pōhā, associated with toheroa.

6.2 Methods

Field collections

Toheroa

In September 2020, seventy-two adult toheroa (*Paphies ventricosa*; > 70 mm shell length*)* were collected from the intertidal area of Ripiro Beach, on the West Coast of Te Ika-a-Māui, Aotearoa New Zealand. They were held in aerated seawater, in a 20L plastic fish bin with lid, for transport to the University of Waikato, Tauranga (approximately 6 hours transit). The toheroa were then held in filtered and aerated seawater, in a temperature controlled water bath (13-14°C), for an acclimation period of 5 days. Water was changed daily and the bivalves were not fed during this period. The toheroa collected for experimentation were weighed and measured and Condition Index was calculated after completion of the experiment.

Rimurapa

Durvillaea spp.[50] (New Zealand Bull Kelp, rimurapa) blades (enough material to make 12 pōhā) were collected at low tide from Brighton Beach, Ōtepoti (Dunedin) on the East Coast of Te Waipounamu. The blades were washed with filtered seawater to remove sand and epibionts. Rimurapa material was then patted dry with tissue, rolled, packaged with cold pads and transported to the University of Waikato in Tauranga (approximately 36 hours transit).

Experimental design

The following experiment incorporated eight treatments described below (Table 6.1) with each treatment carried out in triplicate and each replicate containing three toheroa. Treatments will hereafter be referred to by the abbreviations provided in Table 6.1.

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[50] As I was unable to undertake genetic analysis to ascertain the species of *Durvillaea*, I have identified the algae used in this experiment to genus level.

Table 6.1 displays the eight treatments, codes and associated factors, within the experiment. All treatments contained toheroa (*Paphies ventricosa).* Codes descriptions are as follows: pōhā + seawater (P-SW), pōhā inverted + seawater (PI - SW), pōhā + Aerial exposure (P-AE), pōhā inverted + aerial exposure (PI-AE), seawater (SW), seawater + daily antibiotics (SW-AB), aerial exposure (AE), aerial exposure + pre-administered antibiotics (AE-AB).

Treatment	Code	Pōhā	Seawater	Antibiotic
1	SW	-	Y	-
2	SW-AB	-	Y	Y
3	AE	-	-	-
4	AE-AB	-	-	Y
5	P-SW	Y	Y	-
6	PI-SW	Y	Y	-
7	P-AE	Y	-	-
8	PI-AE	Y	-	-

Treatment descriptions

Pōhā/pōhā inverted/no pōhā

Of the eight treatments, four used pōhā to hold live bivalves. *Pōhā* (P-AE and P-SW) treatments were used in the traditional sense (see Chapter 5 for description, thalli is split open and used), while in the pōhā inverted treatments (PI-AE and P-SW) the split thalli were turned inside out, with the outer tissue of the kelp exposed to the toheroa (Figure 6.1). For the four non-pōhā treatments, toheroa were held in 1L glass jars with loosely fitted (not airtight) lids.

Preparation of pōhā

The Blades of rimurapa to be used as pōhā were cut into 12 similar sized pieces and measured (Appendix C; Table C 1). The thalli were then split through the central tissue, along and down the width of the blade, to form an airtight bag (see Chapter Five for making a pōhā). Holes were punched around the openings of the fresh pōhā and cable ties threaded through, allowing the entrance of the pōhā to remain slightly open and accessible, while also creating a form of handle used to suspend them (Figure 6.1).

Sea Water /Aerial Exposure

Of the eight treatments, four incorporated seawater incubation of toheroa, while the other four held the toheroa under aerial exposure (no seawater). Two seawater treatments were kept in jars (SW, SW-AB), while two were held in pōhā (P-SW, PI-SW). To mirror these, two aerial treatments held toheroa in jars with no seawater (AE, AE-AB) and two in pōhā with no seawater (P-AE, PI-AE). Aerial exposure treatments were each lined with a folded and wet paper towel to maintain moisture.

Antibiotic

The pharmaceutical grade, broad scale antibiotic Chloramphenicol was administered to two of the eight treatments (AE-AB, SW-AB). Throughout the experiment, the antibiotic was kept at a working solution of 50mg/L (dried powder mixed with filtered water) and was applied to seawater via pipette.

The nine toheroa held in the AE-AB treatments (three per replicate) were held separately from other toheroa during the acclimation period. These individuals received 5mg/L of Chloramphenicol in the early morning for two days and following this, antibiotic was increased to 10mg/L for the last two days, before the experiment commenced (total of four days of antibiotic treatment). Doses were based on previous shellfish experiments using this antibiotic (de Zwaan et al., 2002; Barbarro and de Zwaan, 2008; Yamada et al., 2016).

Seawater replicates which received antibiotic treatment (SW-AB, N=3), were given 5mg/L Chloramphenicol when the experiment first began (at 0 hours) and thereafter received a dose of 10mg/L once daily for the remainder of the experiment.

Experimental set up and procedures

Treatments were placed in a temperature controlled, freshwater bath set at 13°C (ambient coastal temperature).

Pōhā treatments

Four 40L plastic bins were filled with filtered seawater and placed in the water bath where they were acclimated to water bath temperature and held under constant aeration. Seawater within bins was not changed during the duration of the experiment. The pōhā were suspended within these bins filled with seawater, by ropes, to ensure kelp tissue (a) was kept at a constant temperature, (b) was not exposed to freshwater and (c) did not become desiccated.

Aerial exposure treatments

A weighted 40L fish bin was held in the water bath and aerial exposure treatments (1L glass jars with no seawater) sat in these. Seawater jar treatments were placed directly into the water bath. All seawater treatments held temperature acclimated, previously aerated and UV filtered seawater (1L per replicate). The initial DO reading of 8.16 mg/L was taken at 0 hours, immediately after aeration was removed from the acclimating filtered seawater. This was then transferred into each replicate for seawater treatments. After seawater was transferred to each treatment, no water changes occurred.

Two LED floodlights were fixed to wooden frames above the water bath, sitting directly above the treatments. Light intensity from the natural white LED floodlights (CCT = 4000K) was measured, using a LiCor Li1500 meter with a LiCor Li192 PAR sensor, at approximately 150 (Range: 100-200) µmole photons m^{-2} s^{-1}, at the level of the light/pōhā interface, throughout the experiment. Treatments were exposed to ~10 hours of continuous light during each 24 hour period.

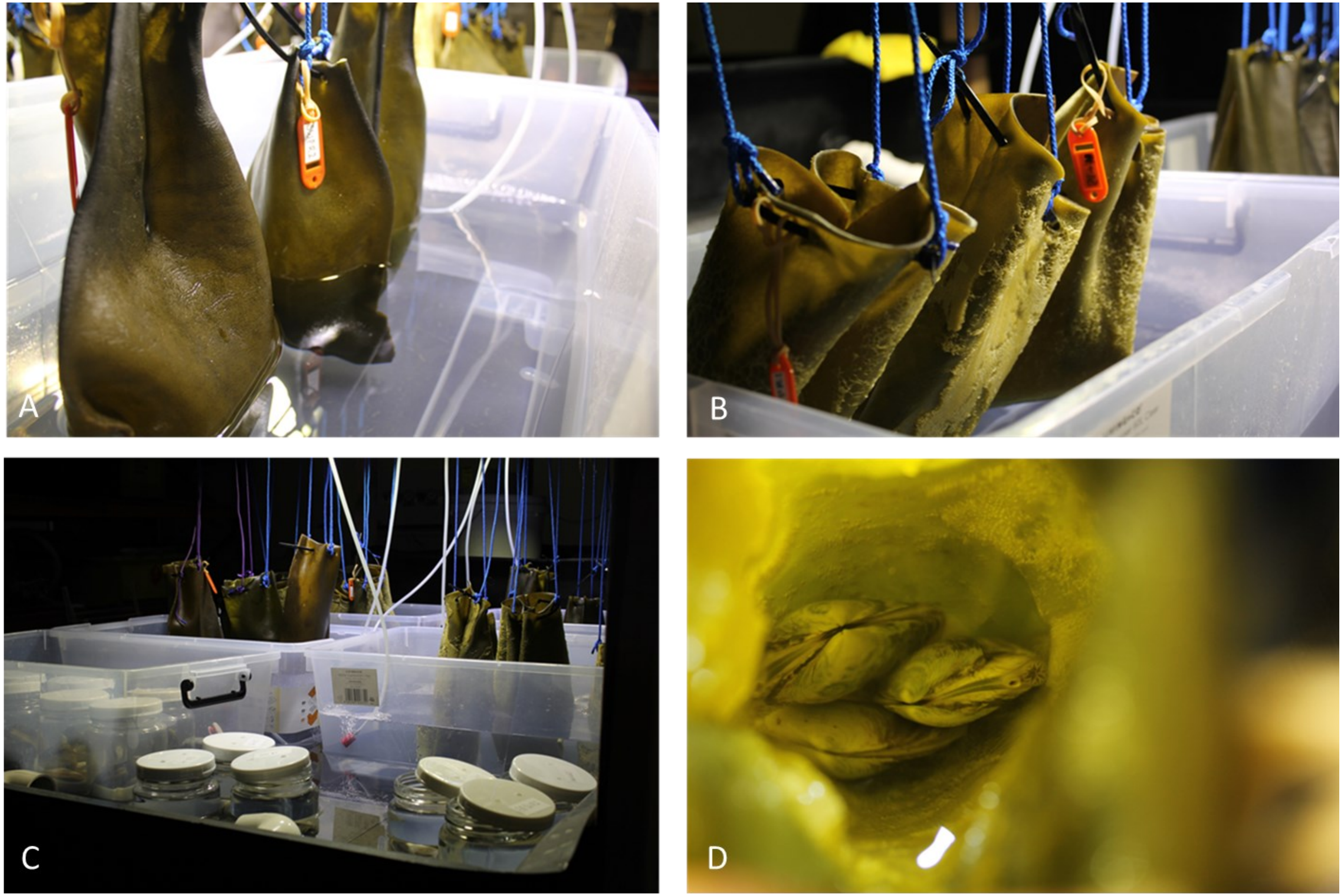


Figure 6.1 A: traditional pōhā treatment, B: inverted pōhā, C: water bath set up, D: toheroa in seawater pōhā treatment.

DO (mg/L) and temperature (˚C) were measured intermittently (one or two hourly over a period of 10 hours in each treatment on the first day of the experiment) using a PreSens Fibox 4, with attached and calibrated oxygen and temperature probes. Measurements were taken from within the pōhā bags and jars. DO was not measured outside of the pōhā. Once anoxia was established in all seawater experiments, gas measurements were stopped. Temperature was measured with six HOBO data loggers thereafter. Throughout the experiment temperature was measured at an average of 13.7 °C (Range: 12.1 °C -15.9 °C). Salinity of seawater was measured at 35 ppt at 0 hours of the experiment.

DO fluxes were measured as a proxy of both the photosynthetic activity of the algal blades and as an indication of bivalve respiration within the pōhā. To assess DO concentrations through time in the presence of bivalves with and without pōhā, change in DO concentration of seawater treatments were further analysed.

Replicates were checked daily for mortalities and individuals were considered deceased if they failed to respond to probing stimuli. A metal rod was used to stroke the mantle of each individual and if signs of valve shutting were not observed, they were removed from the experiment. The experiment began on Wednesday 16 September 2020 and was terminated after 14 days.

Condition Index

The *dry flesh weight:dry shell weight* Condition Index % is a widely used condition index that is universally applicable and easily standardized. The use of dry tissue weights eliminates the bias of water content fluctuation within tissues. The index can give meaningful indications about the physiological state of a bivalve, with a low value inferring that major energetic effort has been expended. As such, this can be a good biological indicator of stress placed on an animal, from exposure to poor environmental conditions or disease, or from production and release of gametes (Lucas and Beninger, 1985; Marsden, 2000).

CI% values were calculated using the following equation (Matozzo, 2012):

$$CI\% = \frac{dry\ tissue\ weight}{dry\ shell\ weight}\ x\ 100$$

Marine agar bacterial culture

Lawn culture methods were used to grow a suite/sub-sample of aerobic marine bacteria associated with different treatment incubations. Lawn or spread cultures are used to grow discreet colonies of microorgansims, from a small sample volume, which are distributed evenly over an agar surface. The number of colony forming units (CFU) are then counted as an indication of type and abundance of bacteria present in a sample (Sanders, 2012).

Trial One; day three sampling

The first bacteria samples taken from bivalve individuals occurred on the third day of the experiment. For each replicate, a bivalve individual was removed from its treatment and a swab sample was taken, where a sterile wooden swab was lightly brushed over the mantle and outer periostracum for 10 seconds. Swab samples were immediately placed in sterile glass vials, with 4ml of sterile (autoclaved) seawater and sealed. Vials were then each vortexed for 10 seconds to create a suspension of cells for spreading on agar (Sanders, 2012).

Within a sterile fume hood, a 1:100 ml two-fold serial dilution was undertaken for each sample using sterile seawater. Pre-poured 90 mm Marine Agar (2216) plates (Fort Richard Laboratories) were used to cultivate aerobic, heterotrophic marine bacteria. Room temperature agar plates were inoculated with a 200ul aliquot from a serial diluted (10^{-2}) sample. Lawn/spread protocol followed aseptic techniques for plating bacteria as recommended by Sanders (2012) using an L shaped metal spreader. Inoculated agar plates where sealed with parafilm, inverted and placed in an incubator at 30^{o}C, under dark conditions. Inoculation of marine agar for each replicate was undertaken in duplicate (Wille et al., 1996), with a total of 48 plates.

Bacterial growth on agar plates were photographed using a Canon EOS 60D, at 24 (Day One), 48 (Day Two) and 72 (Day Three) hours of incubation.

Trial Two; day five sampling

A second trial was undertaken on the fifth day of the experiment, taking swab samples only from the aerial treatments. Seawater treatments were not sampled as these treatments were undergoing different degrees of degradation (pōhā thalli were beginning to disintegrate in some replicates and seawater jar treatments were turning black due to sulphide accumulation). This was due to and further confounded by proliferation of anaerobic bacteria which could not be cultivated with this methodology. All methods in this second trial were as described above (trial one) with two differences. In trial two, individuals were swabbed for 5 seconds (instead of 10 seconds) and samples were shaken by hand instead of vortexed. It was apparent from trial one that swabbing for 10 seconds would lead to high bacterial counts and flooding of the plates with CFUs across all treatments.

Bacterial Analysis

The photographs of each agar plate were imported into Adobe Photoshop 2021 (Version 22.3.1) to be enhanced. The colour range of the colonies was isolated and the contrast increased to better identify and differentiate bacterial colonies. These were used as a supplementary visual aid, alongside the original images. All images were further analysed for bacterial growth and presence by quantitative and qualitative methods.

Grid-point Intercept (GIP) cover analysis of agar plates

As colonies were quick to grow (often > 300 CFUs per plate) it was not feasible to conduct full counts of each plate. Instead, a Grid-point Intercept (GPI) (Hulvey et al., 2018) methodology was developed to quantify type and abundance of bacterial growth, represented as a Relative Colony Abundance score (RCA). This provided a proportional estimate of agar plate surface cover. This methodology enabled time-effective and accurate quantification in order to compare bacterial growth associated with different treatments. The quantification of bacterial colonies within this methodology were purely for comparative purposes (relative abundance) and were not designed to determine total number of bacteria (CFU ml^{-1}) present within each sample. An assessment was conducted to determine if the GPI methodology was estimating consistent RCA counts between agar replicates. Details of this assessment can be found in Appendix C (Table C 3 and Figure C 1). This assessment confirmed that the GPI methodology produced consistent RCA counts between plates and was sufficient in producing useful estimates for comparison.

The original images of all agar plates were identically cropped (to the edge of the agar medium), to insure uniform placement when overlaying with a grid. These were then analysed using ImageJ (Java version 1.8.0_112). The first cropped image was brought into ImageJ and a scale was set, measuring 90mm across the diameter (actual size) of the agar plate. A 10mm by 10mm grid was overlaid on this image, producing a 646-point grid across the visual field of the agar medium (Figure 6.2). These settings were stored as a template and overlaid on all subsequent images brought into ImageJ.

All intersected colonies on a plate were identified and counted. Colonies falling within 0.25mm of an intercept point were included as this was an appropriate measure to insure an accurate representation of coverage. Counts which were produced for each replicate were then divided by 646 (total number of intercepts), to produce an RCA score between 0 and 1.

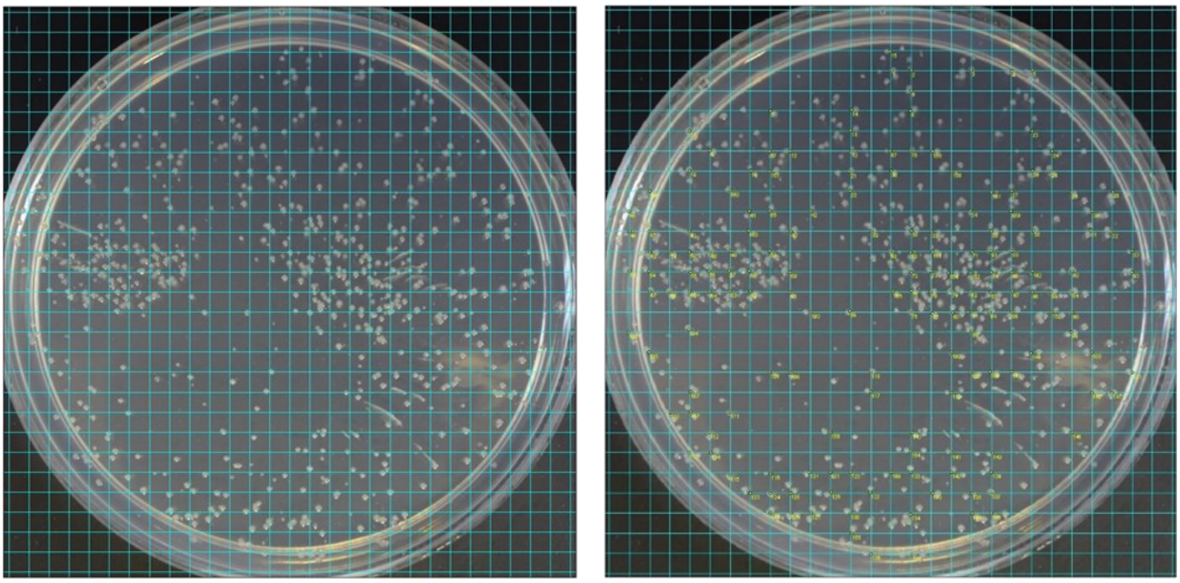


Figure 6.2 Example of grid template overlaid on agar replicate P-AE 1-2 at 24 hours growth (left) and Grid-intercept point counts of the same plate (right).

Bacterial subtyping

The division of similar bacterial strains (bacterial typing) into subgroups (Busch and Nitschko, 1999) was undertaken using macroscopic morphology, namely pigment. Differentiation of colony colour became apparent at 48 hours, after which visual taxonomic subgroups (VTS hereafter) of colonies were identified daily (see Appendix C, Table C 4 for all VTS and Figure 6.3 for an example of colony subtypes). Further qualitative descriptions of differing VTS, such as speed of growth and phases, size, shape and texture were also noted (Ahern, 2018).

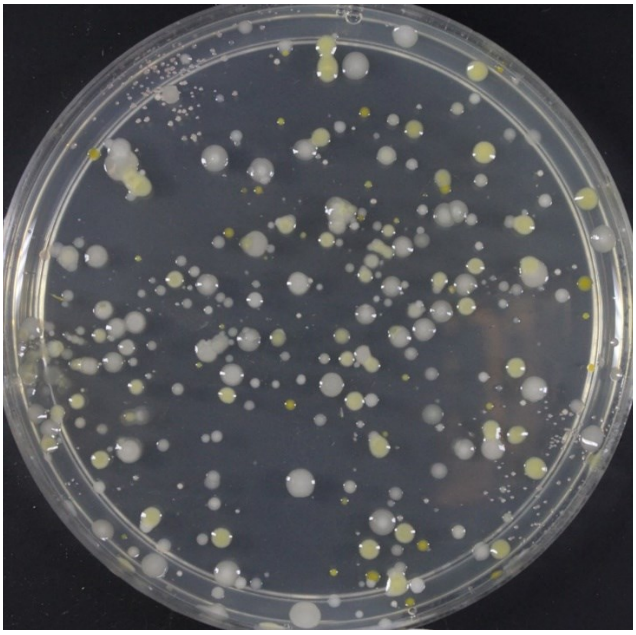


Figure 6.3 Example of agar plate with subtypes (Treatment: AE1, three days of growth)

VTS (community data) were recorded using the same GPI methods as above. If more than one type of colony was found to intersect a grid point, both were counted and represented in the VTS data.

Statistical analyses

Dissolved Oxygen

To visualise the data, DO averages (±SE) of all seawater treatments were plotted against time, in a line graph. Several Kruskal-Wallis Rank Sum Tests, followed by post hoc Dunn tests were undertaken comparing each treatment (P-SW, PI-SW, SW-AB and SW) at each sampling interval (Appendix C, Table C 4). DO values were also pooled into pōhā (P) and no pōhā (NP) groups, and DO averages (±SE) at each sampling interval were displayed in a bar graph. Multiple One-Way ANOVAs were undertaken in Minitab® 18 on these groups for each sampling interval, to compare the effect of kelp presence on DO concentration through time. Where assumptions of normality were not met, a Johnson transformation of the data was undertaken.

Bivalve measurements

Length and Condition Index of pōhā and non-pōhā treatments were analysed for statistical differences between bivalves within these groups using One-way ANOVAs.

Bacterial colonies

To visualize differences in relative colony abundance by treatment, plots of RCA scores at 24 and 48 hours were produced for trial one. Visualisations of trial two also included RCA scores at 72 hrs. Counting of daily growth on agar plates ceased if colonies appeared to be reaching Phase C (stationary phase) or Phase D (death phase) of growth (Holt, 1977).

RCA scores calculated at 24 hour growth for Trial One failed to meet assumptions of normality and equal variance, therefore a non-parametric Kruskal-Wallis test was undertaken in R (Version 4.0.2) to compare the effects of different treatments on bacterial growth. Following this, a post-hoc Dunns test (Dinno, 2017) was performed. A Bonferroni correction was not used as, for the current experiment, it may be considered too conservative. Bonferroni corrections are important when a large number of tests are carried out without an *a priori* hypothesis. The results of the individual post-hoc tests were important (between individual treatments) and avoiding a type II error seemed more appropriate (Armstrong, 2014).

As the RCA scores produced from trial two had small replicate sizes (n=3), comparative testing was not undertaken. Descriptive statistics were presented along with plots of growth by day for discussion. Presence and absence of bacterial subgroups for each treatment and trial were also presented.

Multivariate analysis

Visual taxonomic subgroups (VTS) of both trials were analysed, as multivariate community data, in the software PRIMER v7 with the add on PERMANOVA+1. The data from Trial One at 48 hours of bacterial growth and Trial Two at 48 and 72 hours of growth were analysed separately. Each data set was transformed to the fourth root and a Bray-Curtis dissimilarity matrix was applied, as Bray-Curtis can be used when underlying assumptions of normality are not met (Clarke and Warwick, 2001). Unconstrained PCO (Principal Co-ordinate Analyses) were performed on fourth root transformed Bray-Curtis matrices for all data sets. Corresponding PCO ordinations were then overlaid with associated vector plots of correlated VTS.

6.3 Results

Bivalve measurements

Rates of toheroa mortality varied with treatment (Figure 6.4). Mortality was first recorded in the PI-SW treatment at 5 days of incubation, followed by SW and P-SW treatments. The individuals within aerial treatments (with and without pōhā) were found to survive longer than seawater treatments, the exception being the SW-AB treatment where no mortality was recorded. This treatment was terminated at 14 days. Individual treatments were terminated at different times as based on degradation of algal tissue or water quality.

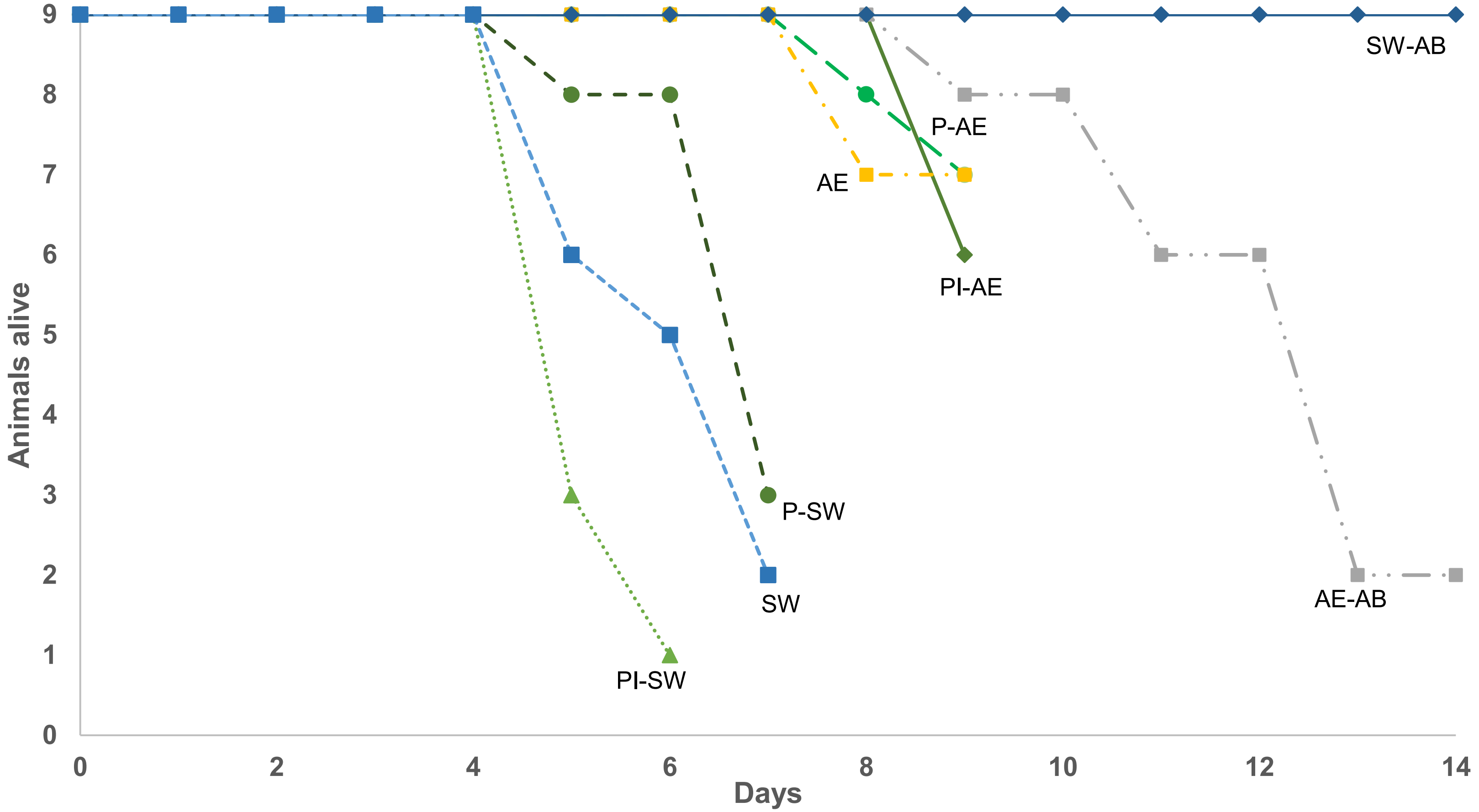


Figure 6.4 displays mortalities of bivalves (*Paphies ventricosa*) in each treatment (Three replicates per treatment, three animals per replicate). Stop in trend line indicates the termination of that treatment (animals were still alive at time of termination). PI-SW: inverted pōhā with seawater, SW: seawater, P-SW: pōhā with seawater, PI-AE: inverted pōhā aerial exposure, AE: aerial exposure, PI-AE: inverted pōhā aerial exposure, P-AE: pōhā aerial exposure, AE-AB: aerial exposure with antibiotic, SW-AB: seawater with antibiotic.

Toheroa length ranged from 69 mm to 90 mm with a mean length of 76.9 mm. CI% ranged from 10.2 – 33.01%, with a mean percentage of 25.87. One-way ANOVAs comparing bivalves grouped in either pōhā or non-pōhā treatments found no significant differences between both bivalve length (P = 0.320) and CI% (P = 0.319) between the two groups. Bivalve length and Percentage Condition Index are reported in Appendix C, Table C 1).

Dissolved Oxygen Measurements

DO declined steadily in all treatments for the first four hours (Figure 6.5). At that point, DO in pōhā treatments stabilised, while DO in non-pōhā (glass jar) treatments continued to decline. From the four hour point onwards, there were significant differences in DO between pōhā and non-pōhā treatments (One-way ANOVAs; Table 6.2), with pōhā treatments showing significantly higher average DO values than jar treatments.

Statistical analyses identified significant differences among several treatments through time (see Table 6.2 for post hoc Dunn’s tests). The P-SW treatment displayed higher DO concentrations than other treatments throughout the experiment (Figure 6.6). PI-SW and SW were not found to be statistically different at 9 hours, although PI-SW was found to have higher values (Figure 6.6). At five, seven and nine hours, significant differences were found between either one or both pōhā treatments (PI-SW and P-SW) and non-pōhā treatments (SW and SW-AB), while no differences were found between non-pōhā treatments through time (Appendix C; Table C 4).

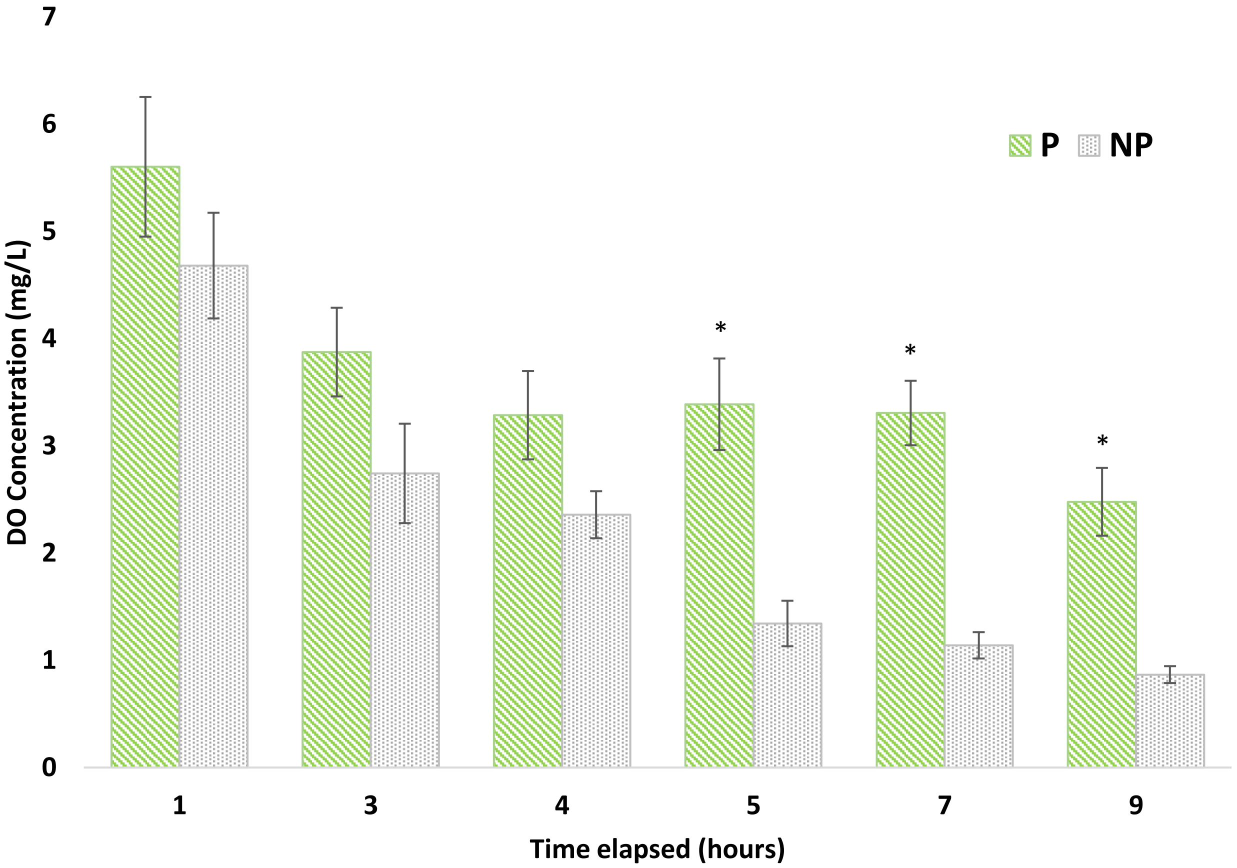


Figure 6.5 Bar chart displaying average values of measured DO concentration (±SE bars) for two groups (N=6 per group, P=Pōhā, NP=No Pōhā) over time. P group consisted of kelp bags, while NP consisted of jars, with all replicates filled with filtered seawater and housing three toheroa (*Paphies ventricosa*). Asterisks indicate significant difference between group ($P<0.005$).

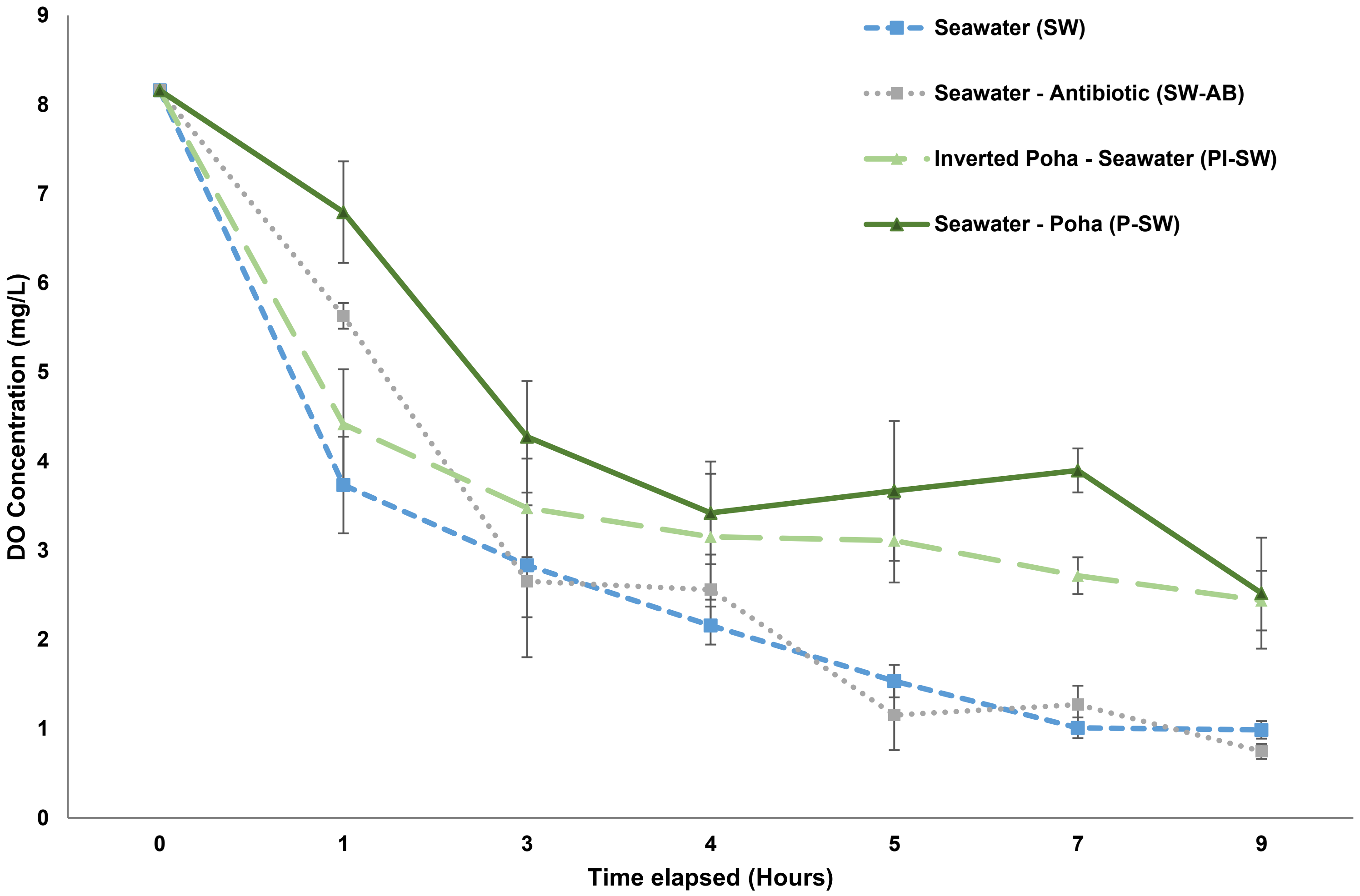


Figure 6.6 Average DO concentrations (±SE bars) treatments over time (n=3; SW: Seawater in glass jar, SW-AB: Antibiotic seawater in glass jar, PI-SW: Seawater inverted pōhā and P-SW: Seawater pōhā) through time. Each treatment held filtered seawater and three toheroa (*P. ventricosa*).

Table 6.2 Post hoc multiple comparisons Dunn's test comparing treatments for each time interval sampled. Treatments with statistically significant p-values are in bold. P<0.05 is represented by one asterisk, P<0.005 is represented by two.

1 hour	SW-AB	SW	PI-SW
SW	0.044		
PI-SW	0.182	0.214	
P-SW	0.154	**0.0033****	**0.027***

3 hours	SW-AB	SW	PI-SW
SW	0.454		
PI-SW	0.248	0.285	
P-SW	**0.044***	0.056	0.154

4 hours	SW-AB	SW	PI-SW
SW	0.197		
PI-SW	0.41	0.14	
P-SW	0.14	**0.026***	0.197

5 hours	SW-AB	SW	PI-SW
SW	0.367		
PI-SW	**0.015***	**0.035***	
P-SW	**0.011***	**0.027***	0.454

7 hours	SW-AB	SW	PI-SW
SW	0.367		
PI-SW	0.087	**0.044***	
P-SW	**0.008***	**0.003****	0.154

9 hours	SW-AB	SW	PI-SW
SW	0.214		
PI-SW	**0.011***	0.07	
P-SW	**0.004****	**0.035***	0.367

Bacterial analysis

Relative Colony Abundance (RCA) scores varied considerably between treatments. The lowest average RCA score at 24 hours was recorded in the treatment AE-AB (Trial 1; 0.14 ± SE 0.02) and AE (Trial 2; 0.048 ± 0.04). The highest RCA score at 24 hours was recorded in the PI-AE treatment for both trials (0.37 ± 0.039 and 0.17 ± 0.025). A total of nine visual taxonomic subgroups (VTS) were identified from all bacterial incubations, with each subgroup likely consisting of a number of heterotrophic marine bacteria species. A table of all identified VTS with photos and qualitative descriptions is provided in Appendix C (Table C 6). The results of marine bacterial culture analyses are presented by trial, below.

Trial One – day 3 sampling

Kruskal-Wallis tests were undertaken on trial one RCA scores for each day of growth (24 hours and 48 hours). Post hoc Dunn's tests identified significant differences between treatments (Table 6.3) at 24 hours (Kruskal-Wallis x^2 = 25.73, P<0.001). Full table of post-hoc Dunn's Tests (R outputs) can be found in Appendix C (Table C 5).

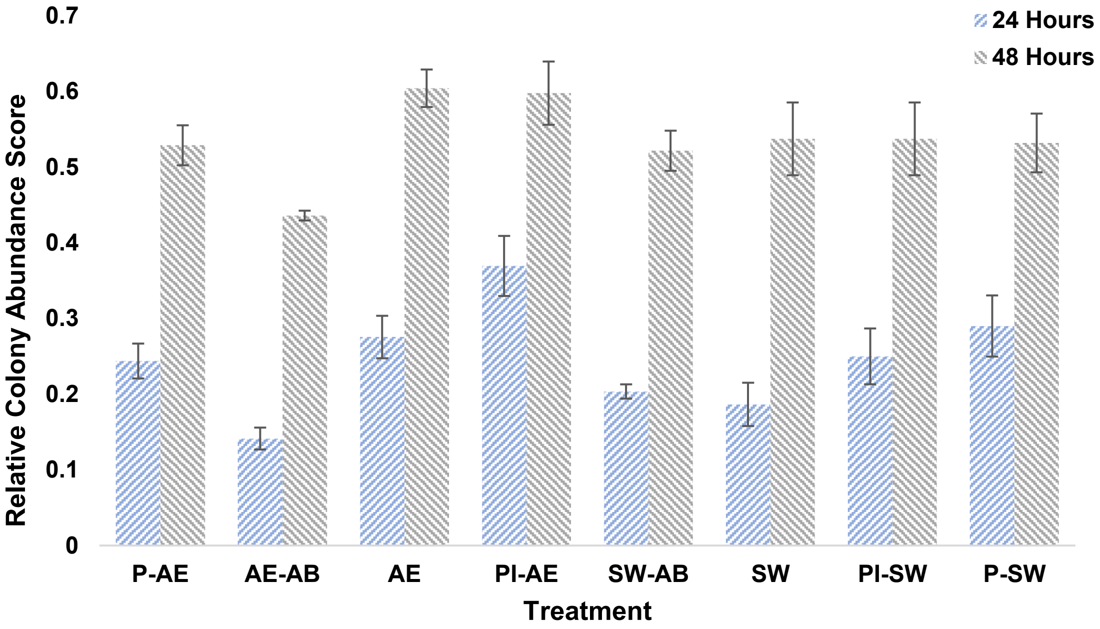


Figure 6.7 Average RCA scores at 24, 48 hours bacterial cultivation, displaying mean and ± SE bars (Standard Error, n=6) for each treatment. AE = Aerial Exposure, AE-AB = Aerial exposure with antibiotic, P-AE = Aerial exposure in pōhā and PI-AE = aerial exposure in inverted pōhā. P-SW = Pōhā with, PI-SW = Inverted pōhā with seawater, SW = Seawater in glass jar, SW-AB = Seawater in glass jar with antibiotic.

Table 6.3 Table displays multiple comparisons post-hoc Dunn's Test, comparing each treatments relative colony abundance score (RCA) (N=6) at 24 hours growth. P<0.05 is signified by one asterisk, P<0 .005 is signified by two.

	AE-AB	SW-AB	AE	PI-AE	P-AE	SW	P-SW
SW-AB	0.0744						
AE	**0.0008****	**0.0425***					
PI-AE	**>0.0001****	**0.0029****	0.1512				
P-AE	**0.0058***	0.1394	0.261	**0.0474***			
SW	0.0647	0.4712	**0.0495***	**0.0037****	0.1561		
PI-SW	0.0444	0.3983	0.0715	**0.0063****	0.2047	0.4264	**0.0347***
P-SW	**0.0002****	**0.0191***	0.3629	0.248	0.1611	**0.0227***	

Statistical analysis showed that treatment AE-AB had a significant effect on bacterial growth, (Figure 6.7) with AE-AB displaying the lowest RCA scores. In trial one, P-AE was found to have the second lowest RCA scores in the aerial treatments, followed by AE and PI-AE. PI-AE abundance appeared to be higher than others, with significant differences found between PI-AE and five other treatments (Figure 6.7).

At 48 hours, no significant difference was found from the Kruskal-Wallis analysis (x^2 = 12.8472, P<0.08), although the post-hoc Dunn Test did identify marginally significant differences between AE-AB and several other treatments, including: AE (P = 0.0232), PI- AE (P = 0.0403), SW (P = 0.0256) and P-SW (P = 0.0389) (see Appendix C).

At 24 hours, P-SW had a marginally significant effect on RCA scores, with higher abundances displayed in Figure 6.7. Although P-SW colony abundance is higher at 24 hours, this difference was no longer apparent after 48 hours, with little difference in RCA scores across seawater treatments.

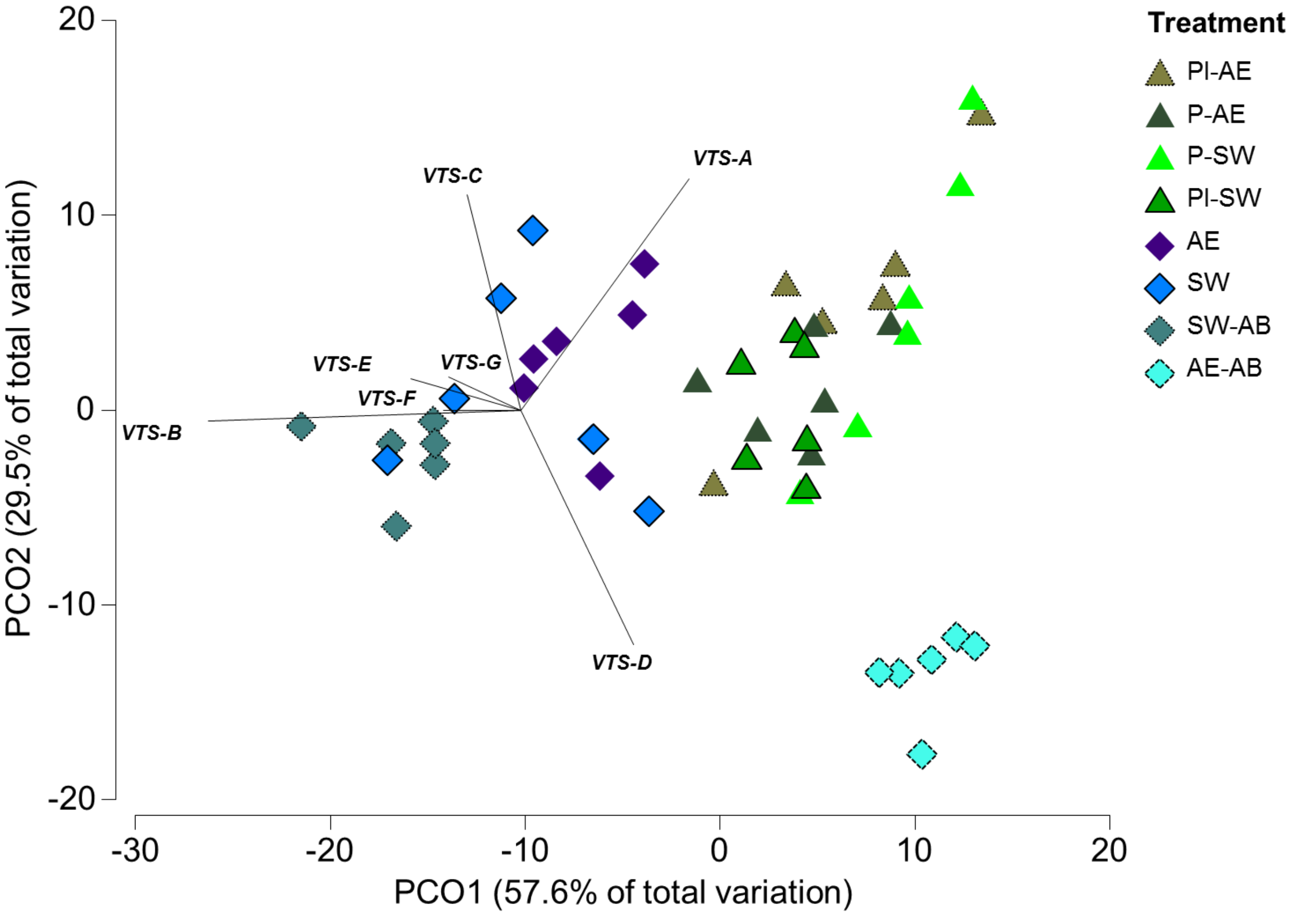


Figure 6.8 Principal Co-ordinates Ordination (based on Bray-Curtis distances of fourth root transformed Visual Taxonomic Subgroups (VTS) data) of the first trial. Plot is overlaid with associated vector plots of correlated subgroups (Pearson ρ = < 0.3). The first two PCO axes explain 57.6% and 29.5% of the variability in the resemblance matrix. See appendix for descriptions of VTS.

Pōhā treatments cluster together within the PCO ordination (Figure 6.8) and are clearly separated from non-pōhā treatments, indicating that colony subgroup structure differed between these groups. The first two principal components of the ordination together explained 79.9% of the variation of the VTS data between different treatments. Along the PCO2 axis, pōhā treatments are characterized by VTS-A and to a lesser extent VTS-C, although VTS-A was a subgroup prevalent across all treatments. Along the PCO1 axis, non-pōhā treatments SW, SW-AB and AE are characterised by VTS-B, and to a lesser extent, VTS-E,F and G. Along the PCO1 axis, all replicates in the treatment AE-AB cluster together and are very clearly characterised by the subgroup VTS-D, this distinguishing them from all other treatments.

Trial Two – day 5 sampling

Figure 6.9 indicates a uniform increase in RCA scores at each time interval. AE treatments have lower RCA scores, while PI-AE have the highest.

The PCO ordination (Figure 6.10) of bacterial subgroups at 48 hours shows a clustering of replicates from pōhā treatments, while non-pōhā treatments show more of a spread within the ordination. Differences in VTS assemblages between pōhā and non-pōhā treatments are indicated by minimal overlap between the two groups. VTS associated with P-AE and PI-AE included VTS-A and VTS-C, while VTS associated with AE and AE-AB included VTS-B, D,E,G and H. The PCO ordination of colony abundance at 72 hours (Figure 6.10) indicated a small shift in VTS assemblages. One replicate from PI-AE was found to have a slight association with dark yellow colonies (VTS-D), pulling it closer to AE-AB reps in the ordination along the PCO1 axis.

Replicates from other pōhā treatments appear to be associated with VTS-A and C, while non-pōhā treatments are associated with a larger assemblage of VTS. This could be visualized from inspection of agar plates (Figure 6.11). Small Pink colonies (VTS-H; Appendix C; Table C 6) were observed for the first time, in AE replicates at 72 hours growth, this VTS characterizing two AE replicates along the PCO1 axis.

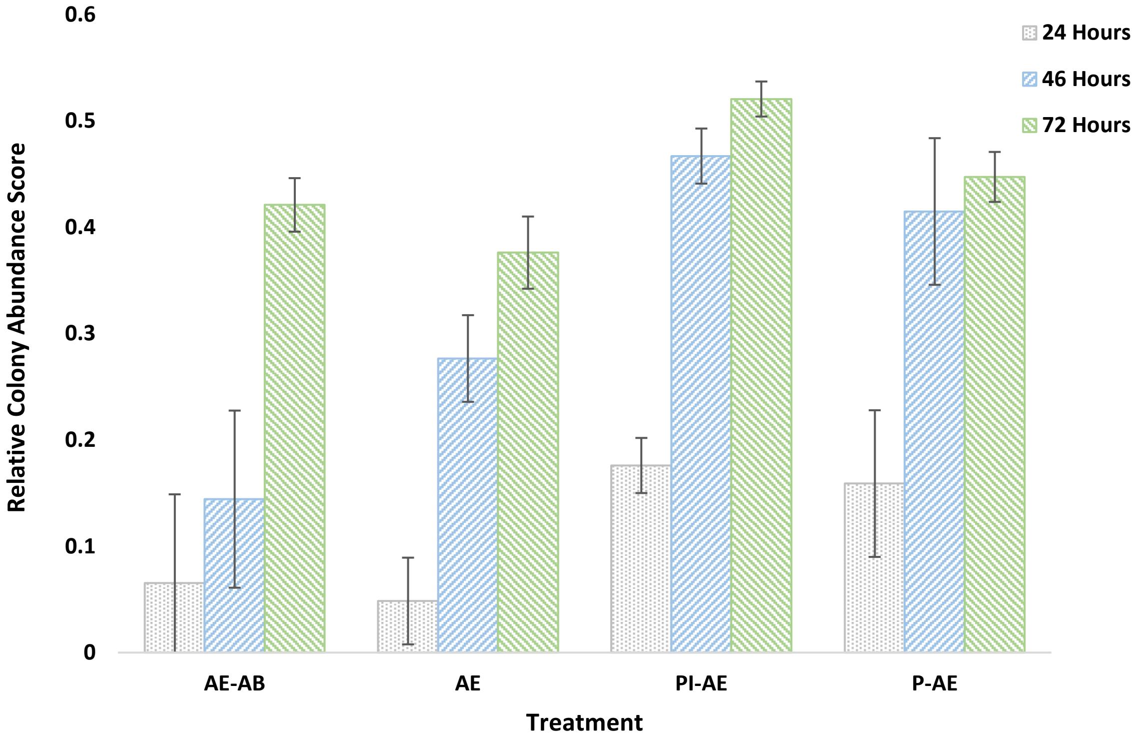
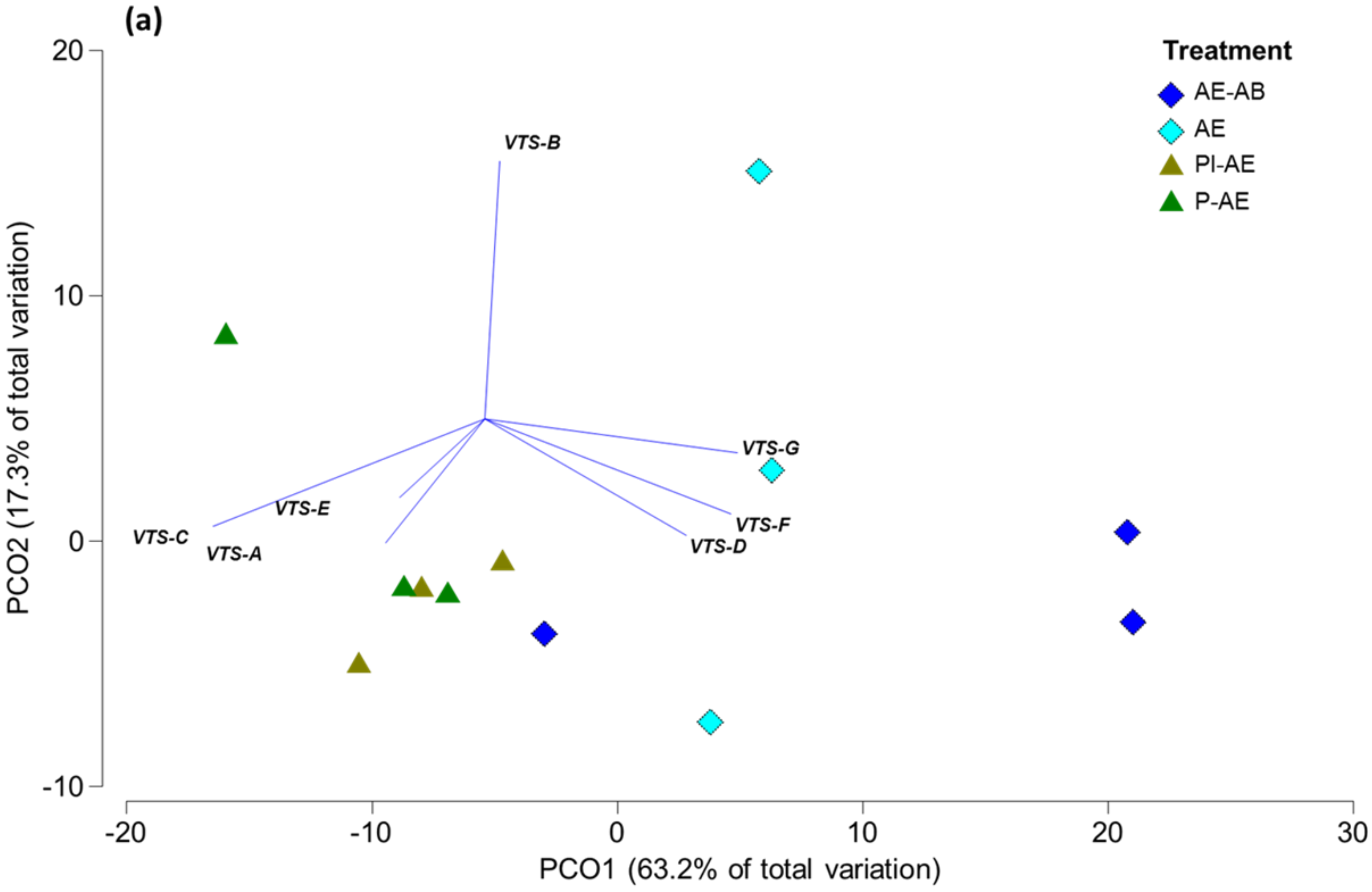


Figure 6.9 RCA scores at 24, 48 and 72 hours bacterial cultivation displaying mean and ± SE bars (n=3) for each treatment. AE; Aerial Exposure, AE-AB; Aerial exposure with antibiotic, P-AE; Aerial exposure in pōhā and PI-AE; aerial exposure in inverted pōhā.


(a)
Treatment
AE-AB
AE
PI-AE
P-AE
VTS-B
VTS-G
VTS-F
VTS-D
VTS-E
VTS-C
VTS-A
20
10
0
-10
-20
-10
0
10
20
30
PCO2 (17.3% of total variation)
PCO1 (63.2% of total variation)

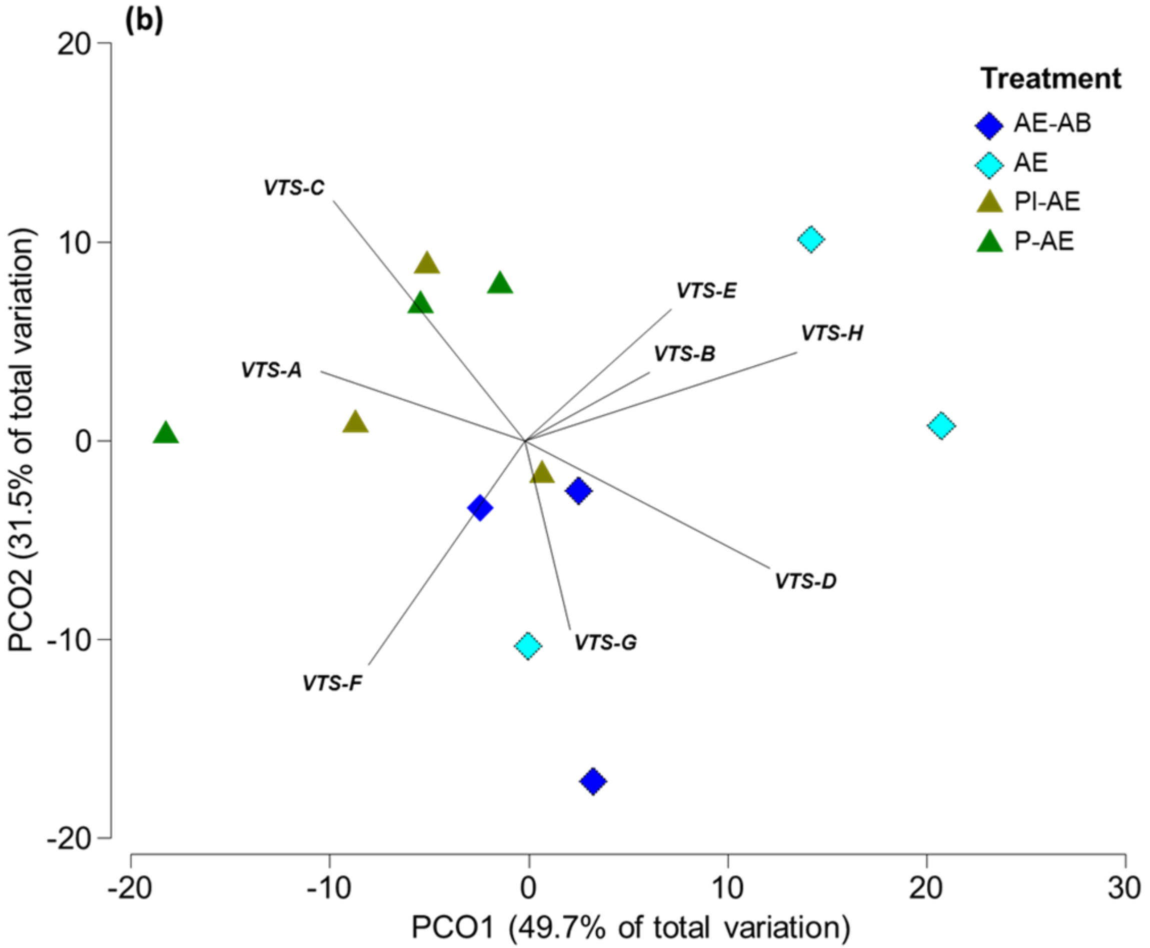


Figure 6.10 Principal Co-ordinates Ordinations of the Second Trial at 24 hour and 48 hours growth. Ordination based on Bray-Curtis distances of fourth root transformed Visual Taxonomic Subgroup data. Plots are overlaid with associated vector plots of correlated subgroups (Pearson ρ = < 0.5). Ordination (a): 48 hour growth; the first two PCO axes explain 63.2% and 17.3% of the variability in the similarity matrix. (b): 72 hour growth; the first two PCO axes explain 49.7% and 31.5% of the variability found.

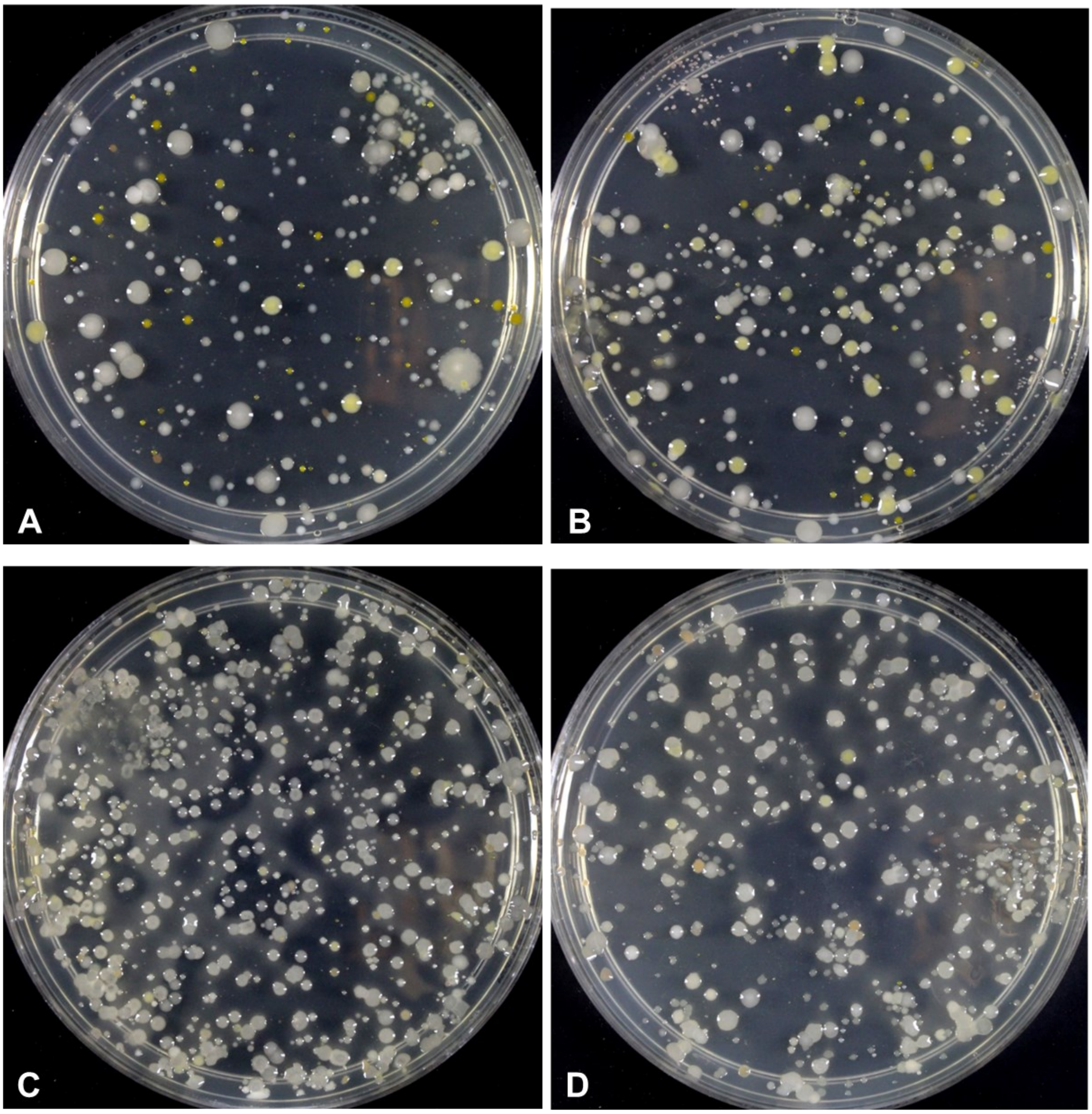


Figure 6.11 Examples of bacterial growth on Marine Agar (2116) of trial two aerial treatments at 72 hours of incubation (dark conditions, 30ºC). A= AE-AB3, B= AE1, C= PI-AE3 and D= P-AE1.

6.4 Discussion

Māori are known to have developed many novel technologies over hundreds of years, some of which were tools used in resource management (Williams, 2016). Such tools include vessels to aid in transport of resources, with the utilization of these continuing to be relevant and of use today. This experiment explored the concept of using one such technology, the pōhā, to hold live bivalves. The experiment revealed that when pōhā are newly made, filled with seawater and exposed to sufficient PAR light, that photosynthetic activity of the algal tissue was able to maintain DO inside the pōhā despite bivalve respiration. When comparing bacterial colonies associated with pōhā and non-pōhā treatments, a clear difference in colony assemblages were identified between the two groups, indicating that the presence of pōhā influenced bacterial growth associated with the toheroa.

Photosynthesis and respiration of pōhā and toheroa

The respiratory behaviours of toheroa that were observed in previous experiments (Chapter Four) indicated that when held in seawater, toheroa individuals are likely to continuously filter, and when DO is available, aerobically respire. This was demonstrated by both behaviour and a consistently marked decrease in DO in a short space of time. DO uptake by toheroa was most evident when comparing respiration rates of toheroa and tuatua (*Paphies subtriangulata*), in which tuatua individuals were found to frequently and randomly cease aerobic respiration even in the presence of highly aerated seawater (Chapter Four). It is with this reasoning that it is highly likely all individuals were opportunistically filtering and respiring, when DO was available, in seawater treatments of this experiment.

When treatments were separated into two groups, based on the presence of pōhā, the corresponding DO measurements reflected some interesting trends through time. DO was found to steadily decline in all treatments for the first four hours. After this point, DO appeared to stabilize across pōhā treatments, while it continued to decline within non-pōhā treatments, with significant differences found between these two groups from four hours onwards. Taking into account the algal blades, the toheroa and the associated microbiota of each, the amount of live biomass is far greater within pōhā treatments, than in non-pōhā treatments. If the algal tissue of the pōhā was not photosynthetically active, or was respiring, a steep drop in DO would be expected, along with a net loss of DO over time well below that of non-pōhā treatments, and this would be reflected in Figure 6.6. Of benefit to the study would have been pōhā filled with seawater, with no toheroa, as a further control for photosynthetic activity. Unfortunately, the number of algal blades that could be transported to the laboratory was limited.

A decline in DO across all treatments was observed up until the four hours mark when DO stabilised in pōhā treatments just above hypoxic levels (~3mg/L). This indicates that a compensation point was reached, where algal photosynthetic activity was occurring at a rate where it is able to sit at equilibrium with the respiration of the toheroa, and DO levels were able to be maintained. It is likely that toheroa respiration rates also slowed, a physiological response to lower DO levels. In Chapter Four, it was found that when DO levels reached approximately 4 mg/L, DO uptake by toheroa decreased (indicative of oxyregulatory behaviour).

When comparing the two pōhā treatments, DO was found to be slightly higher over time in P-SW treatments than in PI-SW treatments. Chlorophyll is more concentrated on the outer layers of the rimurapa tissue which may explain the higher photosynthetic rates recorded in P-SW treatments. Previous studies of the photobiological characteristics of *Durvillaea antarctica* have found that the brown alga has several adaptations for efficient light use. This includes having high thallus light absorptance, due to the thickness of the thalli and to the high concentration of pigments in the tissue. The species exhibits photosynthetic saturation at low irradiance and is therefore able to photosynthesise efficiently even under low light intensity (Cruces et al., 2012; Tala et al., 2019).

Pōhā influences on bacterial growth

The first bacteria cultivation trial (toheroa swab samples taken after three days of being held in pōhā) found that antibiotic treatments held in air experienced the lowest amount of colonial growth, while inverted pōhā held in air had the most. However, at 48 hours, there appeared to be little difference between treatments. It is interesting to note that both PI-AE and P-SW treatments had higher counts at 24 hours, yet at 48 hours bacterial colony counts are similar to other treatments. This initial slowing of growth within these replicates may indicate that pōhā and the associated algal biofilm may have had an inhibitory effect on slower growing bacteria types. The highest bacterial counts found in inverted pōhā is likely a reflection of the addition of microbes within the seawater, which were associated with the outer tissues biofilm.

Bacterial biodiversity, as indicated by VTS assemblage data, varied between treatments. Non-pōhā groups were characterized by a wider variety of colony types. Pōhā treatments were found to be characterized by a smaller set of subtypes including grey/transparent/white (VTS-A) colonies and to a lesser extent orange colonies (VTS-C). The VTAs prevalent in pōhā treatments (Grey/transparent/white colonies) were dominant across all treatments, making up the majority of colonies counted and were in the order of hundreds. VTS-A colonies are likely to be a number of different heterotrophic marine bacteria (Ahern, 2018) and were grouped in the same subgroup as they were often difficult to differentiate when manually counting. This VTS appears to be representative of opportunistic, faster growing bacteria.

As non-pōhā treatments were characterized by a different suite of VTS, it is clear that the presence of pōhā influenced bacterial colony growth and composition. VTS associated with non-pōhā treatments also appeared to be more diverse, including light yellow, dark yellow, brown, red and pink colonies. These colonies were occasionally identified in some pōhā reps, but were not significant in characterizing these treatments.

The aerial antibacterial treatment was clearly characterized by VTS-D, a smaller, dark yellow highly distinguishable colony, while the seawater antibiotic treatment appeared to be associated with light yellow colonies (VTS-B). From the results, it is clear that the modes of action for inhibiting or effecting bacterial growth is different between the antibiotic used and the algal tissue. Several colonies associated with antibiotic treatments were slower growing, smaller and of distinguishable pigments (see Figure 6.8 and Appendix C, Table C 6). The converse of this was found for pōhā treatments, with plates appearing to have lower diversity and more growth of VTS-A.

Bacteria associated with toheroa and pōhā

Chloramphenicol is considered a broad-spectrum antibiotic which can act on both gram-positive and gram-negative bacteria, interfering with bacterial protein synthesis (de Zwaan et al., 2002). Using a PCR-based approach, de Zwaan et al., (2002) analysed bacteria present in anoxic seawater incubations containing the live bivalve *Mytilus edulis*. The predominant groups identified were Sulphate Reducing Bacteria (SRB) *Desulfobacteria* and *Desulfobulbus* spp.. These SRB are typically gram-negative and are able to metabolize fatty acids including propionate which is a product of anaerobic metabolism.

De Zwaan et al., (2002) found that the opportunistic bacteria within the incubations, which became pathogenic under prolonged anoxia, were associated with and introduced by the bivalves. Chloramphenicol was able to inhibit bacterial growth and associated bivalve degradation, whereas the presence of only sterile water could not. This is also the case for the current study, as the seawater used was filtered and UV treated. All bacteria grown would be associated with the toheroa, or the algal microbiome. De Zwaan et al., (2002) suggests that SRBs are not the bacterial group responsible for pathogenic proliferation and disease in the bivalves, although once mortality is reached, due to pathogen proliferation, this would stimulate excessive growth of SRB.

Coffin at al., (2021) analysed the endogenous bacteria which accelerated oyster (*Crassostrea virginia*) mortality under anoxic conditions, using 16s rRNA amplicon sequencing. Under static anoxic conditions, the bacterial genera associated with antibiotic (chloramphenicol) bivalve incubations were *Desulfotalea, Acrobacter, Slackia, Desufofaba* and *Vibrio*. Bacteria associated with static bivalve incubations with no antibiotic included *Alkaliphilus, Desulfovibrio, Vibrio, Spaerochaeta and Bacteriodes*. It is likely that these anaerobic bacteria were present in the toheroa incubations, but would not have been cultured as the methods used were specific to aerobic bacteria.

The aerobic bacteria identified by Coffin et al. (2021) may also have been cultured in the current study. In flow-through bivalve incubations (aerobic), Coffin et al. (2021) identified the bacteria associated with antibiotic treatments to be *Vibrio, Desulfotalea, Alkaliphilus* and *Flavobacterium*, while bacteria associated with non-antibiotic treatments were *Desulfovibrio, Alkaliphilus, Spraerochaeta, Vibrio* and *Flavobacterium*. Toheroa microbiomes have found been found to contain the common bacteria was *Spirochaeta*, while Mycoplasmataceae, Endozoicomonadaceae, *Vibrio* and *Psychrobacter* are also bacterial groups associated with the genus *Paphies* (Bennion, pers. comms.; Biessy et al., 2020). *Vibrio* taxa have been suggested to be potential producers of Tetrodotoxin in bivalves (Biessy et al., 2020). Typing bacterial species associated to pōhā and non-pōhā treatments in the current study would have been very beneficial, particularly to ascertain if the bacteria which are inhibited by pōhā are known pathogens to shellfish. If this was the case, pōhā would certainly be promoting bivalve health.

Evidence suggests that regulatory functions related to health, development and resilience of macro-algae are aided by epiphytic bacteria (Gaitan-Espitia and Schmid, 2020; Egan et al, 2013; Tujula et al, 2010). Conversely, if bacterial biofilms compromise the algal tissue and photosynthetic ability, it may expose the host to new diseases and pathogens as its health deteriorates (de Mesquita et al., 2019). Bacteria that may otherwise be commensal with their macroalgal host, may accelerate thalli degradation when the algae is under conditions of stress, infection or undergoing organic breakdown (Egan et al., 2013).

Secondary metabolite and the role of phlorotannins (PHT) in brown algae

Secondary metabolites produced by brown algae, such as phlorotannins, play important roles in defence against microbial attack, particularly when the tissue is exposed to stress. A study undertaken in Qingdao, China by Wei et al. (2016) examined the antimicrobial mechanisms of phlorotannins in the brown algae *Sargassum thunbergii* on a marine bacterium *Vibrio parahaemolyticus*. The antibacterial activity of low molecular weight phlorotannins and their role in bacterial damage were assessed. The study found that ions and proteins could leak out of cultured bacteria cells when exposed to the *S. thunbergi* extracts, suggesting an increase in cell permeability was induced in the bacterium and that cell membranes were critically damaged. *Vibrio parahaemolyticus* is a pathogen with a worldwide distribution, frequently associated with human infections and bacterial disease in aquaculture species. Findings within this study may have important implications for the consideration of low weight phlorotannin applications in marine aquaculture.

Many studies have undertaken crude extracts of algal material to directly screen for antimicrobial activities. These studies have provided valuable insight into the diversity of bioactive metabolites produced by algae, however the understanding of the natural delivery of these metabolites, along with their ecological relevance in inhibiting localised bacteria, is often much less understood (Lam et al., 2008).

Large algae such as *Durvillaea* spp. have complex morphological adaptations, with different parts of their structure exposed to different stresses. The anatomic features of the blades of *Durvillaea* spp. allow them to float on the surface of the water, increasing the blades exposure to temperature and UV stress. It has been found that the anti-oxidative capacity of phlorotannins can be essential to algal blades during times of such stress. Cruces et al. (2012) found that the induction of soluble phlorotannins in *Durvillaea antarctica* was triggered by increases in temperature and this study supported the role of phlorotannins in metabolic adaptations to environmental stress.

A study by Lüder and Clayton (2004) simulated wounding of a brown alga species *Ecklonia radiata*, to investigate the healing process. The results suggested that phlorotannins had three major functions in wound healing; sealing, structural healing and anti-herbivore attack. Phlorotannins were found to surface and accumulate during the early stages of wounding in *E. radiata*, their role serving as a sealing function and prevention against microbial attack. A similar study undertaken by Halm et al. (2011) assessed the responses of mechanical wounding and exposure of UV radiation to the brown alga *Laminaria hyperborea*. Fluorescence microscopy of living tissue showed that within the wound area, there was a clear accumulation of phlorotannins over the course of the experiment. The presence of phlorotannins at the early stage of tissue healing, which involved gluing of the wound, indicated these metabolites had a clotting mechanism, helping in sealing the wounded region. It is also suggested that at this stage, further release of phlorotannins may aid in preventing bacterial infection. Phlorotannin leakage was identified at the wound surface from the second day onward, where the tissue medulla was sealing.

The implications of these studies to the physio-chemical constituents of pōhā are interesting to note. During pōhā production, when the thallus is split open, phlorotannins may have the potential to accumulate at the tissue surface and leak from the wounded inner thalli. In this instance, the inner contents of the pōhā may be exposed to newly induced antimicrobial metabolites.

Secondary metabolites are clearly prevalent within the tissue of brown algae but of interest to the current study is the role of metabolites at the thallus surface and extension into the surrounding environment. Several studies have assessed the antimicrobial effects of waterborne macroalgal metabolites to a spectrum of potential bacterial colonizers (Lam et al., 2008). Lam and Harder (2007) investigated the efficacy of waterborne antimicrobial metabolites from nine marine macroalgae (red, green and brown) on eubacterial planktonic communities in seawater. To achieve this, bacteria were cultured in both algal-treated and non-algal-treated seawater and the planktonic bacterial community richness was compared. Community composition of bacteria was found to be affected by algal treatments and bacterial densities (excluding one red alga, *Porphyra*) were reduced by 20-50% compared with natural seawater. Lam and Harder (2007) concluded that epibiotic bacteria can be targeted much farther from the algal thallus then previously assumed.

Further research by Lam et al (2008) investigated the hypothesis that antimicrobial algal metabolites may target specific bacterial phyla. Bacterial phyla which were found to be most affected by algal presence belonged to the CFB (Cytophaga, Fusobacterium and Bacteriodes) and *Roseobacter* clade, with the results demonstrating the strong effects of waterborne macroalgal metabolites against a prominent group of marine bacteria, *Roseobacter*, which is particularly prevalent in coastal regions (Wagner-Döbler and Biebl, 2006, Lam et al., 2008). It could be postulated that this bacteria was present and potentially affected by the pōhā within the current study.

A study by Sneed and Pohnert (2011) assessing the structural influences of a green algae to its surrounding bacterioplankton community found that algal regulation of bacteria does not involve elimination of the entire bacterial community as would antibiotics, but rather it influences different strains of bacteria, using different modes of action. It is suggested that a combination of factors, including the alga morphology, secondary metabolites and properties of the thallus surface all contribute to the changes in community composition that was found.

Bacterial communities associated with brown algae are also potential sources of diverse bioactive compounds. Genera linked to algae include *Pseudomonas, Pseudoalteromonas, Stenotrophomona, Vibrio, Alteromonas, Shewanella, Streptomyces* and *Bacillus*, these having evolved in a highly competitive micro-habitat with limited space. Bacteria such as these have developed counteractive defences, such as producing allelochemicals to prevent other epibionts from colonizing and these secondary metabolites may also aid in protecting the macroalgal host (Egan et al., 2013; de Mesquita et al., 2019).

It is clear from the above studies that algae have a huge potential to influence bacteria both at the aglal-water interface and within the plankton. The mechanisms of these are still largely unknown (Sneed and Pohnert, 2011) but the bacterial results of the current study indicate that the algal tissue of the pōhā bags were effecting bacterial growth and this may be occurring at the algal tissue-water interface, within the seawater or potentially having a direct effect on bacteria within or on the toheroa. Further to this, antibacterial metabolites are likely only a part of the mechanisms at work, with algae associated bacteria likely to be playing active roles in the difference observed as well.

6.5 Concluding remarks

Provided there is enough PAR available, the short-term effects of holding toheroa in a raw pōhā filled with seawater is that the pōhā may be a source of oxygen, replenishing DO which would be removed by the respiration of toheroa. This would only be for a short amount of time, as after the kelp has been turned into a pōhā the tissue begins to degrade. The rimurapa used in the current study had travelled under non-controlled temperature for 36 hours prior to being processed. If the pōhā was utilized immediately after it had been harvested, the results may have been different. This could include the potential for higher and longer DO levels maintained by the photosynthetically active tissues of the fresh blade, along with the potential for stronger or longer responses of phlorotannin synthesis and accumulation. Traditionally, pōhā would have been used immediately after harvesting.

Pōhā are often curated, undergoing several drying and rehydrating processes to become a long-term receptacle for storage and transport. The consequences of the curation processes for the action of secondary metabolites is at present unknown, as is the role that these metabolites might play in aiding food preservation.

Toheroa treated with antibiotics survived the entire experiment (14 days) with a likelihood of surviving longer. This is over double the LT_{50} of animals incubated in seawater without antibiotics. The results found here are in alignment with previous research (Chapter Four), in that bacterial proliferation and disease is the driving force for bivalve mortality. Water quality deterioration (for example, sulphide accumulation) in the incubation medium of the study was not a determining factor of survival time in the presence of, or with the pre-treatment of, chloramphenicol.

The seawater retained from both pōhā and non-pōhā treatments were startling different in appearance. The water within the pōhā did not appear to accumulate the black sulphides compared to jar treatments. The water appears to have been altered by its residence within the pōhā, but the implications of this are beyond the scope of the current study. Brown algae are well known as biomonitors and biosorbents, as they can accumulate high concentrations of metals. Sulphated polysaccharides are a main binding group in brown algae (Brinza et al., 2007; Andrade et al., 2010) and biosorption of H_2S metal precipitate may have been occurring, via the polysaccharides modes of action.

Figure 6.12 Water retained after experiment, the left jar is from a pōhā seawater replicate and the right jar is water from a non-pōhā seawater replicate.

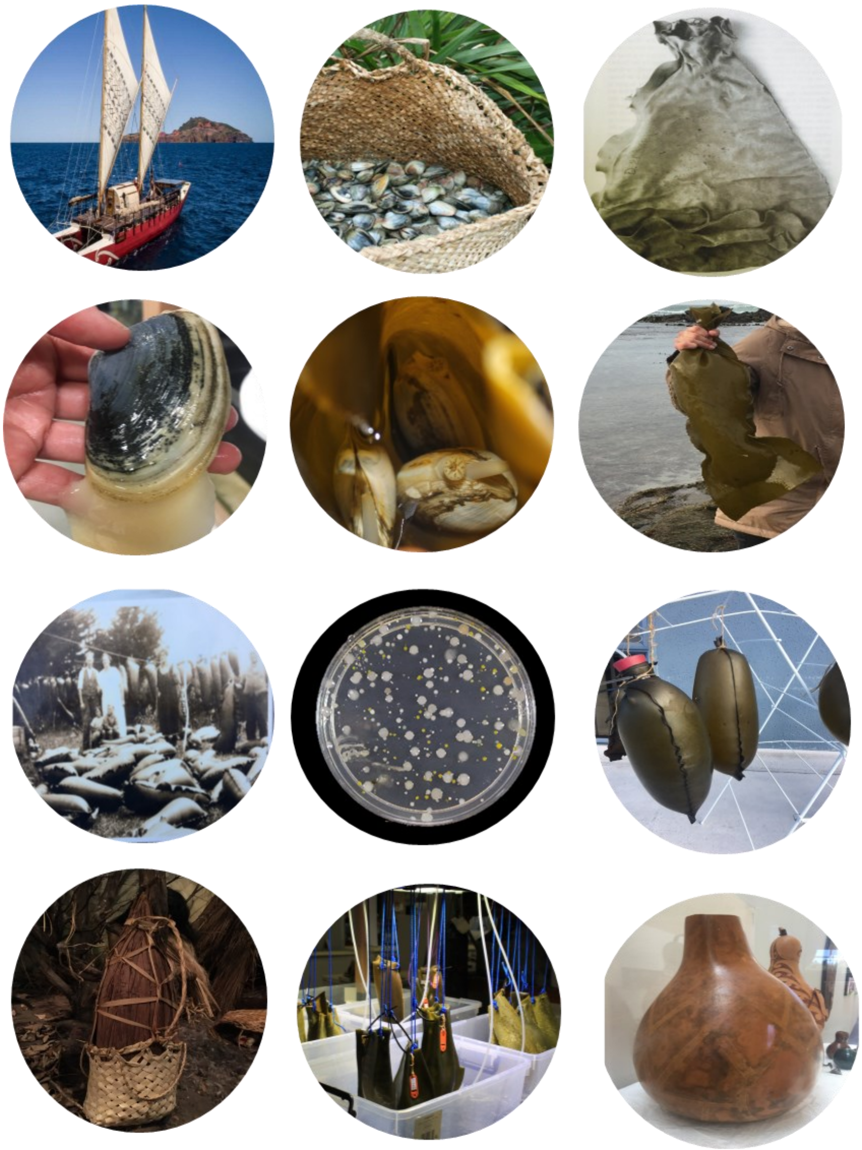
Toheroa survivability within pōhā did not appear to be different than treatments without pōhā, although several replicates were terminated when animals were still alive. The way in which this experiment was conducted was not conducive to promoting thalli tissue preservation, for example, the lack of water changes. Many iterations of this experiment, with a variety of algal treatments, could have been executed, particularly to better avoid tissue degradation. Within a real-world context, pōhā preparation and utilisation would have likely been handled, stored and treated differently. Fresh pōhā being used over long-distances to hold shellfish is unlikely, however fresh pōhā may be of great benefit for short-term storage. The experiment identified characteristics of the algae that may aid in or influence bivalve health.

Kōrero tuku iho given about the uses of pōhā for re-seeding, suggest that raw pōhā were used in much the same manner as the ecological role of rimurapa along the coastlines. Pōhā may provide protection and nurture the toheroa in their new location in order to help them acclimate. Reseeding of spat is suggested to have been undertaken in such a manner, where pōhā were drilled with holes and anchored along the shoreline, to allow for acclimation and slow release of the juveniles. The ecological value of rimurapa is entrenched in its whakapapa (Chapter Five). This is direct evidence of how the ecological mātauranga of different species is reflected in whakapapa, whakataukī and kōrero tuku iho, and that this knowledge, filtering down through generations, has scientific based environmental applications.

When considering long-distance transport as a restoration tool, a variety of receptacles may have been used, to transport toheroa and other kaimoana species, by land, by waka or by both. Pōhā may have been the last link in the chain when undertaking such translocation practices. When considering the use of raw pōhā as a temporary wharenui or home for bivalves, such as toheroa, characteristics of the brown algae investigated in this experiment may contribute to their protection.

Chapter Seven

Discussion



7.1 Summary

Hundreds of years before our time, Māori were employing an array of different strategies which allowed them to successfully manage the natural resources of Aotearoa (New Zealand). Although these management models or approaches evolved in an era which was wildly different from the cultural, environmental and economic world we now inhabit, there is huge contemporary benefit to understanding these practises and the knowledge base on which they were built. Translocation of marine shellfish is an example of one such management tool. In this thesis I examine the evidence for long-distance transport and translocation of the bivalve, toheroa (*Paphies ventricosa*) by Māori prehistorically, as hypothesised by Ross et al. (2018). I have assembled academic and indigenous knowledge, incorporating a broad range of disciplines and knowledge systems, in alignment with the interconnected and interdependent values of Te Ao Māori.

Chapters Two and Five explore concepts of traditional resource management practices, by diving deep into the kōrero tuku iho (oral traditions), the first written accounts of Māori prehistory and the collective mātauranga of two taonga resources; toheroa and rimurapa. Anthropological, historical and traditional knowledge was combined to explore the human elements of long-distance toheroa translocation. Specifically, I sought to better understand why early-Māori would be compelled to undertake such a feat, as well as the capacity and opportunities they would have had to undertake long-distance transport of live bivalves prehistorically.

To support this translocation theory, I sought to determine the prehistorical distributions of toheroa populations across Aotearoa (New Zealand), with the use of archaeological tools. Chapter Three presents a broad scale desktop study of shell middens across Aotearoa in which the primary focus was toheroa. Archaeological databases were used to determine if the toheroa midden record within Murihiku was consistent with toheroa being endemic to the south. Here I aimed to understand the presence and use of the species by Māori in the earliest phases of the prehistoric sequence.

In Chapters Four and Six, I explored the physiology of toheroa, with an overarching goal of understanding how these animals may respond to long-distance transport and the stressors that they may face. These took shape in the form of *in situ* experiments and are the first of their kind for toheroa. The importance of such experiments have been highlighted, when considering future translocation and aquaculture practices. Chapter Six combines Western science and mātauranga pōhā/rimurapa to explore the use of traditional methods in transport and translocation practices.

Having not broached the disciplines of archaeology and anthropology before this thesis, my awareness has been heightened to the true importance of looking towards the past for answers in regards to our marine species and their environments. Further to this, looking to Indigenous peoples, who have influenced, shaped and been shaped by marine resources, is an invaluable part of any research undertaken within environmental spaces. The collective tīpuna of Māori were ecologists, they were geologists, navigators and engineers. They were aquaculturists, horticulturists, medicinal practitioners, the list goes on; and they were connected to the natural world in a way that academic scientists can only dream of being. Māori continue to work actively in all of these roles, as they carry the mātauranga of their ancestors with them into the future.

7.2 Archaeology, kōrero tuku iho, ecology and beyond

Imagine how rich we would be, if we all shared [51]

Whakapapa

Toheroa were an important resource to even the earliest occupants of northern regions. This is heavily reflected in traditional narratives, whakatuiki (proverbs) and whakapapa (genealogy/ancestry) in northern Māori's cultural history. Although an important taonga to Murihiku (Southland) iwi today, no such narratives, whakataukī or whakapapa was found in the current study regarding toheroa in the south. This could be explained by a later introduction of toheroa to Murihiku, leading to less time and opportunity of the resource to shape southern Māori identity.

Kōrero tuku iho and archaeology

Aotearoa was one of the last major land masses to be occupied by humans and as such has a uniquely short prehistory. Because of this, existing oral traditions of Māori can provide insights into the lives and behaviours of even the earliest occupants. Archaeological tools in coastal areas can complement such oral traditions and contribute significantly to hypotheses about the deep past, such as the "translocation hypothesis".

Within Aotearoa, interest in archaeology, other than human artefacts, has fluctuated through time. Davidson (1967) suggests that "*at various stages the influence of scientists educated in other disciplines has been beneficial*", stating that the study of middens in modern archaeology has been shaped by contributions from several different fields. Chapter Three utilises archaeological insights in a novel way, by analysing midden deposits to challenge an ecological and cultural hypothesis.

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[51] John Aramete Wairehu Steedman, 1996

The presence of hundreds of toheroa shell midden along the West Coast of Te Ika-a-Māui, adjacent to known toheroa populations, indicate that this resource has been utilized extensively by Māori in these areas. Along the South Coast of Te Waipounamu, toheroa midden of this nature does not appear to exist. From the top of Te Ika-a-Māui, 968 middens were identified in the current study and of these middens, 40% were found to either have toheroa present, or consist entirely of toheroa. Along the South Coast of Te Waipounamu, 122 middens were identified and of these, only 6.5% contained toheroa. Toheroa shells were also absent from pre-human beach deposits within Murihiku. The general absences of toheroa shell midden and deposits lends itself to the notion that toheroa are not endemic to the area and may have been introduced to the South Coast by Māori. What is yet to be clarified is the exact time periods to which toheroa were present along the South Coast of Murihiku. Further research, incorporating midden surveys of the coastline, along with radiocarbon dating of any toheroa midden found, would add great value to Chapter Three.

The current study has largely focused only on archaeological sites which had toheroa present, rather than cultural artefacts. Artefacts and cultural lithic material from archaeological surveys of Te Aupōuri (the Far North of Te Ika-a-Māui) have been deposited at the Auckland Institute and Museum. Coster and Johnston (1976) remark that these may be of value for future research, to determine the sources of the stone materials used by Māori in the Far north. This may be directly applicable to the current study, particularly to assess the sources of argillite adze found within these sites and the potential for this argillite to have been originally sourced from Riverton in Murihiku. This may provide further evidence of Māori presence and trade between the Far North and the southern coast of Aotearoa.

Through kōrero tuku iho, archaeological investigations and historical accounts, it is clear that long-distance voyages from the north to the south were undertaken multiple times during the prehistoric sequence (Chapter Two). Within Aotearoa, there is evidence for widespread early transport of industrial stone, such as obsidian, across the entire country. Archaeological sites identified within this study provide evidence for Te Ika-a-Māui obsidian (and thus the presence of northern iwi) within Murihiku in the 14th to early 15th century. This indicates that there was occupancy in the southern most areas of Aotearoa, in the earliest phases of the prehistoric sequence, by people who had come from or were closely connected to northern communities.

The legitimacy of such travel has been proven in contemporary settings by traditional Māori waka navigators (tohunga whakatere waka). The speed at which ancestral waka can travel has been determined via contemporary voyages utilizing traditional waka-hourua and navigation methodologies. From this knowledge, it was established that a trip from the west coast of Te Ika-a-Māui to the southern beaches of Murihiku would take approximately 8 days, without stops. This is a very achievable journey in which to incorporate successful long-distance transport of shellfish species such as toheroa.

Toheroa physiology

While the opportunity to transport live bivalves has been made evident, the ability of toheroa to withstand prolonged periods of time out of their natural habitats was less known. Successful long-distance transport and translocation would be contingent on the bivalve's ability to cope with and combat stressors exposed to during this process. *In situ* experiments measured multiple biomarkers to determine the physiological responses of toheroa to a suite of stressors likely to be linked to transportation (Chapter Four). From respirometry experiments, toheroa were found to be opportunistic oxyregulators, maintaining a consistent respiration rate under lowered oxygen tension, until a threshold of hypoxia was reached. This response is in alignment with the ecology of the species within their natural habitat, where they are likely to experience long periods of emersion and when exposed to aerated seawater, will undertake opportunistic aerobic respiration. The closely related bivalve tuatua (*Paphies subtriangulata*) is ubiquitous across Aotearoa and not under threat. To determine if the species would be a good proxy for toheroa in future experiments tuatua individuals were subjected to the same respirometry experiments. Tuatua responded much differently to toheroa, with the animals exhibiting respiration responses reflective of oxyconformity, indicating they may not be the best proxy (Chapter Four).

When toheroa are exposed to anoxia, or are held under aerial exposure, a number of physiological and behavioural mechanisms are employed to prolong survivability under these conditions (Chapter Four). When held under anoxic conditions and treated with antibiotics, toheroa were able to switch to anaerobiosis and survive for extended periods of time (mor than two weeks). Toheroa are also able to withstand prolonged periods of starvation. From this study it is clear that when removed from their habitat, the leading causes of health deterioration, particularly when exposed to temperatures outside of their thermal window, is bacterial proliferation (of most prevalence when held in anoxic water) and desiccation. These are risks that could be easily mitigated during transport.

The current study found that toheroa with a lower dry weight Condition Index % (CI%) had a lower survival rate in general. Previous research has found that toheroa have higher CI% in colder months (Redfearn, 1974; Bennion, pers. comms.). With this in mind, it would be more beneficial to undertake long-distance transport of toheroa in colder months.

Traditional tools for transportation and translocation

When transporting and translocating species, innovative tools would have been required, particularly different vessels to hold toheroa. The pōhā; a natural kelp bag fashioned from the large brown algal species *Durvillaea* spp. (rimurapa), is a southern Māori technology said to have been used in transporting and re-seeding toheroa prehistorically. The traditional knowledge, prehistoric and historic uses of rimurapa by southern Māori are wide and varied, with the resource having been managed and cultivated for many generations by southern Māori. Contemporary use of pōhā and rimurapa (southern Bull Kelp) has included the successful reseeding of seagrass to new areas by local hapū in Te Waipounamu.

While there are many historical accounts of pōhā being used for translocating shellfish (Chapter Five), the details of exactly how they were used are missing, both in the literature and in the memories of the knowledge holders with whom I was lucky enough to speak to. To explore the concept of holding kaimoana in pōhā, an *in situ* experiment was undertaken. This experiment explored the biochemical and bacterial implications of holding live bivalves within raw pōhā bags (Chapter Six).

The experiment revealed that when pōhā were newly made, filled with seawater and exposed to sufficient PAR light, photosynthetic activity of the algal tissue was able to maintain dissolved oxygen (DO) inside the pōhā, replenishing DO which was quickly removed by bivalve respiration (Chapter Six). When considering the antibacterial potential of the pōhā, several characteristics of the brown alga may play antimicrobial roles, including secondary metabolites and algal biofilms. Macro-algal secondary metabolites are known to have a marked effect on bacterial colonisation, being a strong selective force for community composition (Lam et al. 2008). Further to this, metabolites have been found to extend beyond the thallus, capable of effecting bacteria in the plankton (Sneed and Pohnert, 2011). Marine agar cultures of shellfish swabs taken during the experiment indicated that bacterial growth in pōhā, comparative to non-pōhā treatments, was markedly different. It was clear that the biofilm of the pōhā, or the secondary metabolites released by pōhā, influenced bacterial community composition. These results indicate that pōhā have the potential to be a natural antimicrobial agent against some bacterial subtypes.

It is unlikely that Pōhā would have been used in the manner with which they have been in the experiment (filled with seawater and left to stagnate), as this led to rapid deterioration of the kelp. Further to this, rimurapa blades used in this experiment had undergone 32 hours of transport under non-temperature controlled conditions, so the results found here may not fully represent the photosynthetic and antibacterial potential of a fresh pōhā. Nevertheless, the biochemical and bacterial results found here have direct implications for the functionality of pōhā.

The current study has only investigated pōhā in its raw form. Traditionally pōhā are often curated, undergoing several drying and rehydrating processes to become a long term receptacle for storage and transport. I consider the “pōhā experiment” a trial study. Many iterations of this experiment could have been undertaken. For example, trials could have incorporated the following; comparing the use of raw and curated (dry) pōhā described in Chapter Five, incorporating water changes and burial trials after incubation, the use of other traditional vessels (see below) to hold bivalves and actual transportation of animals within differing vessels.

The *in situ* experiments undertaken within this thesis involved planned mortalities of the species’ in question. Although much was learnt from the experiments presented in Chapters Four and Six, they are not in alignment with a kaupapa Māori approach or ethos. Future experiments relating to this research should strive to have a common purpose of sustaining life, rather than taking the animals to their physical limits in which they cannot recover.

In Chapter Five, examples of how rimurapa and pōhā could be used to translocate and reintroduce species to new areas is shown by Wakefield (2008) providing direct evidence of pōhā as a translocation tool. When considering the use of raw pōhā as a temporary whare or home for bivalves, characteristics of the brown algae investigated in Chapter Six may contribute to their protection, at least on a short term scale. Kōrero tuku iho surrounding the uses of pōhā for re-seeding, suggest that raw pōhā were used in much the same manner as the ecological role of rimurapa along the coastlines. Pōhā may provide protection and nurture the toheroa in their new location in order to help them acclimate. One exercise that could be undertaken is to follow traditional methods presented in Chapter Five. This would involve collecting toheroa spat and placing them in pōhā with holes drilled into the thallus. These could be weighted down in intertidal areas with stones, for slow release of spat into the environment.

Long-distance transport and translocation of toheroa may have been undertaken with a variety of traditional tools touched on within this thesis, such as pātua, kete whiri (flax/harakeke woven basket specifically for shellfish), hue (gourd) and pōhā. As highlighted in Chapter Four, key to the health of the bivalves would be mitigating bacterial proliferation and desiccation. Bioassays of harakeke (*Phormium tenax*) methanol extracts, one of the most used plant fibres by Māori, have exhibited antibacterial properties (Calder et al., 1986). Utilizing containers made from plants such as harakeke and rimurapa may provide natural forms of bacterial management.

Although toheroa can survive extended periods under adverse conditions (Chapter Four), care would have been needed to result in successful relocations of animals to new shorelines.

Stress to toheroa individuals could be avoided by undertaking a variety of preventative actions, including routine water flushes, or periodic exposure to new seawater, being kept out of direct sunlight, intermittently cleaning toheroa in fresh seawater or introduction of a non-toxic/natural antibacterial agent, and being transported in colder months. This could be as simple as holding the bivalves in a kete whiri and suspending in coastal waters there by replenishing dissolved oxygen, counteracting the potential oxygen debt (Sobral and Widdows, 1997) and flushing the animals along a journey. While possibly not the main vessel in which toheroa were translocated, pōhā may have been the last link in the chain of shellfish translocation. A variety of receptacles may have been used to transport toheroa and other kaimoana species, by land, by waka or by both.

Further considerations of pōhā

An attempt was made to extract *Durvillaea* spp. tissue, using a number of solvents, via sonification. Marine bacterial bioassays were undertaken with these extracts but they failed to work. For future thought, running antibacterial bioassays on successful extracts of raw and curated *Durvillaea* spp. tissue samples could further assess the species antibacterial potential. The implications of this, in terms of the preservation capacity of pōhā (in particular, pōhā-tītī) which is already well documented, would be of great value. Further to this, tests such as these may prove again the scientific capacity and understanding which Māori practitioners of pōhā would have amassed prehistorically (Chapter Five), regarding the properties of rimurapa in food preservation.

The current research has proven that raw pōhā can influence the bacterial composition of its surrounding environment, although the benefits of this to toheroa and other bivalves, when being held inside pōhā bags, is yet to be understood. Undertaking DNA meta-barcoding of samples from the pōhā experiment would have benefited the current study. This would have enabled identification and comparison of bacterial types which were present in pōhā treatments vs jar treatments and potentially identify any bivalve pathogens present. The effects of pōhā on grazers such as the gastropod pāua (*Haliotis* spp.) are suggested to be harmful to the animals foot (Pirker, pers. comm.), which is in alignment with secondary metabolite roles as defence against active herbivory (Chapter Five and Six). As bivalves are filter and deposit feeders, they are un-likely to be affected by these metabolites in the same way.

7.3 *Durvillaea spp.*: a new theory

Humans have been transporting species to non-native ecosystems, both intentionally and by accident, for millennia. The relocation and domestication of a species by humans is a potential speciation mechanism. Domestication of species has resulted in the emergence of many novel species, some of which are the world's most agriculturally important crop species (Bull and Maron, 2016). During domestication, a key component is the role of sustained human activity in the propagation and care of plants and animals (Zeder et al., 2006).

The translocation and successful horticulture of plant species by prehistoric Māori has been well documented (Roskruge, 2007; Shepherd et al., 2016). The transport and successful cultivation of the kūmara is a classic example of this. In a tropical environment, the kūmara would flower, produce seeds and these would be propagated the following season. Within Aotearoa, kūmara are unable to flower due to the climate, and cultivation must be done a different way. Root stocks are instead kept over winter, encouraged to shoot and these are planted out in spring for the new season. Early-Māori would have quickly adapted to this new form of cultivation after transporting the species to a new, temperate climate. Another plant of significance which was bought to Aotearoa by Māori is the hue (gourd; *Lagnaria siceraria*). This species is also limited by climate factors, and could generally only be cultivated in northern areas. It is a testament to the scientific knowledge and agricultural ability of Māori that they were able to transport and adapt tropical species to a temperate climate (Roskruge, 2007).

We consider speciation to be occurring when a lineage splits, becomes reproductively isolated and forms genetically distinct sub-populations. However, it is difficult to define exactly when such an event has or is occurring, due to the vagueness surrounding differences in sub-populations that have slightly different traits and those that have divergent lineages. Human mediated speciation rates cannot currently be quantified, although numerous studies have found that human activities have influenced species' evolution (Bull and Maron, 2016). Bull and Maron (2016) compiled a review of anthropological activities resulting in populations becoming distinct from other populations of the same species, potentially driving speciation. It is known that humans can drive contemporary evolution[52] significantly faster than through natural selective forces (Stockwell et al., 2003). Bull and Maron (2006) suggest that human activities can directly and indirectly produce reproductive barriers of different kinds (physical, geographical), while applying selective pressures (by age, type, size) and this can result in the development of new traits in a sub-population and eventual genetic divergence.

Plant species which have been domesticated (cultured into crops), generally exhibit lower genetic diversity to their wild relatives. Such lack of diversity found within Ōreti toheroa has led to the "toheroa translocation hypothesis" and the idea that southern populations were

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[52] ***Contemporary evolution**: heritable trait evolution observed in contemporary time (i.e. less than a few hundred generations).* Taken from Stockwell et al. (2003).

brought about by human intervention (Ross et al., 2018). There are considered to be two broad stages in crop evolution, in which diversity can be lost following domestication, although these are the simplification of complex and on-going processes. These include an initial bottleneck occurring, creating a subset from wild populations and, following this, selection of desirable traits during continued domesticity leading to further loss in genetic diversity (Gross et al., 2014; Shepherd et al., 2016).

Shepherd et al. (2016) investigated the effects of domestication bottlenecks on a plant species endemic to Aotearoa. Rengarenga (New Zealand rock lily; *Arthropodium cirratum*) is a perennial lily-like herb which grows in coastal areas, on rocky outcrops and cliff edges. The plant is insect pollinated with an ability to self-pollinate and the natural distribution of rengarenga is restricted to the north of Te Ika-a-Māui. South of this, rengarenga is usually associated with pre-European archaeological sites and gardens and is often found growing with karaka (*Corynocarpus laevigatus*), this species known to be cultivated by Māori. It is suggested that rengarenga found outside its natural distribution may be the result of prehistorical translocations by Māori (Heenan et al., 2004). Shepherd et al., (2016) suggest that although no phenotypic differences between wild and translocated populations are apparent, it is possible that traits not easily recognised may have been selected for, including rhizome size and palatability. Shepherd et al., (2016) suggests that rengarenga is in the early stages of domestication, with Māori translocating the species beyond its natural range for cultivation as a food supply and significantly increasing its distribution, including from the north to Te Waipounamu. This was tested by examining chloroplast diversity and structuring in natural populations, assessing how much diversity may have been retained across multiple translocation sites and the relationship between translocated sites and Māori settlements.

The variation in chloroplast haplotypes between sub populations were assessed using PCR amplification and sequencing. It was found that of the 29 haplotypes detected in the species sampled, only two of these haplotypes were found at sites considered to have derived from translocations by Māori and even in the early stages of domestication, results indicated that a large amount of chloroplast diversity had been lost.

Samples taken from sites within the species natural distribution demonstrated high chloroplast diversity, with Shepherd et al. (2016) suggesting that the phylogeographic pattern of the species observed may be the result of initial population expansion, followed by population bottlenecks, leading to genetically distinct populations. The extent to which diversity is lost due to domestication bottlenecks is dependent on several factors. This includes the number of individuals in the founding population and the duration of the bottleneck event (Zeder et al., 2006). Several reasons are suggested to explain low chloroplast diversity found within rengarenga sub-populations that are considered to be translocated. This included the physical isolation of new sub-populations preventing gene flow between wild and cultivated populations and that the plants were sourced from a narrow area. It could be postulated that sub-populations of rengarenga may be undergoing species divergence through bottleneck domestication.

To yield products for human use from plant and animal resources, people are able to drive rapid evolution; through relocation, domestication, artificial selection and grooming of physiological traits (Gross et al., 2014). Harvesting is a strong directional selective force with respect to phenotypic traits and this selection may cause contemporary evolution within harvested populations, particularly if harvest rates exceed natural mortality rates (Stockwell et al., 2016).

In chapter five I discuss the research of Fraser et al. (2010, 2012), who present a newly identified species of *Durvillaea* spp., *D. poha*, named for the traditional uses of its broad “cape” like blades, to make pōhā. From DNA extraction, amplification and sequencing of *D. Antarctica* and *D. poha* individuals, Fraser et al. (2012) found that mitochondrial (Cytochrome c oxidase I) haplotype diversity in *D. poha* was relatively low compared with other monophyletic groups within *D. Antarctica.* Here, I present a new hypothesis; that *Durvillaea antarctica* sub-populations have been domesticated by southern Māori prehistorically, thus facilitating the divergence of the species and potential speciation, through selectively propagating and grooming lineages which were most desirable (Gross et al., 2014). This may have occurred through the transplantation (translocation) of *Durvillaea* spp. to new areas and through harvesting and gardening of the endemic species over generations. These processes may have been developed as a fundamental part of the mahika kai of the resource (Chapters Two and Five) to produce the distinctive trait of broad and distinct lamina needed to make pōhā, and to ensure good condition of the rimurapa was maintained (discussed in Chapter Five). If true, this may be one of the earliest first forms of algal aquaculture to have occurred within Aotearoa and a novel example of human-mediated speciation, at the hands of Māori.

Fraser et al. (2010, 2012) suggests that the restricted distribution of *D. poha* may be due to the morphology of the blades, limiting the species ability to drift long-distances. The blades of *D. poha* are described as: always flattened and never cylindrical in cross section (Fraser et al., 2011; Velásquez et al., 2019), i.e. the perfect physiology to make pōhā. *D. poha* can be found in a band above *D. antarctica* on semi-sheltered coasts of the rocky intertidal, while it is also found in the absence of other *Durvillaea* species “*in relatively sheltered locations such as inside the mouth of harbours and bays”* (Velásquez et al., 2019). The specific distributions in sheltered harbours and bays, is of interest, as these areas were likely to be highly accessible to coastal Māori occupants prehistorically (perhaps the convenience of these locations were by selection?). The distributions described are in general, easily reached by humans for harvest and management, particularly in comparison to other species of this genus. *Durvillaea* spp. have high reproductive potential and rapid growth rates (Chapter Five), which may indicate the species are an excellent candidate for human-mediated speciation and contemporary evolution. Future transplantation experiments to explore this concept could be relatively easy to undertake, for example, utilizing harakeke lines of rope to bind manually detached whole individuals (Holdfast, stipe and blade) to boulders in a new area. The movement of whole boulders with rimurapa attached could also be explored. This could be undertaken with hapū who are worried about the deterioration of rimurapa health.

7.4 Concluding remarks

When I began this thesis, I sought to provide evidence for, understand and reclaim knowledge pertaining to translocations of toheroa in the deep past. This research has achieved those objectives and more. Specifically, I have provided evidence for the long-distance translocation, ancient aquaculture and prehistoric management of a taonga marine species, toheroa. This thesis is novel and contributes to our growing understanding of traditional resource management in Aotearoa. The experiments undertaken are the first of their kind for toheroa and tuatua and highlight the complexities of intertidal surf clam physiology, which have implications when considering the suitability for the shellfish in differing aquaculture grow out systems and for management via translocations. While I have not been able to determine definitively whether toheroa in the south are solely a consequence of Māori translocation, the evidence presented here is consistent with that hypothesis.

This thesis reclaims traditional knowledge regarding marine management of taonga species and highlights several possible avenues for future research. Under current management, the toheroa fishery will likely remain closed for the unforeseeable future. Exercises involving translocation and re-seeding of toheroa beds, in particular hapū led exercises of this nature, may prove beneficial in supporting toheroa population management. Land-based aquaculture may also be a viable option in the future, with research into the viability of such aquaculture currently being undertaken (Ross, pers. comm.). The physiological tolerances and behavioural responses highlighted within this thesis (Chapters Four and Six) provide information which may assist such practices going forward. Further to this, it may be of great benefit to include traditional tools in the collection and acclimation of spat or adults to grow out facilities. It is essential that hapū and iwi be involved in every step of such activities.

From this body of research and the mātauranga with which it is underpinned, we can accept that Māori have undertaken long-distance transport and translocation of plant and animal resources. Ascertaining if Māori established toheroa populations in the south is a more difficult question to answer. Traditional practices such as this is clearly fitting with Polynesian and Māori resource management. This thesis has proven that toheroa are physically robust enough to handle such a voyage. Multiple opportunities for such a journey most certainly existed, while the countless novel technologies (waka hourua, pōhā, kete whiri etc.) developed by Māori would have facilitated such an activity. As demonstrated through archaeological analysis, the absence of toheroa in southern middens does not support the current school of thought that toheroa are endemic to the south. It may not be possible to pinpoint specifics regarding who, when and how long-distance translocations occurred prehistorically. However, of more importance here, is that we can learn from traditional practices such as translocation and where appropriate incorporate them into contemporary management of toheroa and other taonga aquatic species.

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Appendix A

Table A 1 Displays all place names, corresponding locations, Local Authority Association and direct references were available, that have been searched for toheroa (*Paphies ventricosa*) midden.

Place name (Search term)	Location	Island	Local Authority Association	References
Piwhane/Kapowairua (Spirits Bay)	Te Paki, Aupōuri Peninsula	Te Ika-a-Māui	Far North District Council	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Takapaukura (Tom Bowling Bay)	Te Paki, Aupōuri Peninsula	Te Ika-a-Māui	Far North District Council	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Paengarehia (Twilight Beach)	Te Paki, Aupōuri Peninsula	Te Ika-a-Māui		
Te Oneroa-a-Tōhē (Ninety Mile Beach)	West Coast, Te Aupōuri Peninsula	Te Ika-a-Māui	Far North District Council	Ross (2017)
Whangapē	West Coast, North Auckland Peninsula	Te Ika-a-Māui	Far North District Council	Redfearn (1974)
Otaipango/Hendersen Bay	East Coast, Te Aupōuri Peninsula	Te Ika-a-Māui		
Mitimiti	West Coast, North Auckland Peninsula	Te Ika-a-Māui	Far North District Council	Redfearn (1974)
Ahipara	West Coast	Te Ika-a-Māui	Far North District Council	
Waipoua (Ripiro)	West Coast, Northland (North of Dargaville)	Te Ika-a-Māui	Far North District Council	
Dargaville	West Coast, Northland (North of Dargaville)			
Omamari (Ripiro Beach)	West Coast Northland	Te Ika-a-Māui	Kaipara District Council	
Baileys Beach, Ripiro (Moi-a-toa?)	West Coast Dargaville. Northland (Taitokerau)	Te Ika-a-Māui	Kaipara District Council	Ross et al., (2017)
Glinks Gully (Ripiro)	Te Kopuru, West Coast Northland	Te Ika-a-Māui	Kaipara District Council	
Pouto, Ripiro	West Coast Northland	Te Ika-a-Māui	Kaipara District Council	
North Kaipara Peninsula/Pouto Point	West Coast, Pouto	Te Ika-a-Māui	Kaipara District Council	
South Kaipara Head	West Coast	Te Ika-a-Māui	Kaipara District Council	Leighton (1975), Johnson (2000)
Muriwai (Te Oneone Rangatira)	West Coast of the Auckland Region	Te Ika-a-Māui	Auckland Council	Ross et al., (2017)
Bethells Beach	West Coast of the Auckland Region	Te Ika-a-Māui	Auckland Council	
Waitākere	West Coast	Te Ika-a-Māui	Waitākere District Council	
Piha	West Coast, North Auckland Peninsula	Te Ika-a-Māui	Auckland Council	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974), Morrison (2008)
Pollok	West Coast, North Auckland Peninsula	Te Ika-a-Māui	Auckland Council	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Tokerau Beach	Karikari Peninsula, Doubtless Bay, East Coast Northland	Te Ika-a-Māui	Auckland Regional Council	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)

Te Arai	East Coast	Te Ika-a-Māui	Auckland Regional Council	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Ōhope	East Coast	Te Ika-a-Māui	Whakatāne District	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Rangitāiki River	East Coast	Te Ika-a-Māui	Whakatāne District	
Ōpōtiki	East Coast	Te Ika-a-Māui	Ōpōtiki District	Morisson (2008)
Porangahau (Te Paerahi Beach)	East Coast (Hawkes Bay)	Te Ika-a-Māui	Central Hawkes Bay District	Wakefield and Walker (Ngati Kere) 2005
Mahanga Beach				
Mahia				
Kāpiti- Horowhenua	Rangitīkei River to Waikanae Beach	Te Ika-a-Māui	Horowhenua District	Morisson (2008)
Tangimoana	Rangitīkei	Te Ika-a-Māui	Horowhenua District	Morisson (2008)
Foxton Beach				
Waitārere Beach	Waitārere/Foxton	Te Ika-a-Māui	Horowhenua District	Morisson (2008)
Hokio Beach	Kāpiti- Horowhenua Coast			Morisson (2008)
Ōtaki Beach	Kāpiti- Horowhenua Coast			
Te Horo Beach	Kāpiti- Horowhenua Coast			
Peka Peka	Kāpiti- Horowhenua Coast	Te Ika-a-Māui	Kāpiti Coast District	
Raumati	Kāpiti- Horowhenua Coast			
Waikanae	Kāpiti- Horowhenua Coast			
Bruce Bay	West Coast	Te Waipounamu		
Karamea	West Coast, 30 km North of Karamea	Te Waipounamu	Tasman District?	Redfearn (1974)
Kahurangi Point	West Coast, North of Karamea	Te Waipounamu	Tasman District	Redfearn (1974)
Kaiapoi	East Coast	Te Waipounamu	Waimakariri District Council	
Kaikōura	East Coast	Te Waipounamu	Kaikoura District	
Hampden	East Coast	Te Waipounamu	Southland district	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Moeraki	East Coast	Te Waipounamu	Otago District	
Waiko1uiti	East Coast	Te Waipounamu	Southland District	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Long Beach	East Coast	Te Waipounamu	Southland District	Hoby (1933), Cassie (1995), Street (1971), Redfearn (1974)
Invercargill (Waihopai)	South Coast	Te Waipounamu	Southland District	
Ōreti	South Coast, Invercargill. Southland (Murihiku)	Te Waipounamu	Southland District	

Bluecliffs Beach	Te Waewae Bay South Coast. Southland (Murihiku)	Te Waipounamu	Southland District	
Orepuki Beach	Te Waewae Bay	Te Waipounamu	Southland District	Futter (2011)
Sandhill Point (Hakapureirei)		Te Waipounamu	Southland District	
Riverton/Aparima		Te Waipounamu	Southland District	
Jacobs River Estuary		Te Waipounamu	Southland District	
Bluff		Te Waipounamu	Southland District	
Colac Bay/Oraka	Murihiku	Te Waipounamu	Southland District	
Wakaputa Point	Murihiku	Te Waipounamu	Southland District	
Waimatuku Mouth	Waimatuku (Ōreti)	Te Waipounamu	Southland District	Garvan (1997)
Dummys Beach		Te Waipounamu	Southland District	
Waikawa Bay	Murihiku	Te Waipounamu	Southland District	

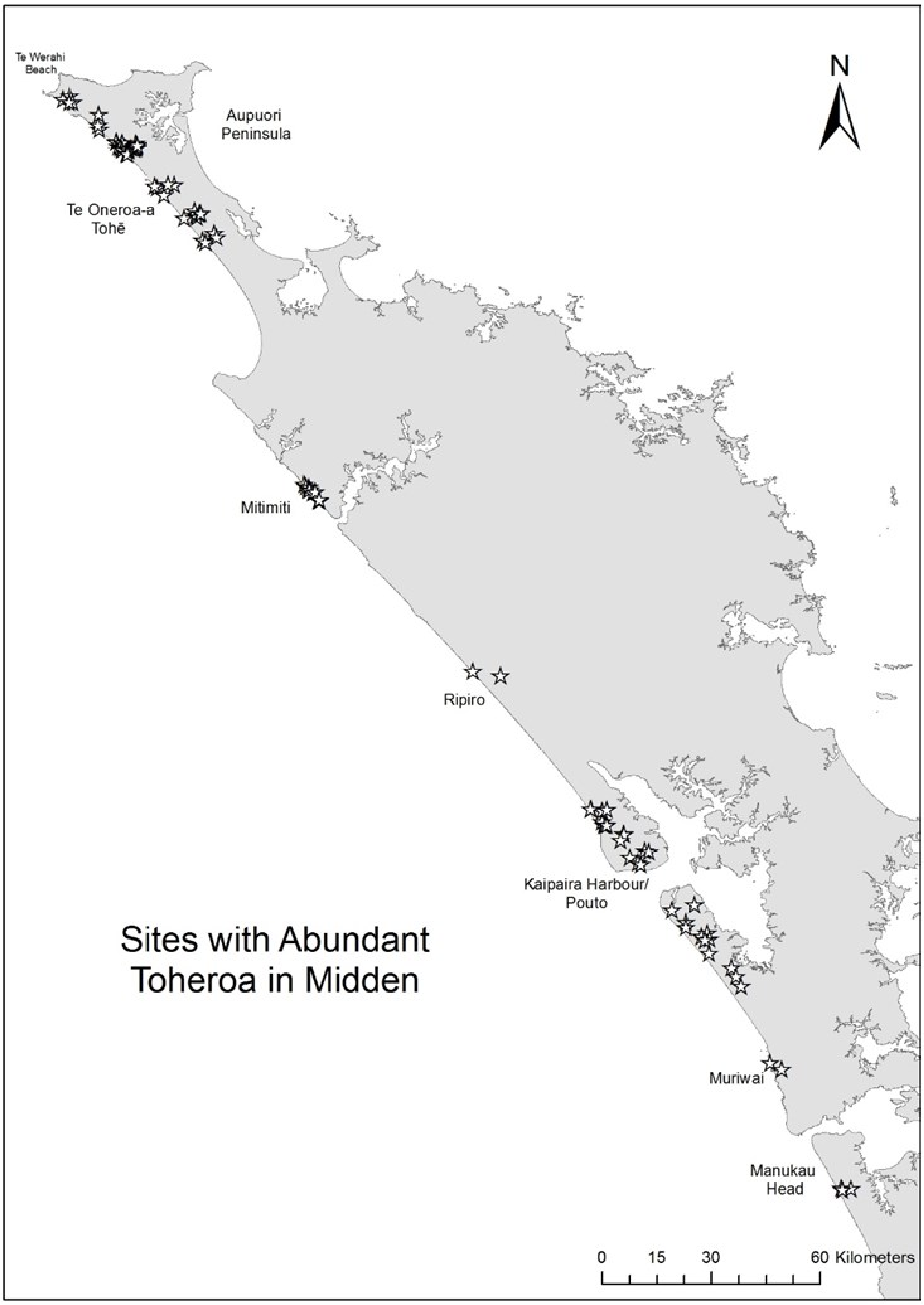


Figure A 1 midden sites with toheroa identified as abundant in midden, the predominant species, or midden consisting only of toheroa across all sites identified in survey.

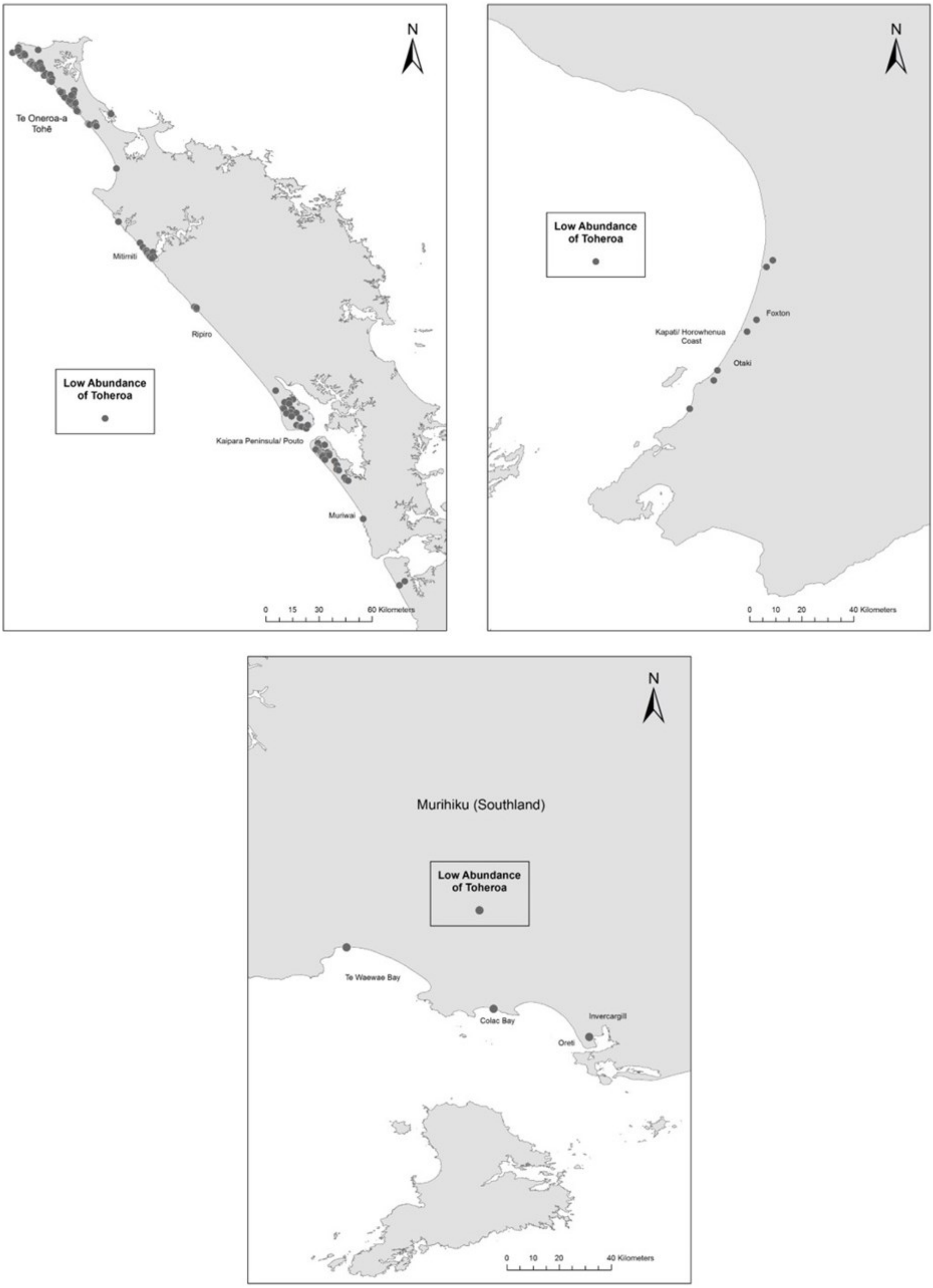


Figure A 2 Far North and West Coast (Top Left), Kāpiti/Horowhenua Coast (Top Right) and Murihiku coastline (Bottom) displaying midden sites with low abundances and/or lack of species predominance.

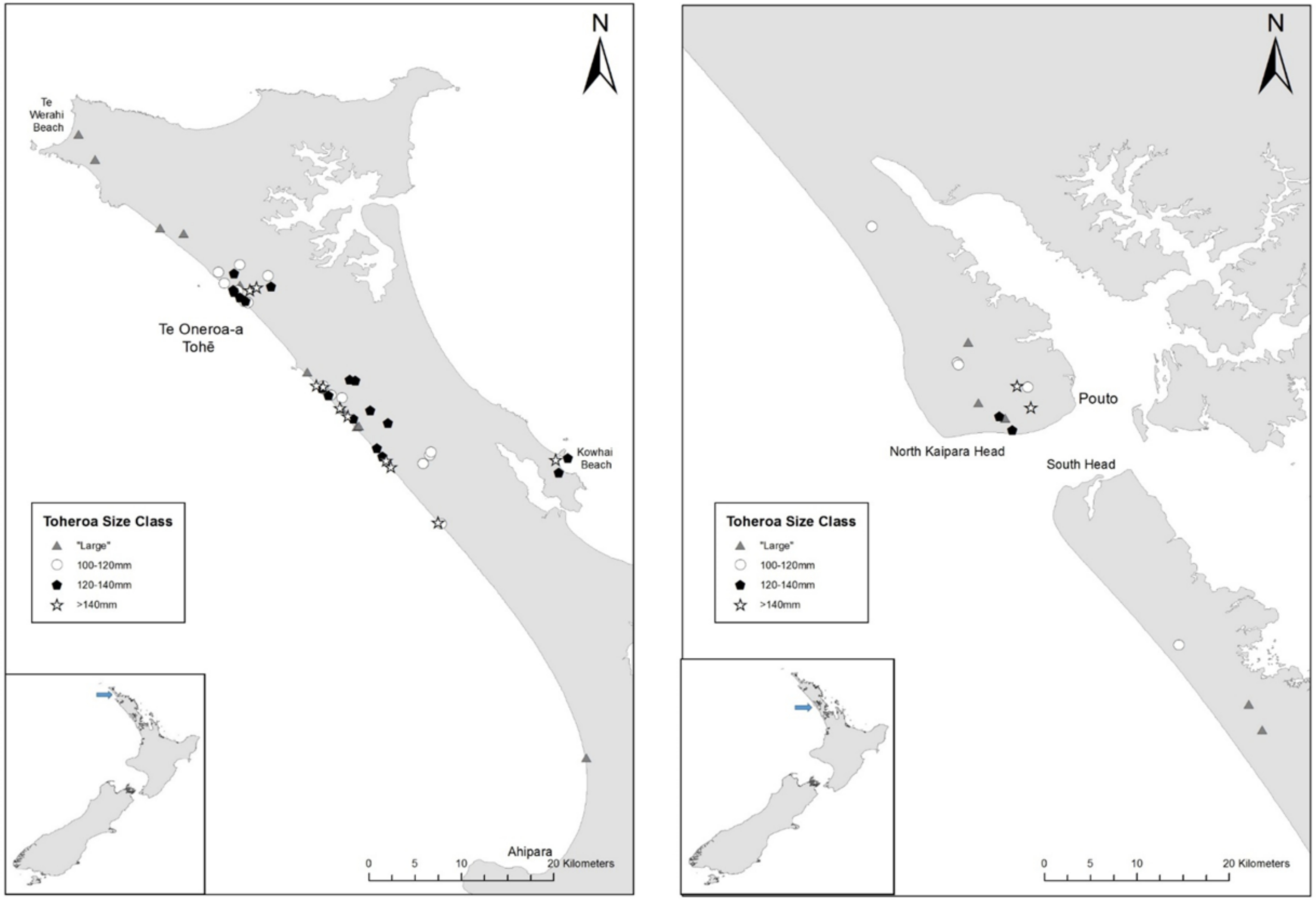


Figure A 3 Sites along the West Coast of Te Ika-a-Māui with size classes of toheroa shell (length in mm), noted in site descriptions as large or measuring >100 mm.

Appendix B

Table B 1 bivalve measurements and dry tissue weight Condition Index % for tuatua (*Paphies subtriangulata*) and toheroa (*Paphies ventricosa*) from all respirometry (static and intermittent-flow) trials.

Replicate	Trial	Length (mm)	Width (mm)	Dry weight (g)	Dry tissue weight (g)	Shell weight (g)	CI%
ToheR1	Static	85	52	42.13	7.78	34.35	22.6492
ToheR2	Static	80	49.5	32.7	6.89	25.81	26.69508
ToheR3	Static	80	48.5	28.05	6.33	21.72	29.14365
ToheR4	Static	88.5	54	43.52	8.4	35.12	23.918
ToheR5	Static	78	51.5	31.53	6.76	24.77	27.29108
ToheR6	Static	86.5	55	41.59	7.75	33.84	22.90189
ToheR7	Static	87	57	48.33	9.94	38.39	25.89216
ToheR8	Static	77	49	28.01	5.91	22.1	26.74208
ToheR9	Static	81	50	37.09	7.63	29.46	25.89952
Tua1	Static	54	36	19.24	1.52	17.72	8.577878
Tua2	Static	56	36.5	15.6	1.93	13.67	14.11851
Tua3	Static	58	36.5	31.51	1.82	29.69	6.13001
Tua4	Static	56	37	19.18	1.76	17.42	10.10333
Tua5	Static	39.5	37.5	23.32	1.9	21.42	8.870215
Tua6	Static	54	35	18.92	1.58	17.34	9.11188
Tua7	Static	55	34	15.97	1.505	14.465	10.40442
Tua8	Static	58.5	36.5	22.97	1.76	21.21	8.297973
Tua9	Static	53.5	33	17.74	1.48	16.26	9.102091
Tua10	Static	57	35	18.28	1.85	16.43	11.25989
TuaR11	Static	56	37	22.85	2.327	20.523	11.3385
TuaR12	Static	59	37	20.59	1.9	18.69	10.16586
TuaR14	Static	52	35	16.74	1.44	15.3	9.411765
TuaR15	Static	53	32	17.57	1.53	16.04	9.538653
TuaR16	Static	54.5	34	15.29	1.47	13.82	10.63676
ToheFlush1	Intermittent-flow	89	56.5	46.88	8.56	38.32	22.3382
ToheFlush2	Intermittent-flow	84	54	35.24	7.93	27.31	29.03698
ToheFlush3	Intermittent-flow	92	55	50.38	9.33	41.05	22.72838
TuaFlush1	Intermittent-flow	60.5	38.5	28.7	1.93	26.77	7.209563
TuaFlush2	Intermittent-flow	56.5	33	20.64	1.505	19.135	7.865169

Table B 2 respiration rates of tuatua (*Paphies subtriangulata*) replicates at different time intervals and under different oxygen levels.

Rep	Time elapsed (minutes)	O2 conc. mg/L	Respiration Rate (mg O_2 g DW $^{-1}$h^{-1})	Rep	Time elapsed (minutes)	O2 mg/L	Respiration Rate (mg O_2 g DW $^{-1}$h^{-1})
P.sub R1	20-30	8-7	0.535696	**P.sub R3**	170-180	7-6	0.191455
P.sub R1	40	8-7	0.711015	**P.sub R3**	210-220	7-6	0.266619
P.sub R1	60	8-7	0.097399	**P.sub R3**	240-250	7-6	0.697749
P.sub R1	80-90	8-7	1.243465	**P.sub R3**	270	6-5	0.073746
P.sub R1	110-120	8-7	0.818155	**P.sub R3**	290-300	6-5	0.314838
P.sub R1	130-140	7-6	0.310055	**P.sub R3**	330-340	6-5	0.408438
P.sub R1	170-180	7-6	0.472387	**P.sub R3**	370	6-5	0.402766
P.sub R1	210-220	7-6	0.461024	**P.sub R4**	400-410	8-7	0.107782
P.sub R1	240-250	6-5	0.097399	**P.sub R4**	20-30	8-7	0.776594
P.sub R1	270	6-5	0.43505	**P.sub R4**	40	8-7	0.357757
P.sub R1	290-300	6-5	0.123373	**P.sub R4**	60	8-7	0.375209
P.sub R1	330-340	6-5	0.345768	**P.sub R4**	80-90	8-7	0.459558
P.sub R1	370	6-5	0.594136	**P.sub R4**	110-120	8-7	0.095984
P.sub R1	400-410	5-4	0.486997	**P.sub R5**	130-140	8-7	0.174516
P.sub R1	20-30	5-4	0.960844	**P.sub R5**	20-30	8-7	0.584968
P.sub R2	40	8-7	0.276853	**P.sub R5**	40	8-7	0.23893
P.sub R2	60	8-7	0.50485	**P.sub R5**	60	8-7	0.230691
P.sub R2	80-90	8-7	0.298567	**P.sub R5**	80-90	8-7	0.368008
P.sub R2	110-120	8-7	0.472279	**P.sub R5**	110-120	8-7	0.288364
P.sub R2	130-140	7-6	0.352852	**P.sub R5**	130-140	8-7	0.115346
P.sub R2	170-180	7-6	0.293139	**P.sub R5**	170-180	7-6	0.337798
P.sub R2	240-250	7-6	0.075999	**P.sub R5**	210-220	7-6	0.258155
P.sub R2	270	7-6	0.21714	**P.sub R6**	240-250	8-7	0.307589
P.sub R2	290-300	7-6	0.559135	**P.sub R6**	20-30	8-7	1.523252
P.sub R2	330-340	6-5	0.260568	**P.sub R6**	40	8-7	1.296183
P.sub R2	370	6-5	0.203569	**P.sub R6**	80-90	7-6	0.302758
P.sub R2	400-410	5-4	0.561849	**P.sub R6**	110-120	7-6	0.391063
P.sub R2	440	5-4	0.369138	**P.sub R11**	150-160	7-6	0.306665
P.sub R3	470	8-7	0.135712	**P.sub R11**	190-200	7-6	0.063692
P.sub R3	20-30	8-7	0.825386	**P.sub R12**	20-30	8-7	0.851361
P.sub R3	40	8-7	0.544584	**P.sub R12**	60	7-6	1.087546
P.sub R6	130-140	7-6	0.334296	**P.sub R12**	80-90	7-6	0.582221
P.sub R7	170-180	8-7	0.359525	**P.sub R12**	110-120	6-5	0.851361
P.sub R7	20-30	8-7	1.033599	**P.sub R12**	150-160	6-5	0.505324
P.sub R7	60	8-7	0.843888	**P.sub R12**	190-200	6-5	0.506697
P.sub R7	80-90	7-6	0.477549	**P.sub R12**	210-220	5-4	0.708552
P.sub R7	110-120	7-6	0.157002	**P.sub R12**	240-250	5-4	0.43392
P.sub R7	130-140	7-6	0.320547	**P.sub R12**	270	5-4	0.411949
P.sub R7	170-180	7-6	0.245316	**P.sub R12**	290-300	4-3	0.477861
P.sub R9	210-220	8-7	0.137377	**P.sub R12**	330-340	4-3	0.005493
P.sub R9	20-30	8-7	1.12616	**P.sub R12**	370	4-3	0.107107
P.sub R9	60	8-7	0.715443	**P.sub R14**	20-30	8-7	0.831727
P.sub R9	80-90	7-6	0.463713	**P.sub R14**	60	8-7	0.662677

P.sub R9	130-140	7-6	0.263323	**P.sub R14**	80-90	8-7	0.513913
P.sub R9	150-160	7-6	0.536582	**P.sub R14**	110-120	7-6	0.574771
P.sub R9	190-200	7-6	0.649198	**P.sub R14**	150-160	7-6	0.682963
P.sub R9	210-220	7-6	0.046371	**P.sub R14**	190-200	7-6	0.603509
P.sub R9	240-250	6-5	0.271603	**P.sub R14**	210-220	6-5	0.933157
P.sub R10	290-300	8-7	0.213639	**P.sub R14**	240-250	6-5	0.311052
P.sub R10	20-30	8-7	0.375443	**P.sub R14**	270	6-5	0.317814
P.sub R10	60	8-7	0.280181	**P.sub R14**	330-340	6-5	0.104811
P.sub R10	80-90	8-7	0.532344	**P.sub R15**	20-30	8-7	0.775372
P.sub R10	130-140	7-6	0.516934	**P.sub R15**	60	8-7	0.613836
P.sub R10	150-160	7-6	0.798516	**P.sub R15**	130-140	8-7	0.155074
P.sub R10	170-180	6-5	0.392253	**P.sub R15**	150-160	8-7	0.659066
P.sub R10	210-220	6-5	0.268974	**P.sub R15**	170-180	7-6	0.335995
P.sub R10	270	6-5	0.302595	**P.sub R15**	210-220	7-6	0.575068
P.sub R10	290-300	6-5	0.308199	**P.sub R15**	240-250	7-6	0.323072
P.sub R11	20-30	8-7	0.391587	**P.sub R15**	270	7-6	0.484608
P.sub R11	60	8-7	0.467074	**P.sub R16**	20-30	8-7	0.33957
P.sub R11	80-90	8-7	0.330254	**P.sub R16**	60	8-7	0.472735
P.sub R11	110-120	7-6	0.36328	**P.sub R16**	80-90	8-7	0.52933
P.sub R3	60	8-7	0.604148	**P.sub R16**	110-120	8-7	0.545976
P.sub R3	80-90	7-6	0.243928	**P.sub R16**	130-140	7-6	0.572609
P.sub R3	110-120	7-6	0.212728	**P.sub R16**	170-180	7-6	0.392836
P.sub R3	130-140	7-6	0.317674	**P.sub R16**	190-200	7-6	0.499368

Table B 3 respiration rates (mg O_2 g DW $^{-1}$h^{-1}) of toheroa (*Paphies ventricosa*) replicates at different time intervals and under different oxygen levels.

Rep	**Time (min)**	**O2 (mg/L)**	**Respiration Rate (mg O_2 g DW $^{-1}$h^{-1})**	**Rep**	**Time (min)**	**O2 (mg/L)**	**Respiration Rate (mg O_2 g DW $^{-1}$h^{-1})**
P. ven R1	20-30	8-7	0.140249	**P. ven R5**	80-90	4-3	0.92443
P. ven R1	40	7-6	1.110544	**P. ven R5**	110-120	3-2	0.531123
P. ven R1	60	6-5	0.666899	**P. ven R5**	130-140	3-2	0.235348
P. ven R1	80-90	6-5	0.185091	**P. ven R5**	170-180	3-2	0.135166
P. ven R1	110-120	5-4	0.895877	**P. ven R5**	210-220	3-2	0.016962
P. ven R1	130-140	4-3	0.599159	**P. ven R5**	240-250	2-1	0.125095
P. ven R1	170-180	3-2	0.343467	**P. ven R6**	20-30	7-6	1.082191
P. ven R1	210-220	2-1	0.393079	**P. ven R6**	40	6-5	0.91857
P. ven R1	240-250	2-1	0.177458	**P. ven R6**	60	6-5	0.717633
P. ven R1	270	2-1	0.041979	**P. ven R6**	80-90	5-4	0.57602
P. ven R1	290-300	2-1	0.093499	**P. ven R6**	110-120	4-3	0.367428
P. ven R2	20-30	7-6	1.160048	**P. ven R6**	130-140	4-3	0.103339
P. ven R2	40	6-5	0.953121	**P. ven R6**	170-180	3-2	0.233948
P. ven R2	60	5-6	0.862198	**P. ven R6**	210-220	3-2	0.084202
P. ven R2	80-90	4-3	0.861153	**P. ven R6**	240-250	3-2	0.348291
P. ven R2	110-120	4-3	0.23828	**P. ven R6**	270	2-1	0.045929
P. ven R2	130-140	3-2	0.436847	**P. ven R7**	20-30	7-6	0.784395

P. ven R2	170-180	3-2	0.070543
P. ven R2	210-220	2-1	0.160944
P. ven R2	240-250	2-1	0.244551
P. ven R2	270	2-1	0.183936
P. ven R2	290-300	2-1	0.108689
P. ven R3	20-30	7-6	0.765106
P. ven R3	40	7-6	0.644827
P. ven R3	60	5-4	1.109236
P. ven R3	80-90	4-3	0.690488
P. ven R3	110-120	4-3	0.875361
P. ven R3	130-140	3-2	0.552391
P. ven R3	170-180	2-1	0.190441
P. ven R3	210-220	2-1	0.224966
P. ven R3	240-250	2-1	0.160372
P. ven R3	270	2-1	0.189327
P. ven R3	290-300	2-1	0.028956
P. ven R4	20-30	8-7	0.897155
P. ven R4	40	6-5	1.52138
P. ven R4	60	4-3	1.372755
P. ven R4	80-90	3-2	0.531447
P. ven R4	110-120	3-2	0.329677
P. ven R4	130-140	2-1	0.199968
P. ven R4	170-180	2-1	0.049992
P. ven R4	210-220	2-1	0.009008
P. ven R4	240-250	2-1	0.063053
P. ven R4	270	2-1	0.102686
P. ven R5	20-30	8-7	1.132215
P. ven R5	40	6-5	1.17992
P. ven R5	60	5-4	0.909588
P. ven R7	60	5-4	0.976524
P. ven R7	80-90	4-3	0.230237
P. ven R7	110-120	4-3	0.373937
P. ven R7	130-140	3-2	0.354089
P. ven R7	170-180	3-2	0.238177
P. ven R7	210-220	2-1	0.142906
P. ven R7	240-250	2-1	0.074629
P. ven R7	270	2-1	0.03652
P. ven R8	20-30	8-7	0.180571
P. ven R8	60	8-7	0.422114
P. ven R8	80-90	7-6	0.325966
P. ven R8	110-120	7-6	0.467843
P. ven R8	130-140	7-6	0.093803
P. ven R8	170-180	6-5	0.230404
P. ven R8	210-220	6-5	0.267339
P. ven R8	240-250	6-5	0.321275
P. ven R8	270	5-4	0.419769
P. ven R8	330-340	5-4	0.180571
P. ven R9	20-30	8-7	0.497608
P. ven R9	60	6-5	0.81902
P. ven R9	80-90	5-4	0.635079
P. ven R9	110-120	5-4	0.482118
P. ven R9	130-140	5-4	0.182004
P. ven R9	170-180	4-3	0.090034
P. ven R9	210-220	4-3	0.12779
P. ven R9	270	4-3	0.160706
P. ven R9	290-300	4-3	0.042597
P. ven R9	330-340	4-3	0.079385

Table B 4 intermittent flow respirometry data for toheroa and tuatua.

Species	Time elapsed	Oxygen (mg/L)	Respiration Rate (mg O_2 g DW $^{-1}$h^{-1})	Species	Time elapsed	Oxygen (mg/L)	Respiration Rate (mg O_2 g DW $^{-1}$h^{-1})
Toheroa	20	7.6	0.410302	**Tuatua**	110	6.3	1.050414
Toheroa	40	6.6	0.785969	**Tuatua**	40	7.03	0.58492
Toheroa	20	6.46	1.161636	**Tuatua**	210	6.75	0.091326
Toheroa	30	6.39	0.829486	**Tuatua**	240	6.63	0.130284
Toheroa	30	6.01	0.934282	**Tuatua**	30	7.8	0.804637
Toheroa	20	7.55	0.55584	**Tuatua**	60	7.45	0.693427
Toheroa	40	6.47	0.928282	**Tuatua**	90	7.06	0.716324
Toheroa	20	6.7	1.173754	**Tuatua**	110	6.89	0.663989
Toheroa	30	6.1	0.96308	**Tuatua**	40	7.53	0.632916
Toheroa	30	7	0.617746	**Tuatua**	70	7.2	0.582217
Toheroa	20	6.02	1.463609	**Tuatua**	100	6.8	0.77847
Tuatua	20	7.8	1.457551	**Tuatua**	130	6.51	0.536425
Tuatua	40	7.61	0.423423	**Tuatua**	30	7.78	0.461195
Tuatua	60	7.2	1.023271	**Tuatua**	60	7.55	0.451382
Tuatua	90	6.75	0.700276				

Table B 5 Dry tissue weight Condition Index % of toheroa from the mortality experiment. SW-AB-A = Seawater- Antibiotic-Anoxia, AE = Aerial Exposure, CTRL = control and SW-A = Seawater- Anoxia.

Replicate	Width (mm)	Length (mm)	Depth (mm)	Whole Dry Weight (g)	Dry Tissue Weight (g)	Shell Weight (g)	Condition Index %
SW-AB-A1	49	81	21	36.17	5.77	30.4	18.98026
SW-AB-A2	48	76	17	24.78	4.65	20.13	23.09985
SW-AB-A3	54	87	21	45.64	6.33	39.31	16.10277
SW-AB-A4	48	77	20	29.12	4	25.12	15.92357
SW-AB-A5	52	87	17	43.15	7.05	36.1	19.52909
SW-AB-A6	47.5	79.5	20	28.82	4.51	24.31	18.55204
AE1	54	86	24.5	46.82	5.93	40.89	14.50232
AE2	51	82	23	37.77	5.58	32.19	17.33458
AE3	44	70	17	21.38	3.87	17.51	22.10166
AE4	52	84	20	37.96	5.807	32.153	18.06052
AE5	51	82	23	37.71	5.006	32.704	15.307
AE6	51	81.5	24	36.15	5.82	30.33	19.18892
CTRL1	50	82	20	33.096	4.978	28.118	17.70396
CTRL2	47.5	76	20	29.138	4.648	24.49	18.97918
CTRL3	50	84	24	38.322	6.448	31.874	20.22965
CTRL4	49	83.5	29	39.621	5.981	33.64	17.77943
CTRL5	42	76	18	29.274	3.792	25.482	14.88109
CTRL6	52	82	20	46.289	7.995	38.294	20.87794
SW-A	50	79	17.5	34.799	5.55	29.249	18.97501
SW-A	53	82	19.5	38.113	6.116	31.997	19.11429
SW-A	56	85.5	20	42.971	6.23	36.741	16.95653
SW-A	45.5	70	16	23.867	3.643	20.224	18.01325
SW-A	44.5	68.5	21.5	21.073	3.26	17.813	18.30124
SW-A	55.5	93	18	52.535	9.33	43.205	21.59472

Table B 6 Kruskal-Wallis Rank Sum test of toheroa (*Paphies ventricosa*) respiration rate Respiration Rate (mg O2 g DW -1h-1) vs O2 integer, with post hoc Dunn Test (Dinno, 2017) undertaken in Rstudio (RStudio Core Team, 2020).

```
Kruskal-Wallis chi-squared = 38.0604, df = 6, p-value = 0


                           Comparison of RR by Oxygen

Col Mean-|
Row Mean |        2-1         3-2         4-3         5-4         6-5         7-
6
---------+-----------------------------------------------------------------------
--
     3-2 |  -2.173536
         |    0.0149*
         |
     4-3 |  -3.032536  -0.638305
         |    0.0012*     0.2616
         |
     5-4 |  -4.201387  -2.053892  -1.555793
         |    0.0000*    0.0200*     0.0599
         |
     6-5 |  -4.797557  -2.453598  -1.949074  -0.268227
         |    0.0000*    0.0071*     0.0256     0.3943
         |
     7-6 |  -3.852847  -1.899731  -1.426481   0.017764   0.270080
         |    0.0001*     0.0287     0.0769     0.4929     0.3935
         |
     8-7 |  -3.451503  -1.623822  -1.160831   0.200299   0.449030   0.17444
1
         |    0.0003*     0.0522     0.1229     0.4206     0.3267     0.430
8

alpha = 0.05
Reject Ho if p <= alpha/2
```

Table B 7 Kruskal-Wallis Rank Sum test of tuatua (*Paphies subtriangulata*) Respiration Rate (mg O2 g DW -1h-1) vs O2 integer, with post hoc Dunn Test (Dinno, 2017) undertaken in Rstudio (RStudio Core Team, 2020).

```
Kruskal-Wallis chi-squared = 13.8447, df = 4, p-value = 0.01


                          Comparison of RR by Oxygen

Col Mean-|
Row Mean |        4-3         5-4         6-5         7-6
---------+--------------------------------------------
     5-4 |  -1.614701
         |     0.0532
         |
     6-5 |  -0.866015   1.349763
         |     0.1932     0.0885
         |
     7-6 |  -1.302699   0.830595  -0.956521
         |     0.0963     0.2031     0.1694
         |
     8-7 |  -2.144200  -0.392385  -2.973090  -2.452881
         |    0.0160*     0.3474    0.0015*    0.0071*

alpha = 0.05
Reject Ho if p <= alpha/2
```

Table B 8 displays the number of times different behaviours were observed for each treatment over the entire experiment (12 days). SW-AB-A = Seawater-Antibiotic-Anoxia, AE = Aerial Exposure, CTRL = control and SW-A = Seawater- Anoxia.

Behaviour	CTRL	SW-AB-A	SW-A	AE
Foot fully retracted	53	6	9	81
Foot Probing	16	7	2	0
Foot Visible	54	2	4	8
Foot Extended	24	84	38	4
Both siphons fully retracted	20	6	3	17
Inhalant fully retracted	25	5	4	18
Exhalant fully retracted	58	7	3	28
Inhalant Visible	99	4	7	47
Exhalant Visible	61	6	6	36
Siphons visible	56	4	5	32
Exhalant extended	3	44	34	5
Exhalant extended	0	40	34	5
Siphons slightly extended (1-3cm)	8	37	8	22
Siphons suspended in seawater (extending towards top of jar)	0	6	3	0
Siphons extended and resting on bottom of jar	0	15	14	0
Inhalant flaccid	0	0	0	13
Exhalant flaccid	0	0	0	17
Outer mantle swelling (mantle retaining water)	42	4	4	7
Valves and Mantle open	6	6	1	14
Outer mantle flaccid (out of valves) or gaping	0	0	0	30
Valve contraction/clapping/closure	3	0	0	9
Both siphons open (00)	11	4	3	8
Inhalant siphon open (IO)	12	12	5	37
Exhalant siphon open (EO)	28	7	4	12
Total number of sampling times across all replicates	**134**	**92**	**52**	**94**

Appendix C

Table C 1 Width and length of rimurapa blades used to make pōhā replicates.

Replicate	Length (mm)	Width (mm)
P-AER1	320	100
P-AER2	310	130
P-AER3	320	210
PI-AER1	300	170
PI-AER2	400	130
PI-AER3	380	160
P-SWR1	320	230
P-SWR2	320	130
P-SWR3	330	130
PI-SWR1	240	120
PI-SWR2	340	130
PI-SWR3	320	140
Average	325	148

Table C 2 Length and dry tissue weight Condition Index % of 69 toheroa individuals. Four individuals from replicates PI-AE1, PI-AE3, AE1 and AE3 were unable to be measured as they failed to be freeze dried effectively.

Replicate	Length (mm)	CI%	Replicate	Length (mm)	CI%	Replicate	Length	CI%
P-AE1	77.50	29.08	**AE-AB1**	74.00	24.77	**PI-SW2**	82.00	29.48
P-AE1	75.00	22.81	**AE-AB1**	74.00	24.77	**PI-SW2**	75.00	25.75
P-AE1	76.00	25.91	**AE-AB1**	87.00	24.30	**PI-SW2**	77.50	33.02
P-AE2	77.50	14.71	**AE-AB1**	72.00	27.33	**PI-SW3**	71.00	26.21
P-AE2	71.00	28.72	**AE-AB2**	90.00	27.12	**PI-SW3**	73.00	23.73
P-AE2	76.00	25.18	**AE-AB2**	74.00	25.81	**PI-SW3**	74.00	26.89
P-AE3	69.00	29.16	**AE-AB2**	77.00	13.48	**SW1**	72.00	27.37
P-AE3	79.00	28.89	**AE-AB3**	82.00	31.03	**SW1**	76.50	28.04
P-AE3	75.00	30.00	**AE-AB3**	78.00	30.66	**SW1**	72.00	29.66
PI-AE1	73.00	24.39	**AE-AB3**	87.00	25.43	**SW2**	72.00	27.09
PI-AE1	86.00	26.53	**P-SW1**	90.00	21.62	**SW2**	85.00	28.80
PI-AE2	78.00	23.90	**P-SW1**	80.00	31.41	**SW2**	74.00	27.80
PI-AE2	76.00	30.06	**P-SW1**	72.00	24.07	**SW3**	85.00	27.75
PI-AE2	72.00	26.75	**P-SW2**	71.50	27.30	**SW3**	75.00	10.21
PI-AE3	72.50	27.81	**P-SW2**	86.00	26.39	**SW3**	71.50	27.81
PI-AE3	71.00	21.69	**P-SW2**	69.00	29.37	**SW-AB1**	79.00	27.10
AE1	70.00	14.19	**P-SW3**	71.00	24.96	**SW-AB1**	82.00	27.21
AE1	84.00	23.15	**P-SW3**	71.00	25.52	**SW-AB1**	75.00	23.02
AE2	75.00	24.28	**P-SW3**	83.00	27.73	**SW-AB2**	70.50	20.40
AE2	74.00	25.26	**PI-SW1**	80.50	26.82	**SW-AB2**	76.00	21.21
AE2	78.00	30.77	**PI-SW1**	75.50	27.46	**SW-AB2**	82.00	23.75
AE3	81.00	25.21	**PI-SW1**	86.00	23.84	**SW-AB3**	81.00	27.52
AE3	76.50	27.54	**PI-SW2**	82.00	29.48	**SW-AB3**	78.00	32.66
AE3	76.50	27.54	**PI-SW2**	75.00	25.75	**SW-AB3**	71.00	24.86

An assessment was conducted to determine if the Grid-point Intercept methodology was estimating consistent and accurate relative abundances between agar replicates. Growth at 24 hours for the second trial produced countable colonies (between 30 and 300). Full colony counts from these agar plates were compared with GPI generated colony counts, to assess the effectiveness of the GPI methodology in estimating equal proportions of bacterial colony cover between each agar plate.

Full counts of each agar plate (n=12) were undertaken and compared with GPI counts from the same agar plate. These were both plotted (Figure C 1) and were found to follow the same trend across all replicates. The total GPI counts (representing colony coverage estimates) were then converted to a percentage of the whole counts. Percentages were compared across the twelve agar replicates to assess accuracy of using GPI methodology to equate relative colony cover.

A difference of 6.74% was found between the highest and lowest percentage, while the average GPI count was found to cover 33.23% (SE 0.65) of total colonies present on a plate (Table C 3). The majority of the percentages fell between 30 and 35%, (a difference of approx. 5%). This gives indication that the GPI methodology is sufficient in producing useful estimates for comparison, from a sample size of 12.

Table C 3 Table of whole counts, GPI counts and percentage coverage of GPI counts of each replicate

Replicate	Total colony count	Total Grip-point Intercept count	GPI count Percentage of total colonies
AE-ABR1	125	39	31.20
AE-ABR2	203	71	34.98
AE-ABR3	49	17	34.69
AER1	114	37	32.46
AER2	64	22	34.38
AER3	99	35	35.35
PI-AER1	475	152	32.00
PI-AER2	416	144	34.62
PI-AER3	149	45	30.20
P-AER1	276	80	28.99
P-AER2	473	169	35.73
P-AER3	174	60	34.48
Average			33.26

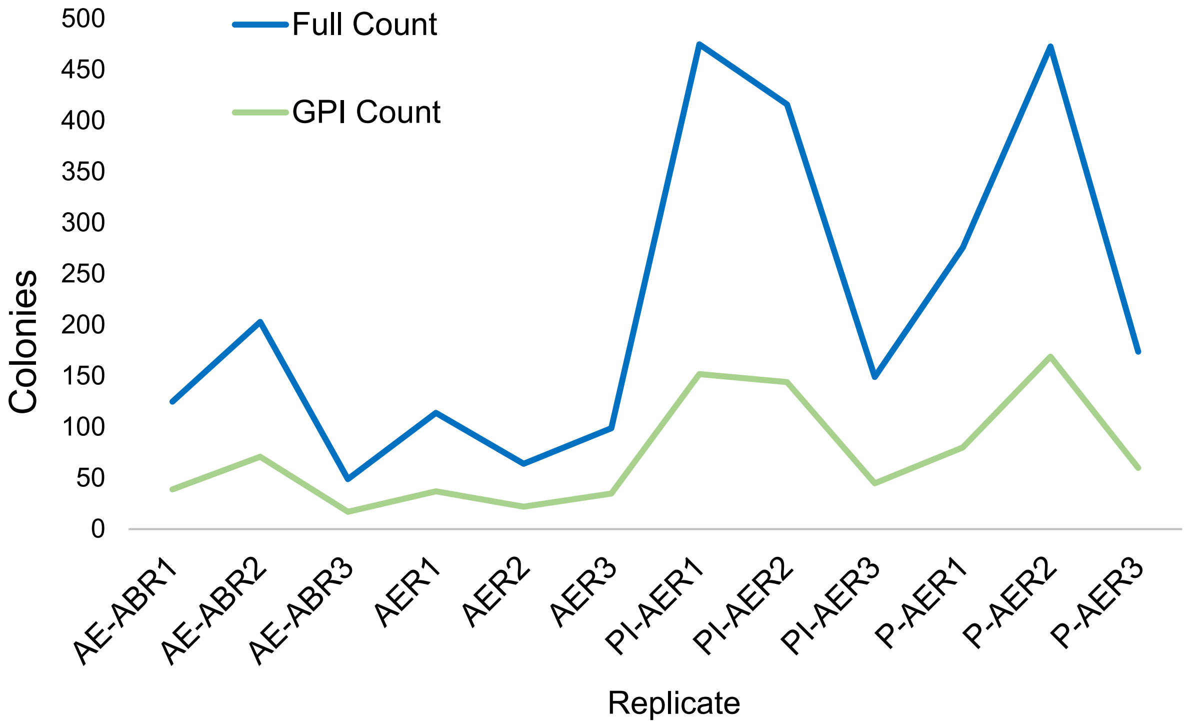


Figure C 1 Full counts and total GPI counts of bacterial colonies for 12 agar replicates.

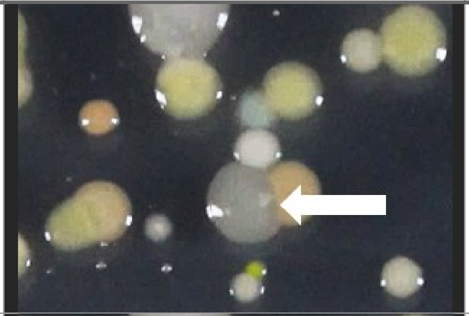
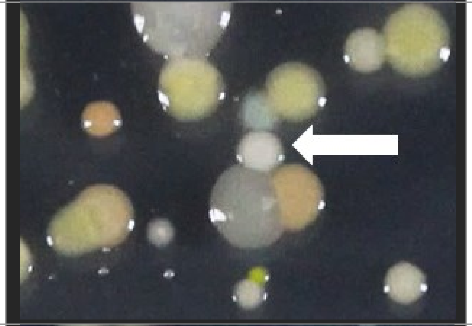
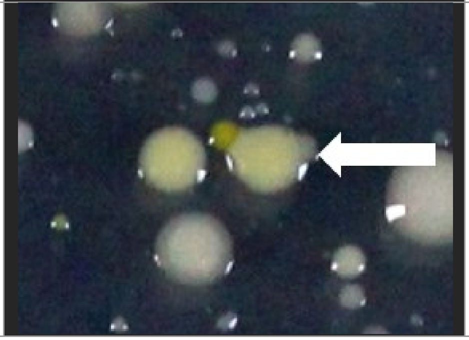
Table C 4 Descriptive statistics; multiple One Way ANOVAs of dissolved oxygen values from two groups (DF,1; N=6 per group; Pōhā vs No Pōhā), based on time elapsed. P<0.005 signified by asterisk.

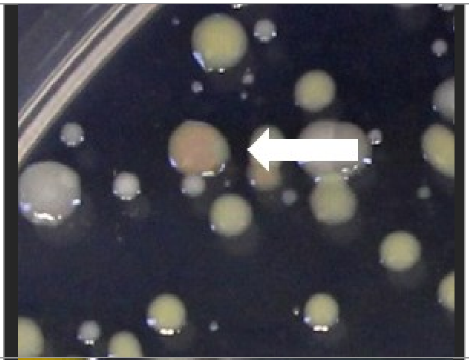
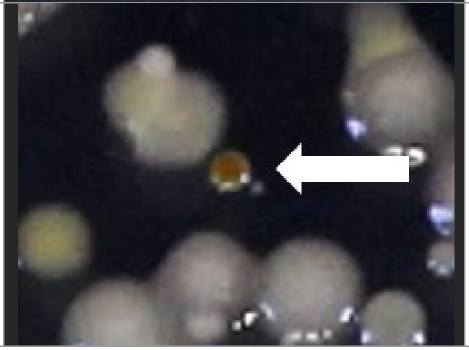
Time Elapsed	**Dissolved oxygen (Mean ± SE)**		**F-Value**	**P-Value**	**Johnson Transformed**
	Pōhā	**Non-Pōhā**			
1 Hour	5.603 ±0.651	4.682±0.493	1.27	0.286	N
3 Hours	3.875±0.413	2.743±0.463	3.32	0.098	N
4 Hours	0.499±0.352	0.567±0.389	4.11	0.07	Y
5 Hours	3.388±0.427	1.343±0.212	18.39	**0.002***	N
7 Hours	3.307±0.300	1.140±0.122	44.57	**<0.000***	N
9 Hours	0.670 ±0.152	0.781±0.162	6.13	**0.002***	Y

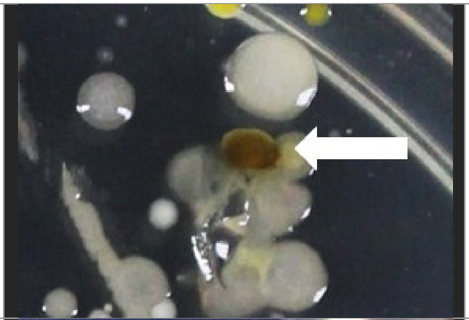
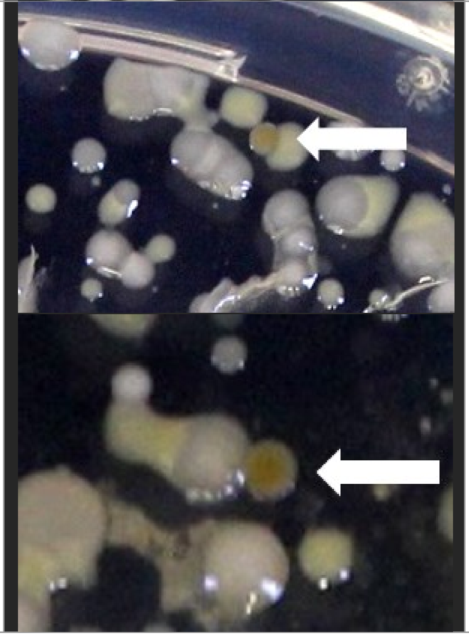
Table C 5 R output for Kruskal-Wallis rank sum test and post hoc Dunns Test. Trial One: comparing statistical differences of univariate RCA data between treatments for 24 hour and 48 hour colony growth.

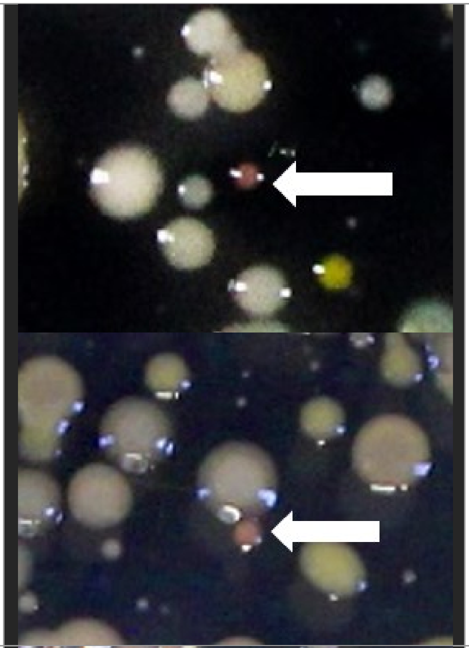
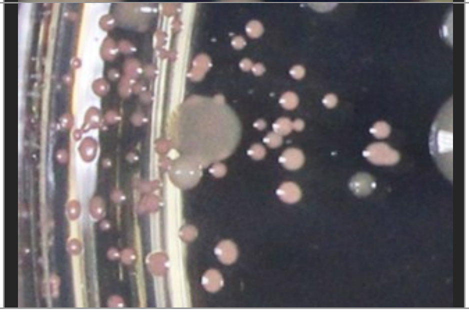
```
Growth at 24 hours
Kruskal-Wallis chi-squared = 25.7317, df = 7, p-value = 0


                         Comparison of x by Treatment
                                (No adjustment)
Col Mean-|
Row Mean |       ABAE       ABSW         AE       AEIP        AEP         SW
---------+------------------------------------------------------------------
    ABSW |  -1.443924
         |     0.0744
         |
      AE |  -3.166319  -1.722395
         |    0.0008*     0.0425
         |
    AEIP |  -4.197694  -2.753770  -1.031374
         |    0.0000*    0.0029*     0.1512
         |
     AEP |  -2.526867  -1.082943   0.639452   1.670826
         |    0.0058*     0.1394     0.2613     0.0474
         |
      SW |  -1.516120  -0.072196   1.650199   2.681573   1.010747
         |     0.0647     0.4712     0.0495    0.0037*     0.1561
         |
    SWIP |  -1.701768  -0.257843   1.464551   2.495926   0.825099  -0.185647
         |     0.0444     0.3983     0.0715    0.0063*     0.2047     0.4264
         |
     SWP |  -3.516987  -2.073062  -0.350667   0.680707  -0.990119  -2.000866
         |    0.0002*    0.0191*     0.3629     0.2480     0.1611    0.0227*
Col Mean-|
Row Mean |       SWIP
---------+-----------
     SWP |  -1.815219
         |     0.0347

alpha = 0.05
Reject Ho if p <= alpha/2

Growth at 48 hours
Kruskal-Wallis chi-squared = 12.8472, df = 7, p-value = 0.08


                         Comparison of x by Treatment
                                (No adjustment)
Col Mean-|
Row Mean |       ABAE       ABSW         AE       AEIP        AEP         SW
---------+------------------------------------------------------------------
    ABSW |  -1.639796
         |     0.0505
         |
      AE |  -3.145521  -1.505725
         |    0.0008*     0.0661
         |
    AEIP |  -2.980510  -1.340714   0.165010
         |    0.0014*     0.0900     0.4345
         |
     AEP |  -1.835747  -0.195950   1.309774   1.144763
         |     0.0332     0.4223     0.0951     0.1262
         |
      SW |  -1.949192  -0.309395   1.196329   1.031318  -0.113445
         |     0.0256     0.3785     0.1158     0.1512     0.4548
         |
    SWIP |  -1.949192  -0.309395   1.196329   1.031318  -0.113445   0.000000
         |     0.0256     0.3785     0.1158     0.1512     0.4548     0.5000
         |
     SWP |  -1.763554  -0.123758   1.381966   1.216955   0.072192   0.185637
         |     0.0389     0.4508     0.0835     0.1118     0.4712     0.4264
Col Mean-|
Row Mean |       SWIP
---------+-----------
     SWP |   0.185637
         |     0.4264

alpha = 0.05
Reject Ho if p <= alpha/2
```

Table C 6 Table of Visual Taxonomic Subgroups (VTS) with photos and qualitative descriptions. Growth is the time in which a VTS colony is first distinctive with the naked eye from the beginning of agar plate incubation. Sizes are an approximation (Small: 1-2mm, Medium: 3-4 mm, Large: >5 mm).

Visual Taxonomic Subgroup Code	Image	Pigment	Colony Size	Form (shape, texture, elevation)	Growth	Notes
VTS-A		Grey /Transparent	Medium-large	Circular, irregular after several days growth. Convex when smaller, often flat and raised	Primary colonizer, 24 hours	Grey and Pale/White have been grouped together. These were the most abundant colonies and were often difficult to differentiate while manually counting. This group is likely to represent many different species (Ahern, 2018).
VTS-A		Pale/White	Medium	convex, circular and irregular	Primary colonizers, 24 hours	
VTS-B		Light Yellow	Medium - large	circular, flat and raised	Primary colonizers 24-48 hours	

VTS-C		Orange	Medium	circular, colonies can also become irregular, flat and raised	24-48 hours	
VTS-D		Dark Yellow	Small - medium	Circular, convex	48 hours	
VTS-E		Dark Brown	Small- medium	circular, irregular, flat, raised	48-72 hours	

					
VTS-F		Brown/Light brown	Small-medium	irregular, margins sometimes rough, flat	48-72 hours

VTS-G		Red	Small-medium	Circular, flat and raised	48-72 hours	
VTS-H		Pink	Small - medium	Circular and irregular. Convex, larger colonies flat and raised	72 hours	