The recruitment dynamics of post-settlement juvenile toheroa and the potential applications for aquaculture.

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Master of Science (Research) in Ecology and Biodiversity

at

The University of Waikato

by

Marieka van der Lee

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2022

Abstract

Managing the recovery of threatened species due to anthropogenic disturbance is one of the most challenging problems in ecological monitoring. Researching species ecology is vital to help us improve ecosystem health and subsequently develop better management strategies in the environment. Humanity is entirely reliant on ecosystem services for food security. With the world population expected to reach ten billion by 2050, there is a growing need for more sustainable food sources. With the exploitation of many environmental resources worldwide, aquaculture has been championed as a sustainable option for future seafood production. In New Zealand, the toheroa (*Paphies ventricosa*) has been identified as a potentially valuable asset to the aquaculture industry and for possible conservation strategies via the implementation of reseeding populations with hatchery-reared spat.

Toheroa faced inadequate resource management and exploitation in the 1900s which ultimately led to the closure of an important recreational, cultural and commercial fishery. However, toheroa populations have failed to recover despite over 40 years of protection. It has been proposed that the continued decline of toheroa populations is not due to a lack of juvenile recruitment. Very little is known about juvenile toheroa recruitment, and there is no available information that could facilitate restoration management or determine the appropriate action to take for monitoring juvenile populations. From both a conservation and an aquaculture perspective, understanding the underlying ecology will be pivotal for future endeavours.

My thesis aimed to investigate the distribution dynamics of post-settlement juvenile toheroa on Ripiro Beach and the potential applications for aquaculture. Population surveys were conducted on Ripiro Beach in February and May to establish a sampling methodology that accurately captures the juvenile population both spatially and temporally. Surveys on vertical substrate stratification significantly affected both density and shell size with increasing sediment depth. Additionally, in contrast to the hypothesis formed on the basis of traditional knowledge that juvenile distribution is limited to the dunes and upper intertidal, spat appeared to have far more varied littoral distributions than previously theorised. The data from these surveys were used to make estimates of the total juvenile population on Ripiro Beach with attention to changes spatially (habitat type), temporally (seasonally), and by size cohorts (mm). My results indicated that toheroa populations are not recruit-limited. Estimates for the total February population ranged between 580 (±190) million and 650 (±200) million. By May, large abundance losses (> 90%) dropped the estimated population to between 30 (±15) million and 37 (±17) million, indicating significant bottleneck mortality during the early growth stages. However, the high abundances of small spat (< 5 mm) indicate that toheroa aquaculture is potentially viable. In aid of future aquaculture applications, I investigated how handling, harvesting, and different transportation methods could impact toheroa health, survival, or performance. This experiment aimed to mimic real-world applications wherein juvenile spat would be harvested and ongrown in hatcheries. To do this, I utilised the burrowing behaviour of juvenile toheroa as a quantitative indicator of stress. I found that if appropriate storage methods were implemented, initial handling and harvesting had a greater impact than actual transportation.

The research in this thesis demonstrated that populations do not appear to be recruit-limited. Furthermore, the findings indicate that aquaculture built on the foundation of wild-harvested juveniles is potentially viable. However, further research is required in order to quantify potential annual recruitment variation both spatially and temporally. Additionally, in order to establish a conservation approach, we must first define the niche requirements of toheroa to determine the obstacle (or obstacles) inhibiting recovery.

Acknowledgements

To begin with, I would like to express gratitude for the experience of gaining such an educational experience. There are many people I would like to thank for their guidance and help that made this thesis possible. Firstly, to my supervisors Dr Phil Ross, Dr Hazel Needham. Hazel, thank you for your input, encouragement, and positivity. Phil, thank you for the amazing opportunity to be a part of something as special as the iconic toheroa, their charisma made the long drive up north well worth it. Thank you for your wisdom and guidance during this process, it couldn't have been done without you.

Thank you to all of Team Toheroa. I would like to thank those who spent hours on the beach with me helping to collect my data during surveying, one of the many parts of being an ecologist requires being hunched over a sieve. Thank you, Ethan and Martyn for being of great assistance and putting in the hours on the beach with me.

To my family, Mum and Dad, thank you for all the love and support you've given me over the years. To my brothers, Jacob and Luke, thank you for always making me laugh when I need it. I would like to thank my lovely Oma, morning coffees with you always leave me feeling brighter. To my friends, Helena, Brittnee, Charlotte, Nicole, Caleb, Kelsey, and Dylan, thank you for rallying me through this thesis.

This research could not have been completed without the aid of a University of Waikato Research & Enterprise Study Award.

Table of Contents

List of Figures

List of Tables

1 Chapter 1 – General introduction

1.1 Introduction

One of the defining ecological problems of our time is the management of deteriorated ecosystems instigated by anthropogenic activity (Ellis, 2015). Preserving threatened and endangered species has moved to the forefront of modern ecology (McCay *et al.,* 2003). Understanding the importance of ecological processes is key to successful management, conservation, and restoration practices in the environment (Ellis, 2015; Jackson *et al.,* 2001). Large-scale connectivity links habitats both spatially and temporally, cumulative stressors such as exploitation, habitat modification, eutrophication, and urbanisation have altered environments to extremes (Thompson *et al.,* 2017; Sheaves, 2009). Researching species ecology helps us to improve ecosystem health through better management and subsequently preserving and supporting important ecosystem services (Daily & Matson, 2008).

Food security is one of the key ecosystem services provided by the environment (Porter *et al.,* 2009). Over the past decades, we have seen an increased urgency to understand how to successfully feed a growing population without depleting environmental resources (Lytle, 2009). Sufficient resource management must be delicately balanced with sustainability to ensure quality of life for current and future generations. Increasing seafood production has been identified as a key strategy for sustaining the world's increasing human population. However, failure in natural resource management has resulted in reduced biodiversity and depletion of wild populations to alarming levels, particularly in the marine environment (Berchez *et al.,* 2016; Jennings, 2004). In many cases, fishing has collapsed populations of species that play fundamental roles in ocean ecosystems, causing trophic cascades that alter the food web (Baum & Worm, 2009). By 2050, the world population will have grown to almost ten billion people, and with it comes the demand for food sources to increase production by 50% compared to its present (Smaal *et al.,* 2019). With these forecasted production requirements and declining natural stocks, aquaculture has been championed as a sustainable option for future seafood production.

1.2 Aquaculture worldwide

Aquaculture is the controlled cultivation of aquatic organisms such as fish, molluscs, crustaceans, algae, and aquatic plants (Calixto *et al.,* 2020; Frankic & Hershner, 2003). At present, half of the fish consumed around the world is produced by aquaculture, surpassing global fisheries capture for commercial seafood revenues (Calixto *et al.,* 2020; Froehlich *et al.,* 2017). In 2018, farmed seafood production reached 82.1 million tonnes globally, with Asia at the forefront of production contributions (Rocha *et al.,* 2022). The industry's rapid growth rate has been attributed to declining catches from traditional fisheries coupled with the increasing world population (Frankic & Hershner, 2003; Tal *et al.,* 2009). Globally, people recognise the valuable asset that the environment provides as life-support services for our current and future populations. However, the sustainability challenge remains a point of contention (Daily & Matson, 2008). In the absence of sufficient management strategies and quotas, there has been a decreasing trend in the catch rates of marine shellfish, which has in some cases led to stock collapse (Caddy *et al.,* 2003; Lotze, 2004). In order to utilise ecosystem services with an expanding human population, there is an ever-growing need for sustainable aquaculture. Bivalve aquaculture is increasing globally, often utilising wild-caught juvenile recruitment from oysters, clams, scallops, and mussels (Gallardi, 2014). The majority of the world's juvenile spat used in marine aquaculture is sourced from the wild (South *et al.,* 2020a). Additionally, the threatened state of many marine bivalve species has adapted aquaculture techniques to progress restoration methods into facilitating hatchery-reared animals (Konisky *et al.,* 2011). For example, North America restoration programmes have focused on seeding and on-growing clam spat (*Mercenaria mercenaria*) in industrialised nurseries (Manzi *et al.,* 1986). Similar techniques have been implemented in the Great Bay Estuary (USA); conservation measures for the eastern oyster (*Crassostrea virginica*) included releasing hatchery-grown spat onto restored substrates (Konisky *et al.,* 2011).

1.2.1 Aquaculture in Aotearoa New Zealand

Aquaculture has become a significant primary industry in Aotearoa New Zealand (hereafter 'NZ') over the past 40 years (South *et al.,* 2020a). Collectively, Greenshell^{TM} mussels (GSM) (*Perna canaliculus*) and Chinook (king) salmon

(*Oncorhynchus tshawytscha*) produce over NZD $400 million in revenue (Symonds *et al.,* 2019). In NZ, the green-lipped mussel (*Perna canaliculus*) contributes >70% of export product annually, and the juvenile mussel spat is primarily harvested from the wild on the shore of Te Oneroa a Tohe (Ninety Mile Beach; Alfaro *et al.,* 2010). There are aspirations to increase the production and value of the aquaculture industry in NZ (to a $3 billion industry by 2035), and for this to happen there is a need to develop new aquaculture species. One species which has long been considered to be a potentially valuable aquaculture target is the toheroa (*Paphies ventricosa*) (Newcombe *et al.,* 2015; Ross *et al.,* 2018a).

1.3 Toheroa

1.3.1 Toheroa biology and ecology

Toheroa are large intertidal surf calms that were once considered a rich and inexhaustible kaimoana (seafood) (Murton, 2006). They were a staple food source for Māori and are an iconic and taonga (treasured) species in NZ (Futter, 2011). Toheroa feature large in mātauranga Māori (traditional Māori knowledge) and have been known by many names, including moeone, tohemanga, taiwhatiwhati roroa, tupehokura, and roroa (Hamilton, 1908; Murton, 2006; Ross *et al.,* 2018a). They were revered by Māori, who often made long journeys purely to gather toheroa (Williams, 2004). They were typically shucked, then dried or smoked (Stace, 1991). Many Māori consider toheroa to be a part of their whakapapa (genealogy), valued like a member of the family, eliciting strong kaitiakitanga (guardianship) (Smith, 2013). Extensive populations of toheroa were once present on exposed west-facing surf beaches of Taitokerau (Northland), the Kāpiti-Horowhenua coast, and on the south coast of Murihiku (Ross *et al.,* 2018b; Williams *et al.,* 2013a) (Figure 1). The largest North Island populations have historically been Te Oneroa a Tohe (Ninety Mile Beach), Ripiro (Baylys or North Kaipara Beach), Muriwai, and the Kapiti-Horowhenua Beaches (Akroyd *et al.,* 2002). In the South Island, significant populations were found at Oreti Beach and Bluecliffs in Te Waewae Bay (Redfearn, 1974).

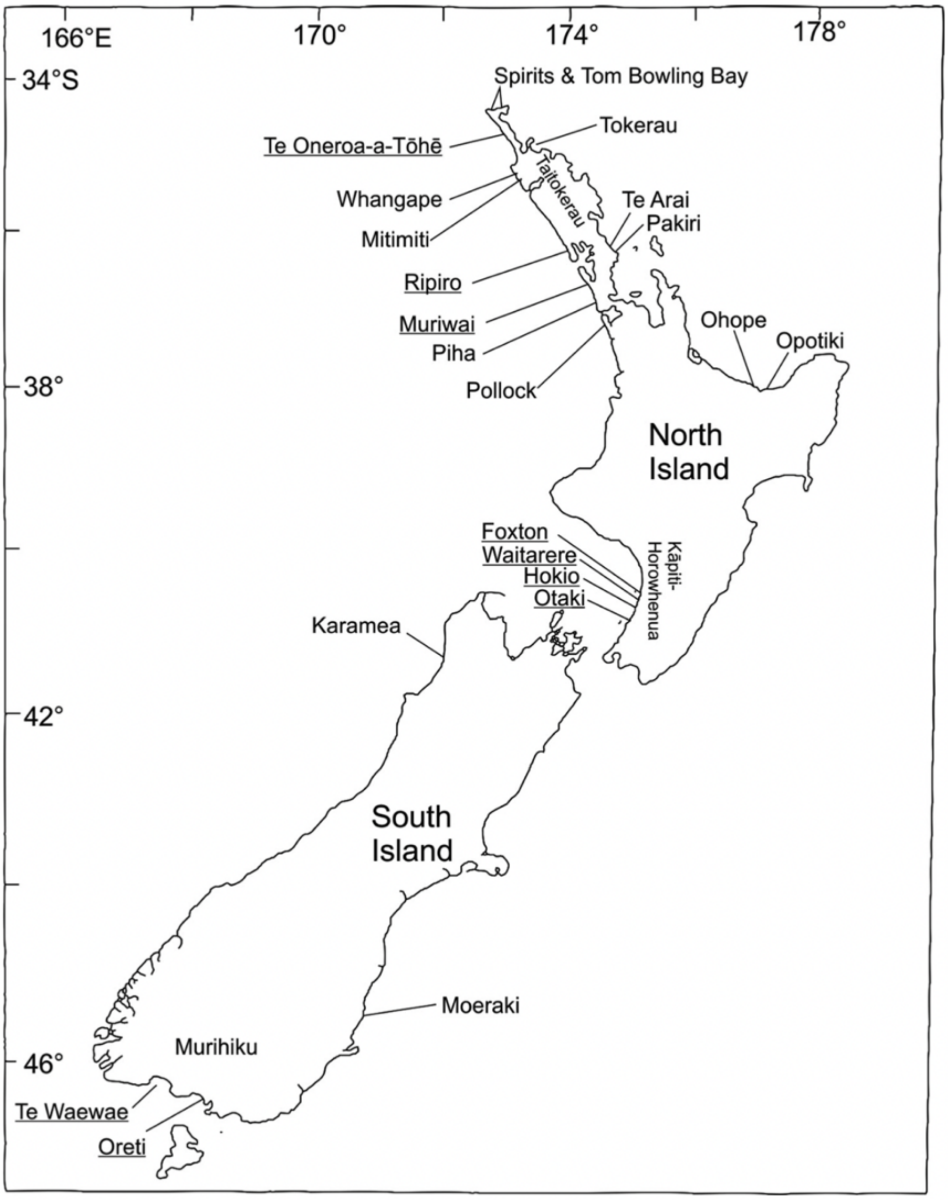


Figure 1: The distribution of toheroa in New Zealand, major populations are underlined. Figure reproduced from: Ross *et al.* (2018a).

Toheroa are bivalve molluscs endemic to NZ from the Mesodesmatidae family of the order Venerida (Redfearn, 1974). They are the largest clam species in NZ. Other species of the *Paphies* genus include; pipi (*Paphies australis*), tuatua (*Paphies subtriangulata*), and the southern deep water tuatua (*Paphies donacina*) (Ross *et al.,* 2018a). Of the four species, the pipi is the easiest to differentiate morphologically, with a pronounced elliptical shell shape (Sidwell, 2002). In comparison, toheroa and tuatua have similar morphology and are often misidentified. Tuatua shells are angular, whereas toheroa are ovately wedge-shaped with pronounced curvature along both the dorsal (either side of the hinge) and the ventral margin (Figure 2) (Redfearn, 1974; Sidwell, 2002).

Figure 2: Left – Juvenile toheroa and tuatua that show shell morphological differences. Right – Adult toheroa with foot (or tongue) extended. Animals found on Ripiro Beach in February 2022. Photo by author.

Toheroa have valves that do not completely close, the gaps between valves are covered by mantle folds which can appear pink in some individuals (Rapson, 1954; Redfearn, 1974). They are generalist suspension feeders, consuming organic debris and phytoplankton from the water column (Cassie, 1955). They have two independent siphons which are long compared to the other members of the *Paphies* genus (Rapson, 1952). The siphons are extendable, highly contractable, and either extend slightly above the surface or sit flush with the stratum during feeding (Gadomski, 2017) (Figure 3). The outer aperture of the larger inhalant siphon is encircled by complex tentacles which serve as a filter to inhibit the passage of larger undesirable particulate matter (Gadomski, 2017). Water and food particles are drawn into the mantle cavity for sorting (Rapson, 1952). The role of the smaller exhalent siphon is to discharge deoxygenated water, faeces, and non-digestible or excess food particles bound by mucous (pseudofaeces) (Gadomski, 2017). Toheroa have a large muscular and triangular foot (or tongue) which enables them to burrow rapidly into the sand (Redfearn, 1974). Adult individuals can burrow to depths greater than 20 cm below the surface (Kondo & Stace, 1995).

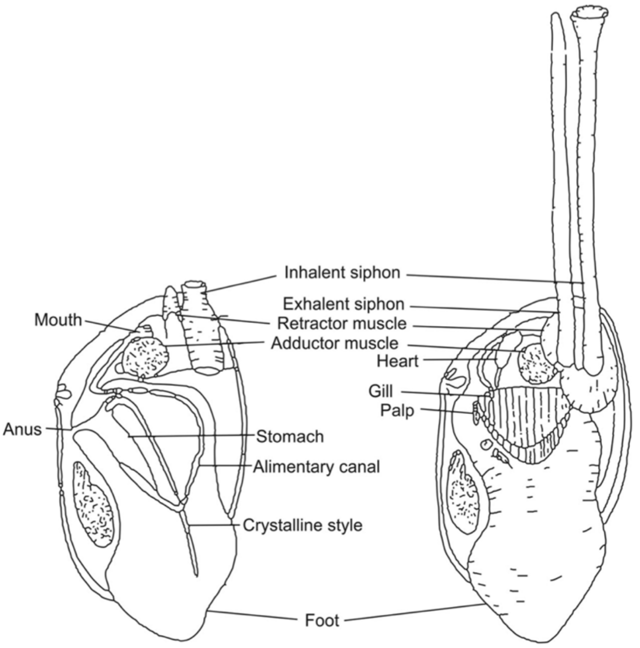


Figure 3: The internal anatomy of toheroa (*Paphies ventricosa*), with the left valve and mantle removed. Figure reproduced from Rapson (1952).

In the past, northern toheroa were known to grow to sizes of up to 180 mm (Cook, 2010) but rarely exceed 100 mm in the present day (Williams *et al.,* 2013a). Southern toheroa have smaller populations but have been known to reach lengths of up to 100-150 mm (Ross *et al.,* 2018a). Other members of the *Paphies* genus, like *P. donacina* can grow to 110 mm, *P. subtriangulata* to 80 mm, and *P. australis* to 100 mm (Cook, 2010). Subfossil archaeological evidence found at many northern beaches left by early Māori present large and well-preserved shell middens, bearing testimony to the popularity of toheroa (Figure 4) (Hayward & Records, 1975; Morrison & Parkinson, 2008). Some middens and pre-human shell deposits contain very large shells (commonly exceeding 150 mm), which are heavier and bulkier than any live animals recorded recently in the same locations (Morrison & Parkinson, 2008; Ross *et al.,* 2018a). Some believe these may be an extinct sub-species of toheroa, whereas others believe that modern toheroa no longer reach these sizes due to environmental changes (Cassie, 1955; Williams *et al.,* 2013a). Like many bivalves, toheroa have patchy distributions that vary spatially and temporally. They are known to primarily inhabit the intertidal zone (Redfearn, 1974). There has been speculation that subtidal populations exist which may contain larger individuals; however, there is no direct evidence to support this (Morrison & Parkinson, 2008).

Figure 4: Archaeological shell middens found on Ripiro Beach in February 2022. Photo by author.

1.3.2 Reproduction and recruitment

Toheroa are gonochoristic, they have separate sexes and sex does not change during an individual's lifetime (Smith, 2003). However, some hermaphrodite individuals have, on rare occasions, been observed (Redfearn, 1974). They have distinct stages of gonad development and sexual maturity varies by age, size, and location (Redfearn, 1974; Ross *et al.,* 2018a). Toheroa reproduction is achieved through broadcast spawning, gametes (both eggs and sperm) are released into the water column for external pelagic fertilisation (Futter, 2011; Redfearn, 1974). Similar to other temperate bivalves, environmental cues such as changes in water temperature and food abundance are thought to be the primary influence for spawning patterns (both onset and duration) (Redfearn, 1974). During a single spawning event, adult females are thought to release 15-20 million eggs (Redfearn, 1982; Ross *et al.,* 2018a). Toheroa larvae are planktonic, exhibiting varying pelagic larval durations across different locations (Ross *et al.,* 2018a). Northern toheroa have a duration of about 3 weeks, whereas the pelagic period of southern toheroa is thought to be nearer to 6-7 weeks (Gadomski *et al.,* 2015; Redfearn, 1982). Embryonic morphology and larval stages for toheroa have been described in depth by Gadomski *et al.* (2015) and Redfearn (1982). After the pelagic period, larvae settle out of the water column and onto the swash zone, where they metamorphose into juvenile spat (Redfearn, 1974).

1.3.3 Settlement and distribution

Settlement defines the phase when spat transition from the pelagic zone to the benthos. For toheroa, this typically occurs two months after the spawning period when they have reached 2 mm in length (Redfearn, 1974; Williams *et al.,* 2013a). During any tidal stage, juvenile spat are collected by wavefronts and carried up the beach by the surf before being deposited onto the shore (Redfearn, 1974). Spat then dig themselves into the substrate using their foot, utilising the period when each wave recedes from the shore (10-20 mm depth) (Redfearn, 1974; Ross *et al.,* 2018a). Initially, they struggle to maintain solid purchase within the sediment, frequently being resuspended from the substrate due to the turbulent surf (Redfearn, 1974). Sometimes toheroa can anchor themselves to benthos by attaching byssus thread (secreted filament bundles) to sand grains (Williams *et al.,* 2013a). It is widely believed that new recruits inhabit the upper littoral near the high tide mark and progressively move further down the beach as they grow in length (Redfearn, 1974).

1.3.4 The decline of toheroa

The discovery of toheroa by Pākehā (New Zealanders of European descent) ultimately caused their demise. In the late 1800s, recreational fishery grew substantially across NZ (Murton, 2006; Ross *et al.,* 2018a). The early 1900s saw the rise of commercial harvesting operations established near the west coast settlement of Te Kopuru (Southern end of Ripiro Beach), and at Ninety Mile beach (Trego-Hall *et al.,* 2020; Williams *et al.,* 2013a; Williams *et al.,* 2013b). Canned toheroa quickly became widely desired and renowned for their taste. Whole tongues and the favoured ‘Toheroa Soup’ was an internationally exported delicacy (Cassie, 1955; Murton, 2006). Māori tribes (iwi) and subtribes (hapū) of the region expressed concern regarding the wasteful method and depletion of toheroa beds, but they were largely rebuffed (Murton, 2006; Trego-Hall *et al.,* 2020). From 1913, toheroa fisheries regulations were implemented incrementally (Murton, 2006). By the mid-1900s, toheroa populations had reduced and were no longer viable (Stace, 1991). Commercial operations largely ceased by 1969, with the last cannery closed in 1971 (Redfearn, 1974; Williams *et al.,* 2013a). With toheroa populations failing to recover despite these management steps, recreational harvest faced heavy restrictions, and closure soon followed in the period through 1971 to 1980 (Williams *et al.,* 2013a; Williams *et al.,* 2013b). Toheroa management has been under the Customary Fisheries Regulations since 1996, with the collection of toheroa now almost entirely prohibited (Futter, 2011). Harvesting of toheroa is now restricted to customary take by Māori, with Tangata Tiaki (Māori customary fisheries appointees) authorising permits mainly for tangi (funerals) and hui (meetings) (Futter, 2011; Ross *et al.,* 2018a). Despite being protected for more than 40 years, toheroa have failed to return to their former abundance (Williams *et al.,* 2013a; Ross *et al.,* 2018a).

1.3.5 Potential aquaculture applications for toheroa

The failure of toheroa populations to recover, despite provided protections, has prompted discussions of alternative restoration measures, including the potential for hatchery-reared spat to be used for reseeding the toheroa beaches (Newcombe *et al.,* 2015; Ross *et al.,* 2018a). In the North, there has been some evidence that recruitment is not the limiting factor for recovery, but is actually attributed to post-settlement juvenile mortality (Ross *et al.,* 2018a). If so, there is potential for toheroa spat to be harvested from the beach the same way mussel spat is, and then on-grown in hatchery facilities. There has been some interest from iwi and hapū in whether toheroa spat can be implemented into the aquaculture industry (Ross *et al.,* 2018a). This opportunity has the potential to be culturally, ecologically, and commercially valuable. Propagation of wild-sourced toheroa spat could liberate an available resource, and the research required could fill knowledge gaps of the intricate underlying ecology of toheroa (Yongqiang *et al.,* 2019).

1.4 Research significance

For such an iconic species, there is relatively little known about the ecology of toheroa. The comprehensive research that forms the foundation of known toheroa ecology was conducted around the time that populations were declining in the 1950s - 1970s (Cassie, 1951; Cassie, 1955; Rapson, 1952; Rapson, 1954; Redfearn, 1974; Redfearn, 1982). However, no available literature captures the current recruitment dynamics of post-settlement juvenile toheroa. Typically, toheroa-centric literature includes surveys conducted for stock assessment, with adult toheroa (~75 mm) as the primary target (Williams *et al.,* 2013a). More recent research has emerged that aims to understand the underlying factors inhibiting recovery (Bennion *et al.,* 2022; Cope, 2018; Gadomski, 2017; Gadomski *et al.,* 2015; Vallyon, 2020). The purpose of this research project is to generate new knowledge that will inform discussions about the viability of toheroa aquaculture and build upon existing toheroa ecology in general. Specifically, juvenile recruitment. There is a particular need to better understand the dynamics of toheroa recruitment and post-settlement growth and mortality. This will inform discussions around the viability of wild spat harvest from an aquaculture perspective and the ethics of harvesting spat of a struggling species from both a conservation and a cultural perspective.

1.5 Thesis aims and structure

The aim of this thesis is to investigate the dynamics of post-settlement juvenile toheroa recruitment on Ripiro Beach and the potential applications for aquaculture. In order to do this, we first need to develop an effective survey methodology that targets juvenile toheroa spat before conducting surveys to quantify distributions spatially and temporally. We want to understand how juveniles are distributed across and along the littoral zone, and within different habitats present on the beach. From these survey results, we will be able to estimate the number of juvenile toheroa recruiting to the beach and assess rates of natural mortality and aquaculture viability. Lastly, I will look at different methods that could be used to transport juvenile spat from the beach to an aquaculture facility.

1.5.1 Thesis structure

In **Chapter 2,** I conduct pilot surveys that aim to develop a sampling methodology optimised to target juvenile toheroa. I investigate how density and shell size changes with increasing sediment depth. I also investigate how juveniles are distributed along the littoral zone.

In **Chapter 3,** I conduct a survey to investigate the spatial and temporal distribution patterns of juvenile toheroa spat on Ripiro Beach. I utilise the methodology developed in Chapter 2 to further investigate how juveniles are distributed along the littoral zone. I also investigate how abundance is affected by different environmental habitats and over the recruitment season.

In **Chapter 4,** I aim to estimate the population size of juvenile toheroa recruitment on Ripiro Beach. Population estimation was categorised over time scales, habitat types, and size cohorts. Population estimates were used to investigate juvenile mortality rates and asses the viability of wild spat harvest for aquaculture.

In **Chapter 5,** I investigate different transportation methods for live toheroa by analysing burrowing behaviour as a response to handling stress. The aim is to understand how toheroa react to different treatments and assess the best method for transporting wild harvested toheroa spat from the beach to potential aquaculture facilitates.

In **Chapter 6,** I discuss the overall findings and conclusions of the research in this thesis. I summarise my thoughts on the viability of wild spat harvest for aquaculture, the potential limitations of my thesis and my recommendations for future research.

1.5.2 Permits

My thesis is a part of a much larger body of research, my supervisor Dr Phil Ross has obtained a special permit (SP706-2) from the Ministry of Primary Industries to gather toheroa for research purposes. Dr Ross has also been working in collaboration with and is supported by the local iwi and kaitiaki (Te Roroa and Te

Uri o Hau) for research on Ripiro Beach regarding toheroa. An animal ethics application was submitted to the University of Waikato Animal Ethics Committee, but no permission was needed for the collection of an invertebrate.

2 Chapter 2 – Pilot surveys

2.1 Introduction

Bivalve molluscs are highly productive marine invertebrates and are distributed anywhere from the high-intertidal to the deep ocean floor (Ripley & Caswell, 2008). Broadcast spawning bivalves produce an abundance of larvae to prepare the population for unpredictable adverse conditions (Andresen *et al.,* 2014). High spat mortality is often considered symptomatic of juvenile bivalve recruitment (Ripley & Caswell, 2008). Regarding annual recruitment variation, the quantity of offspring is not always considered proportional with increasing stock size of reproductively fit adults (Andresen *et al.,* 2014). In high-dispersal taxa, such as marine broadcast spawners with a pelagic larvae phase, a high degree of variation in recruitment can be expected from year to year (Luttikhuizen *et al.,* 2003). Researching spawning and recruitment dynamics can help us understand the responses of populations to stochasticity (Ripley & Caswell, 2008), which can lead to the development of effective conservation and species preservation strategies (Asadi *et al.,* 2018).

Juvenile toheroa spat typically settle onto the shore two months after the spawning period when they have reached 2 mm in length (Redfearn, 1974). It is widely believed that new toheroa recruits inhabit the upper shore and progressively move further down the beach as they grow in length (Redfearn, 1974; Williams *et al.,* 2013a). Smith (2003) observed that juvenile high-density clusters (<32 mm shell length) often inhabited comparatively higher shore zones above adult beds. Additionally, Redfearn (1974) also reported that dense juvenile populations tend to be separated from the adult population forming dense concentrations on the high-tide mark, In contrast, no such spatial relationship has been consistently observed, toheroa from all cohorts have been seen distributed together (Beentjes, 2010b; Williams *et al.,* 2013a). Māori lore in Taitokerau defines two story's regarding toheroa reproduction and settlement; spat are born into the endemic dune grass pingao (*Ficinia spiralis*) (seeds are shaped like toheroa spat) and spinifex (*Spinifex sericeus*) (Stace, 1991). In another story, on the highest of tides, spat are carried up shore with the surf and deposited on the dunes where the juveniles seek refuge and grow in the nursery habitat of the grasses (Stace, 1991). Then, toheroa are transported in spring onto juvenile beds. Spat held within the pingao are blown onto the upper-intertidal, and cross-shore winds transport spat held within the tumbleweed-like seed heads of the spinifex across the beach through numerous streams along northern beaches (Ross *et al.,* 2018a; Stace, 1991).

Monitoring the distribution and abundance of toheroa populations has been carried out for more than 70 years. However, no research has been conducted regarding the distribution dynamics of juvenile toheroa. The majority of the available information regarding toheroa surveys indicates the use of littoral stratification with systematic transect design. These surveys allow for good coverage in regard to the distribution of the population along the intertidal zone. Such designs have proved successful on Ripiro Beach (Akroyd *et al.,* 2002; Akroyd *et al.,* 2008; Williams *et al.,* 2013a), Ninety Mile Beach (Morrison & Parkinson, 2008; Williams *et al.,* 2013a), Muriwai (Akroyd *et al.,* 2008), and some southland surveys (Beentjes, 2010a; Beentjes, 2010b). However, no such survey has been conducted that targets juvenile recruits <30 mm, typical surveys excavate the sediment surface without sieving the contents leaving a significant proportion of the population unrecorded. It is unknown if toheroa populations have continued to decline due lack of juvenile recruitment. In order to approach the subject of aquaculture, we must first understand the underlying ecology of juvenile spat. At present, no literature has quantified how spat are distributed across the littoral region. Limited information is available regarding the burrowing depth of juvenile spat, most observations are made anecdotally when surveying adult populations (Redfearn, 1974; Rapson, 1952). Conventional knowledge states that spat form dense aggregations near high tide or within the dunes. The first step in quantifying recruitment patterns for aquaculture purposes is to design an effective survey technique that accurately captures the population.

2.1.1 Aims and research purpose

The purpose of this research is to conduct pilot surveys to fill knowledge gaps regarding the spatial distribution dynamics of post-settlement juvenile toheroa. I aim to understand how increasing sediment depth affects abundance and shell size. I aim to test the hypothesis that juveniles are separated from the adult population, forming discrete bands adjacent to the dunes. The findings from this research will be used to establish an effective survey technique that aims to have wider implications for restoration and aquaculture purposes.

To do this the following research questions will be investigated:

(1) What are the distribution dynamics of juvenile spat abundance with increasing sediment depth?

(2) What are the distribution dynamics of shell size with increasing sediment depth?

(3) Do juvenile spat form beds along the high tide zone, separate from the adult population?

2.2 Methods

2.3 Study location – Ripiro Beach

Ripiro Beach (Dargaville) has long since been recognised as a toheroa hotspot both historically and present day. It is known to yield some of the highest recorded abundances of toheroa (Akroyd *et al.,* 2008). For this reason, many toheroa-centric studies have been conducted on Ripiro Beach (Akroyd *et al.,* 2002; Akroyd *et al.,* 2008; Cope, 2018; Redfearn, 1974; Vallyon, 2020; Williams *et al.,* 2013a). Ripiro is a recognised state highway, and at 72 kilometres, it is the longest drivable beach in NZ (Redfearn, 1974). Ripiro is situated on the North Island's west coast in the Taitokerau region, stretching from Maunganui Bluff in the north to Kaipara North Head (Poutō peninsular) in the south.

With a fairly flat profile, Ripiro is a dissipative beach with a littoral width varying considerably between 100 – 300 m and is orientated in a North West direction (Williams *et al.,* 2013a). The exposed nature of the coastline to the Tasman Sea creates continuous wave action with prevailing winds and swells from the southwest, resulting in a highly turbulent surf zone (Redfearn, 1974; Williams *et al.,* 2013a). Swells from the Southern Ocean drive longshore drift to the north, but is also known to sometimes switch to the southeast (Cope, 2018). The sedimentology consists of hard-packed fine sand, and the beach is backed by large sandstone cliffs reaching heights of up to 150 m (Figure 5) (Williams *et al.,* 2013a). On the Poutō Peninsula in the south, cliff faces give way to ephemeral wetlands in the foredunes (Champion & Reeves, 2008), with a well-established pine forest plantation (*Pinus radiata*) in the catchment (Farnsworth *et al.,* 1975). Kaitiaki (guardians) from the region have noticed the disappearance of toheroa beds in areas adjacent to commercial forestry operations (Williams *et al.,* 2013b).

Figure 5: Sandstone cliffs and stream outlet on Ripiro Beach in February 2022. (Drone photo by E. Russell).

Ripiro Beach undergoes erosional periods where heavy wave action results in the movement of sand to offshore bars (Cope, 2018). Gentle undulating contours are created along the coast by intersecting embayments, streams, and small creeks, which are usually laterally adjoined by encroaching ridges from cliff faces (Cassie, 1955; Williams *et al.,* 2013a). Freshwater outflow onto the shore creates lowered depressions on the littoral zone which enables the sand to remain saturated during low-tide, the greatest densities of toheroa are habitually found on these damp patches (Cassie, 1955).

Pilot surveys were conducted on an area of Ripiro known as Baylys Beach (S 35°57.358', E 173°44.622'). Baylys Beach is situated within close proximity to a small urban settlement that is about 13 km from Dargaville (Figure 6). This site has a consistent stream outlet onto the beach, it is backed by tall cliffs on either side of the gully with houses and pasture extending beyond.

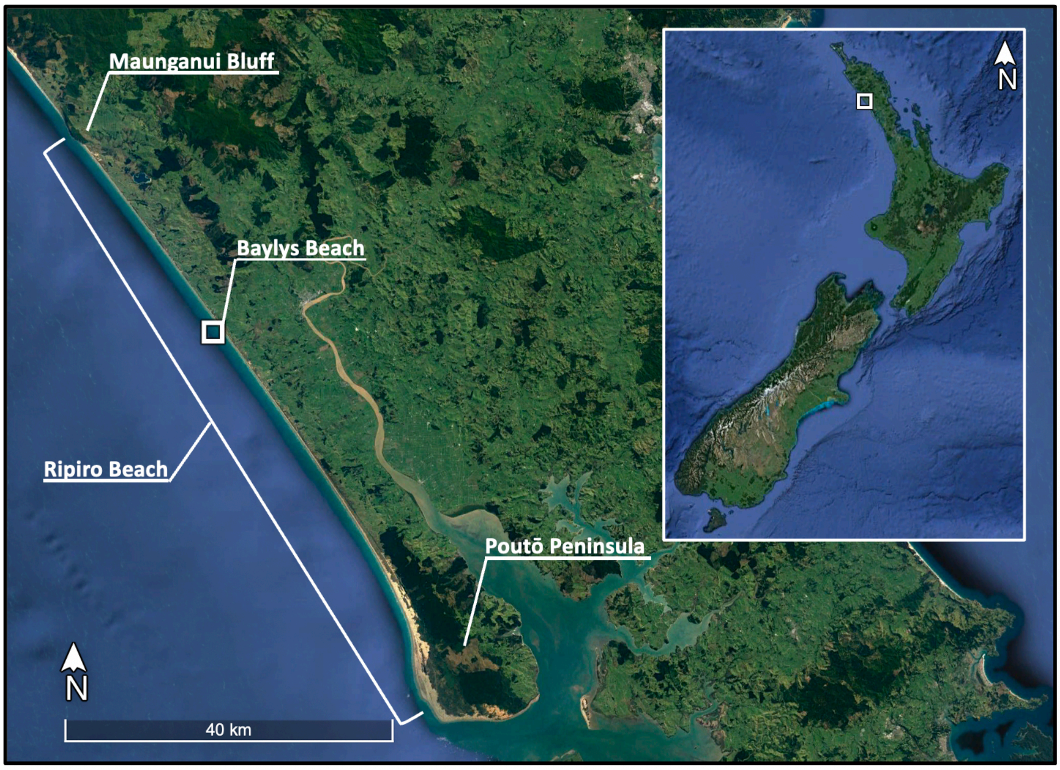


Figure 6: Map displaying the section of Ripiro Beach where pilot surveys were conducted. Image retrieved from Google Earth.

2.3.1 Sampling methodology

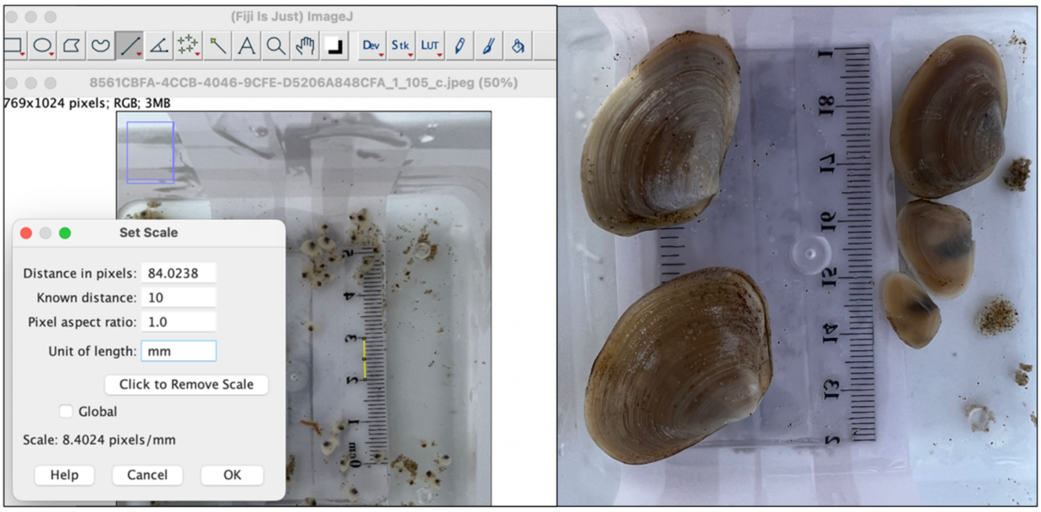
Fieldwork was conducted on Baylys Beach in February 2022. Preliminary sampling involved excavating the sediment surface on a known toheroa bed at four different depths, 0-2 cm, 2-5 cm, 5-10 cm, and 10-15 cm. Observations obtained from this informed the vertical zonation juveniles tend to inhabit within the substrate; depth parameters were then optimised for surveying juvenile spat. Quantifying vertical zonation was determined using substrate stratification, consisting of three margins, 0-2 cm, 2-5 cm, and 5-10 cm. Three replicate quadrats of 0.5 m x 0.5 m (0.25 m^2) were placed randomly on the centre of the bed. The sand was excavated with flat-end plastic shovels and sieved in water through a 1 mm mesh sieve (Figure 7). Due to the small size of toheroa spat, it was not a suitable choice to attempt to measure and count them on-site, the task would be too time-consuming, and you would lose the battle with the incoming tide. Instead, the spat were transferred into clear plastic containers with rulers attached underneath. Photos were taken from above the containers for later analysis.

To define littoral zonation, as typical with other toheroa surveys on Ripiro Beach, due to the wide littoral width, a transect was placed perpendicular to the shore to encompass the full tidal range (low tide – high tide). Quadrats were placed systematically along a 150 m stretch with 10 m intervals. Two depth margins were optimised from the depth stratification survey, 0-2 cm and 2-5 cm. Plots were then sieved and analysed following the aforementioned method. All collected toheroa were returned to their sampled location.

Figure 7: Fieldwork conducted on Ripiro Beach in February. Photo by P. Ross.

2.3.2 Statistical Analysis

Toheroa length and abundance were determined post-field work using photo analysis software in Fiji ImageJ (Version 2.1.0/1.53c) (Schindelin *et al.,* 2012). The individual toheroa were counted manually using the ruler attached to the bottom of the containers to set a scale, pixel distance was automictically converted into millimetres (Figure 8). RStudio (Version: 2021.09.0) was used to test the effect that sediment depth had on abundance and shell size. The toheroa mean size (mm) and density (0.25 m^2) data for each depth margin were tested for normality using the Shapiro-Wilk normality test, and all assumptions were met. Analysis of variance (ANOVA) were performed; the independent factor was sediment depth with either three levels (0-2 cm, 2-5 cm, 5-10 cm) or two levels (0-2 cm and 2-5 cm). The dependent variables were density and shell size respectively. RStudio (Version: 2021.09.0) was also used for running Tukey HSD contrasts to determine statistically significant relationships between sediment depth, abundance, and size. The accepted level of significance for all tests was $p \leq 0.05$. Descriptive tables and graphical data visualisation were generated in Microsoft Excel and RStudio. Bar charts and box plots were formulated to show the difference in shell size and density with increasing sediment depth and along the littoral zone.



Distance in pixels: 84.0238
Known distance: 10
Pixel aspect ratio: 1.0
Unit of length: mm
☐ Global
Scale: 8.4024 pixels/mm

Figure 8: Photos taken of toheroa collected on Ripiro Beach that were later analysed in Fiji ImageJ.

2.4 Results

2.4.1 Depth stratifications

On Baylys Beach, the three plots sampled randomly on the bed yielded significant results. The three depth stratifications (0-2 cm, 2-5 cm, 5-10 cm) proved fundamental for portraying distribution patterns of vertical zonation in the benthos. Increased depth had a negative effect on toheroa abundance (Figure 9). The mean density of toheroa per 0.25 m^2 in the top 0-2 cm was 99.67 (± 21.8), at 2-5 cm it was 6.33 (± 4.5), and at 5-10 cm it was 1 (± 0) ($n = 321$) (Table 1). The 0-2 cm margin contained 93% of the sampled population, the next layer at 2-5 cm contained only 6.3 %, and the 5-10 cm margin held just 0.94 %. ANOVA analysis determined that only the 0-2 cm margin had a significant effect on density ($p < 0.01$), whereas the 2-5 cm and 5-10 cm margins were not significant ($p > 0.05$) (Table 2). A Tukey HSD comparison depicted strong relationships between 0-2 cm - 2-5 cm and 0-2 cm - 5-10 cm depths ($p < 0.01$) (Table 2). However, the interaction between 2-5 cm - 5-10 cm was deemed not significant ($p > 0.05$).

Conversely, increasing depth had a positive effect on shell size (Figure 9). Mean shell size increased from 4.17 mm (± 0.1) (0-2 cm) to 6.48 mm (± 4.47) (2-5 cm) to 78 mm (± 6.86) (5-10 cm) (Table 1). However, it should be noted that only one individual was found in each 5-10 cm replicate. ANOVA analysis for the mean shell size and depth relationship showed that only the 5-10 cm margin was statistically significant ($p < 0.01$), whereas 0-2 cm was not ($p > 0.05$), and 2-5 cm was nearly significant ($p = 0.055$) (Table 2). A Tukey HSD comparison confirmed this by stating that the interaction between 0-2 cm – 2-5 cm was not statistically significant ($p > 0.05$). Furthermore, both 0-2 cm – 5-10 cm and 2-5 cm – 5-10 cm interactions were highly significant ($p < 0.01$). These depth stratifications confirm a strong correlation between lowered density and increasing size with depth (Figure 10).

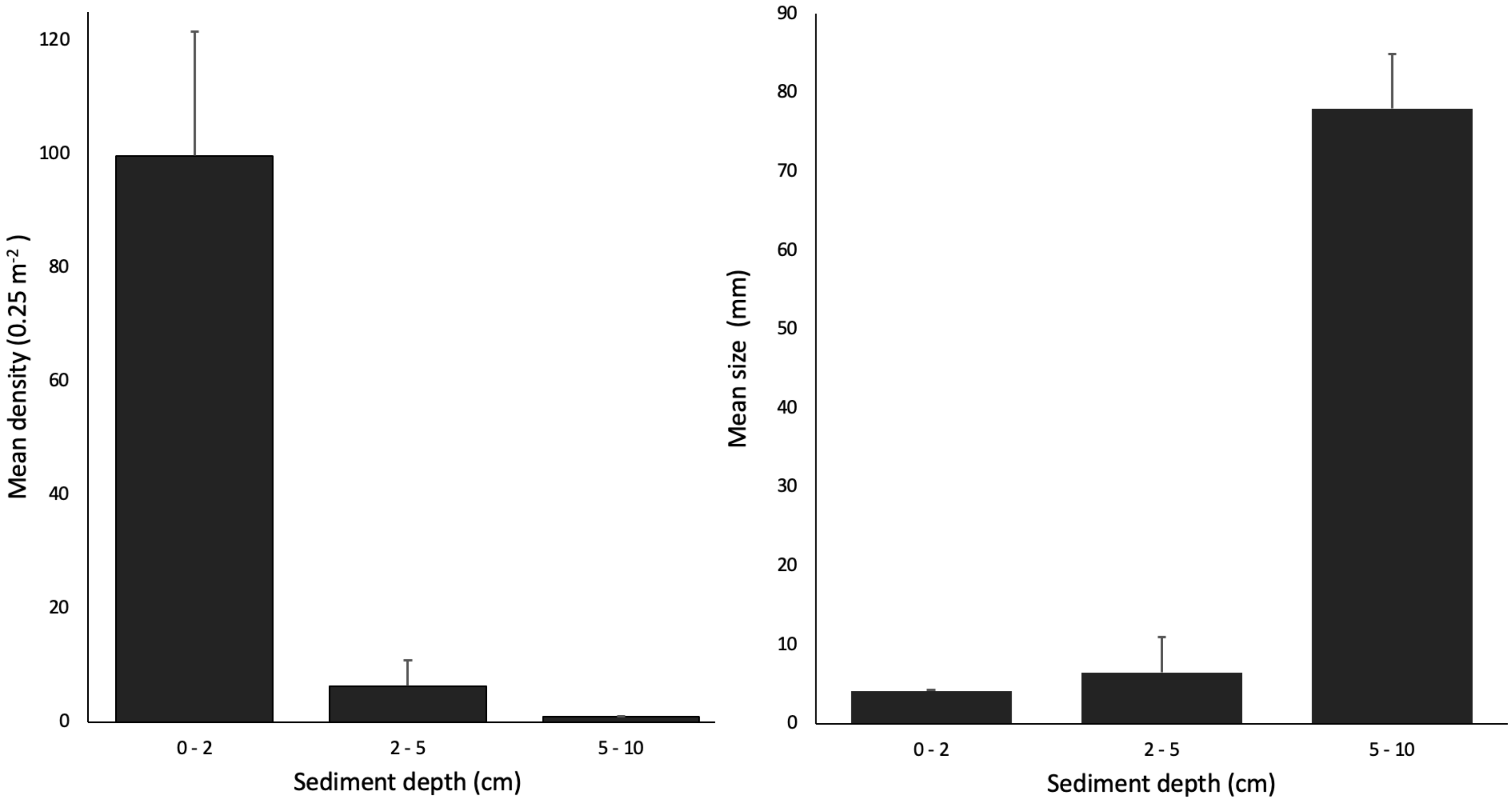


Figure 9: Left - Mean density of toheroa per 0.25 m^2 quadrats at three different depths. Right - Mean toheroa shell size per 0.25 m^2 quadrats at three different depths. Error bars represent standard deviation (*n=321*).

Table 1: Summary of mean density (0.25 m^2) and mean shell size (mm) data from the three depth stratifications on Baylys Beach in February ($n = 321$).

Mean shell size (mm)			
	Sediment Depth		
	0-2 cm	2-5 cm	5-10 cm
Plot 1	4.29	11.61	83.93
Plot 2	4.1	3.44	70.48
Plot 3	4.12	4.39	79.56
Mean	4.17	6.48	78
SD (σ)	0.1	4.47	6.86
SE (±)	0.06	2.58	3.96
Density (0.25 m^2)			
	Sediment Depth		
	0-2 cm	2-5 cm	5-10 cm
Plot 1	104	6	1
Plot 2	119	11	1
Plot 3	76	2	1
Mean	99.67	6.33	1
SD (σ)	21.8	4.5	0
SE (±)	12.6	2.6	0
Percentage of sampled population (%)	93.15	5.92	0.93
Total Abundance	321		

Table 2: Summary of ANOVA and Tukey HSD comparisons for the three depth stratifications on Baylys Beach in February ($n = 321$).

ANOVA		
	Depth	***p*-value**
Density (0.25 m^2)	0-2 cm	<0.01**
	2-5 cm	>0.05
	5-10 cm	>0.05
Shell Size (mm)	0-2 cm	>0.05
	2-5 cm	0.055 *
	5-10 cm	<0.01**
Tukey HSD		
Density (0.25 m^2)	0-2 cm - 2-5 cm	<0.01**
	0-2 cm - 5-10 cm	<0.01**
	2-5 cm - 5-10 cm	>0.05
Shell Size (mm)	0-2 cm - 2-5 cm	>0.05
	0-2 cm - 5-10 cm	<0.01**
	2-5 cm - 5-10 cm	<0.01**

* Nearly significant, ** Significant

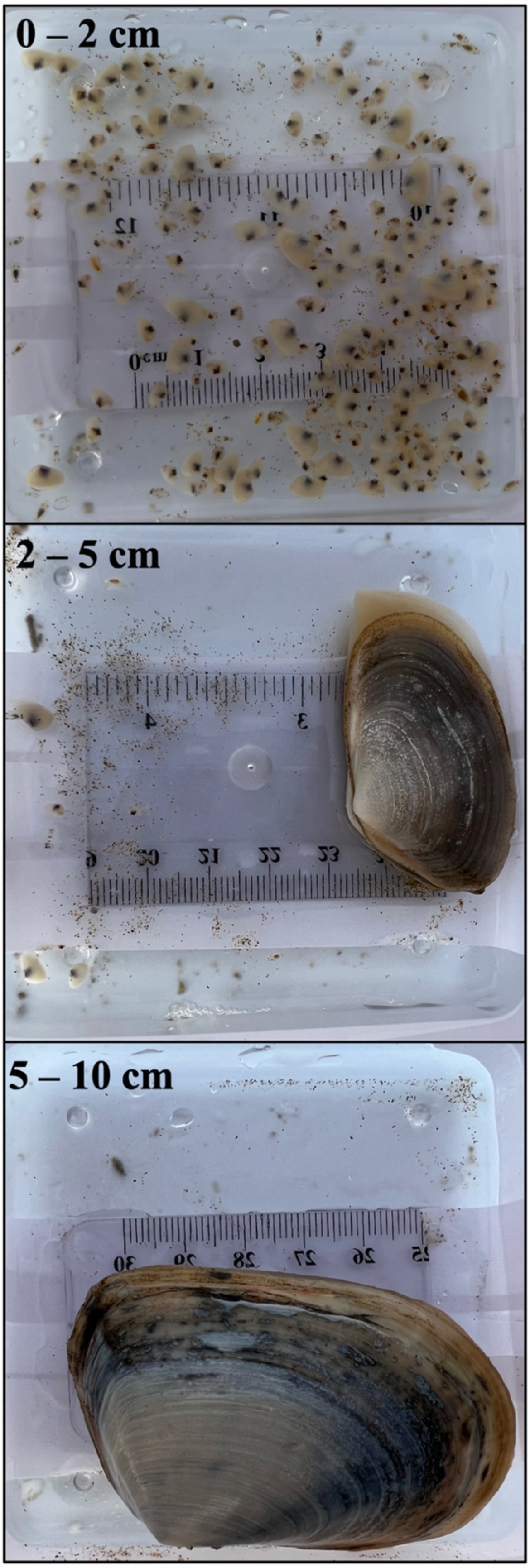


Figure 10: Example quadrat from the three different sediment depth stratifications on Baylys Beach.

2.4.2 Littoral distributions

The two sediment depth stratifications along the whole transect on Baylys Beach in February portrayed the same distribution patterns. The top 0-2 cm yielded 1,217 toheroa, with only 109 in the 2-5 cm margin (*n*=1,326) (Table 3). The 0-2 cm margin had a mean density of 76.1 (± 70) per 0.25 m^2, compared to 6.88 (± 7.79) per 0.25 m^2 for 2-5 cm margin (Figure 11). The 0-2 cm margin contained 91.78 % of the sampled population, with only 8.2 % in the 2-5 cm margin. ANOVA analysis for density distributions between the two depths was significant ($p < 0.01$). In contrast to the hypothesis that juveniles are limited to the high tide and dunes, they were distributed along the entire littoral width. There appeared to be a strong bimodal distribution at both depths, with peak densities situated on either side of the transect centre (mid-tide). The highest recorded density was situated just above mid-tide. The mean shell size increased from 3.84 mm (± 2.79) to 5.89 mm (± 6.78) with increasing sediment depth (0-2 cm to 2-5 cm) (Table 4) (Figure 12). ANOVA analysis for mean toheroa shell size between the two depths was significant ($p < 0.05$).

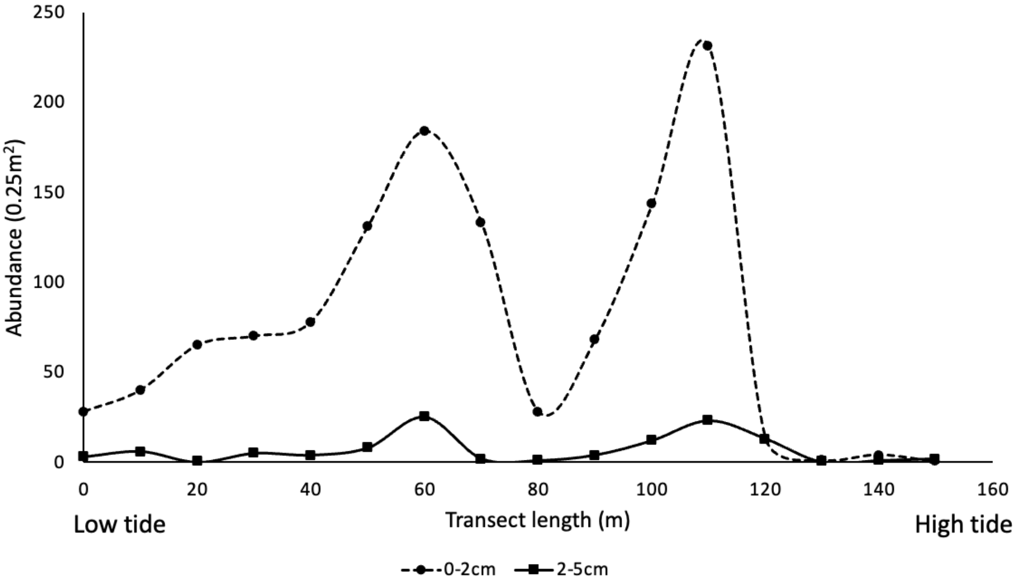


Figure 11: Line graph representing significant difference ($p < 0.01$) in the density of toheroa per 0.25 m^2 at different sediment depths along the transect. The density of toheroa is higher in the top 0-2 cm (*n=1,326*).

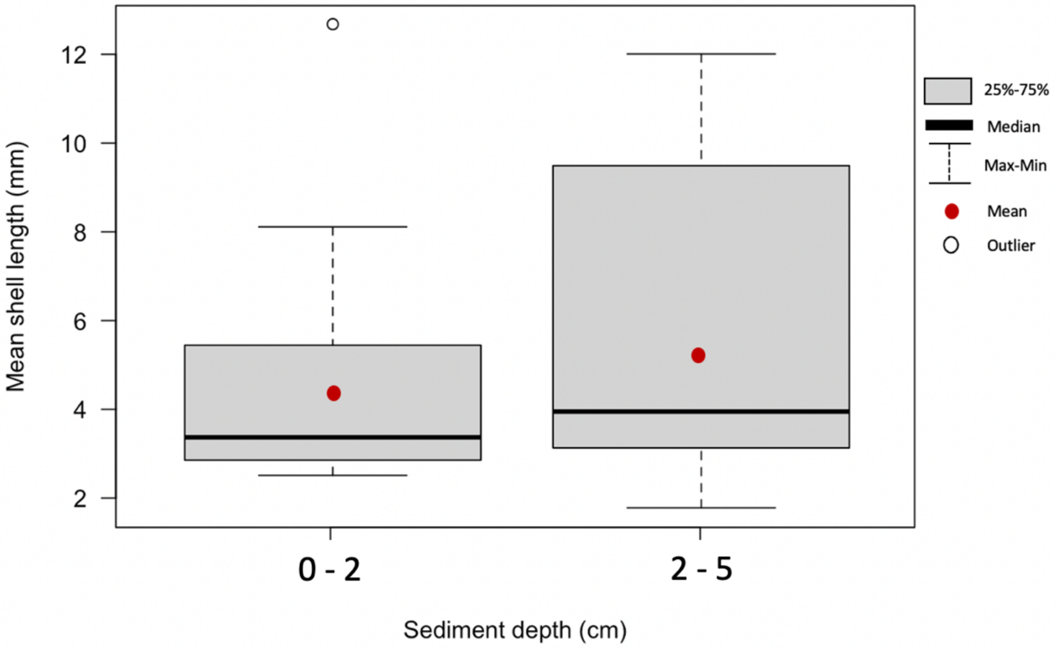


Figure 12: Box plot representing significant ($p < 0.05$) difference in the median shell length of toheroa per quadrat (0.25 m^2) at different sediment depths (*n=1,326*).

Table 3: Summary of mean density (0.25m^2) data obtained from depth stratifications on the transect on Baylys Beach in February (*n=1,326*).

Depth	Count	Mean Density (0.25 m^2)	SD(σ)	SE (±)	Max (0.25 m^2)	Min (0.25 m^2)	Percentage of population (%)
0-2cm	1,217	76.1	70	17.5	232	0	91.78
2-5cm	109	6.88	7.79	1.95	25	0	8.22

Table 4: Data summary of mean shell (mm) size from the depth stratifications on Baylys Beach in February (*n=1,326*).

Depth	Mean Size (mm)	SD(σ)	SE (±)	Max (mm)	Min (mm)
0-2 cm	3.84	2.79	0.08	31.623	1.001
2-5 cm	5.89	6.78	0.65	42.29	1.302

2.5 Discussion

The aim of this chapter was to investigate the distribution of juvenile toheroa in order to establish a new methodology optimised for spat sampling. The pilot surveys proved fundamental for portraying juvenile toheroa distribution dynamics both along the littoral zone and vertically within the substrate. The depth stratifications conducted within the substrate portrayed a strong negative relationship between increasing depth and decreasing density for juvenile toheroa. The top 0-2 cm margin contained upwards of 90 % of the sampled population (92 % and 93 % respectively), and the decline in density between the 0-2 cm and 2-5 cm margins was abrupt. For the three-depth margin stratification, only the 0-2 cm margin was found to have a significant effect on density. Furthermore, the relationships between 0-2 cm – 2-5 cm and 0-2 cm – 5-10 cm were significant but 2-5 cm – 5-10 cm was not significant. The density distribution changes for the depth stratification (0-2 cm and 2-5 cm) along the whole transect was significant. This indicates that the density of juvenile toheroa is predominantly held within the top 0-2 cm of the substrate. This coincides with anecdotal comments from Redfearn (1974) and Williams *et al.* (2013a) for juvenile spat distributions. Additionally, Rapson (1952) observationally stated that juveniles appear to inhabit the top ¾ inches of sediment (1.9 cm). However, this is the first study to quantitively define substrate stratification for juvenile toheroa.

The depth stratifications also presented a strong relationship between sediment depth and shell size. The three-depth pilot survey (0-2 cm, 2-5 cm, and 5-10 cm) indicated that increasing depth is correlated with increasing shell size. However, even though abundance significantly declined with depth, size was less affected between the 0-2 cm and 2-5 cm margins. The 0-2 cm was not significant and the 2-5 cm was nearly significant. Whereas the population composition changed significantly by 5-10 cm, with only one large adult sampled per replicate. However, the insignificant result likely reflects the large adult shell size increase. For example, on the transect, where there were only two margins, the difference in the mean shell size between 0-2 cm and 2-5 cm was deemed significant. There was a mean difference of about 2 mm between the 0-2 cm and 2-5 cm depths. The high abundance of smaller toheroa likely indicates freshly settled recruits (~ 2 mm) on the surface that are unable to burrow deeper into the sediment. It could also represent bottleneck mortality of earlier spawned cohorts during the 0-5 mm growth period, thereby decreasing the population at 2-5 cm (Philippart *et al.,* 2003; Rapson, 1952; Redfearn, 1974). Bivalve burrowing depth is known to be proportional to shell size, larger adults and individuals with a higher body mass index occupy greater depths (Kranz, 1974). For example, field studies in Chesapeake Bay (USA) of three different bivalves (*Mya arenaria, Macoma balthica*, and *Macoma mitchelli*) found a tendency for larger individuals to be situated deeper in the sediment (Blundon & Kennedy, 1982).

The results from this study did not support the hypothesis that juvenile toheroa are limited to the dunes and high-tide zone. Spat were found along the entire intertidal. However, they displayed well-defined modes of high density on either side of the mid-tide, with peak density just above the mid-tide. These findings coincide with observations from Cassie (1951), who believed that there has been some evidence to cast doubt on the high-tide zone as the dominant habitat for juvenile toheroa. Additionally, observations made by Williams *et al.* (2013a) on Ripiro Beach found midlittoral adult beds containing all sizes of toheroa. However, this is the first study to investigate and quantify whether the traditional knowledge regarding littoral distributions is representative of actual populations. Observed littoral distribution patterns for juvenile toheroa from my research are summarised in Figure 13.

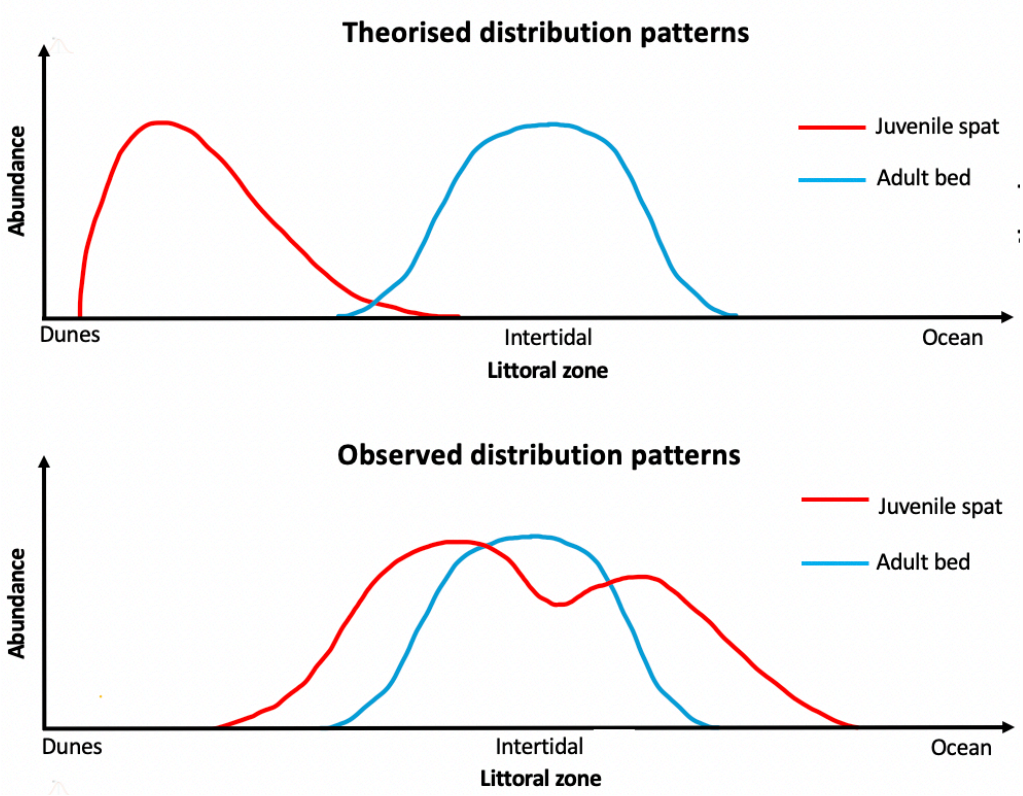


Figure 13: Schematic plots showing previously theorised distribution patterns compared to observations made on Ripiro Beach in 2022.

2.5.1 Conclusion

Prior to this study, current literature would have informed a survey technique that only sampled from the upper littoral. The results from my research now indicate that to capture the population accurately, the entire intertidal must be surveyed. For the first time, both vertical substrate stratification and littoral distribution dynamics of post-settlement juvenile toheroa spat have been defined. These findings can have wider-reaching implications for both conservation monitoring and aquaculture. Ripiro Beach has a wide littoral width, sieving quadrats can be a time-consuming task when it requires walking over 100 m from the sampling site to reach the water. This pilot survey helps limit unnecessary sieving, we know that spat predominantly inhabit the top 0-2 cm of sand, with the 0-5 cm margin capturing the entire population whilst excluding larger adults. Therefore, subsequent survey design on Ripiro Beach can be optimised for only the surface layers. Additionally, because they cover such a wide littoral range, I would advise that systematic transects are implemented into future survey designs. These results successfully aided in establishing a new sampling technique for juvenile toheroa spat. In Chapter 3, I will apply these techniques to determine whether these observations are consistent across other locations on Ripiro Beach.

3 Chapter 3 – Spatial and temporal distributions

3.1 Introduction

The coastal area is dominated by tidal fluctuations that form defined niche conditions along the littoral region (Dyer *et al.,* 2000; Klein, 1985). Environmental conditions range from fully aquatic to fully terrestrial across the length of the shore, resulting in patterns of intertidal zonation that have been well-documented worldwide (Harley & Helmuth, 2003). A variety of factors influence intertidal zonation; temperature (Harley & Helmuth, 2003), salinity (Druehl, 1967), wave exposure (Stephenson & Stephenson, 1961), substrate composition and orientation (Raimondi *et al.,* 1988), and tidal dynamics (Dyer *et el.,* 2000). In addition, emersion time is a key predictor for the distribution and survival of many benthic marine species (Dyer *et al.,* 2000; Harley & Helmuth, 2003). Typically, the distribution of surf clam species are often confined to the same zonation (Harley & Helmuth, 2003). This is thought to be attributed to either active habitat selectivity or differential mortality due to unfavourable conditions (Dyer *et al.,* 2000).

As similar with other temperate bivalves, toheroa populations are known to vary in both density and across a range of spatial scales, thus, approximating abundance and distribution can be problematic (Williams *et al.,* 2013a). The position of beds along Ripiro Beach are known to be variable, with higher densities to the South of the beach in some years (Akroyd *et al.,* 2008), and to the North in others (Akroyd *et al.,* 2002). Patchy distributions of adult populations are thought to be correlated with the suitability of substrate, they are often found in dense aggregations on the intertidal zone (Cummings *et al.,* 1998; Hughes, 1970). Toheroa usually occupy beaches of similar morphological features; a wide low lying shore (dissipative beach), exposed turbulent surf, cliff or dune backed, freshwater outflow (streams), high phytoplankton concentrations, and fine uniform grain size (0.21–0.33 mm) (Rapson, 1952; Williams *et al.,* 2013a). A consistent factor has always been the appearance of large toheroa beds on locations with sufficient freshwater flow onto the beach (Redfearn, 1974; Rapson, 1952). It has been theorised that these habitats provide toheroa the ability to evade unfavourable environmental conditions, preventing desiccation and utilising thermal refuge (Redfearn, 1974; Rapson, 1952; Cope, 2018).

Currently, no available literature explores stream association with juvenile spat. In order to further establish sampling methodology, it is crucial to understand how differential habitats affect the distribution patterns of juvenile toheroa. Restoration and conservation practices will be ineffective if the underlying recruitment ecology is not defined. Additionally, the viability of aquaculture can only be discussed if adequate recruitment monitoring methodology is implemented.

3.1.1 Aims and research purpose

The purpose of this study is to apply the knowledge gained from the pilot surveys in Chapter 2 to assess whether there is consistency across other locations. I aim to investigate the distribution dynamics of post-settlement juvenile toheroa both spatially and temporally on Ripiro Beach. I want to further explore the hypothesis that juveniles inhabit the upper littoral between the dunes and high tide. I aim to investigate if, like adults, juvenile abundance is stream-associated. Lastly, I want to investigate how distributions change over the recruitment season.

To do this, the following research questions will be investigated:

(1) How is juvenile size and abundance distributed both spatially and temporally along the littoral zone?

(2) Do juvenile spat favour habitats with stream outflow onto the beach like adults?

3.2 Methods

Surveys were conducted on Ripiro Beach, a full description of the chosen study location is detailed in Chapter 2.

3.2.1 Site Selection criteria

Prior to surveying, sites known from previous field explorations were located (P. Ross, personal communication, February, 2022), a four-wheel drive vehicle was driven along the length of the beach in search of toheroa beds. Beds were defined by analysing the morphology of the sediment surface. As typical with other toheroa surveys, in conjunction with stream outlets, the presence of twin siphon holes were used to identify locations of high density. Two adjacent holes (one smaller than the other) appear on the surface after feeding during tidal changes (Figure 14).

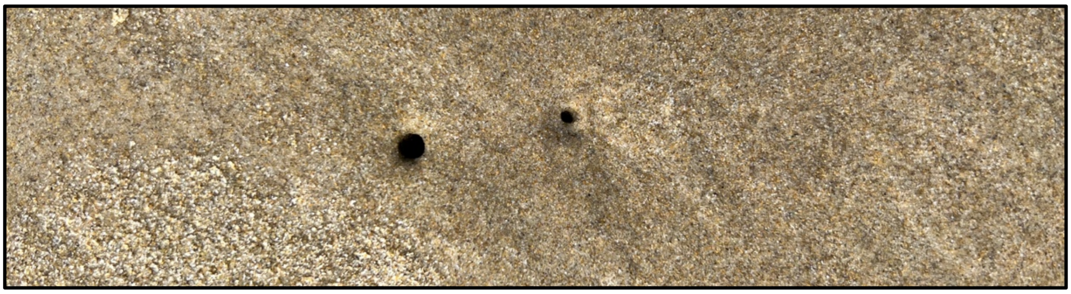


Figure 14: Example of twin siphon holes found on Ripiro Beach.

Sampling sites were divided into two different habitats; adult beds situated on stream habitats, and non-stream habitats that had no freshwater seepage or adult population. This choice was made so that juvenile distribution patterns on adult stream beds could be compared to locations that are considered environmentally unfavourable. In total, five stream habitats and one non-stream habitat were chosen, covering a 14.7 km stretch of the beach (Figure 15).

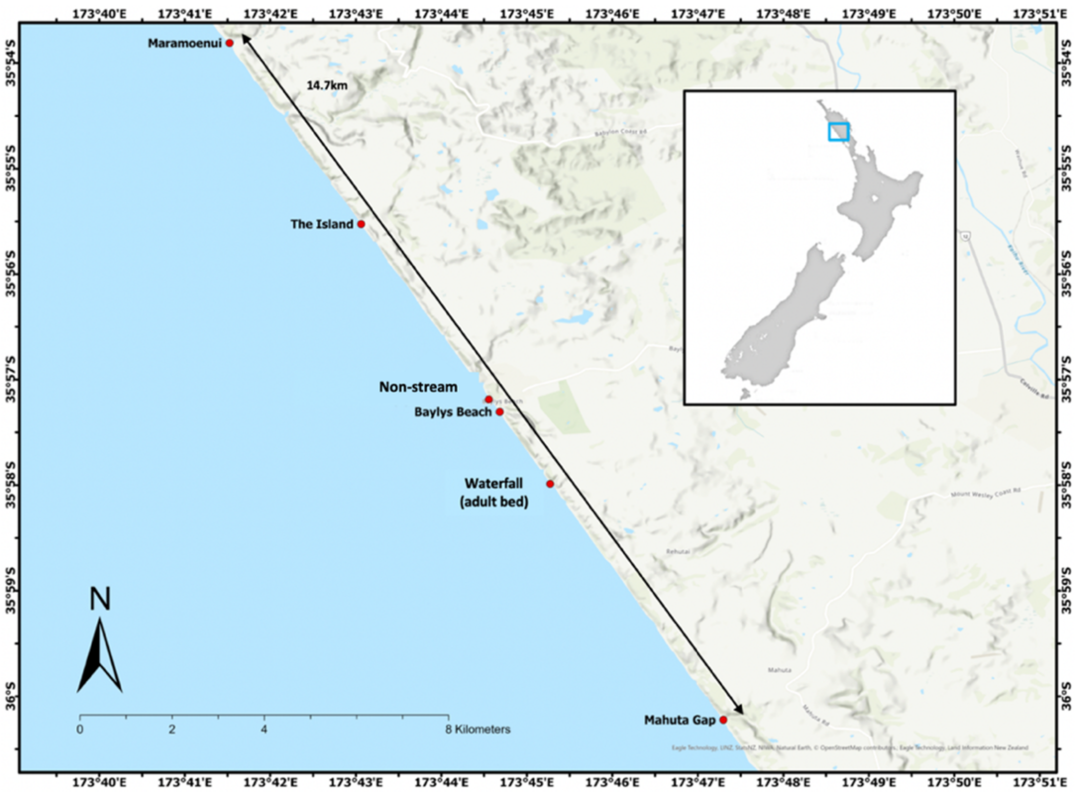


Figure 15: Map displaying the section of Ripiro Beach where the survey was conducted. Red dots represent sampling locations, arrow shows the length of the beach the sampling covered (14.7 km). Coordinate system: WGS 1984 Web Mercator (auxiliary sphere). Spatial data obtained from ArcGIS pro: World Topographic Map.

Baylys Beach (S 35°57.358', E 173°44.622')

Baylys Beach is situated within close proximity to a small urban settlement (Figure 16). It is located next to a main road access point, making it a high-traffic zone for both pedestrians and vehicles. This site has a consistent stream outlet onto the shore, it is backed by tall cliffs on either side of a gully with houses and pastures extending beyond.

Non-stream (S 35°57.211', E 173°44.546')

The non-stream habitat chosen was situated on an area of the beach that had no stream outlet. Additionally, there were also no apparent siphon holes on the sand surface. This location was slightly more elevated than the others, with the cliff face encroaching further onto the beach. Because of this, the littoral width is reduced in comparison to stream locations.

Maramoenui (S 35°53.809’, E 173°41.522')

Maramoenui was the most northern sampling location, with an adult bed and a consistent stream supply to the beach. The site is backed by a significant gully with cliffs on either side of the outlet, the catchment extends into pasture.

The Island (S 35°55.5251’, E 173°43.0625’)

The island was the second most northern sampling location, it was located on a stream outlet backed directly by pasture. Hardstone cliffs protrude slightly onto the shore from the southern side of the outlet.

Mahuta Gap (S 36°0.22’, E 173°47.3’)

Mahuta Gap was the most southern sampling location, situated on a stream outlet that also doubles as road access for vehicles. The outlet is backed by stone cliffs and pastures.

The waterfall (S 35°57.9887', E 173°45.2715')

The waterfall was the second most southern location. Fresh water enters the beach by groundwater flow from the cliff face that backs it forming a feature akin to a waterfall.

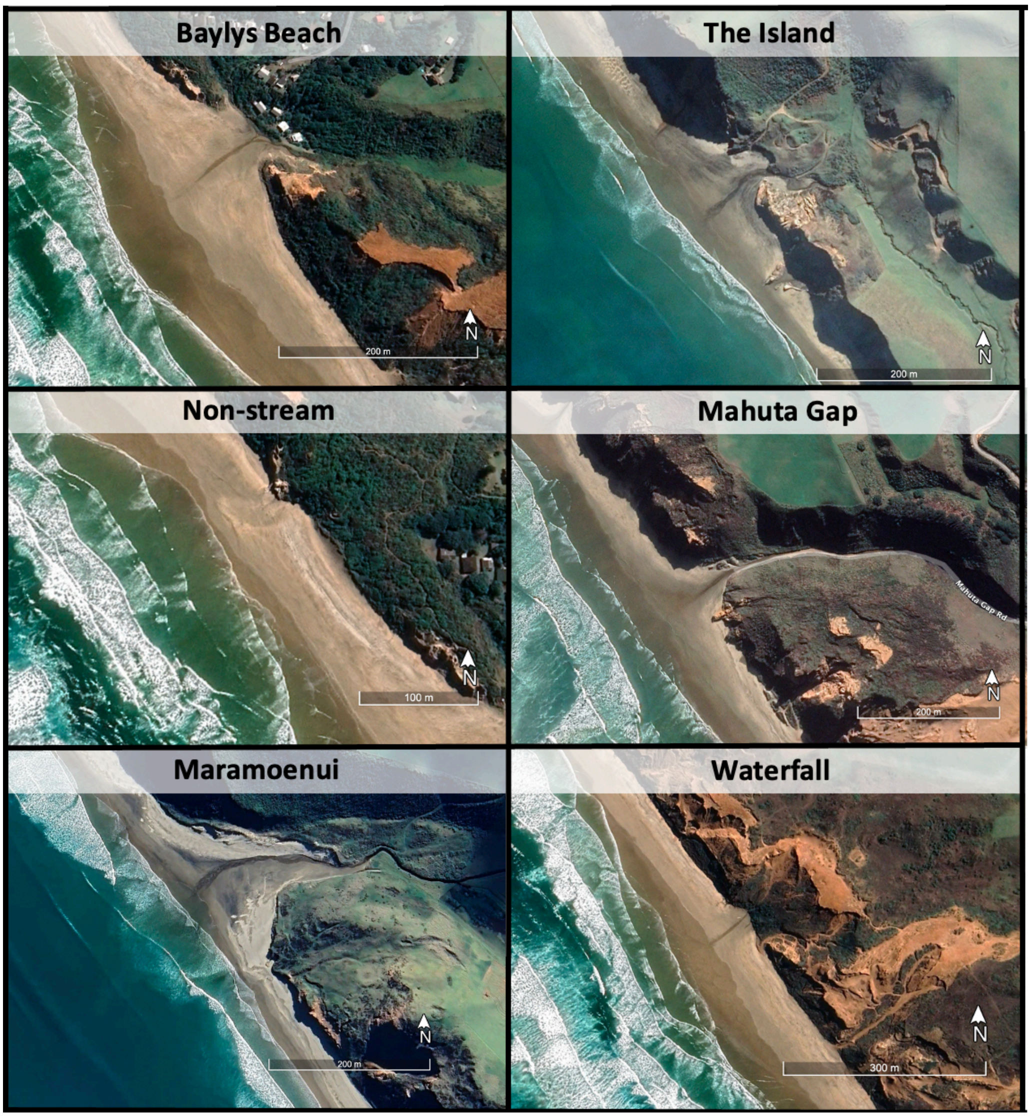


Figure 16: Topography of the different sites sampled in this study. Image retrieved from Google Earth.

3.2.2 Sampling Methodology

Fieldwork was conducted during two phases, 15th - 18th of February 2022, and the 18th – 21st of May 2022. Data obtained from the pilot surveys (Chapter 2) informed the littoral and vertical zonation juveniles tend to inhabit within the substrate, transect allocation and depth parameters were then optimised for surveying juvenile spat. All plots were excavated to 0-5 cm. During February and May, a total of 7 transects were placed along Ripiro Beach, ranging from 50 m to 150 m. Some locations had shorter littoral widths due to the slightly undulating coastline and incoming tide. A total of 78 plots were surveyed. Systematic sampling was implemented by placing 0.25 m^2 metal quadrats on the ground along the length of the transect, intervals of either 5 m or 10 m were chosen (Figure 17). Dimensions of the different transects are given in Table 5. GPS locations were recorded for all sites. The sampling methodology for sediment excavation and analysis (toheroa length and abundance) is as detailed in Chapter 2.

Table 5: Transect dimensions on Ripiro Beach in 2022.

Date	Location	Transect length (m)	Intervals (m)	Number of plots
February	Baylys Beach	150	10	16
	Non-stream	50	5	11
	Maramoenui	120	10	13
May	Maramoenui	120	10	13
	Non-stream	60	10	7
	Mahuta Gap	110	10	12
	The Island	50	10	6

Additionally, a bed was excavated that targeted adult toheroa, the centre of the bed was pinpointed at the epicentre of highest siphon hole density. Two different depth margins were chosen: 0-5 cm to capture juveniles, and 5-10 cm to capture adults. Quadrats measuring 0.25 m^2 were randomly placed on the bed with five different replicates. Firstly, the top 0-2 cm of sediment was excavated with plastic shovels and sieved through a 1 mm mesh sieve in water, then the 5-10 cm margin was excavated by hand. Adult toheroa shell length was measured with callipers and recorded, mean densities were calculated from the replicates.

Figure 17: Drone photos from fieldwork in February on Ripiro Beach. (Photo from E. Russell).

3.2.3 Statistical Analysis

Descriptive tables and graphical data visualisation were generated in Microsoft Excel. Histograms were constructed to portray size frequency distributions of juvenile toheroa across the littoral zone, and size distributions of the adult population.

3.2.4 Map Construction

Distribution heat maps were created using spatial analysist tools in ArcMap GIS (Coordinate system: GCS_WGS_1984). Study site coordinates were exported from google earth as a kml file and imported as a layer, Kriging interpolation was used to display density data from the transects. Location maps were either sourced from Google Earth or were created in ArcGIS Pro (Coordinate system: WGS 1984 Web Mercator (auxiliary sphere). Regional spatial data was obtained from ArcGIS Pro: World Topographic Map.

3.3 Results

3.3.1 Effect of habitat on density and shell size

Overall, the mean density per 0.25 m^2 was lowest on non-stream habitats in both February and May (Table 6). Higher juvenile abundances appeared to be correlated with steam supply to the beach. In February, stream habitats had a mean density of 82.94 (± 76.18) (Baylys) and 101.83 (± 82.37) (Maramoenui), respectively. Whereas mean density was just 45.64 (± 48.69) on the non-stream habitat. The same pattern was observed in May, but at far lower abundances; 3 (± 4.18) (Maramoenui), 13.76 (± 20.5) (Mahuta), and 3.86 (± 5.4) (The Island) for stream habitats, and 2.43 (± 3.05) on the non-stream habitat.

Table 6: Summary of mean density data from all transects in February and May. Sampling depth 0-5 cm.

Date	Location	Mean Density (0.25 m^2)	SD(σ)	SEM (±)	Max	Min	Total abundance
February	Baylys Beach	82.94	76.18	19.05	256	1	1326
	Non-stream	45.64	48.69	14.68	150	0	500
	Maramoenui	101.83	82.37	22.84	297	22	1222
May	Maramoenui	3	4.18	1.16	16	0	35
	Non-stream	2.43	3.05	1.15	8	0	17
	Mahuta Gap	13.67	20.5	5.92	62	0	164
	The Island	3.86	5.4	2.2	16	0	24

The mean shell size was greater on stream habitats compared to non-stream habitats, mean shell size also increased over time from February to May (Table 7). In February, stream habitats had mean sizes of 3.99 mm (± 3.55) (Baylys) and 4.37 mm (± 3.4) (Maramoenui), compared to 3.86 mm (± 2.85) on the non-stream habitat. In May, stream habitats had mean sizes of 10.06 mm (±7.12) (Maramoenui), 8.71 mm (± 3.34) (Mahuta), and 7.13 mm (± 3.27) (The Island), compared to 6.86 mm (± 1.64) on the non-stream habitat.

Table 7: Statistical summary of the mean size of toheroa from the different sampling habitats in February and May. Sampling depth 0-5 cm.

Date	Location	Mean Size (mm)	SD(σ)	SE(±)	Max	Min	Count (*n*)
February	Baylys Beach	3.99	3.35	0.09	42.29	1.001	1326
	Non-stream	3.86	2.85	0.13	40.57	1.08	500
	Maramoenui	4.37	3.4	0.1	49.68	1.05	1222
May	Maramoenui	10.06	7.12	1.2	42.94	2.78	35
	Non-stream	6.86	1.94	0.47	10	4.03	17
	Mahuta Gap	8.71	3.34	0.26	16.38	2	164
	The Island	7.13	3.27	0.67	13.77	3.36	24

3.3.2 Littoral distribution patterns

Littoral distribution proved to be variable and covered a wide littoral range. Most locations had the highest densities within the mid-intertidal to upper-intertidal zone (with the exception of the Island site). On Baylys Beach in February, juveniles were distributed along the entirety of the transect (Figure 18). However, there appeared to be two peaks of high density situated on either side of the transect centre (plots 7 and 12 (50 m distance between)), with the highest density on the upper-intertidal. Lower densities were observed around the low-tide, mid-tide, and high-tide zones.

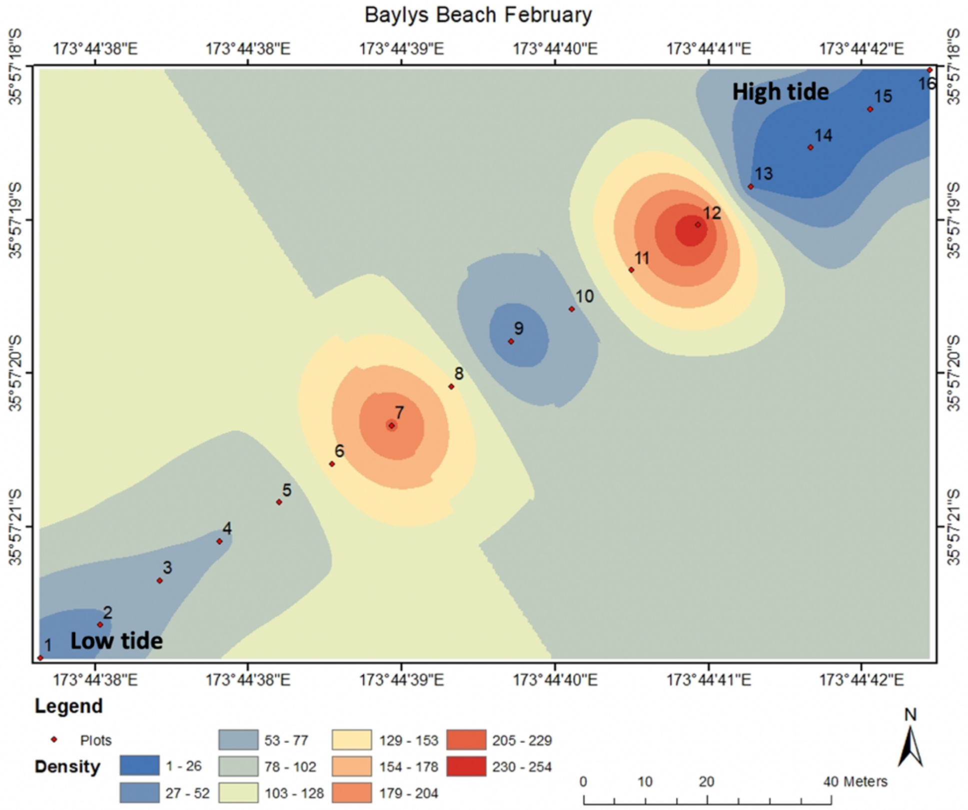


Figure 18: Heat map displaying density distributions on Baylys Beach in February. Numbered labels with circle icons represent plots, with 1 on the low tide zone moving toward the high tide zone. Coordinate System: WGS 1984

Maramoenui was a prolific location in February, juveniles were present along the entirety of the transect (Figure 19). As seen previously on Baylys Beach, there appeared to be two peaks of high density located on either side of the transect centre (plots 4 and 11 (70 m apart)), with the higher abundance on the upper-intertidal. Lower abundances were also observed around the mid-tide, high-tide, and low-tide zones. However, density was greatly reduced in May, the two high abundance locations had receded towards one defined location on the upper intertidal (Figure 20).

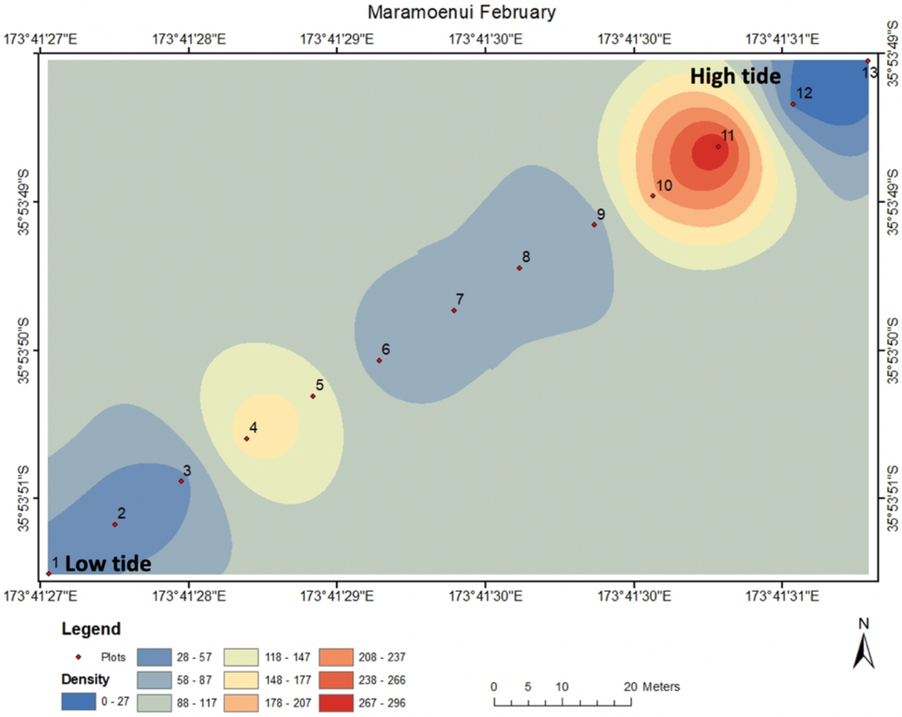


Figure 19: Heat map displaying density distributions on Maramoenui in February. Numbered labels with circle icon represent plots, with 1 on the low tide zone moving toward the high tide zone. Coordinate System: WGS 1984.

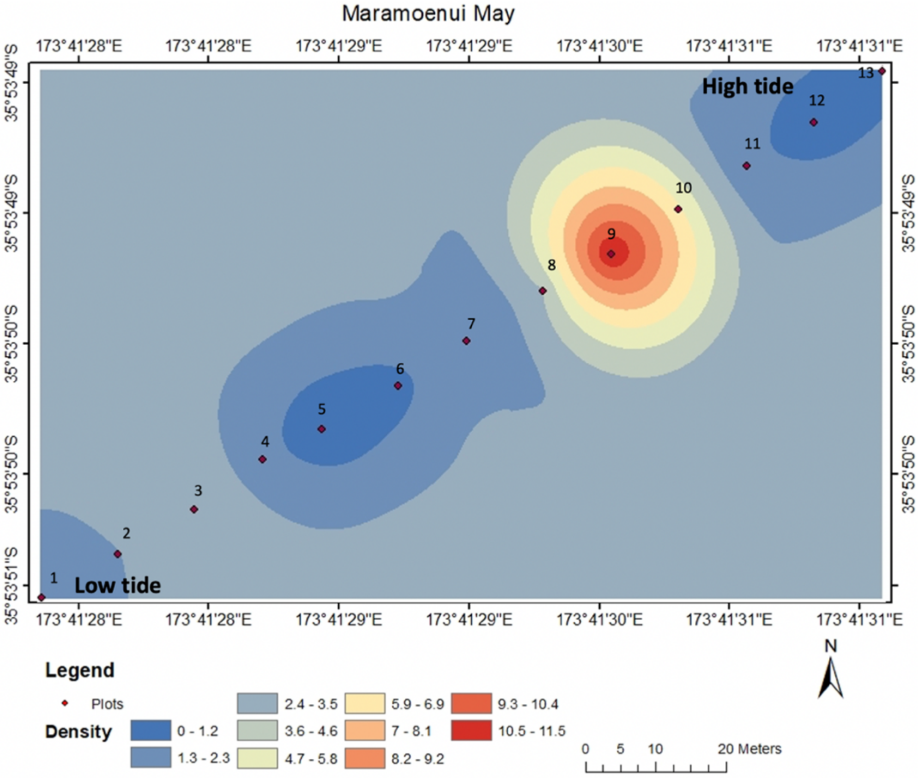


Figure 20: Heat map displaying density distributions on Maramoenui in May. Numbered labels with circle icon represent plots, with 1 on the low tide zone moving toward the high tide zone. Coordinate System: WGS 1984.

In February, in contrast to Baylys and Maramoenui, the non-stream habitat presented one well-defined centric area of high abundance around the mid to low tide zone (Figure 21). There were very few juveniles found on the high-tide and low-tide zones. A similar distribution pattern was observed in May, but with far lower densities (Figure 22). There was only one central zone of density, with no toheroa found on the low and high tide zones.

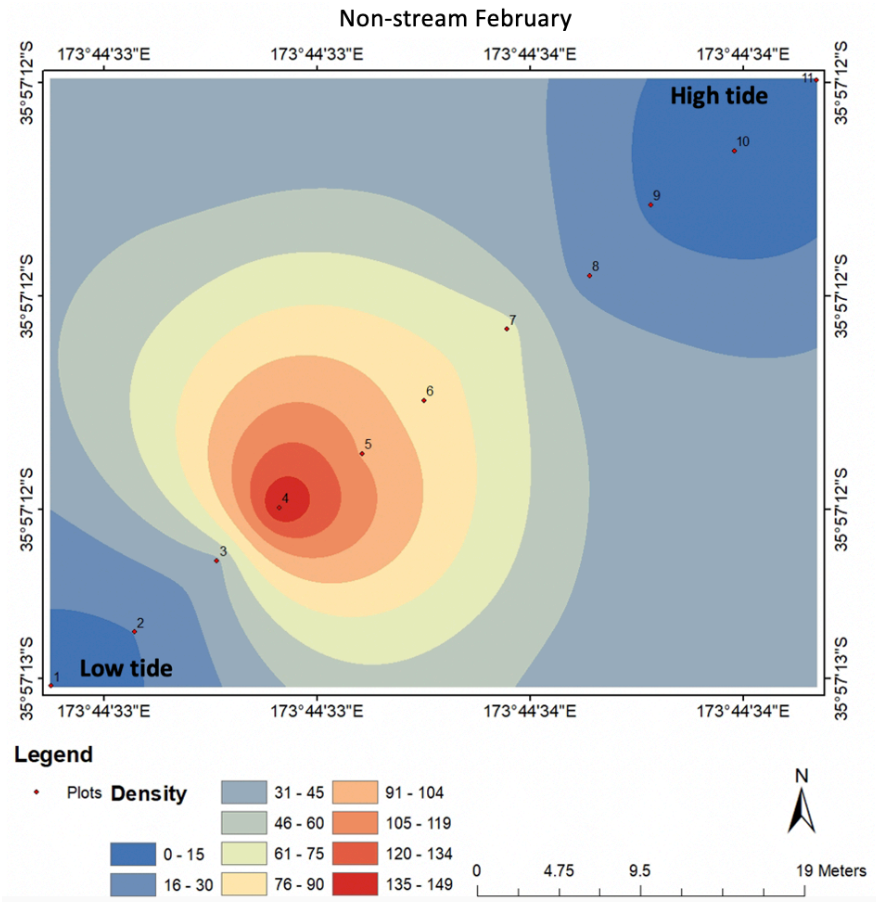


Figure 21: Heat map displaying density distributions on the non-bed site in February. Numbered labels with circle icon represent plots, with 1 on the low tide zone moving toward the high tide zone. Coordinate System: WGS 1984.

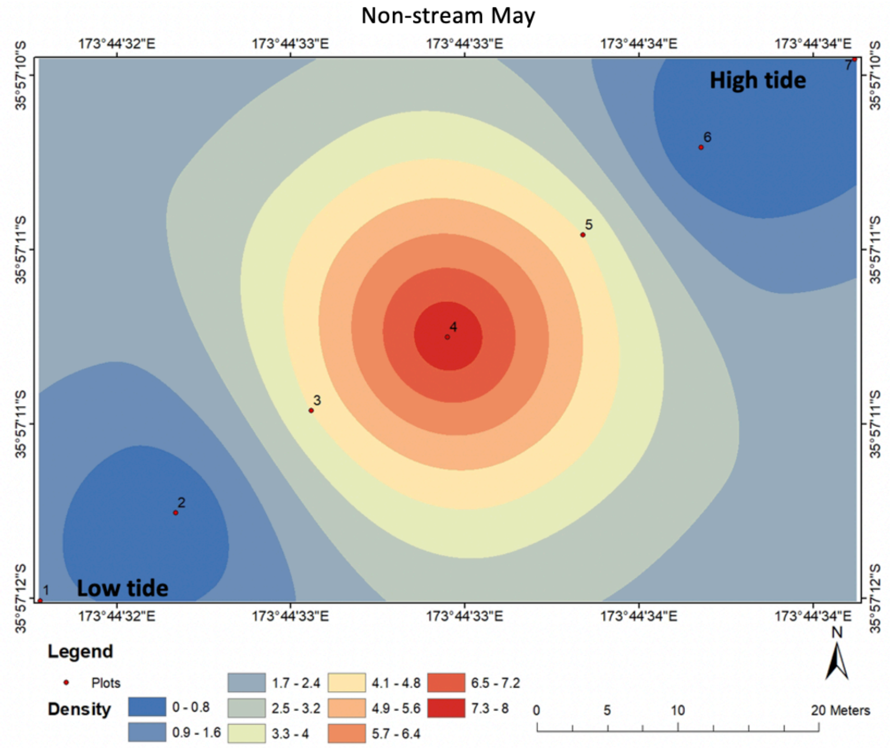


Figure 22: Heat map displaying density distributions on the non-bed site in May. Numbered labels with circle icon represent plots, with 1 on the low tide zone moving toward the high tide zone. Coordinate System: WGS 1984.

Mahuta Gap had the highest density of any transects plotted in May, although it was still significantly less than any location from February (Figure 23). Mahuta gap had one well-defined area of high density that was situated centrally on the mid-tide with a slight skew to the upper-intertidal. Very few toheroa were observed on the low and high tide zones. The Island site in May was the only location that did not show an intertidal zonation, with the upper high tide exhibiting the highest density (Figure 24). However, it should be noted that this density was low with only 16 specimens at the high tide plot (*n=24*).

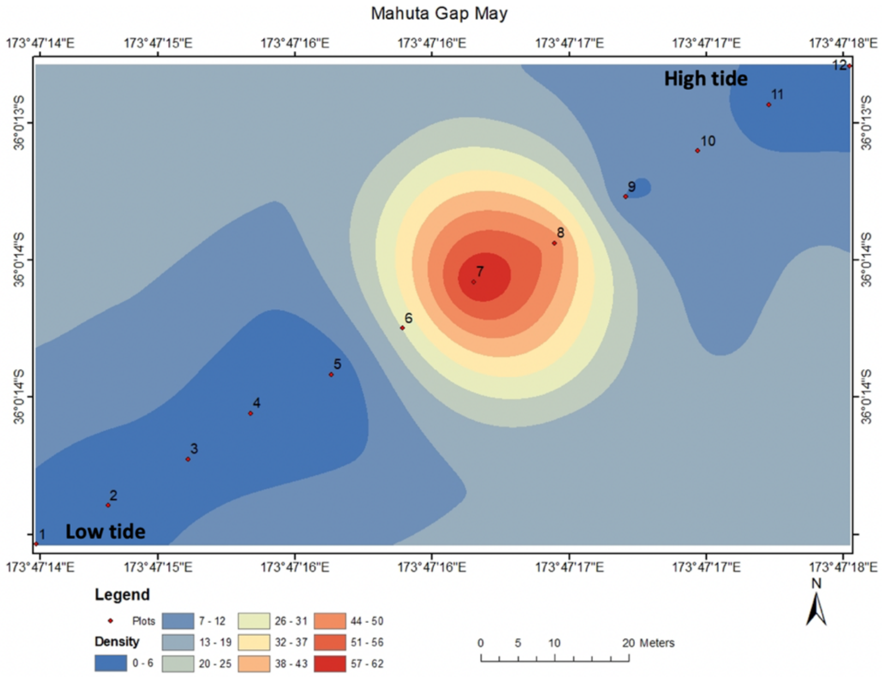


Figure 23: Heat map displaying density distributions on Mahuta Gap in May. Numbered labels with circle icon represent plots, with 1 on the low tide zone moving toward the high tide zone. Coordinate System: WGS 1984.

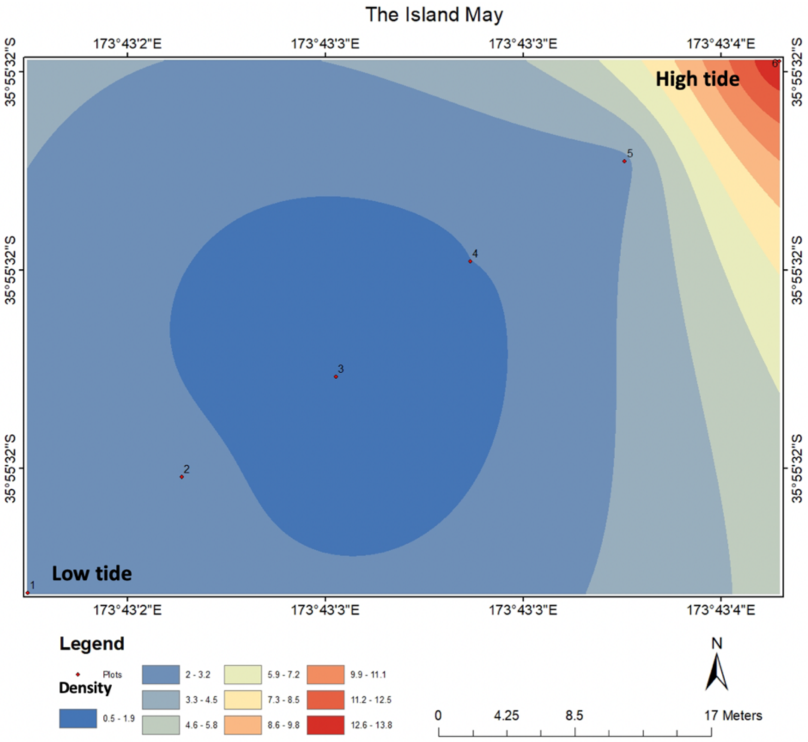


Figure 24: Heat map displaying density distributions on the Island site in May. Numbered labels with circle icon represent plots, with 1 on the low tide zone moving toward the high tide zone. Coordinate System: WGS 1984.

3.3.3 Size frequency distributions

Overall, there appears to be a trend of higher littoral zonation with increasing shell size. Additionally, juveniles from the same cohort typically have aggregated concentrations around the same location on the transect. The dominant size cohort shifted from 0-5 mm to 5-10 mm over time.

Baylys Beach

In February, the 0-5 mm size cohort was the dominant class and displayed a wide distribution with two modes that were on either side either of the transect centre, peak abundance was on the mid-low intertidal (Figure 25). Within the two modes, the highest frequency of 5-10 mm toheroa were skewed toward the upper-midlittoral. Very few toheroa from the 10-15 mm and >15 mm cohort were sampled, of those that were, distribution was situated just below and just above the mid-tide zone.

Maramoenui

In February, there was a high frequency of 0-5 mm toheroa that displayed a wide littoral range (Figure 26). Majority were distributed between two modes, with the highest density near the upper-littoral. The 5-10 mm distribution was more unimodal with a skew towards the upper-midlittoral. Of the toheroa >10 mm, distribution was either upper midlittoral (10-15 mm), or either side of the mid-tide zone (>15 mm). In May, the overall abundance was distributed more evenly between the different cohorts with a higher frequency of larger spat compared to the 0-5 mm cohort abundance in February, likely indicating a decline in spawning. The 0-5 mm cohort had reduced substantially and the distribution was skewed toward the low-tide. Toheroa ranged 5-15 mm were the most abundant and were predominantly distributed on the upper midlittoral. A few toheroa >15 mm were observed around mid-tide to high-tide.

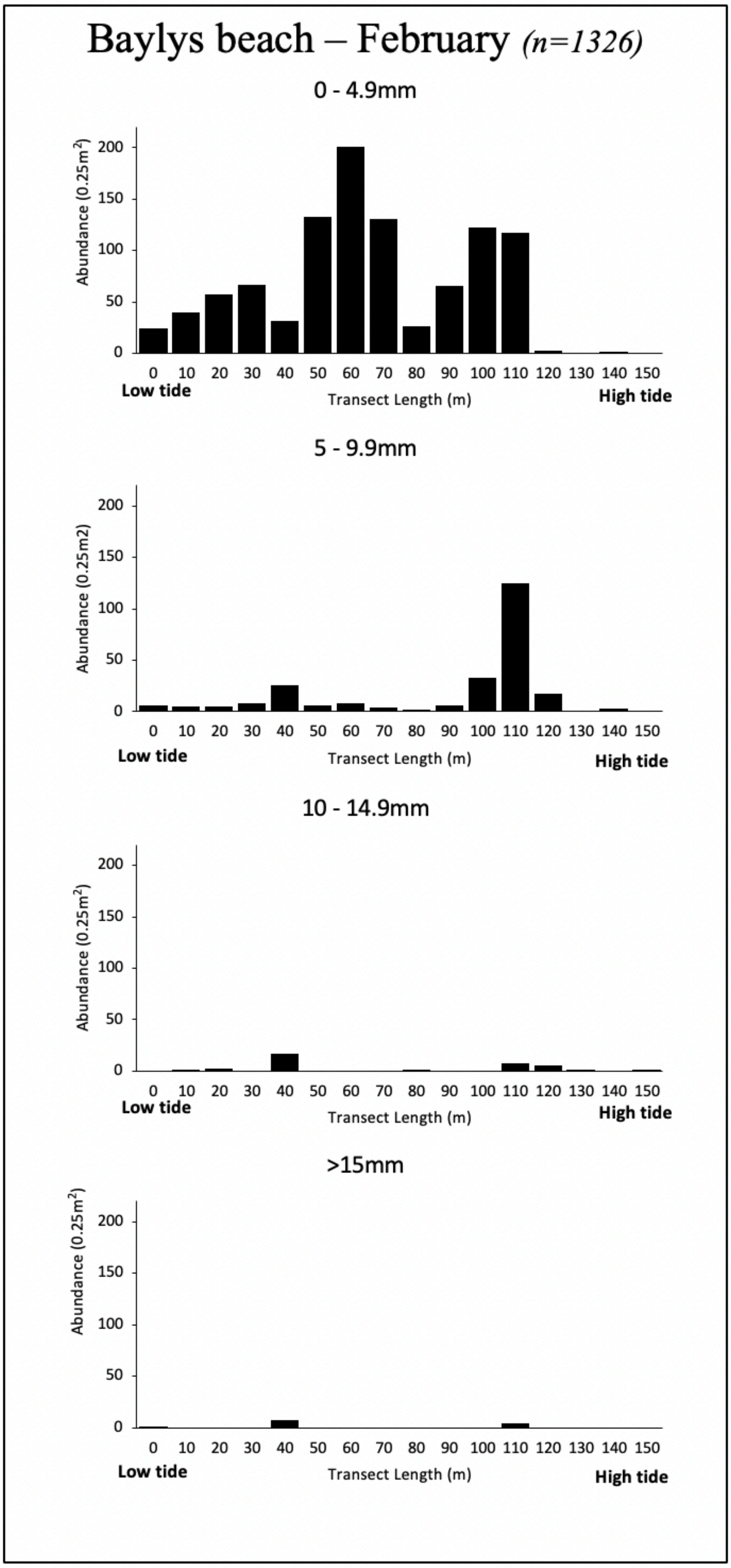


Figure 25: Shell size frequency distributions at Baylys beach in February for 0-5 cm sediment depth. 0 m = low tide.

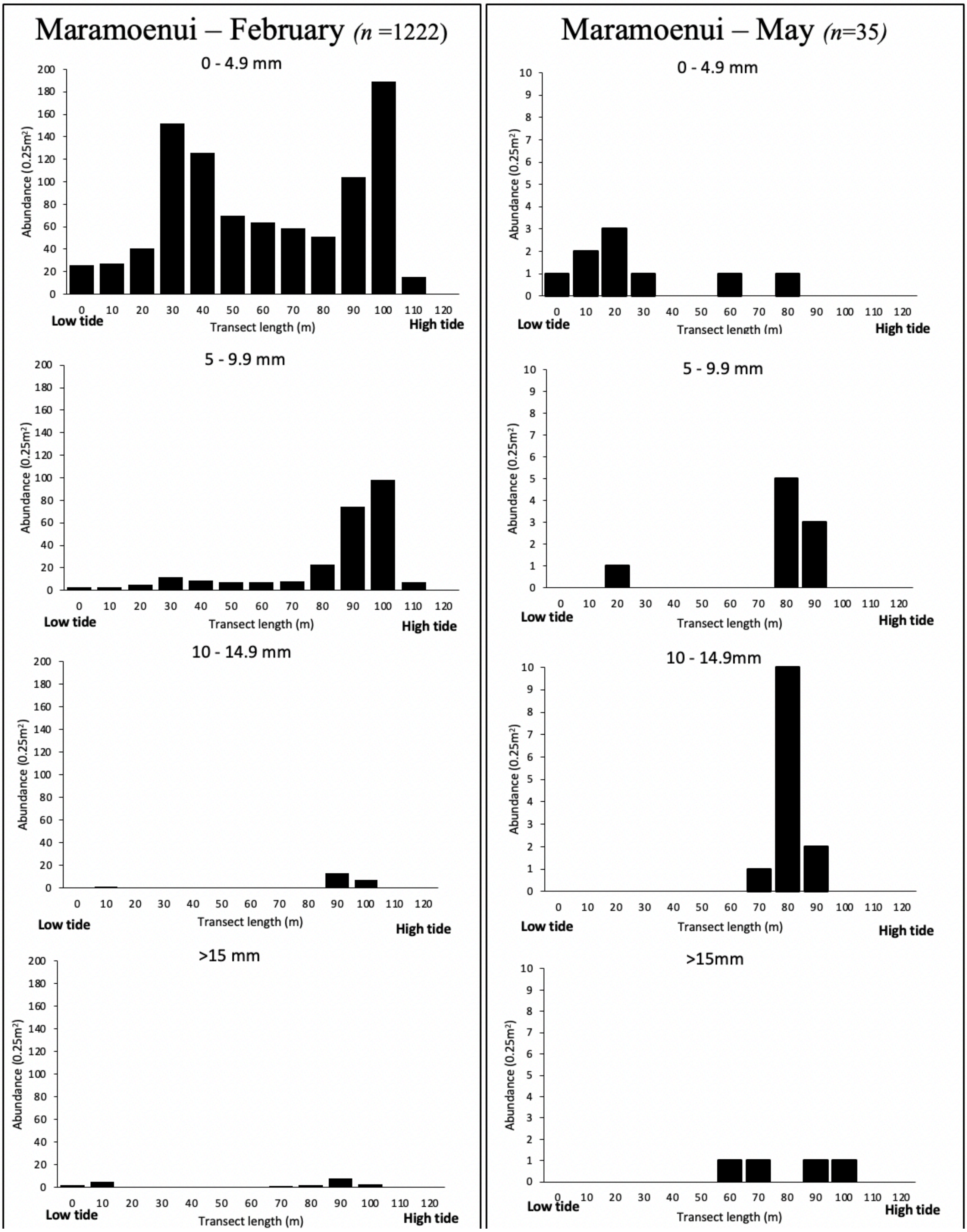


Figure 26: Shell size frequency distributions at Maramoenui, sediment depth 0-5 cm. 0 m = low tide.

Mahuta gap

In May, the 0-5 mm cohort was distributed around mid to low tide (Figure 27). The 5-10 mm and 10-15 mm cohorts had a unimodal distribution around the mid to high intertidal. Only a few >15 mm were found with a relatively central distribution.

The Island

In May, this site was the only transect to have the highest distributions near the high-tide mark (Figure 27). Toheroa ranged 0-10 mm were the most abundant, a few 10-15 mm toheroa were found with the highest density on the high-tide mark. No toheroa >15 mm were found.

Non-stream habitat

In February, there was a unimodal distribution skewed toward the lower intertidal of spat from the 0-5 mm cohort (Figure 28). A small amount of 5-10 mm toheroa also had a unimodal distribution around the mid-tide zone. Very few toheroa >10 mm were observed, and of those that were, the distribution was either just above mid tide (10-15 mm) or just below (>15 mm). Substantially lower densities were observed in May, a small number of 0-5 mm toheroa were situated just below mid tide. The dominant size cohort was 5-10 mm with a central to low tide distribution. No toheroa >15 mm were found. Overall, the non-bed habitat had far fewer toheroa >10 mm than stream habitats. Additionally, they were also distributed lower on the littoral zone.

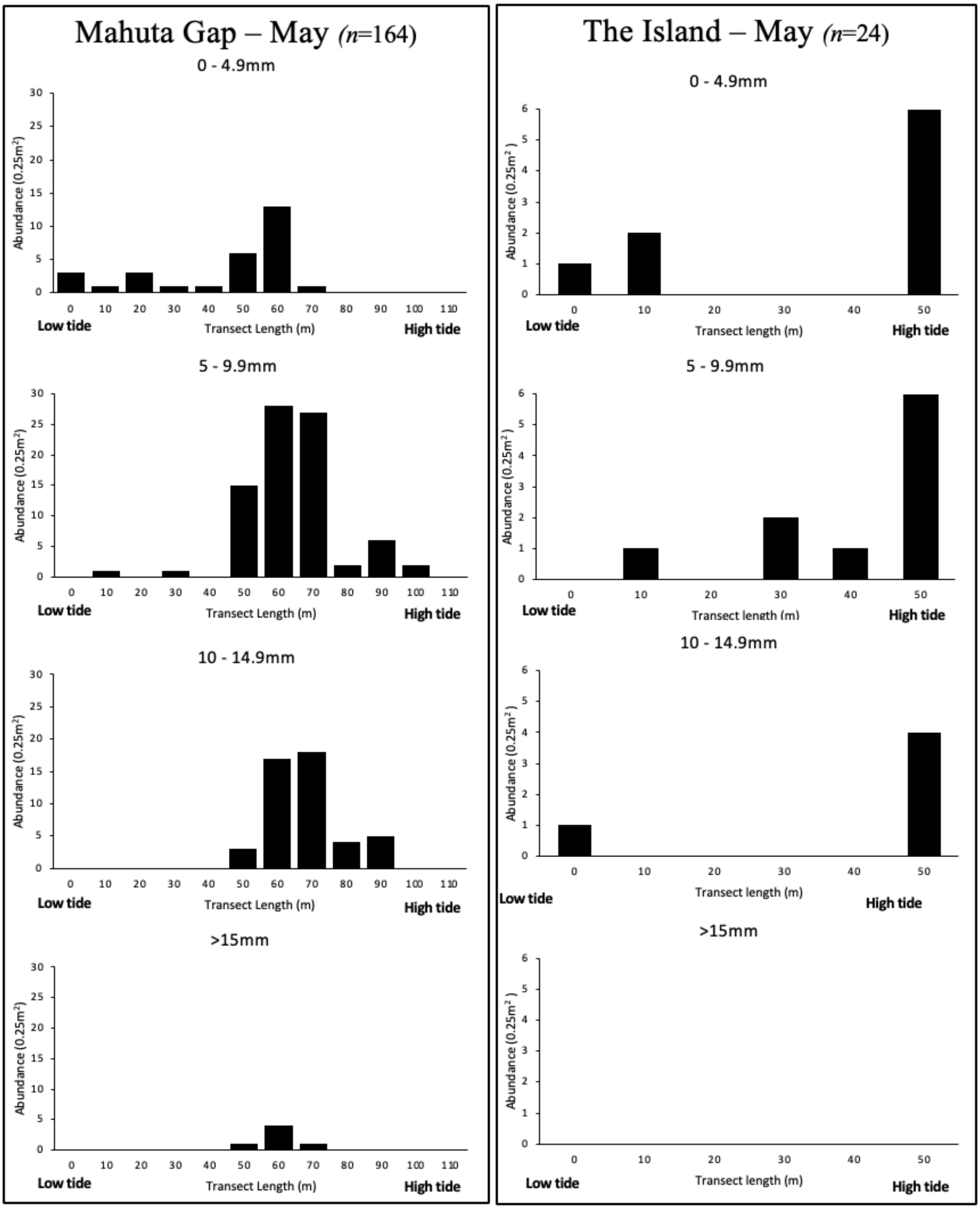


Figure 27: Shell size frequency distributions at Mahuta gap and The Island in May, sediment depth 0-5 cm. 0 m = low tide.

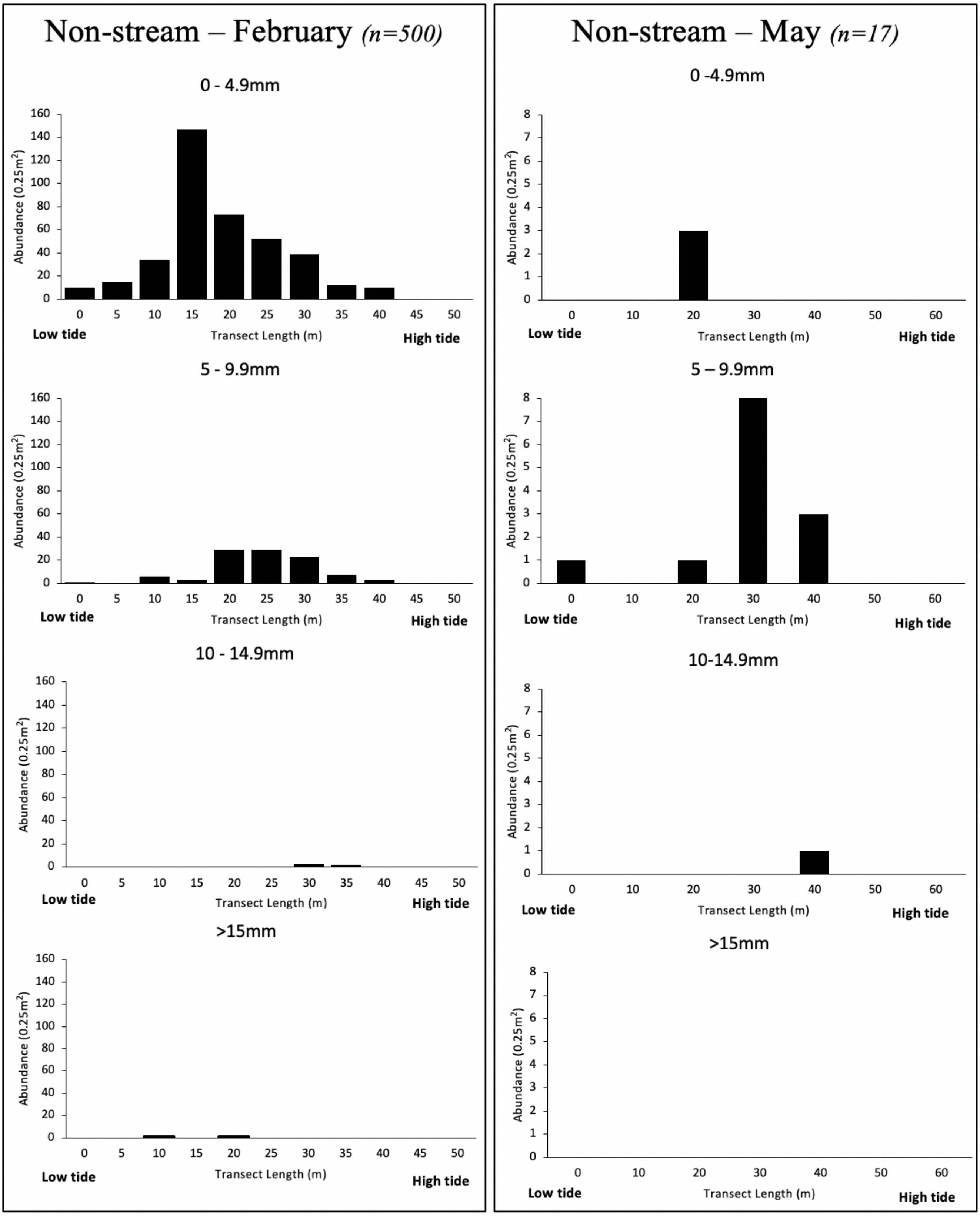


Figure 28: Shell size frequency distributions for the transect on the non-bed habitat, sediment depth 0-5 cm. 0 m= low tide.

3.3.4 Adult toheroa population structure

In May, the adult bed that was excavated yielded relatively high densities of larger individuals (Figure 29, 30). The top 0-5 cm of sand was mostly dominated by toheroa sized 5-30 mm in length. Whereas, the 5-10 cm margin was dominated by toheroa 60-80 mm in length. No juveniles of the 0-5 mm size range were found. The density distribution was nearly 50/50, with 47 % in the 0-2 cm margin and 52 % in the 5-10 cm margin. There's a noticeably lower abundance of toheroa in the 30-60 mm size range.

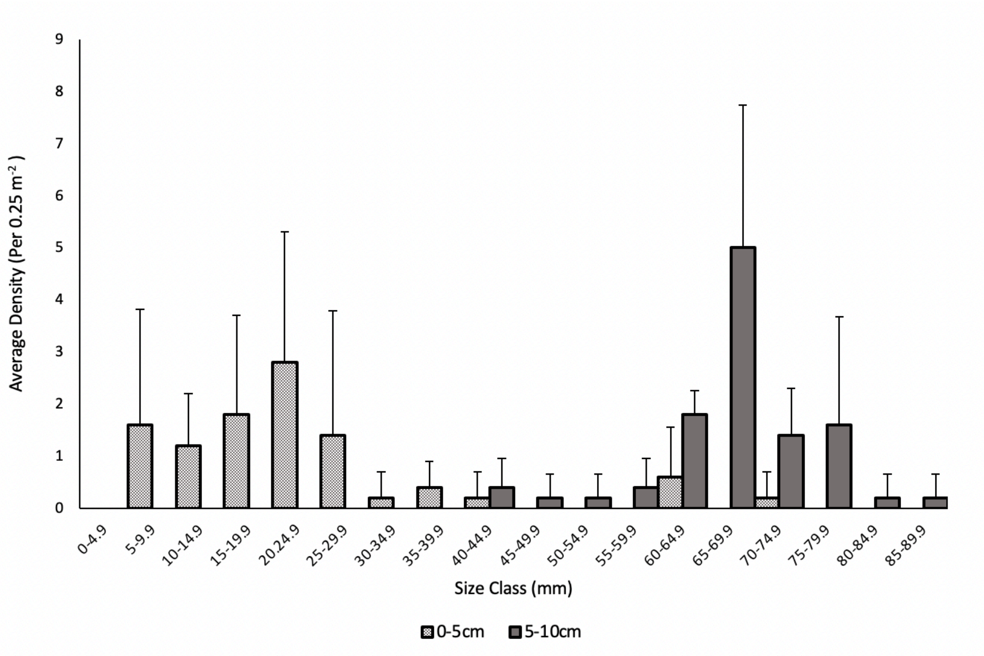


Figure 29: Mean shell size (mm) frequency distributions on the adult bed excavation in May. Two depth stratifications of 0-5 cm, and 5-10 cm sediment depth. Error bars represent standard deviation.

Figure 30: Adult toheroa sampled in May on Ripiro Beach. Photo by author.

3.4 Discussion

This chapter aimed to further investigate the distribution of juvenile toheroa on Ripiro Beach. The results from this study did not support the hypothesis that juvenile toheroa are limited to the high-tide zone. A wide range of distribution patterns were observed, and spat were found along the entire intertidal. In February, stream habitats displayed two well-defined areas of high density situated on either side of the mid-tide, with peak density directly above the mid-tide. Whereas the non-stream habitat only presented one well-defined area of high density around the mid-intertidal. From February to May, juvenile littoral distribution on stream habitats appeared to recede and become aggregated on the mid to high intertidal. This behaviour could indicate that environmental conditions on the upper intertidal are favourable, resulting in lower mortality in these zones. However, it is uncertain whether this is attributed to active habitat selection or differential mortality. Additionally, adult populations are situated further down shore, whether juveniles migrate as they grow or eventually desiccate on these upper intertidal zones is unknown. If mass mortality occurs on these upper intertidal juvenile aggregations, it could explain why populations have failed to recover. Judging by the reduced abundances in May, it points to the end of the major spawning period coupled with juvenile mortality resulting in lower overall abundances.

The non-stream habitat had lower density, lower frequency of larger juveniles, and lower littoral distribution. This is likely attributed to the absence of freshwater seepage onto the beach, which is a well-documented factor affecting adult toheroa populations (Cassie, 1955; Rapson, 1952; Redfearn, 1974). Cope (2018) conducted research regarding the thermodynamics of toheroa beds located on streams at Ripiro Beach, temperatures on the upper intestinal (high-littoral) were comparatively lower than sites without freshwater input. This could indicate why juvenile survival and abundance is higher on streams, lowered temperatures reduce the risk of desiccation. The recruitment season is during the summer months, and substrate saturation and cooler temperatures likely enhance survival. Additionally, increased erosion and saturation in stream locations create embayments and basin-like depression formations which may act to aggregate spatfalls in these areas (Smith, 2003).

The Island site was the only location that fit with the high-tide/dune distribution hypothesis. However, the recorded abundance was low (n = 24). It should be noted that the weather during May sampling for this transect was stormy, strong winds and rough surf appeared to have blown/washed many juveniles up to the high tide mark. Numerous spat were observed laying on the sediment surface that appeared to have been stranded above the surf (had not burrowed). Therefore, the distributions on this site might not be indicative of the whole population.

The size frequency distributions presented a potential correlation between increasing shell size with higher littoral zonation. Juveniles ranged 0-5 mm displayed the widest littoral range. It is likely that newly settled spat (2 mm) are unable to anchor themselves and are frequently redeposited along the shore (Cassie, 1955; Redfearn, 1974). It also appeared that juveniles from the same cohort were aggregated together. However, toheroa larger 15 mm were often situated around the mid-tide zone. Lateral sorting on Ripiro Beach has been observed before, Redfearn (1974) discovered some cases of mono-age beds. This type of separation could indicate different tidal deposits during settlement, where the lateral sorting represents discrete spatfalls (Rapson, 1952). Additionally, passive transport could have occurred when the turbulent surf disturbs the sediment surface resuspending juvenile spat, and successive waves then wash them higher up the beach (Armonies & Hellwig-Armonies, 1992; Redfearn, 1974). Waves dissipate as they progress up shore, the lower energy zone might allow juveniles to better secure themselves in the substrate on higher littoral reaches (Harley & Helmuth, 2003; Redfearn, 1974).

Both Redfearn (1974) and Cassie (1955) reported that often juveniles are separated from the rest of the population forming their own cohort beds during the early stages of growth (first 18 months after spatfall). The excavation of the adult toheroa bed both supports and contradicts this as there were no juveniles of the 0-5 mm size cohort. However, there was a considerable amount from the 5-25 mm range. Because plots were randomly placed centrally on the adult bed and not along a transect perpendicular to the shore, this could mean that 0-5 mm juveniles may have been present above or below the bed, which would fit with some of the observed distribution patterns in this study. It is not uncommon for newly settled surf clams to be spatially separated from adult populations, the closely related tuatua (*Paphies donacina*) also exhibits this behaviour (Marsden, 2002). Juveniles forming separate cohort beds could also represent niche partitioning on the intertidal zone. This occurs when intraspecific interactions cause members of the same species within a population to occupy different distribution patterns, which is often attributed to resource competition (Finke & Snyder, 2008).

Regardless of the reason for juvenile-adult separation, given that larger spat were often situated further up shore, and peak distribution was often adjacent to mid-tide, it indicates that toheroa potentially migrate between different zonations. A survey from Hiddink and Wolff (2002) followed migratory patterns of the bivalve *Macoma balthica* on a tidal flat area of the eastern Dutch Wadden Sea, and two distinct resettlements were observed. Initially, they migrated from the primary low-intertidal settlement towards the high-intertidal nursery. They then relocated again some months later from the high-tidal nursery to the low-tidal and subtidal zone. Such behaviours could indicate toheroa resettlement along the littoral region. It is possible that, after initial pelagic settlement, the toheroa that are too small to maintain purchase are gradually transported up shore due to higher wave energy in the swash zone, then eventually migrate down to the mid-tide. A possible mechanism for migration is thought to be swash riding, entire beds of toheroa have been observed moving along shore (Ross *et al.,* 2018a). This usually occurs on an incoming tide when their siphons extend from the sand ahead of a swash front (forward movement) or after a swash front (backwards movement) (Redfearn, 1974). Once the wave progresses over the bed, toheroa eject themselves from the substrate with their foot and are carried along the shore with the wave (Ross *et al.,* 2018a). Once it recedes, they quickly burrow themselves back into the sand (Redfearn, 1974). Such behaviour has been observed with a North American surf clam (*Donax variabilis*). They appeared to ride only the largest 20 % of waves in response to sound stimuli (Ellers, 1995a; Ellers, 1995b). For toheroa, the mechanism stimulating swash riding is unknown but has been proposed as a response to hydrodynamic changes in pore water pressure (Ross *et al.,* 2018a).

Overall, juveniles were not limited to the high-tide zone, but there did appear to be a trend of peak densities to be situated either on or just above the mid-tide zone. Due to the fact that adult populations are still declining, it could indicate that juveniles do not migrate and these high-density clusters above the mid-tide are actually subject to mortality later on during the growth period. However, the mechanisms driving recruitment distributions are not defined. Whether it is an act of passive transport or active habitat selection remains unknown. More research needs to be conducted on factors affecting spawning and recruitment. Observed littoral distribution patterns for juvenile toheroa are summarised in Figure 31.

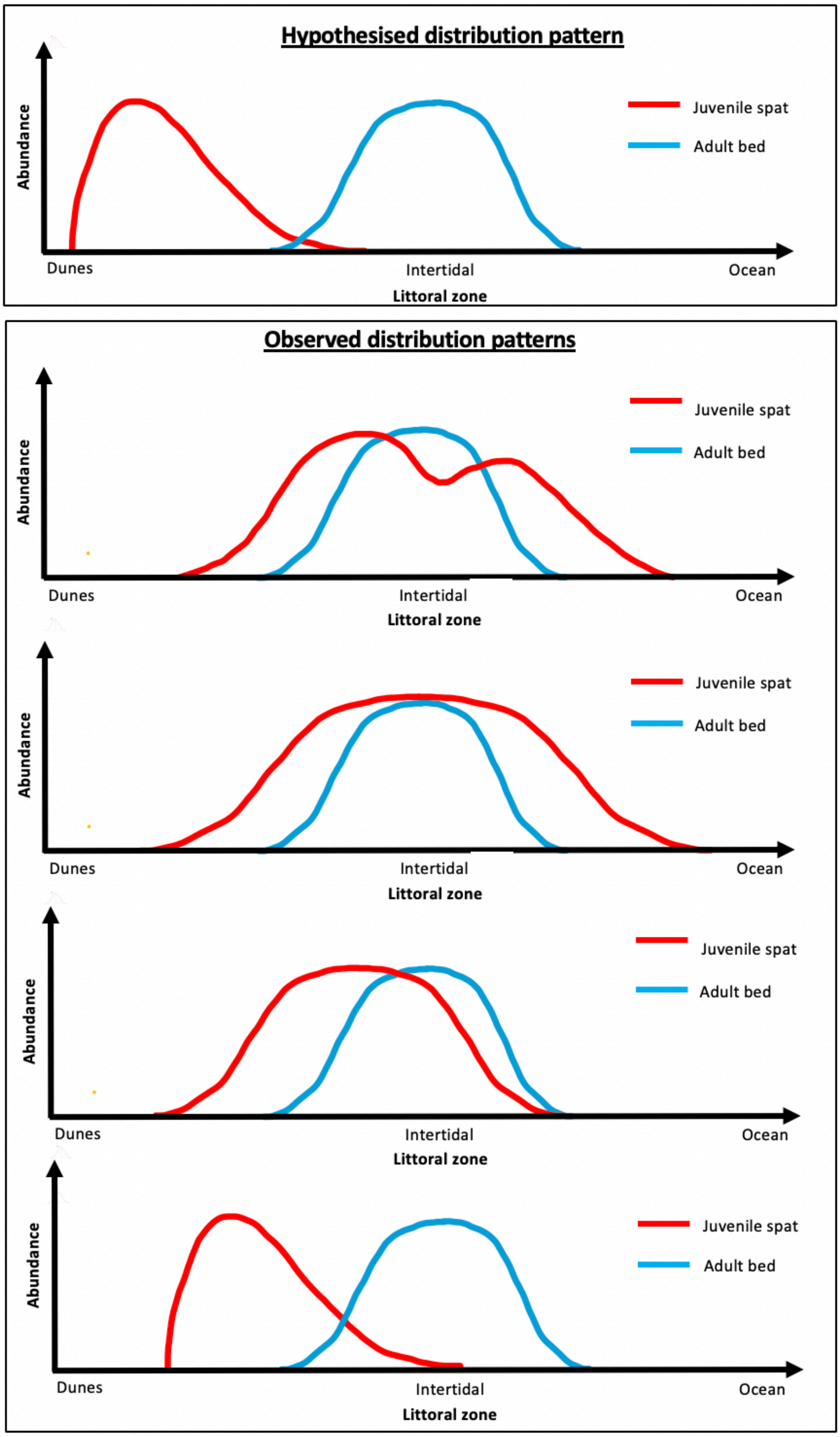


Figure 31: Schematic plots showing previously theorised distribution patterns compared to observations made across the different sites on Ripiro beach in 2022.

3.4.1 Factors affecting spawning and recruitment

Climatic conditions of the coastal zone are largely affected by oceanic conditions, often causing cascading effects on marine ecosystems (Schiel *et al.,* 2016). For northern toheroa, primary gametogenesis is known to occur during autumn and winter, resulting in a major spawning event in early spring (Redfearn, 1974; Smith, 2003). Redfearn (1974) found that the first spawning event during September to February is typically the major reproductive period, but this is known to vary. This coincides with the high abundance of spat ranged 0-5 mm in length sampled in February. However, Redfearn (1974) also observed that significant spatfalls have been recorded in May, June, and July. These occurrences were attributed to favourable environmental conditions. The low densities observed in May in combination with the most abundant size frequency shifting from 0-5 mm to 5-10 mm suggests that the conditions potentially were not favourable at this time.

Gadomski *et al*. (2015) found that toheroa larvae exhibit faster growth in warmer temperatures (12 °C, 16 °C, and 20 °C). Additionally, Redfearn (1974) noted that increasing sea surface temperature from July to October (14 °C to 17 °C) appeared to be a trigger for spawning, with 60-80 % of the population ripe by September - October, and the rest of the population ripening shortly after through October - November. After ripening, partial spawning occurred and then the gonads quickly recycled through to another ripe phase in December - January (sea temperature at 22 °C). Because we know temperature affects larval growth and triggers reproduction, assessing climatic conditions could be a good predictor for toheroa spawning, recruitment, and abundance. For example, the mean sea surface temperature of the Tasman sea has been slowly increasing annually (Ministry for the Environment, 2017). Because Ripiro Beach is situated on the west coast it is exposed to the Tasman sea, warming oceanic temperatures could initiate earlier spawning periods.

A study from Broekhuizen *et al.* (2021) reviewed the potential impact of warming sea surface temperature in the Pelorus Sound of New Zealand. This location is home to the aquaculture farming of Greenshell Mussel™ (*Perna canaliculus*). Unusually large losses of freshly seeded spat were observed during recent oceanic heatwaves. It was discerned that although subantarctic sea waters have remained largely stable, temperatures around the upper regions of New Zealand have risen (0.1–0.4 °C decade^{-1}), with nearshore zones mostly affected (Sutton & Bowen, 2019). Additionally, a study by Philippart *et al.* (2003) found that the population dynamics of intertidal bivalves (*Macoma balthica, Mya arenaria, Cerastoderma edule, Mytilus edulis*) are significantly affected by seawater temperatures. In north-western European estuarine systems, a series of mild winters were followed by low bivalve recruit abundances leading to small adult stocks, rising seawater temperatures affect recruitment by advancing spring spawning and decreasing reproductive output. In a study by del Próo *et al*. (2003), El Niño events had large-scale effects on the recruitment of invertebrates inhabiting the benthos. During a period from 1997-1998, the density of juvenile abalone (*Haliotis fulgens* and *Haliotis corrugate*) drastically declined with the effects of El Niño, exhibiting large variations in shell length. It is thought that El Niño disrupts the pelagic food web and causes mass mortalities, generating temporary changes to species compositions (Arntz & Tarazona, 1990; del Próo *et al.,* 2003). These findings support the theory that climatic conditions drive toheroa spawning. It is likely that in the foreseeable future the effects of global warming may trigger earlier spawning periods. These increasing temperatures could be interpreted as positive for toheroa growth (Gadomski *et al*., 2015). However, mass mortalities of toheroa populations have been known to occur during the summer months throughout the North Island (Williams *et al.,* 2013a). A review of mass mortality for juveniles by Williams *et al.* (2013a) found that individuals of the upper intertidal zone were subject to desiccation during hot weather, this could be a driver of bottleneck mortality of small spat concentrations on the upper littoral.

3.4.2 Limitations and future recommendations

The data quantity was somewhat limited in this study. In future, a comprehensive survey encompassing the full recruitment season would be valuable. The initial plan pre-COVID-19 interruptions was to gather data from October – May on a monthly basis. Additionally, a far greater quantity of transects we going to be sampled. Furthermore, we hoped to put together a bigger team that engaged with locals who were interested in setting up toheroa monitoring programmes. This would have provided a detailed account of spawning onset and duration and informed thorough statistics regarding distribution, migration, and mortality rates for the entire season. The original plan also hoped to define the width of the beds by placing multiple transects per habitat parallel to each other on the littoral zone. Also, multiple transects per habitat type would have been sampled to provide statistically sound points of comparison, choosing multiple non-stream habitats located in-between stream habitats. Due to the fact that bivalve recruitment is known to vary, an ideal methodology would be to gather time series data annually to assess whether these findings are consistent across multiple spawning seasons. Because sampling was conducted during one season, there is no certainty that my results are comparable to other years.

3.4.3 Conclusion

The results from this study have defined juvenile toheroa littoral zonation for the first time. Additionally, they indicate that newly settled juvenile spat have varied distribution patterns along the littoral zone and are not limited to the high-tide zone. There is a trend of higher littoral zonation with increasing size. The mechanisms driving distribution patterns are not defined, but it is likely tidal deposits in the swash zone are the primary reason for settlement along the intertidal zone. Additionally, it is possible that stream outlets on the beach provide favourable conditions that result in higher abundance and survival rates. However, it could also be attributed to the topography of stream outlets forming a basin-like depression that aggregates spatfalls. Whether juvenile distributions are attributed to active habitat selectivity, passive transport, or differential mortality is unknown. However, the findings in this chapter have optimised juvenile sampling techniques, which subsequently have wider implications for both monitoring programmes and aquaculture ventures. In future climatic conditions such as global warming are likely to have a significant effect on recruitment abundance and mortality.

4 Chapter 4 - Population estimates and mortality

4.1 Introduction

Worldwide, the exploitation of ecosystem services has raised concern regarding the condition of our marine environments (McCay *et al.,* 2003). Fisheries management is a complex but necessary process required to ensure sustainability (Björndal & Weintraub, 2004). When developing harvesting strategies for renewable resources, stock assessments form the basis of resource utilisation and aim to mitigate ecosystem deterioration (Gulland, 1983). Conducting regular population estimates ensure natural variation is accounted for, and modelling constraints are implemented to ensure that harvesting rates do not exceed the natural regenerative capacity of the resource (Björndal *et al.,* 2004; Myers & Worm, 2003).

In addition to harvesting wild stock directly for consumption, the wild harvest of juveniles has been introduced as a method to restore or maintain stocks to levels that produce maximum sustainability yield (Myers & Worm, 2003; Ye *et al.,* 2013). Globally, aquaculture has increasingly been identified as a more sustainable approach for seafood production than wild-caught fisheries (Björndal *et al.,* 2004). Many significant commercial aquaculture and stock restoration operations rely on the harvest of wild juveniles (Hair *et al.,* 2002). These include, but are not limited to, tuna, trout, salmon, shrimp, oysters, mussels, scallops, and clams (Hair *et al.,* 2002; Stickney & McVey, 2002). Many aquaculture ventures involve industrialised farming in offshore and inshore coastal waters. For example, in the Mediterranean Adriatic Sea, wild-caught juvenile bluefin tuna (*Thunnus thynnus*) are transported via towing cages to on-growing and farming facilities in nearshore waters (Nakada, 2008). Locally, in New Zealand, wild juvenile mussels (*Perna canaliculus*) are harvested from the shore of Ninety Mile Beach in Northland. Spat washes up intermittently attached to beachcast material in shallow waters; the wild-harvested juveniles are farmed via spat reseeding in longline aquaculture within the inshore coastal waters of the Coromandel (Jeffs *et al.,* 2018).

Many marine shellfish species produce significant quantities of juvenile recruitment, of which a large portion is often subject to mass mortality in the early stages of growth (Underwood & Fairweather, 1989). Because of this, harvesting and farming of juveniles has been established worldwide as a sustainable approach that circumvents the naturally high mortality rates associated with the larval period and post-larvae settlement period (Hair *et al.,* 2002; Shumway *et al.,* 2003). Additionally, utilising wild-harvested juveniles can bypass the high mortality levels associated with spawning induction and spat production within hatcheries (Hair *et al.,* 2002). Stock assessment in bivalve recruitment is necessary to understand and improve recovery and define effective strategies in regulated fisheries (Björndal & Weintraub, 2004).

Stock assessment of toheroa population sizes can be complicated, primarily because they vary considerably both spatially and temporally (Akroyd *et al.,* 2002; Redfearn, 1974). The failure of sustainability management during the 1900s ultimately led to stock collapse (Redfearn, 1974). Since harvesting was banned, some surveys have shown recovery, and others decline. Recovery is thought to be attributed to several years of successful recruitment and the active roles of local Kaitiaki (guardians) managing conservation as customary guardians of the beach (Akroyd *et al.,* 2008). Estimating toheroa populations on Ripiro Beach has been conducted sporadically over the last 70 years; most surveys have been comparable to estimates from the 1960s, implying a static or declining population (Williams *et al.,* 2013a). Estimates have fluctuated between 13 million (Greenway, 1969; Williams *et al.,* 2013a) and >1 million (Akroyd *et al.,* 2002 and references therein). From the most recent survey in 2013, the estimated abundance of toheroa over 40 mm was 12.8 million, of which 1 million were 75 mm (previous legal size) and larger (Williams *et al.,* 2013a).

Toheroa surveys have always targeted adults, often failing to sieve sediment, excluding juvenile toheroa less than 30 mm. Subsequently, this has provided inadequate estimates of juveniles and no comparable statistics regarding recruitment. Currently, very little research covers recruitment abundance or how it changes throughout the recruitment season. There is a significant knowledge gap in factors affecting recovery, and it is mostly unknown whether the declining populations are due to a lack of recruitment or mortality (Williams *et al.,* 2013a, 2013b). At present, no surveys have conducted stock assessments for juvenile toheroa. From a conservation perspective, effective management strategies cannot be established until we understand recruitment ecology. Attaining population estimates will be incredibly important for both restoration and aquaculture purposes. Toheroa already have a history of stock collapse driven by poor fisheries management. Toheroa is a taonga, a protected species, to start harvesting spat from struggling populations could be controversial and have cascading ecological effects if managed poorly. Going forward, we need to know if harvesting juveniles will compromise wild populations. From a cultural and restoration perspective, we need to quantify recruitment to gain acceptance for discussions around the viability of aquaculture. Therefore, it is imperative that we gain a better understanding of the abundance and mortality of juvenile toheroa recruitment on Ripiro Beach.

4.2 Aims and purpose of research

I aim to take a new approach to toheroa conservation on Ripiro Beach. The data generated from the surveys in Chapter 3 will be implemented into a model to estimate the population size of juvenile toheroa, with specific attention to distributional changes temporally (seasonally), spatially (habitat type), and across size cohorts (0-5 mm, 5-10 mm, 10-15 mm, and >15 mm). The estimations will compare how population assemblages change and how this affects abundance and distribution. This study aims to inform discussions around the viability of implementing wild harvested juvenile toheroa spat into the in aquaculture industry.

To do this, the following research questions will be investigated:

(4) Is it possible to generate an estimate of the total population of juvenile toheroa on Ripiro Beach?

(5) How does the abundance of juvenile toheroa change over time, and what does this tell us about mortality rates?

By answering these questions, I hope to gain a better understanding of

1. The viability for toheroa aquaculture based on wild spat harvest?
2. Whether populations are recruit limited – does this explain the failure to recover?

4.3 Methods

4.3.1 Areas included in the model

Population estimates were conducted for the length of Ripiro Beach, a complete description of the chosen study location is in Chapter 2**.** Juvenile spat estimates were made for a 53 km stretch running from Aranga (Maunganui bluff) in the north to Third Stream in the south. I excluded the southernmost 19 km section of the beach as it has quite different characteristics (pine forest plantation in the catchment) with no adult beds and was not comfortable extrapolating out to that area (Figure 32). Quantifying population sizes on Ripiro Beach involved breaking the beach into two different strata based on differential habitat types; streams and non-streams. Streams were identified by trawling the Ripiro coastline on Google Earth; in total, 29 streams were located. The density data generated in Chapter 3 was scaled up and extrapolated for the area of the beach included in the model.

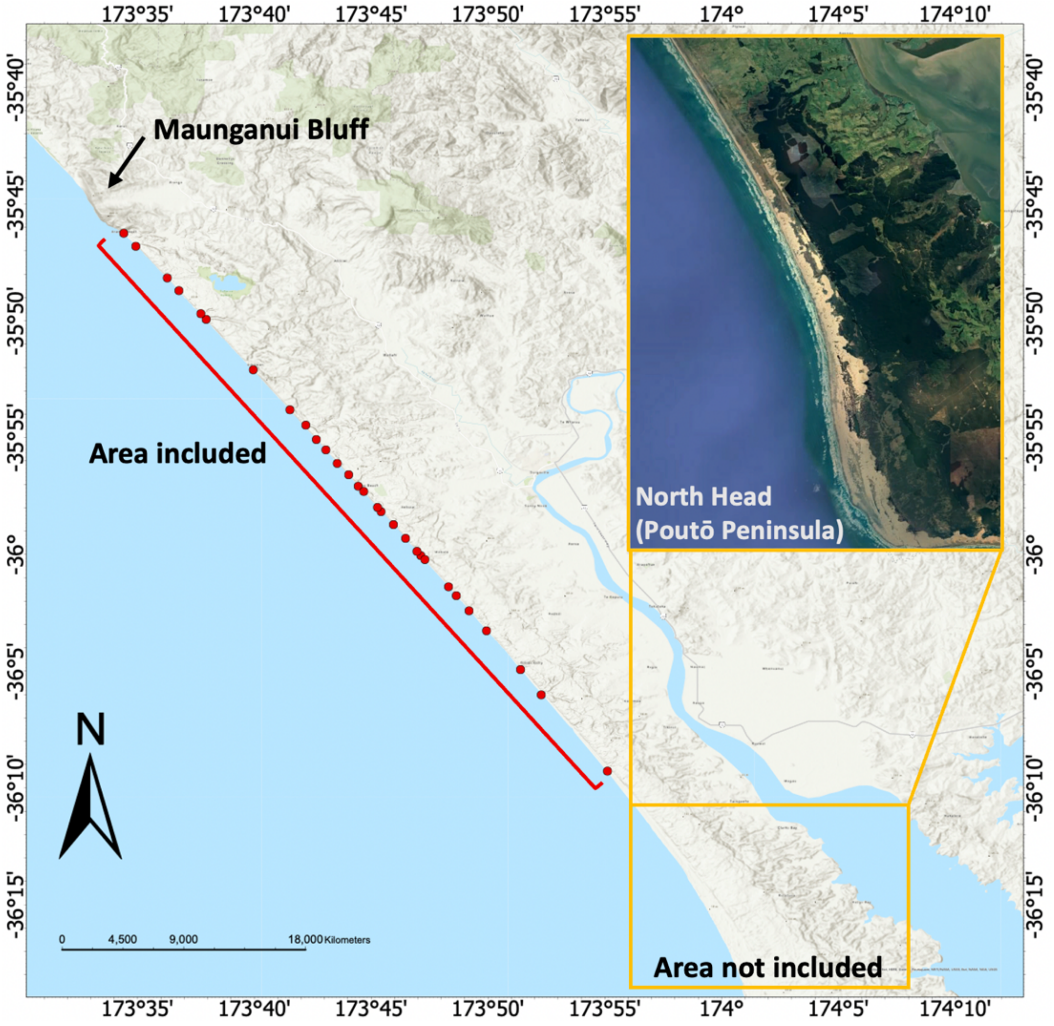


Figure 32: Map of the study location. Red dots represent the 29 streams, and yellow outline represents the beach area that was disregarded for estimation due to different environmental conditions. Map generated in Google Earth and ArcGIS pro, Coordinate system: WGS 1984 Web Mercator (auxiliary sphere). Spatial data obtained from ArcGIS pro: World Topographic Map.

4.3.2 Assumptions of the model

Due to the limitations of the survey data, assumptions had to be made in order to extrapolate. Specifically, the habitat area had to be defined. Determining the size of stream habitats was complicated due to the variability of adult toheroa populations. For Ripiro Beach, there is no consistency amongst the literature defining the size of adult beds. Therefore, population estimates were calculated for two scenarios to cover potential variation between the upper and lower limits. For scenario 1, a conservative lower limit estimate of 10 m widths was chosen for stream habitats. For scenario 2, the stream habitat width upper limit was 100 m. The length of stream and non-stream habitats was defined from the transects from survey data. Ripiro Beach has varied littoral widths, and the incoming tides limited some transect lengths. Embayments on stream habitats create different topography; juvenile toheroa tend to have wider littoral distributions compared to non-stream habitats. Therefore, the length of the stream habitats was standardised to 100 m, and the non-stream habitats were 60 m (Figure 33).

Figure 33: Schematic example of beach profile broken down into habitats; yellow represents streams, and red represents non-streams. Image retrieved from Google Earth.

4.3.3 The model

Population estimates were based on the survey data collected from the transects on Ripiro Beach, full survey methodology is detailed in Chapter 3 (Table 7). Equations for the model were adapted from Akroyd *et al.* (2002).

Table 8: Summary of mean density statistics of toheroa on Ripiro Beach.

Date	Location	Habitat	Mean Density ($0.25\ m^2$)	SD (σ)	SE ($\pm$)	Max	Min	Total abundance
February	Baylys Beach	Stream	82.94	76.18	19.05	256	1	1326
	Non-bed	Non-stream	45.64	48.69	14.68	150	0	500
	Maramoenui	Stream	101.83	82.37	22.84	297	22	1222
May	Maramoenui	Stream	3	4.18	1.16	16	0	35
	Non-bed	Non-stream	2.43	3.05	1.15	8	0	17
	Mahuta Gap	Stream	13.67	20.5	5.92	62	0	164
	The Island	Stream	3.86	5.4	2.2	16	0	24

In order to estimate the total population on Ripiro Beach, scaling factor w_i was calculated with the following formula:

$$w_i = L_i \;x\; t_i$$

Where L_i is the length of the beach that the habitat occupies, and t_i is the width of the beach (transect length) (Table 9).

Table 9: Summary of habitat area parameters for scenarios 1 and 2.

Habitat	Parameters	Scenario 1	Scenario 2
Whole beach	Length	53,000 m	53,000 m
Stream (S)	Number of streams	29	29
	Habitat dimensions	10 m x 100 m (t_i)	100 m x 100 m (t_i)
	Length of beach occupied	290 m (L_i)	2,900 m (L_i)
	Total beach area	29,000 m^2	290,000 m^2
Non-stream (NS)	Length of beach occupied	52,710 m (L_i)	50,100 m (L_i)
	Habitat dimensions	52,710 m x 60 m (t_i)	50,100 m x 60 m (t_i)
	Total beach area	3,162,600 m^2	3,006,000 m^2
Total beach area		3,191,600 m^2	3,296,000 m^2

Thus, the total abundance of toheroa, *M,* was estimated to be:

$$M = \left(\sum_i w_i \; 4M_i \right) \pm SE$$

Where M_i is the mean density of toheroa per quadrat on the transect, multiplied by 4 to scale 0.25 m^2 (0.5 m x 0.5 m) quadrats to the w_i scaling unit (m^2), and *SE* is the standard error.

Calculating Standard Error:

n = Sample size
σ = Standard deviation
SE = Standard error

$$\mathrm{SE} = \frac{\sigma_i}{\sqrt{n_i}}$$

The *SE* of the total estimated population was then scaled for the whole beach as given by Snedecor and Cochran (1989), where SE_i is the standard error of the mean density per quadrat on the transect.

$$\mathrm{SE} = \sqrt{\sum_i w_i{}^2\ 4SE_i^2}$$

The *SE* was also multiplied by 4 to apply the same scale as the estimated density. Final values were obtained by taking a mean from all the transects within the habitat (averages could not be taken for non-stream habitats due to the dataset limitations). Size cohort frequencies were estimated by grouping toheroa by length (0-5 mm, 5-10 mm, 10-15 mm, >15 mm) within each habitat and applying the same aforementioned methodology. Calculations, table summaries, and graphical data visualisation were generated in Microsoft Excel.

4.4 Results

4.4.1 Scenario 1

In February, 98 % of the estimated population was contained within the non-stream habitat and only 2 % within streams (Figure 34). By May, there was a slight habitat shift to 97 % on non-streams and 3 % on streams. The total February population was estimated to be 587.58 (± 188.17) million (Table 10). With 10.26 (± 2.45) million on streams and 577.32 (± 185.72) million on non-streams. There was a 94.6

% reduction by May, with the estimated population dropping to only 31.51 (± 14.92) million. The stream habitat contained 0.79 (± 0.36) million, compared to 30.72 (± 14.56) million in the non-stream habitat. The SE error was higher in May, with a relative standard error (RSE%) of 47.35 % compared to 32.02 % in February. This is attributed to the lower abundance of toheroa sampled, creating higher statistical variability.

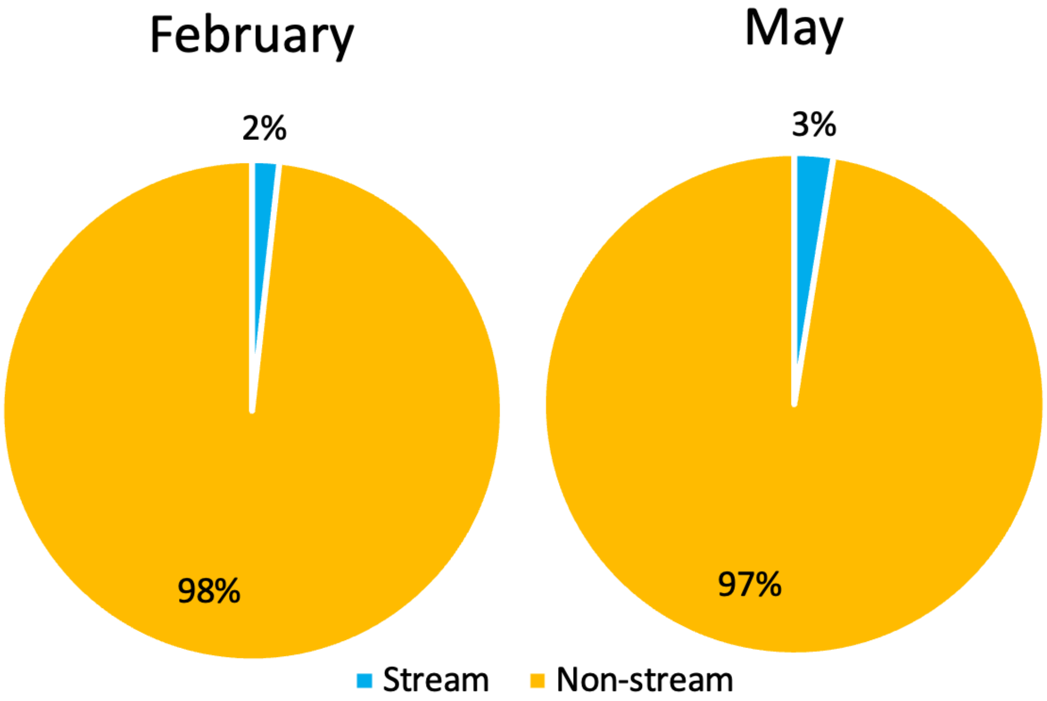


Figure 34: Pie chart for scenario 1 portraying the percentage (%) of the population inhabiting the different habitat types, streams (blue), and non-streams (yellow).

Table 10: Scenario 1 population estimate of juvenile toheroa on Ripiro Beach in 2022.

Habitat	**February**			**May**		
	Million	**SD(±)**	**RSE(%)**	**Million**	**SD(±)**	**RSE(%)**
Stream	10.26	2.45	23.88	0.79	0.36	45.23
Non-stream	577.32	185.72	32.17	30.72	14.56	47.43
Total	**587.58**	**188.17**	**32.02**	**31.51**	**14.92**	**47.35**

In February, when the population was broken down into size cohorts, abundance decreased with increasing size. Inversely, the SE increased with increasing shell size (low sampling abundance, higher statistical variability) (Table 11). The 0-5 mm cohort was the most abundant, contributing to 78 % of the total estimated population (hereafter streams = *S,* non-stream = *NS*) (*S* = 77%, *NS* = 1.34%) (Figure 35). With 450.86 (± 165.92) million in non-streams and 7.82 (± 1.78) million in streams. The 5-10 mm cohort contributed 20% of the total population (*NS* = 19.8%, *S* = 0.34), with 116.13 (± 44.89) million on non-streams and 2.07 (± 0.93) million on streams. The 10-15 mm cohort only comprised 1 % of the population (*S* = 0.97%, *NS* = 0.04%), with 5.69 (± 4.96) million on non-streams and 0.23 (± 0.13) million on streams. The error margins are highest for this cohort, with RSE at 87.1 % (*NS*) and 55.9 % (*S*). The >15 mm cohort had the lowest abundance at only 0.41 % of the population (*NS* = 0.39%, *S* = 0.02%), with 2.28 million (± 1.53) on non-streams and 0.14 million (± 0.07) on streams.

By May, abundance had reduced to 5.62 (± 5.49) million for the 0-5 mm cohort, it dropped to only 17.82 % of the population (*NS* = 17.25, *S* = 0.57). With 5.44 (± 5.4) million on non-streams and 0.18 (± 0.09) million on streams. However, the most abundant size cohort had shifted to 5-10 mm, comprising 75.8 % of the population (*NS* = 74.5%, *S* = 1.3%). Non-streams had 23.49 (± 13.87) million, and streams had 0.41 million (± 0.18). The 10-15 mm cohort contributed just 6.28 % of the population (*NS* = 5.61%, *S* = 0.67), with 0.21 (± 0.13) million on streams and 1.77 (± 1.82) million on non-streams. The SE is high for non-streams because only one toheroa was found within the whole habitat. A small quantity of toheroa > 15 mm was estimated on streams at only 0.1 % with 0.03 million (± 0.02), and none were found on non-streams.

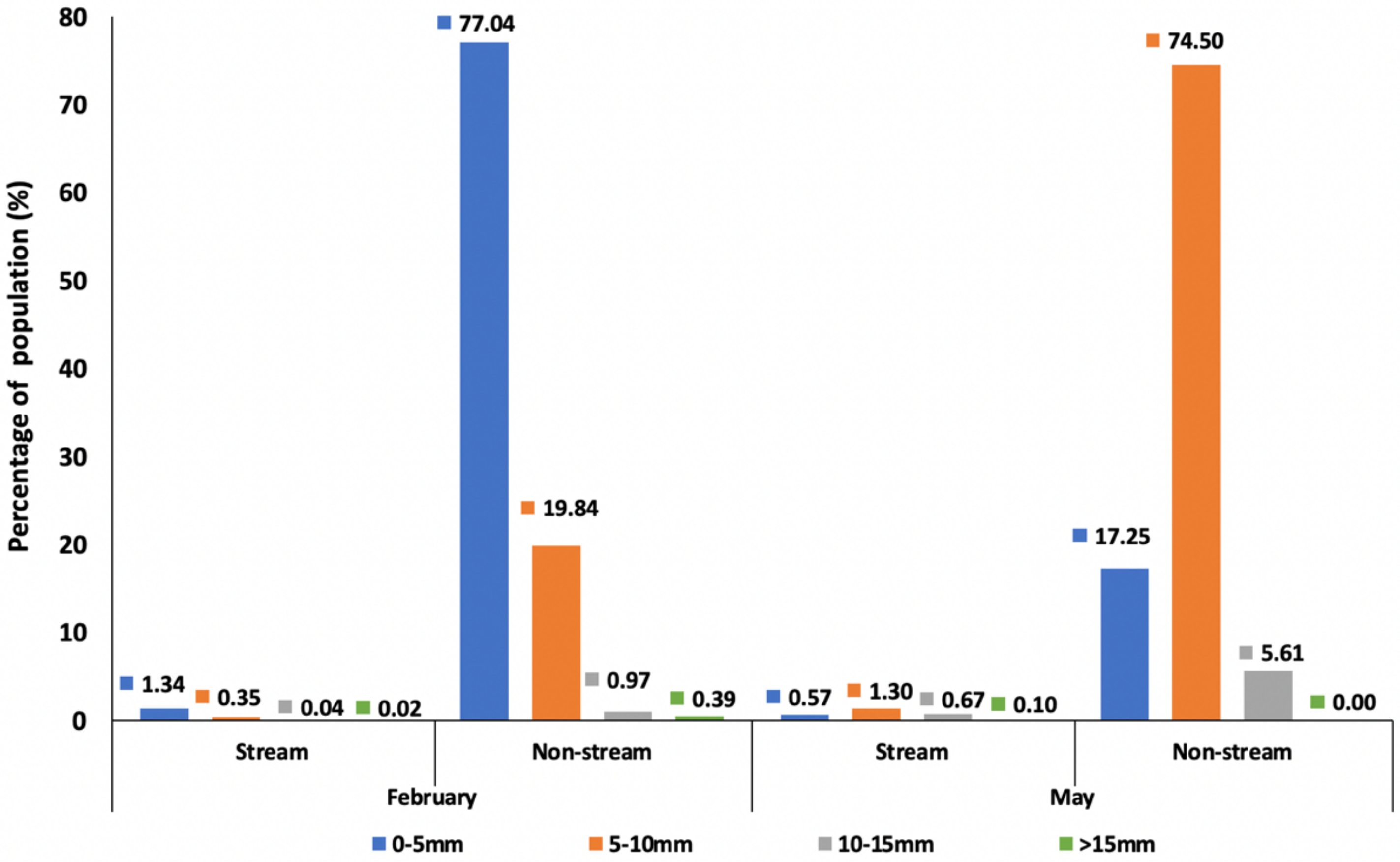


Figure 35: Scenario 1, bar chart portraying the distribution in percentages (%) of cohorts within each habitat from February to May (streams Vs non-streams).

Table 11: Scenario 1 estimation of the juvenile population on Ripiro Beach in 2022 broken down into size cohorts.

Habitat	Size Cohort (mm)	February			May		
		Abundance (Million)	SD(±)	RSE(%)	Abundance (Million)	SE(±)	RSE(%)
Stream	0-5	7.82	1.78	22.79	0.18	0.09	50
	5-10	2.07	0.93	45	0.41	0.18	43
	10-15	0.23	0.13	55.89	0.21	0.13	65
	>15	0.14	0.07	49.12	0.03	0.02	58.22
Non-stream	0-5	450.86	165.92	36.9	5.44	5.4	99.33
	5-10	116.13	44.89	38.66	23.49	13.87	59
	10-15	5.69	4.96	87.1	1.77	1.82*	102.59*
	>15	2.28	1.53	67	0	-	-
Total	0-5	458.68	167.7	36.56	5.62	5.49	97.69
	5-10	118.2	45.82	38.76	23.90	14.05	58.79
	10-15	5.92	5.09	85.98	1.98	1.95	98.48
	>15	2.42	1.6	66.12	0.03	0.02	58.22

* SD (±) is higher because only one animal was found within the habitat.

4.4.2 Scenario 2

In February, 82 % of the estimated population was contained within the non-stream habitat and only 18 % was within streams (Figure 36). By May, the distribution between habitats shifted by 3 %, with 79 % on non-streams and 21 % on streams. The total population was estimated to be 594.91 (± 179.85) million, with 137.63 (± 32.74) million on streams and 457.28 (± 147.11) million on non-streams (Table 12). By May, there was a 94 % reduction in overall abundance, and the population dropped to only 37.15 (± 17.33) million. The stream habitat contained only 7.95 (± 3.48) million, with 29.2 (± 13.85) million on non-streams. The same pattern is observed with increasing SE in May, with the relative standard error (RSE%) at 30.23 % in February compared to 46.65 %. In February, scenario 2 estimates were 63.81 million higher than scenario 1, and 5.64 million higher in May.

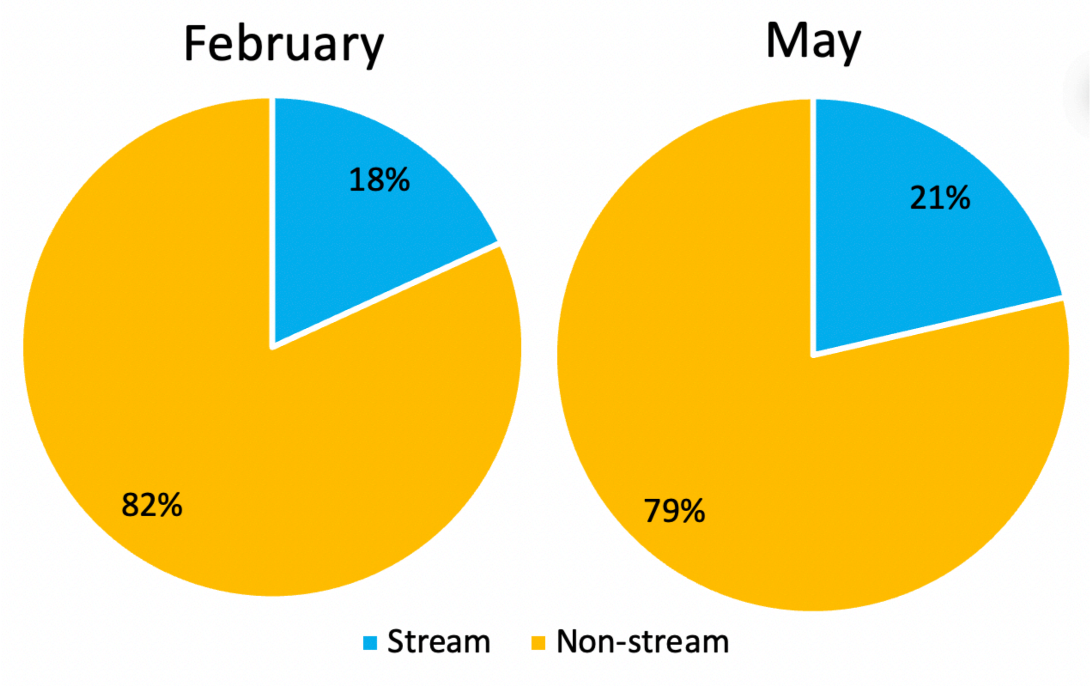


Figure 36: Pie chart for scenario 2 portraying the percentage (%) of the population inhabiting the different habitat types, streams (blue), and non-stream (yellow).

Table 12: Scenario 2 estimated population of juvenile toheroa on Ripiro Beach in 2022.

Habitat	February			May		
	Million	SD(±)	RSE(%)	Million	SD(±)	RSE(%)
Stream	102.66	24.52	23.88	7.95	3.59	45.23
Non-stream	548.73	176.53	32.17	29.2	13.85	47.42
Total	**651.39**	**201.05**	**30.86**	**37.15**	**17.44**	**46.94**

For the cohort distributions in February, abundance decreased with increasing size, and the SE and RSE increased with size. The 0-5 mm cohort was the most abundant, comprising 77.94 % of the total population (*NS* = 60.23%, *S* = 17.71%) (Figure 37). There was an estimated 357.11 (± 131.42) million on non-streams and 104.98 (± 24.02) million on streams (Table 13). The 5-10 mm cohort contributed 20 % of the population (*NS* = 20.16%, *S* = 4.65%), non-streams were estimated to hold 91.98 (± 35.56) million, and streams were 27.57 (± 12.48) million. The 10-15 mm cohort was only 1.3 % of the population (*NS* = 0.76%, *S* = 0.54%), with 4.51 (± 3.93) million on non-streams and 3.19 (± 1.75) million on streams. Only 0.6% of the population were >15 mm (*NS* = 0.3%*,* *S* = 0.3%), with 1.8 (± 1.21) million on non-streams and 1.77 (± 0.89) million on streams.

By May, the 0-5 mm cohort had a significant reduction and only comprised 18.15 % of the population (*NS* = 13.78%, *S* = 4.37%). Estimates declined to 5.17 (± 5.14) million on non-streams and 1.64 (± 0.77) million on streams. The most abundant size cohort shifted to 5-10 mm at 70.52 % of the population (*NS* = 59.51%, *S* = 11.01%). With 22.33 (± 13.18) million on non-streams and 2.21 (± 1.29) million on streams. The 10-15 mm cohort only contributed to 10.37 % (*NS* = 4.48%, *S* = 5.89%), streams had 2.21 (± 1.29) million, and non-streams had 1.68 (±1.73) million. The SE is high because only one toheroa was found in the habitat. Only 0.96 % of the population was >15 mm (*NS* = 0%, *S* = 0.96%), with 0.36 (±0.21) million on streams; none were found on non-streams.

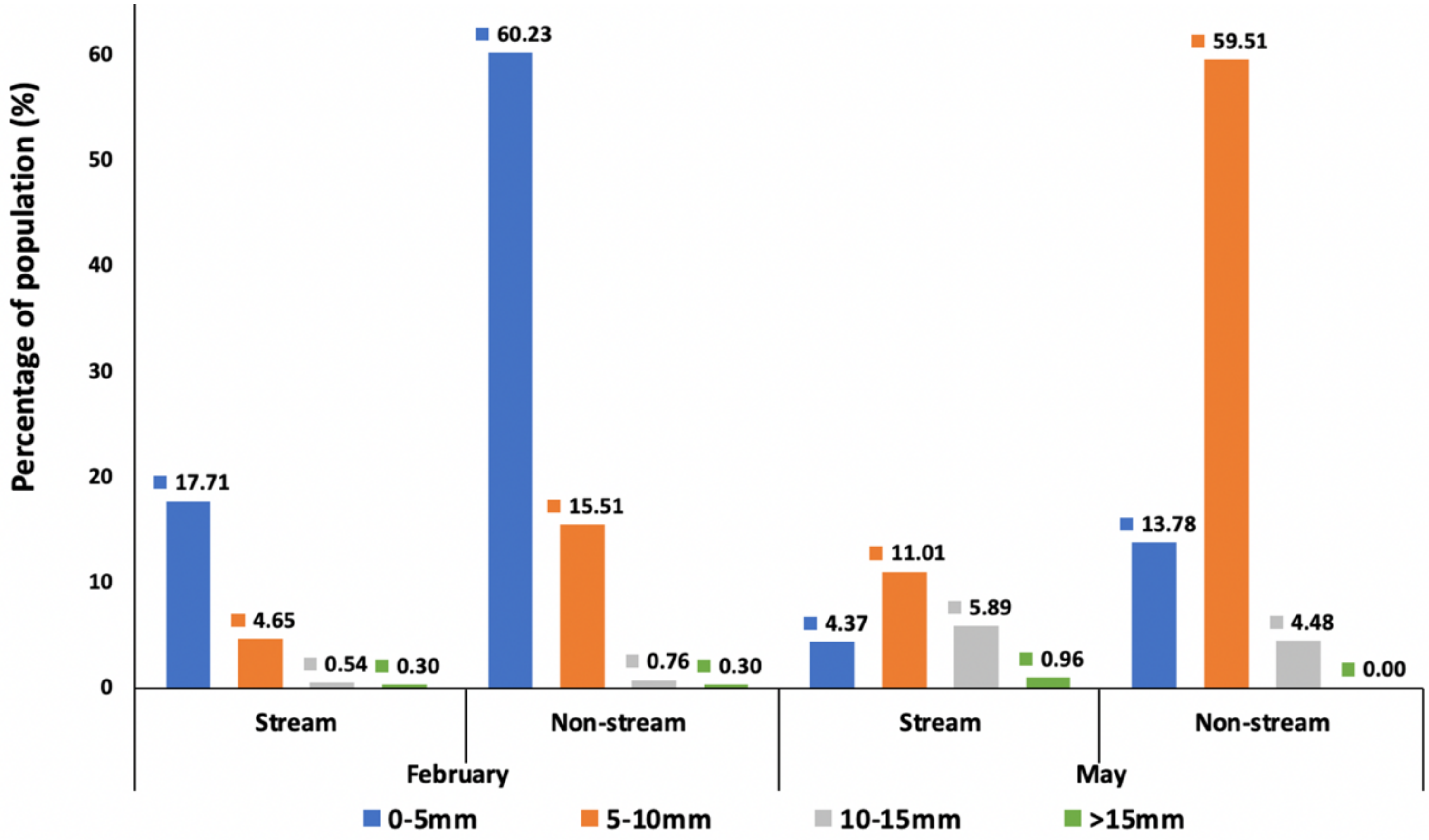


Figure 37: Scenario 2, bar chart portraying the distribution in percentages (%) of cohorts within each habitat from February to May (streams Vs non-streams).

Table 13: Estimates of the juvenile population on Ripiro Beach in 2022 broken down into size cohorts, beach width based on adult bed sizes of 100m.

Habitat	Size Cohort (mm)	February			May		
		Abundance (Million)	SE(±)	RSE(%)	Abundance (Million)	SE(±)	RSE(%)
Stream	0-5	104.98	24.02	22.88	1.64	0.77	47.06
	5-10	27.57	12.48	45.28	4.13	1.73	42
	10-15	3.19	1.75	54.88	2.21	1.29	58.46
	>15	1.77	0.89	50.17	0.36	0.21	57.72
Non-stream	0-5	357.11	131.42	36.8	5.17	5.14	99.33
	5-10	91.98	35.56	38.66	22.33	13.18	59.02
	10-15	4.51	3.93	87.1	1.68	1.73*	102.59*
	>15	1.8	1.21	67	0	-	-
Total	0-5	462.09	155.44	33.64	6.81	5.91	86.78
	5-10	119.56	48.04	40.18	26.46	14.91	56.35
	10-15	7.69	5.68	73.86	3.89	3.02	77.63
	>15	3.57	2.1	58.82	0.36	0.21	58.33

* SD(±) is higher because only one animal was found within the habitat.

4.5 Discussion

The aim of this chapter was to create a model that could be used to estimate the total population of juvenile toheroa on Ripiro Beach. Initial estimates of the population on Ripiro Beach varied depending on the beach area assigned as stream vs non-stream habitat. As there was no available information regarding toheroa bed widths on Ripiro, population estimates were calculated for two scenarios to account for upper and lower limits, one with a conservative average bed width of 10 m and the other with an average bed width of 100 m. Interestingly, stream width had a surprisingly small influence on the total estimate. In February, the estimates between the upper and lower limits ranged between 590 million and 650 million, with only a 60 million difference. This was because either 99 % (scenario 1) or 91 % (scenario 2) of the total beach area was classified as non-stream habitat.

The total population estimate was significantly higher in February compared to May, with a > 93 % decrease in abundance over time. There was also a shift in cohort assemblages and distributional patterns towards the stream habitat. Relative to the area of the non-stream habitat, larger toheroa were scarce (no toheroa >15 mm in May). It is difficult to determine whether this shift in distribution is a function of active habitat selection or differential mortality due to unfavourable conditions (e.g. desiccation). Habitat selectivity could represent ontogenetic niche shifting; adult toheroa populations primarily exist on streams and have been known to migrate via swash riding (Redfearn, 1974; Ross *et al.,* 2018a). However, as there is no definitive answer, the distributional changes in estimates could be assumed to be a combinational effect of differential mortality and ontogenetic behaviour. There was a substantial loss of toheroa from the 0-5 mm cohort. This likely indicates growth, mortality, and the end of the major spawning season. Such factors would explain why the 10-15 mm cohort had the lowest population decrease and shifted to the dominant size cohort in May. However, since all cohorts showed significant declines, mortality is the most probable cause of overall abundance loss.

The primary reason for my study is to determine whether there is viability for toheroa in the aquaculture industry based on the wild harvest of juveniles. With

February estimations >590 million and abundance losses >93%, I believe my study advocates that toheroa populations on Ripiro Beach are not recruit-limited. From an aquaculture perspective, the wild harvest of juvenile toheroa spat appears to be a viable option. However, time sensitivity will be a potential limitation in future. Based on my results, it is likely that the optimal harvesting time is late February. However, due to the unknown seasonal population changes, it could also lie somewhere within or before this timeframe. Furthermore, error margins were higher for May, indicating unreliability in the estimation. Additionally, in real-world applications, even if there were high May abundances, they would be less densely packed, requiring a broader harvesting area. Ideally, harvesting a sufficient amount without needing to cover a large beach area would be more practical and create less environmental disturbance. In February, the non-stream habitat held significantly high abundances, especially for smaller cohorts. Because adults do not survive in these habitats, spat harvesting would not disturb or have any severe ecological impacts on adult populations. The distance between streams is extensive, and it is highly feasible to avoid beds entirely. Ethically, taking larger toheroa will have a greater ecological impact on the population than smaller spat. However, larger spat are more likely to have lower mortality and higher relocation success in hatcheries.

For example, In the Fijian Islands, Erasito *et al.* (2022) looked at the effect of harvesting time on the growth of pearl oysters (*Pinctada margaritifera*). Spat collectors were deployed, and oysters were either left to grow in open waters or were harvested and on-grown in artificial aquaculture panel nets. Smaller growth rates were observed for earlier harvested and relocated oysters than those that remained on open water spat collectors. Additionally, Heslinga *et al.* (1984) looked at the success rate of reseeding hatchery-reared giant clams (*Tridacna derasa*) in Palau; they found that survival was lower with small juveniles, even with protection and husbandry. Supono *et al.* (2020) looked at the effect of different-sized green-lipped mussel spat (*Perna canaliculus*) on retention in aquaculture settings. They found that smaller spat (0.5 mm – 1 mm) had lower retention than larger spat (2 mm – 5 mm). They also found that feeding wild harvested spat prior to re-seeding improves spat condition. Additionally, they found that larger spat had higher success rates for re-seeding on aquaculture farms. Therefore, they suggested only re-seeding larger spat with good nutritional condition whilst nursey culturing smaller spat. This could indicate that freshly settled toheroa spat of 2 mm would have higher mortality rates and lower success during harvest and relocation. For this reason, harvesting should be optimised for taking the largest toheroa possible without compromising the wild population. In February, the non-stream habitat had upwards of 90 million toheroa from the 5-10 mm cohort. This abundance is substantial enough that harvesting even a large quantity would have little impact on the overall population.

Reseeding with hatchery-reared spat has been proposed as an alternative management approach for natural population enhancement and restoration (Newcombe *et al.*, 2015; Ross *et al.,* 2018a). In particular, interest has emerged from Māori groups for culturing this taonga as both a conservation method and a commercial venture (Ross *et al.,* 2018a). Developing commercial spat cultivation could facilitate the application of large-scale reseeding endeavours for natural populations (Nascimento-Schulze *et al.,* 2021). The challenges of adapting existing culture techniques to suit species like toheroa that inhabit high-energy environments have been discussed by Newcombe *et al.* (2015).

Hatchery-based restoration is only viable if the underlying ecology of environmental factors and life history bottlenecks inhibiting the recovery of wild toheroa populations is understood. For example, reseeding toheroa populations is likely ineffective in areas where recruitment rates are high, but mass mortality occurs during the early stages of growth (like Ripiro Beach) (Ross *et al.,* 2018a). Inversely, in locations where recruitment is limited, reseeding populations could surpass the natural obstacles preventing recovery. For example, Wasson *et al.* (2020) looked at Olympia oysters (*Ostrea lurida*) in Elkhorn Slough, an estuary in central California (USA). The population appeared to be recruitment limited, wherein no new juveniles had been overserved in over seven years. Successful population enhancement was achieved using hatchery-reared juveniles from spawning induction of local brood stock, which were later seeded into the estuary.

Unsuitable habitats and deteriorated ecosystems will not support population enhancement; more information is required regarding environmental drivers of toheroa mortality before implementing hatchery-based restoration. For example, one of the most well-documented shellfish restoration case studies in NZ is that of the intertidal cockle *Austrovenus stutchbury*, wherein Cummings *et al.* (2007) transplanted hatchery-reared adult cockles onto previously prolific beds. They found that anthropogenically degraded substrates had low survival, but relatively pristine systems had higher survival rates even a year after transplantation. The viability of stock enhancement with hatchery-reared seed for NZs Pāua *(Haliotis iris*) was explored by Roberts *et al.* (2007). They found that higher mortality rates were observed on unsuitable substrates and locations subject to habitat disturbance. Additionally, larger seed sizes had lower mortality, but increased survival of Pāua larger than 10 mm did not offset the cost associated with longer culturing durations.

Biotic, abiotic, and anthropogenic activity can also have cascading effects on clam aquaculture and wild-caught fisheries. Factors such as diseases (predominantly viruses, bacteria, and protozoa) (Carella *et al.,* 2015), temperature, salinity, and ocean acidification have been known to cause stock collapse (Velez *et al.,* 2016). For example, Ford *et al.* (2002) discovered the Quahog Parasite Unknown (QPX) pathogen in hatchery and nursery tanks for the hard clam *Mercenaria mercenaria* in New Jersey (USA). They found that importing seed from non-local stocks caused mortalities between 26 % to 92 %. With regard to toheroa, the detection of RLOs (Rickettsia-like organisms (bacteria)) and gas-bubble disease (Ross *et al.,* 2017) has raised concern and been implicated with population declines and mass mortalities in Taitokerau (Ross *et al.,* 2018a; Williams *et al.,* 2013b). This could have wider aquaculture implications regarding translocations and reseeding programmes, the spread of pathogens between unaffected populations could induce further mortalities and exacerbate population declines. Additionally, oceanic heatwaves (Broekhuizen *et al.,* 2021) and warming climatic conditions (Philippart *et al.,* 2003) have resulted in mass bivalve juvenile mortality and reduced reproductive output in both wild populations and offshore aquaculture. Furthermore, sediment acidification in coastal nearshore ecosystems has been identified as a mechanism affecting clam mortality, recruitment, and dispersal (Clements & Hunt, 2014). Such factors could negate the success of population enhancement; without understanding the underlying causes for mortality, it is difficult to determine if reseeding toheroa populations would be successful.

While the findings from my research suggest that toheroa aquaculture is viable, confidence in my estimations is limited due to undefined annual recruitment variation and statistical uncertainty. Sufficient quotas and stock assessment must be closely managed to ensure the natural regenerative capacity is not exceeded. Looking through the lens of a conservationist, many of the primary ecological concerns are addressed due to the high abundance of small recruits and the ability to avoid adult populations during harvesting. From a tangata whenua perspective, as I am not a resident of the region, nor a member of local iwi or hapū, it is not within my jurisdiction to decide whether toheroa should be implemented in the aquaculture industry. However, I believe my results indicate that harvesting can be achieved without compromising the wild population. Developing the facilitation of hatchery-reared toheroa could advance our ecological knowledge of juvenile spat. Additionally, aquaculture could reintroduce toheroa as a kaimoana, which might reduce illegal recreational harvesting pressure. Essential factors such as spat size and season time will be crucial when establishing a strategy for harvesting with a low ecological impact but high hatchery success. To manage future conservation practices, we must define the underlying causes of juvenile mortality.

4.5.1 Possible causes for juvenile mortality

Since juveniles were seen in large quantities in February, lack of recruitment does not appear to be the driving cause for the continued decline of toheroa populations. Many marine species worldwide have failed to recover following stock collapse (Froese & Kesner-Reyes, 2002). Research from Hobday *et al.* (2000) looked at the decline of white abalone (*Haliotis sorenseni*), a marine invertebrate once considered inexhaustible that suffered greatly from exploitation. Much like toheroa, deteriorating population size saw the implementation of fisheries regulations. However, it was concluded that reducing the density of the adult population had adverse effects on fertilisation success and increased recruitment failure, which continued through to post fisheries regulations. This observation coincides with the lack of recovery exhibited by toheroa even 40-plus years after the ban on harvesting. However, it does not appear that toheroa have reduced fertilisation success, but rather a bottleneck mortality of juveniles. Factors considered to be prohibiting recovery were summarised by Williams *et al.* (2013b) and included weather, climate, catchment modification, food availability, water quality, and vehicle activity.

It is widely known that catchment modification can severely affect terrestrial-linked marine ecosystems (Tallis *et al.,* 2008). This is typically attributed to pollution, increased sedimentation in freshwater discharge, or stream input diversion and reduction (Roebeling *et al*., 2009). Due to these modifications, fluxes in energy within soft sediments can increase mortality rates of marine benthic communities (Thrush *et al.,* 2006). Globally, coastal and nearshore ecosystems have faced huge increases in agriculture and urbanisation within the catchment, causing significant disruptions to the hydrological cycle (Prosser *et al.,* 2018). It is well documented that toheroa struggle to thrive in locations without ample substrate saturation (Rapson, 1952; Redfearn, 1974). Thus, a factor potentially causing mass mortality could be desiccation due to land use change.

The Ripiro catchment area was once populated by native broadleaf forest (Ross *et al.,* 2018a). Much of this land was cleared by Māori (500-700 years ago), and the remaining fragments were removed by early European settlers (Coster, 1989; Smale *et al.,* 1996). Research from Cope (2018) found that streams modify environmental conditions on Ripiro Beach. Sediment on stream outlets had lower temperatures and reduced distance between the sediment surface and the water table. These two factors likely reduce the risk of desiccation driving higher survival rates and aggregations on streams. This could indicate why lower abundances and fewer toheroa greater than 10 mm were found in non-stream habitats. There have been some local accounts of freshwater diversion due to pumping from coastal bores onto agricultural farmland (Cope, 2018). However, forestry has been primarily blamed for reducing the volume and degrading water quality in the streams that flow onto toheroa beds (Ross *et al.,* 2018a; Smith, 2013).

With upwards of 90% of the population inhabiting the top 5 cm of the sediment surface, as detailed in Chapter 2, beach traffic could potentially cause increased mortalities for juvenile spat. Because Ripiro Beach is a designated state highway, it is frequently subjected to vehicle traffic (Ross *et al.,* 2018a). During fieldwork, cars and four-wheel drive vehicles were often seen driving along the beach, some leaving burnouts on the shore (Figure 38). Ecological impacts of vehicle traffic are known to cause significant environmental management issues on sandy shores, and benthic fauna are often affected interspecifically due to changes to community structure (Sheppard *et al.,* 2009; Taylor, 2013). In the sandy shores of eastern Australia, Schlacher *et al.* (2008) reviewed the changes in body condition and burrowing of the beach clam *Donax delto.* The findings showed that the body mass index was 16% lower in high-traffic zones. Additionally, off-road vehicles substantially impaired the burrowing ability of the clams. Research from Taylor (2013) found that traffic associated with urbanisation had mixed results on clams. Juvenile recruits and abundances of *Amarilladesma mactroides* decreased, and *Donax hanleyanus* juveniles increased with higher urbanisation. Toheroa could be affected by traffic on Ripiro Beach; juveniles are relatively soft-bodied and easy to break (Redfearn, 1974).

Another potential cause for toheroa mortality has been attributed to both avian and pelagic predation. Some of the predators known to toheroa have been outlined as the black-billed gull (*Larus dominicanus*) (Brunton, 1978), red-billed gull (*Larus novaehollandiae scopulinus*), the snapper (*Chrysophrys auratus*), oystercatchers (*Haematopus spp.*), and the short-tail sting ray (*Dasyatis brevicaudatus*) (Rapson, 1952; Redfearn, 1974; Street, 1971). However, Vallyon (2020) looked at the predation effects on toheroa from oystercatchers (*Haematopus ostralegus finschi*) on Ripiro Beach. There appeared to be some localised impacts, but ultimately they were not determined to be the cause for the lack of toheroa recovery.

Figure 38: Burnouts and car tracks on Ripiro Beach in February. Drone photo by E. Russel.

4.5.2 Limitations and future recommendations

Due to the lack of juvenile toheroa surveys, it is impossible to determine whether my estimates are comparable to previous years or even ascertain if the population is still declining. However, I believe the estimates produced from the model I created serve as preliminary indicators of the juvenile population. Due to the impacts of COVID-19, the dataset is limited and lacks sufficient replication; there is limited certainty that these estimates are indicative of the actual population. Whether additional transects and a larger dataset would affect the final population estimate remains unknown. In addition, the largest area on the beach was the non-stream habitat, of which there was only one transect per each sampling period. Therefore, averages could not be taken, which does not allow for statistically confident calculations. Furthermore, if the sampled location held severe under or over-estimates of actual abundances in these habitats, it could drastically alter the results. A comprehensive survey that covered a wider area with replicate transects could reduce some of the standard error from the results whilst also inducing stronger confidence in the estimates. Additionally, the 2021-2022 recruitment season may not accurately represent annual variation. This season may have had higher or lower production compared to other years, it is widely known that toheroa populations exhibit considerable annual variation. There is also a possibility that different spatfalls throughout the spawning season do not have the same quantities, mortality rates, and growth rates. In order to truly assess the viability of aquaculture, successive surveys must be carried out each year to ensure that harvesting does not exceed the natural regenerative capacity. In future, surveys should be conducted throughout the entirety of the season to determine optimal harvesting time to ensure the highest success rates and lowest ecological impacts.

4.5.3 Conclusion

Although these estimates might hold a large margin of error, I believe my research shows that a lack of juvenile recruitment is not the cause for the failed recovery and continued decline of toheroa populations. There was a significant reduction in abundance over time, indicating high mortality rates during the early growth period. Distributional shifts in abundance and cohort assemblages towards streams may reflect active habitat selection or differential mortality due to unsuitable environmental conditions. Reasons for mortality are unknown, but habitat modification, global warming, and desiccation on unfavourable substrates are likely key contributors. My estimates show there is viability for aquaculture applications in the future. However, whether or not such a venture would be successful hinges entirely on the ability to facilitate culturing of small spat (0–10 mm). Additionally, the harvesting period is time-sensitive, recruitment varies annually, and only a small window is open when optimal spat sizes and abundances are present on the beach. Because high abundances were estimated on non-stream habitats, adult beds can be avoided during harvesting. From a cultural and Māori perspective, it is up to them to decide, but based on my results, harvesting is unlikely to compromise wild populations. Further research is required to establish a cost-effective, low-impact strategy that maintains sufficient hatchery success.

5 Chapter 5 – Handling and transportation stress

5.1 Introduction

Aquaculture based on the on-growing of wild harvested juveniles entails a complex handling chain (harvesting, transportation, relocation, growth) wherein the loss of animal condition and high mortality rates are regularly observed (Anacleto *et al.,* 2013; McEwan *et al.,* 2020). Stress induced by mechanical harvesting can elicit severe behavioural and physiological responses. Handling stress is determined to be a threat to animal health when a change in biological condition beyond the normal resting state has adverse effects on behaviours and homeostasis (Barton & Iwama, 1991). For example, in aquaculture, high-stress environments for crab and lobster species have been known to result in cannibalistic behaviours (Wingerter *et al.,* 2013). Additionally, Davis and Schreck (1997) found that the metabolic cost of handling stress resulted in increased oxygen consumption of juvenile coho salmon (*Oncorhynchus kisutch*).

Stressors associated with bivalve handling typically include emersion (air exposure), salinity shock, and physical injury (from harvest or animal interactions) (Wingerter *et al.,* 2013). Injuries such as open wounds and compression fractures from mechanical harvesting can allow for the loss of bodily fluids and increased risk of infection (Basti *et al.,* 2010). To ensure product quality, some species are often held in controlled settings for a period of time prior to transportation (typically seawater) to allow for a return to resting homeostasis post-harvest (Martin *et al.,* 2000; Wingerter *et al.,* 2013). Additionally, this holding period is used for transport preparation conditioning regimes. Wherein purging (fasting but not starving) minimises the discharge of waste during transit (e.g. ammonia) (Basti *et al.,* 2010; Wingerter *et al.,* 2013). A common occurrence with some species is the accumulation of high concentrations of ammonia associated with extended emersion durations (Wingerter *et al.,* 2013). Subsequently, excess amounts are released within 1 hour of re-immersion resulting in adverse physiological conditions during transit.

Long-distance transportation creates a wide range of stress-inducing factors from the moment of harvest to the moment they are consumed. Resistance to physiological collapse declines sharply as these stressors mount (Wingerter *et al.,* 2013). Stress can induce significant quality defects that reduce market value due to product degradation and mortality (Anacleto *et al.,* 2013). Holding and transit durations can vary anywhere from one hour to multiple days (Wingerter *et al.,* 2013). Typical stressors associated with transport include temperature extremes, ammonia poisoning, and physical injury resulting from compression/jostling (Christophersen *et al.,* 2008). The application of inadequate procedures and inferior materials during transit can exacerbate stress and mortality (Wingerter *et al.,* 2013). Therefore, implementing appropriate methodology and holding care are required to maximise success. When introducing a new species into the aquaculture industry, we must first develop a cost-effective transportation protocol that minimises handling stress. Behavioural ecology can be used as a tool to analyse how animals respond to stress-inducing factors and environmental changes within controlled settings. For example, Nickell and Moore (1992) observed eight species of scavenging invertebrates in tank settings to assess their response to altered water velocities on bait attraction.

Due to the dynamic nature of coastal ecosystems, species are subject to harsh conditions that often promote rapid survival responses (Allen & Vaughn, 2009). In marine bivalves, burrowing behaviour is considered an ecological compromise attributed to the harsh nature of the exposed coast they inhabit and a protective measure against predation (Haddon *et al.,* 1987; Kondo & Stace, 1995). Like most benthic bivalves, burrowing behaviour for toheroa consists of a succession of steps as stated by Kondo and Stace (1995): (1) initiation of the foot in a wavy action, (2) penetration of the substrate by the foot, (3) burrowing initiation, (4) erection of the shell, (5) complete burial of the shell, (6) attaining the final position within the substrate. Toheroa orient themselves on a 40°-50° degree angle, with the ventral margin facing the sea and the hinge facing the dunes (Stanley, 1973). Compared to other intertidal surf clams, toheroa display an efficient burrowing performance that reaches depths considered uncommon (>20 cm) (Kondo & Stace, 1995). In order to assess how handling and transportation affect juvenile toheroa, burrowing behaviour can be used as a quantitative indicator of stress. For example, van Gils *et al.* (2009) used the burrowing depth and growth rate of the bivalve *Macoma balthic* as an indicator of predation-induced stress. It has also been observed that bivalves exposed to prolonged stress can have impaired burrowing capabilities (Marin *et al.,* 2005).

5.1.1 Aims and research purpose

The purpose of this study is to gain some understanding of how different transportation methods could impact toheroa health, survival, or performance. To do this, I utilised the burrowing behaviour of juvenile toheroa in response to handling and transportation stress. Currently, there is no research regarding different methods for transporting live toheroa. I aim to outline how mechanical harvesting and different transport treatments of post-harvest juveniles affect burrowing ability. The findings from this study will be used to inform any potential future aquaculture avenues. To do this, I developed three different potential methods of transportation.

The first method I chose was freshly collected seawater from the harvesting site. Many transport methods involve seawater storage facilities. For example, the transportation of juvenile fluted giant clams (*Tridacna squamosa*) has been conducted in plastic bags filled with filtered seawater (Gould *et al.,* 2012). Additionally, studies on transportation methods of live black clams (*Villorita cyprinoides*) also used packing techniques in oxygenated water (Gopal *et al.,* 1985).

For a low-cost, easily sourced option, I used a seawater-dampened cotton cloth (towel). Similarly, materials for the Dungeness crab (*Metacarcinus magister*) involve placing an absorbent pad soaked with seawater on top of the product. Additionally, pacific oysters have been known to be transported in boxes with seawater-dampened towels to ensure sufficient moister and humidity (Wingerter *et al.,* 2013). South *et al.* (2020b) implemented similar techniques when researching the effect of storage on the resettlement of wild-harvest juvenile mussels (*Perna canaliculus*). Experiments were conducted by placing juveniles within an insulated box lined with seawater-dampened towels stored at 20 °C.

Finally, the third option I chose was sand collected directly from the harvest site. I chose this because it better caters to surf clams and mimics the desired niche of toheroa. Toheroa do not like to be exposed, so the ability to remain burrowed within the substrate may be less stressful.

I addressed the following research questions:

(1) Does handling and harvesting stress affect toheroa burrowing ability?

(2) What method is best suited for transporting juvenile toheroa; sand, seawater, or damp cloth?

(3) Does prolonged exposure to transportation stress have an effect on burrowing ability?

5.2 Methods

Toheroa were collected from Baylys Beach in February 2022. A full description of Ripiro Beach is outlined in Chapter 2 (Figure 39).

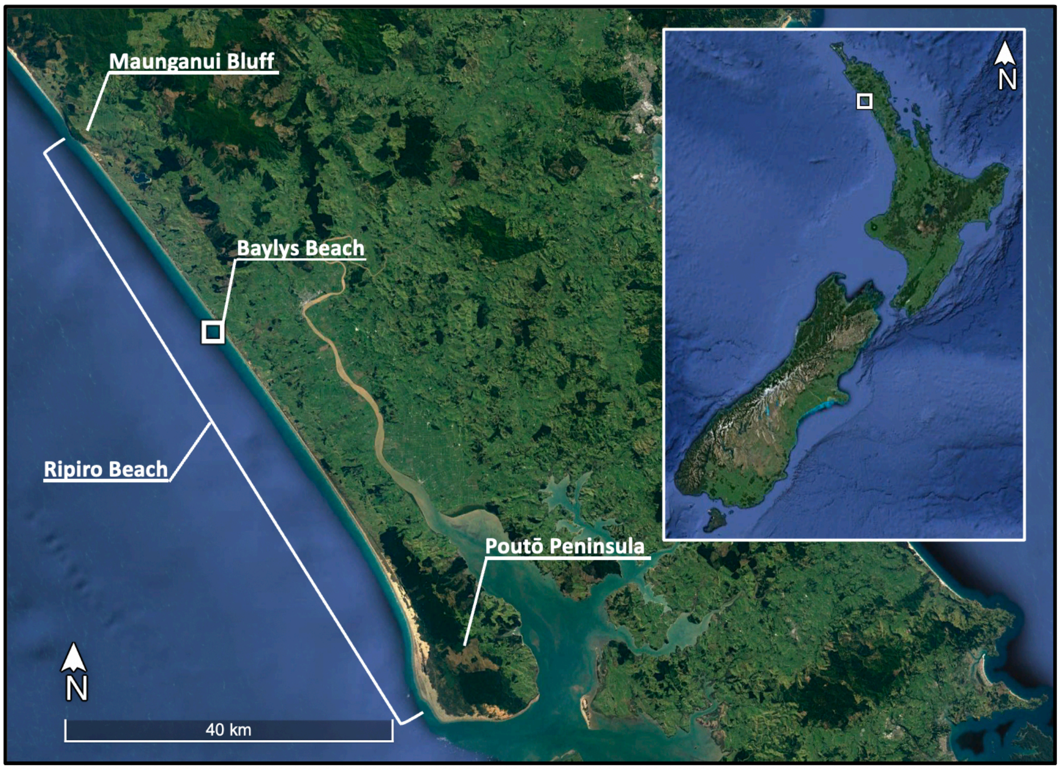


Figure 39: Map displaying the section of Ripiro beach where toheroa were collected from. Image retrieved from Google Earth.

5.2.1 Experimental design

The purpose of this experiment was to mimic real-world applications wherein juvenile spat are harvested from the wild and transported to hatcheries. In order to assess this, I conducted an experiment that analysed the burrowing behaviour after wild harvest, and then again after transportation in three different treatment types. A flow chart describing the methodology I used is detailed in Figure 40.

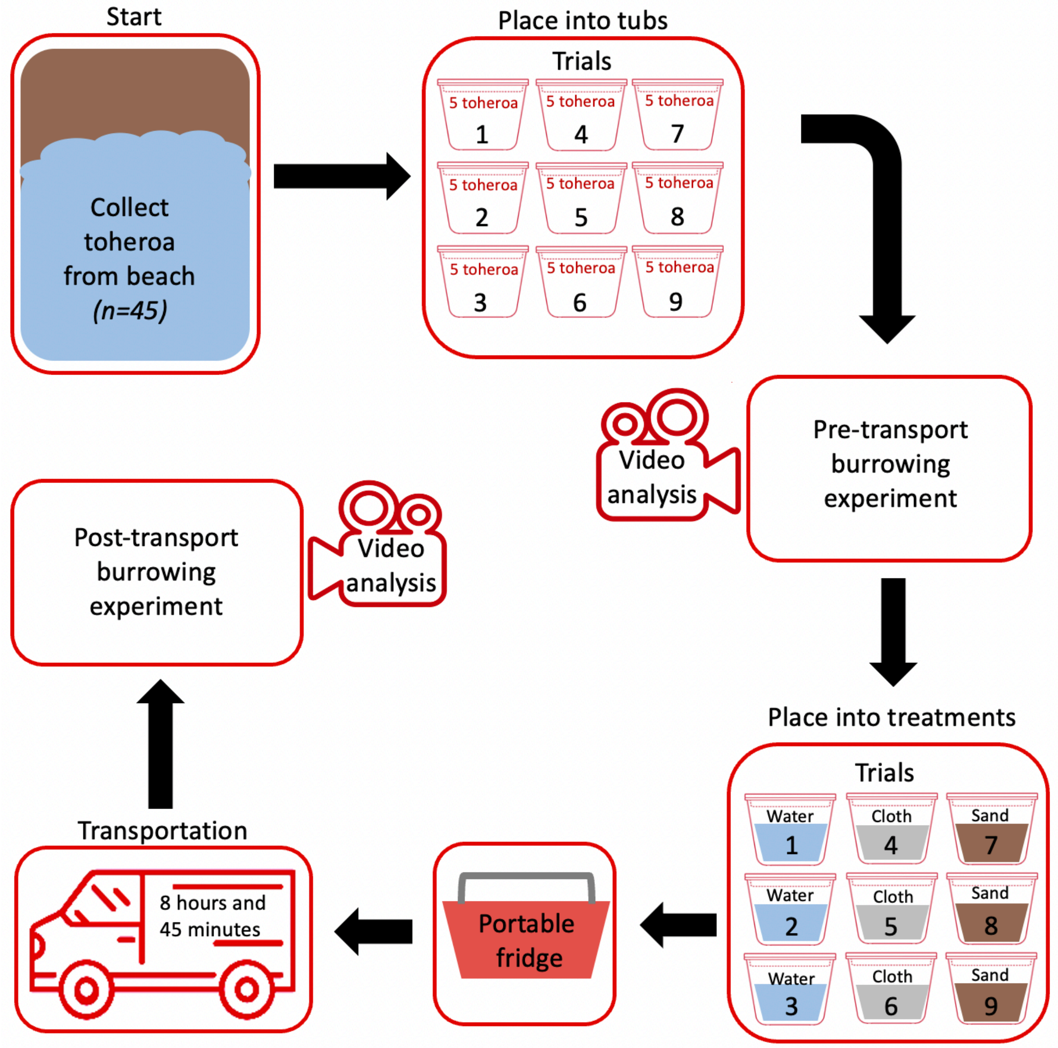


Figure 40: Flow chart describing the experimental design used for analysing burrowing behaviour as a quantitative measure of handling stress. Image by author.

5.2.2 Burrowing analysis

Toheroa were collected by excavating the surface layers of the sand with flat-end plastic shovels atop the toheroa bed, the sand was then sieved through a 1 mm mesh sieve. The chosen size range was 5-10 mm. After harvesting, toheroa were placed into holding tubs filled with seawater collected from the sampling site; they remained inside the tubs for 1.5 hours while in transit and preparation for the experimental setup. A total of nine trials consisting of three replicates which were later assigned to each treatment type post-burrowing analysis. *A* - trials (1, 2, 3; water), *B* - trials (4, 5, 6; cloth), and *C* - trials (7, 8, 9; sand). In each trial, there were five toheroa (45 in total). Prior to treatment methods and transportation, burrowing times were analysed to ensure accurate comparisons between pre-transport and post-transport. This was done to identify any potential bias; if one treatment had significantly slower or faster pre-transport burrowing times, it could affect the post-transport burrowing time interpretation.

For burrowing analysis, a rectangular plastic dish of 10 cm depth was filled with sand, and small plastic trays with mesh bottoms were placed within the dish and subsequently filled with sand (Figure 41). These mesh-bottomed trays allowed for easy removal post-trial by sieving through the mesh. The trays then had 2 cm of seawater poured on top to guarantee the sand would not dry out between experiments, thereby ensuring consistent experimental conditions. The toheroa were slowly placed onto the sand surface. A video was recorded for all trials to ensure accurate measurements were taken. Burrowing behaviour was quantified by the time it took to fully burrow within the substrate upon trial entry. Additionally, burrowing behaviours were also broken down into three successive steps: foot initiation, shell erection, and complete burrowing. This was done to investigate if exposure to stress impaired the burrowing process (e.g. once burrowing was initiated, how long did it take to completely burrow). Any burrowing time taken longer than 5-minutes was assigned as ‘incomplete’. After the pre-transport burrowing trials were completed, the toheroa were placed into their respective treatment type (sand, water, cloth).

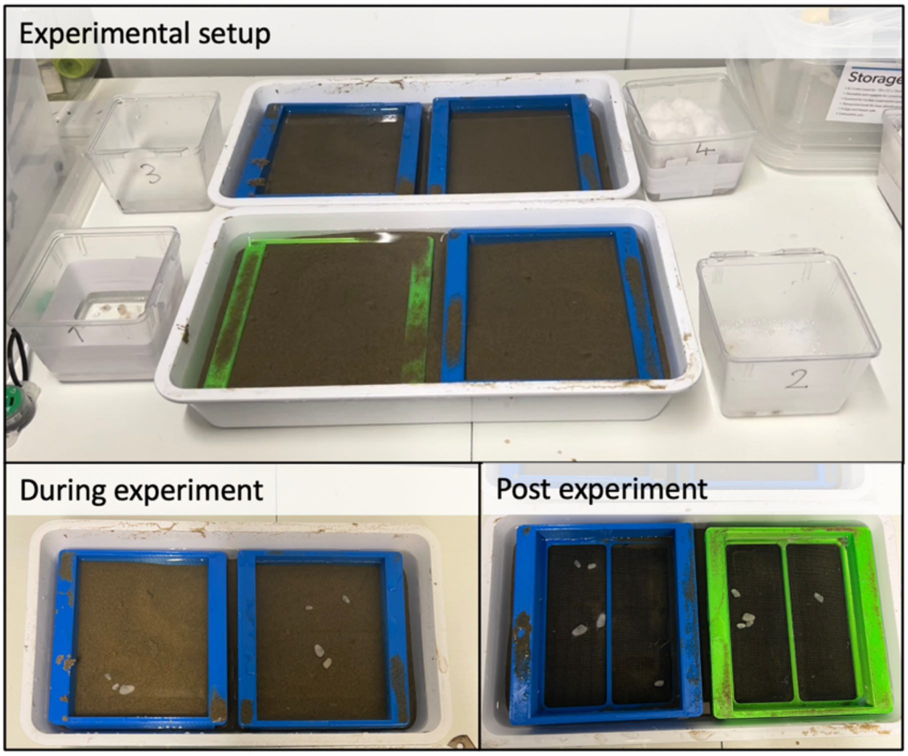


Figure 41: Example of experimental setup for burrowing analysis. Photos by author.

5.2.3 Transportation treatments

In order to determine the effect of transportation stress, three different treatments were chosen. All treatments were conducted in 10 cm x 10 cm plastic tubs (Figure 42). Firstly, freshly collected seawater from the sampling site. Water was filled to the tub's surface and air stones were used to ensure sufficient oxygenation during transit. For the second, a damp cloth was saturated with freshly collected seawater. The material was a 100% cotton towel cut into strips and placed under and atop the toheroa to ensure sufficient moisture was retained during transit. For the third, 3 cm of sand was placed into the tubs. The sand was collected *in situ* at the same location from which the toheroa were harvested (Figure 43). The trials were then distributed between two portable fridges.

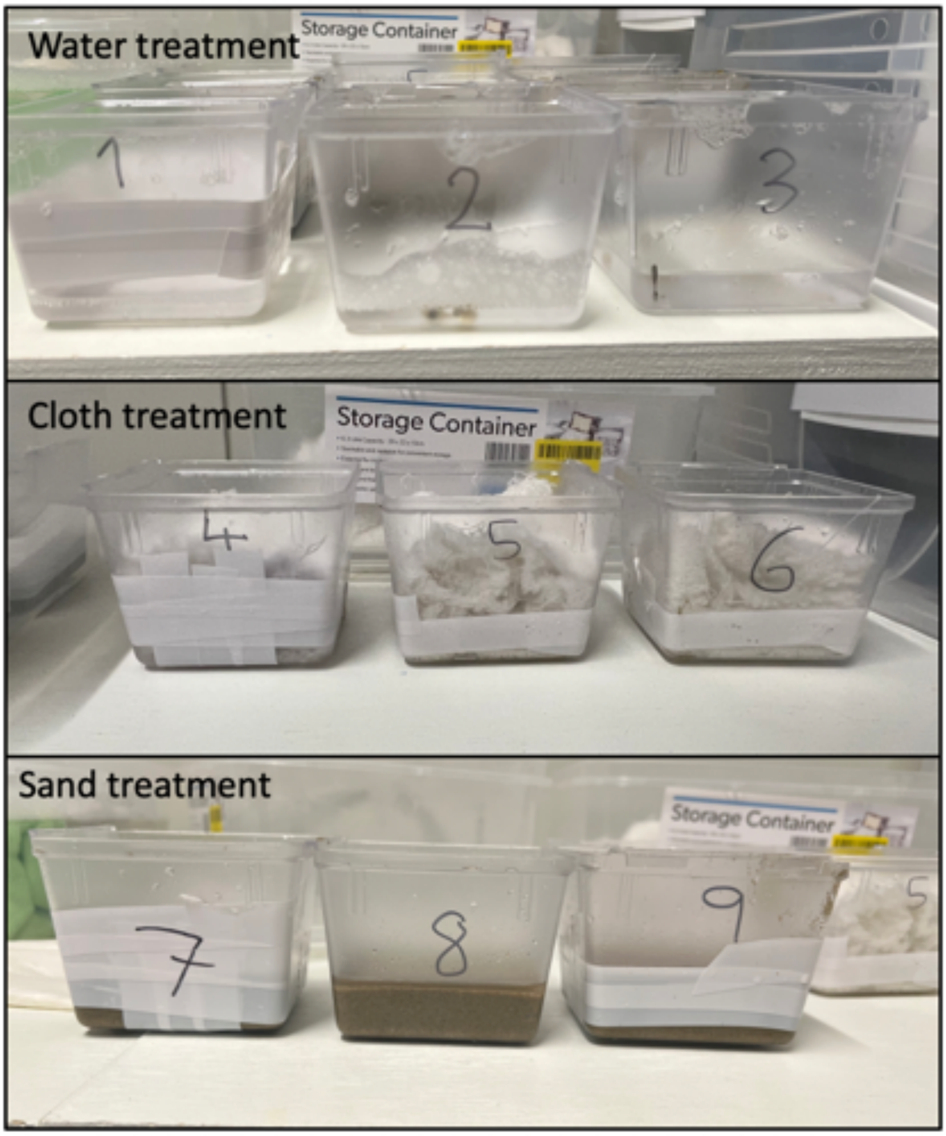


Figure 42: The nine different replicate trials for the three different treatment types (water level is uneven as it was post-trial).

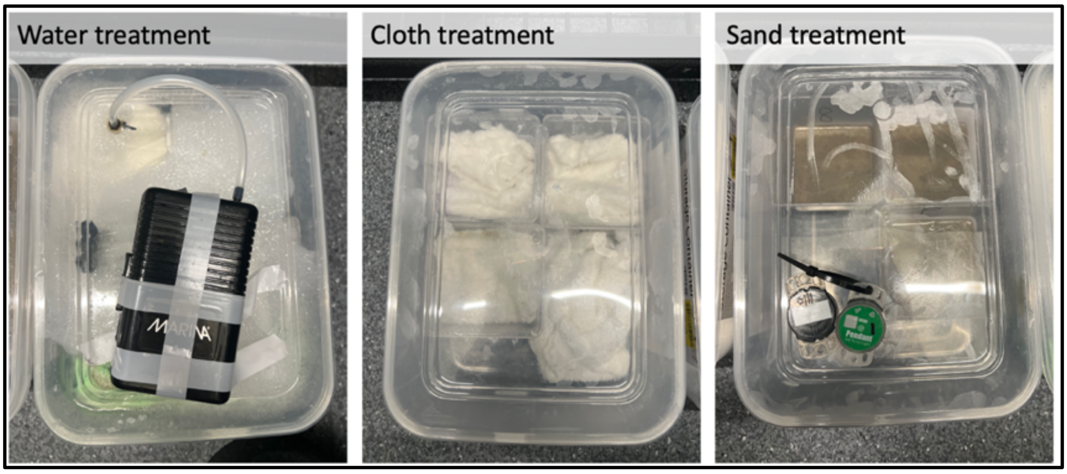
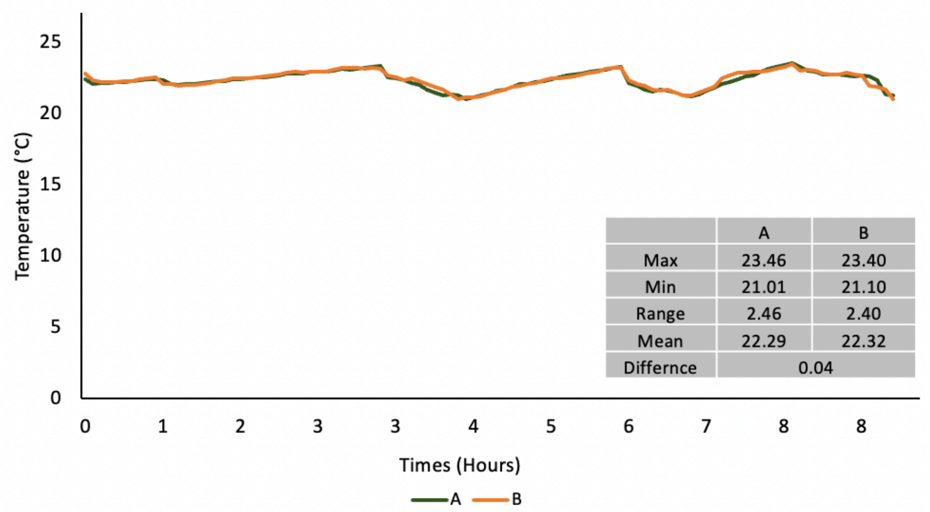


Figure 43: Experimental design during transportation simulation. From left to right - water treatment, damp cloth treatment, sand treatment.

The trials were transported in portable fridges set to 18 °C. HOBO temperature data loggers were placed inside to record any potential fluctuations that could affect the experimental results. The HOBO data loggers recorded temperatures between ~ 21°C and 23.5°C (Figure 44). The max temperature was recorded at 23.40 °C and 23.46 °C, with the minimum between 21.01°C – 21.1°C. The mean temperatures for both fridges had a difference of only 0.04°C. These results can conclude that temperature was consistent across the different treatments, indicating it did not affect the experimental results. The toheroa remained in the portable fridges for 8 hours and 45 minutes during transit. They were then unloaded from the portable fridge and into the lab for post-transport burrowing analysis using the aforementioned method.



	A	B
Max	23.46	23.40
Min	21.01	21.10
Range	2.46	2.40
Mean	22.29	22.32
Diffrence	0.04	

Figure 44: Temperature inside of the portable fridges that the trials were kept in during transportation.

5.2.4 Statistical analysis

Video footage was analysed using time stamps to determine accurate burrowing behaviour. All data was compiled and descriptive tables and bar graphs showing successional burrowing behaviour were generated in Microsoft Excel. RStudio (Version: 2021.09.0) was used to test the effect of treatment type on complete burrowing time. The accepted level of significance for all statistical tests was ≤ 0.05. The toheroa burrowing data for each treatment were tested for normality using the Shapiro-Wilk normality test. Pre-transport burrowing data did not comply with the assumptions of normality (Sand W = 0.8, $p = <0.01$; Cloth W = 0.7, $p = < 0.01$) except for the water treatment (W = 0.85, $p = > 0.05$). Tests indicated that variances were not homogenous. Therefore, a Kruskal-Wallis test was used to compare the median burrowing time (s) of toheroa for each treatment. All post-transport burrowing data met the assumptions of normality (Sand W = 0.92, $p = > 0.05$; Water W = 0.91, $p = > 0.05$). Therefore, an analysis of variance (ANOVA) was performed to compare the median burrowing times (s) for post-transport treatments. To determine if there was any statistical difference from pre-transport to post-transport for the sand treatment, a Mann-Whitney U test was applied as not all data met the assumptions of normality. However, as both pre-transport and post-transport data for the water treatment met assumptions of normality, an ANOVA was performed. As non-parametric statistics were used, box plots were formulated to present the difference in medians between burrowing times and treatment types. For all tests, the independent factor was treatment type (water, cloth, sand), and the dependent variable was burrowing time.

5.3 Results

5.3.1 Analysis of complete burrowing

No significant difference was detected for the median burrowing times between the pre-transport trials *A, B,* and *C* (H = 0.24, $p = >0.05$) (Figure 45). For *A* trials, 53% of the toheroa burrowed within the 5-minute time frame, compared to 80% for *B* trials and 87% for *C* trials. The *B* trials had the fastest mean pre-transport burrowing times at 43.43 (±29.65) seconds, compared to 110.77 (±49.72) seconds for *C* trials and 153.98 (±21.95) seconds for *A* trials. Prior to treatment and transportation, the mean burrowing times for trials *A* and *C* were longer than the post-transport times

(Table 14). This suggests that initial harvesting and handling stress significantly affect juvenile toheroa.

The post-transport burrowing analysis showed that the cloth treatment (*B*) was not a suitable method, no toheroa burrowed within the 5-minute time frame (0%). For the sand treatment (*C*), 73% burrowed and 67% of the water treatment (*A*) burrowed. ANOVA analysis for post-transport times was statistically significant ($p < 0.05$) (Figure 46). The sand (*C*) treatment had the fastest post-transport times at 53.6 (±13.48) seconds, with the water treatment (*A*) at about double the time at 105.75 (±33.77) seconds. However, it should be noted that this could reflect the faster pre-transport times for the *C* trials. On average, the change in burrowing times from pre-transport to post-transport decreased by 57.17 (±43) seconds for the sand treatment (*C*) and 48.08 (±85.2) seconds for the water treatment (*A*) (Table 15). Additionally, there appeared to be far less variation in times for the post-transport burrowing compared to the pre-transport burrowing. For the water treatment, the difference between pre-transport and post-transport burrowing time was significant ($p = 0.05$). However, for the sand treatment, no significant result was detected for the difference between pre-transport and post-transport burrowing time (W = 53.5, $p = >0.05$).

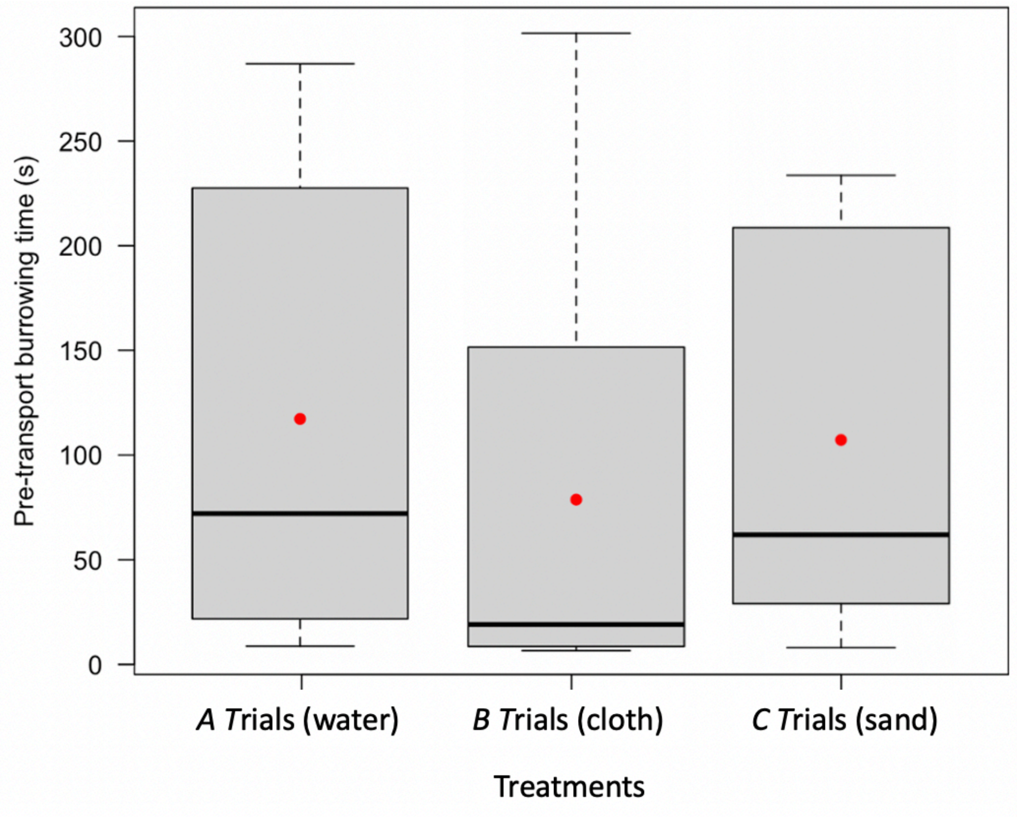


Figure 45: Box plot depicting not-significant difference (H = 0.24, p = >0.05) in median burrowing times (s) for pre-transport.

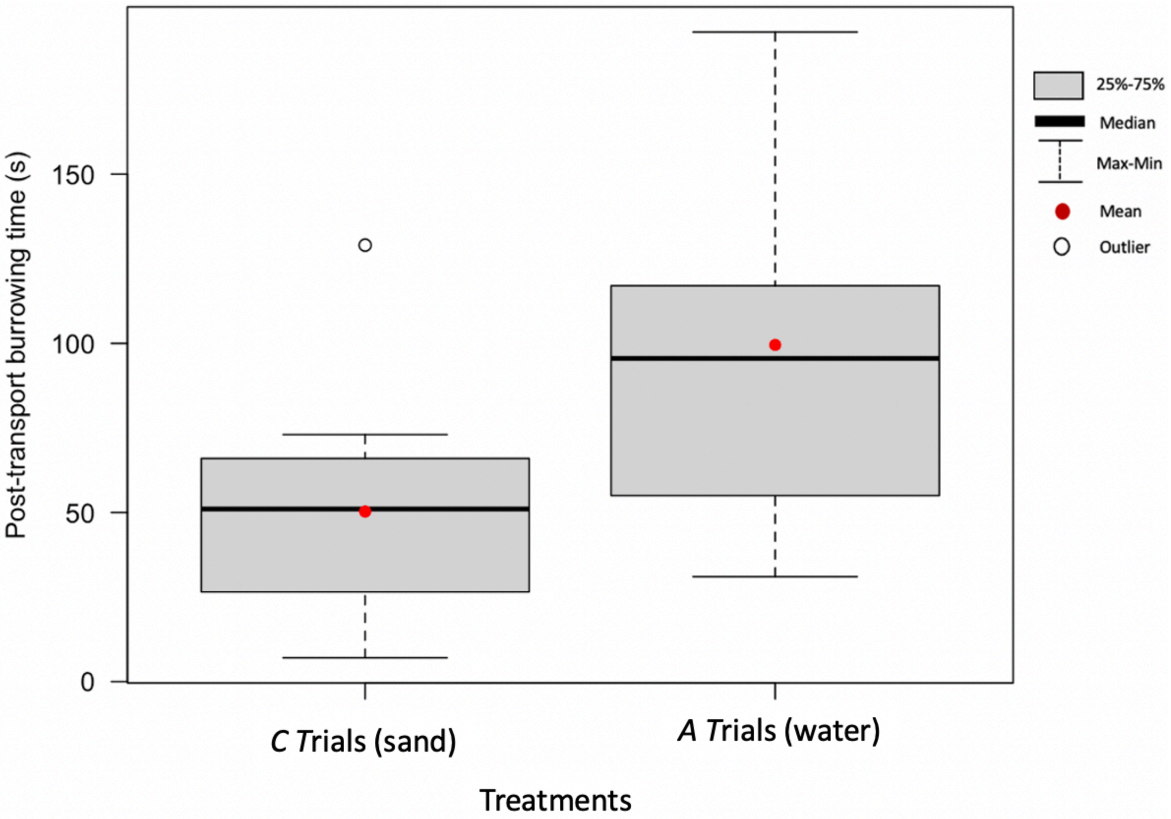


Figure 46: Box plot depicting significant difference (p = <0.05) in median burrowing times (s) for post-transport.

Table 14: Summary of burrowing time statistics. Incomplete burrowing denoted by ' - '.

Pre-transport									
Toheroa in trials	***A* Trials**			***B* Trials**			***C* Trials**		
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	114	251	13	16	8	7	19	8	62
2	214	292	18	23	16	8	99	24	198
3	-	-	34	152	35	9	29	35	212
4	-	-	39	-	13	60	209	35	234
5	-	-	-	-	-	159	-	232	-
Mean	164	271.5	26	63.7	18	48.6	89	66.8	176.5
SD (σ)	70.71	28.99	12.46	76.58	11.8	65.7	87.56	93.01	77.76
SE (±)	50	20.5	6.23	44.21	6.82	29.38	43.78	41.59	38.88
Overall Mean	153.83			43.43			110.77		
SD (σ)	37.39			51.36			86.11		
SE (±)	21.59			29.65			49.72		
Post-transport									
Toheroa in trials	**Water trials (*A*)**			**Cloth trials (*B*)**			**Sand trials (*C*)**		
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	31	55	82	-	-	-	69	7	17
2	40	91	192	-	-	-	73	34	19
3	100	101	-	-	-	-	129	36	51
4	186	117	-	-	-	-	-	63	55
5	-	-	-	-	-	-	-	-	-
Mean	89.25	91	137	-	-	-	90.33	35	35.5
SD (σ)	71.4	26.28	77.78	-	-	-	33.55	16.2	20.29
SE (±)	35.7	13.14	55	-	-	-	19.37	11.71	10.14
Overall Mean	105.75			-			53.61		
SD (σ)	58.49			-			23.35		
SE (±)	33.77			-			13.48		

Table 15: Summary of the change in mean burrowing time (seconds) from pre-transport to post-transport for the different treatments. Incomplete burrowing denoted by ' - '.

Treatment	Trial	Mean pre-transport times	Mean post-transport times	Change	Mean Change	SE(±)
Water (*A*)	1	164	89.25	-74.75	-48.08	85.20
	2	271.5	91	-180.5		
	3	26	137	111		
Cloth (*B*)	4	63.7	-	-	-	-
	5	18	-	-		
	6	48.6	-	-		
Sand (*C*)	7	89	90.33	1.33	-57.16	43.00
	8	66.8	35	-31.8		
	9	176.5	35.5	-141		

5.3.2 Analysis of the successional burrowing steps

Observationally, there was considerable variation in mean burrowing times both across the treatments and within the trials. Although the time frames are small, there was a trend in decreased time between successional burrowing steps from pre-transport to post-transport (Table 16). For the water treatment (*A*), the mean time taken between foot initiation and shell erection decreased by 0.5 seconds from pre-transport to post-transport (Figure 47; Figure 48). Whereas for the sand treatment (*B*), it decreased by 1.25 seconds. Time taken from shell erection to fully burrowed had a 0.04 second decrease in the water treatment (*A*) and 0.92 second decrease in the sand treatment (*C*) from pre-transport to post-transport. From foot initiation to fully burrowed, time decreased by 0.53 seconds for the water treatment and 2.17 seconds for the sand treatment from pre-transport to post-transport. Overall, the toheroa from the sand treatment had a greater decrease than the water treatment.

Table 16: Summary of mean time taken between successive burrowing steps. Foot-Shell = time taken from foot initiation to shell erection, Shell-Burrow = time taken from shell erection to fully burrowed, Foot-Burrow = time taken from foot initiation to fully burrowed. Incomplete burrowing denoted by '-'.

A **Trials (Water)**						
Transport	Foot-Shell		Shell-Burrow		Foot-Burrow	
	Time	SE(±)	Time	SE(±)	Time	SE(±)
Pre	4.58	1.47	7.17	1.3	12	70.41
Post	4.08	0.65	7.13	2.38	11	2.58
Difference	-0.5		-0.04		-0.53	

B **Trials (Cloth)**						
Transport	Foot-Shell		Shell-Burrow		Foot-Burrow	
	Time	SE(±)	Time	SE(±)	Time	SE(±)
Pre	3.08	1.34	9.65	5.28	13	4.84
Post	-	-	-	-	-	-

C **Trials (Sand)**						
Transport	Foot-Shell		Shell-Burrow		Foot-Burrow	
	Time	SE(±)	Time	SE(±)	Time	SE(±)
Pre	4.47	1.31	9.45	2.64	14	3
Post	3.22	0.91	8.53	1.3	12	0.63
Difference	-1.25		-0.92		-2.17	

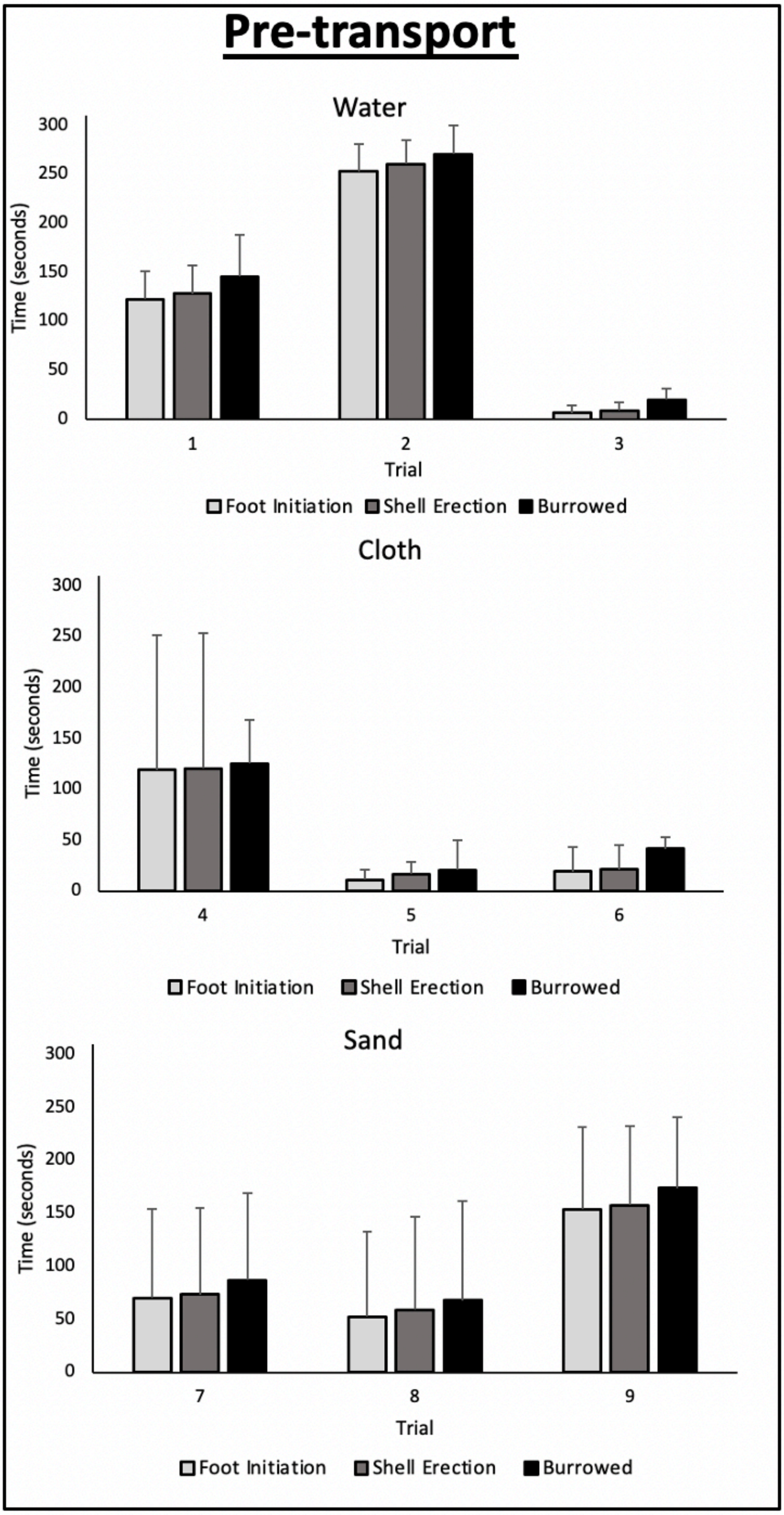


Figure 47: Bar charts showing successional steps of the burrowing process for the different treatment types for pre-transport. Foot initiation = time taken to initiate foot after being placed into trial. Shell erection = time taken till shell erection. Burrowed = time taken to fully burrow. Error bars represent standard deviation.

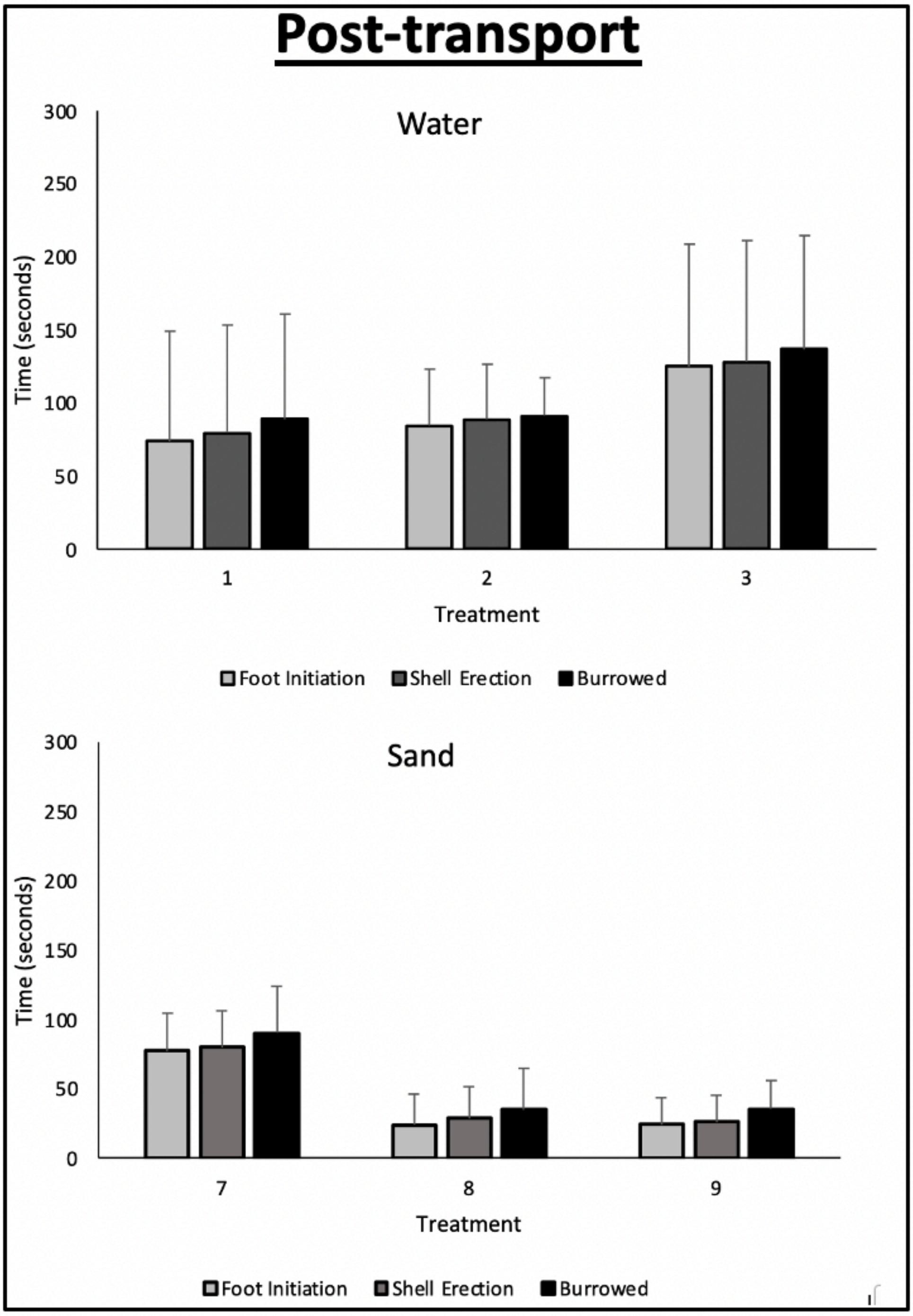


Figure 48: Bar charts showing successional steps of the burrowing process for the different treatment types for post-transport. Foot initiation = time taken to initiate foot after being placed into tray. Shell erection = time taken till shell erection. Burrowed = time taken to fully burrow. Error bars represent standard deviation.

5.4 Discussion

This Chapter aimed to assess the effects of handling, harvesting, and transportation on toheroa health and performance by utilising burrowing behaviour as a quantitative indicator of stress. A key finding from this research is that harvesting and handling do appear to have an immediate effect on juvenile toheroa. While on the beach, when toheroa were disturbed or removed from the substrate burrowing was immediate. However, it was clear from the pre-transport burrowing trials that initial collection impacted burrowing performance. The time frame between harvest and pre-transport burrowing was about 1.5 hours, during this time, the toheroa were held inside tubs containing seawater. However, the lowered burrowing performance is unlikely to be attributed to the holding method as both the water and sand treatment trials had faster post-transport burrowing times. This suggests that the initial harvesting of toheroa will likely elicit a strong physiological stress response when facilitating wild harvest and reseeding in hatcheries. Mechanical harvesting is well-documented to have negative effects in aquaculture operations (Rehman *et al.,* 2017). Nguyen *et al.* (2020) observed that mechanical harvesting of wild mussels stimulated rapid metabolic changes that resulted in increased energy demand, with a prompt transition into anaerobic glycolysis (transformation of glucose into lactate when limited amounts of oxygen are available). Additionally, Marin *et al*. (2005) evaluated the effects of mechanical stress on undersized clams (*Tapes philippinarum*) in aquaculture settings, they observed changes in physiological, biochemical, and behavioural responses that had negative effects on growth, energy demand, and survival. Marin *et al.* (2005) also found that when exposed to prolonged stress, clams exhibited lowered burrowing speed and capability, such as sediment depth and ability to maintain purchase within the substrate.

Overall, it appeared that if adequate storage methods were implemented initial harvesting and handling had a greater effect than transportation. Although, toheroa responded differently to the three treatments. The pre-transport burrowing times for the different treatments were not statistically significant. However, no toheroa from any of the cloth trials burrowed within the five-minute time frame post-transport, which is especially significant considering the cloth trials had the fastest pre-transport times. Furthermore, the sand and water treatments were determined to have a significant difference on burrowing performance post-transport. Both successional and complete post-transport burrowing times were faster for the sand treatment. However, no significant difference was found between the pre-transport and post-transport times for the sand treatment. Whereas for the water treatment pre-transport and post-transport times, a significant difference was detected. Additionally, the sand treatment had faster pre-transport times than the water treatment. It is difficult to determine whether this is a reflection of superior transport methodology or a function of sample group differences. Subsequently, there is limited reason to claim which of the two methods is better suited based on the quantifiable results.

An observation during experimentation showed that when within water many of the toheroa had their siphons and foot extended, it sometimes appeared that they were attempting to dig themselves into the substrate but could not in this environment (Figure 49). This could potentially cause an increased stress response due to over-exertion from increased energy demand. In the sand treatment, once secure in the substrate, they are less likely to exert energy in this way. Additionally, toheroa from the sand treatment had to be removed from the substrate prior to post-transport analysis, which added additional harvesting and handling time. Toheroa from the water and cloth treatments did not have to be disturbed to the same level before the experiment was run. Therefore, it could be argued that toheroa from the sand treatment experienced greater handling stress than the other treatments, which could have lowered their post-transport burrowing performance.

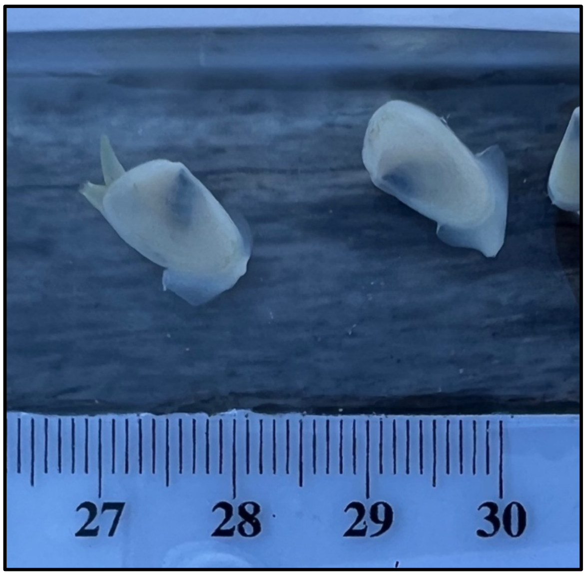


Figure 49: In water treatments, toheroa were often observed with their foot and siphons extended.

The key finding from this experiment was the unsuitability of the damp cotton cloth as a potential transportation treatment. No toheroa burrowed post-transport, indicating significant deterioration to physiological condition. There could be a chance that residual chemicals and contaminants remained on the cloth from the manufacturing process (Shinde *et al.,* 2020). If contaminants were present on the material, then it could have caused adverse physiological stress during transportation. Another possible reason for the lack of burrowing from this material could be that it failed to simulate true niche conditions. Nguyen *et al.* (2020) analysed the effect of immersion and emersion (in seawater) during the transportation of live green-lipped mussels (*Perna canaliculus*). They found that life expectancy and metabolic processes improved following periods of immersion and decreased following periods of emersion. It could also be attributed to the material having low breathability when saturated. Lowered oxygen within the trials could have resulted in lowered burrowing performance (Shumway *et al.,* 1983). If inadequate ventilation was the primary issue, selecting a more appropriate material could fix the problem. For example, post-harvest Abalone (*Haliotis iris*) have successfully been stored in wet hessian materials (Alfaro *et al.,* 2021). This option could be preferential to other methods. Sand and water will either require the removal of the materials from the environment or purchasing and attaining them from independent sources. Additionally, a hessian material would be more cost-effective as the process would be less laborious and would not require sieving, sorting, or disposal of large materials to the same extent once they arrived at the hatchery. Furthermore, a hessian-like material would weigh less and take up less space, thereby optimising transportation procedures.

However, it is also possible that temperature became an issue. The temperature inside the portable fridges was higher than expected (~22 °C (was set to 18 °C)), and sand and water mediums may act as better buffers against elevated temperatures. This could indicate that trials from the cloth treatment might have been in better physiological condition and had higher performance if temperatures were lower. If so, sand or water may be better suited as operations during transit would not require chilled trucks or strict protocols to the same extent. Additionally, choosing a medium that is less sensitive to fluctuations would be optimal. Temperature plays a crucial role in biogeochemical reactions; increasing temperature results in faster biochemical reactions and metabolism, both of which are temperature-dependent (Anacleto *et al.,* 2013; Weber *et al.,* 2008). Similar to other invertebrates, clams are poikilothermic (cold-blooded), meaning their body temperature and metabolic rate is directly influenced by external temperatures (e.g. air and water) (Xiao *et al.,* 2014). For example, a study conducted by Anacleto *et al.* (2013) tested the effect of temperature during transportation for two clam species *Venerupis pullastra* and *Ruditapes philippinarum.* It was concluded that mortality rates were lower at 4 °C compared to 22°C, and they also maintained far better physiological conditions. The temperature inside of the portable fridges was recorded at ~22°C, which is not higher than ambient temperatures within the environment at the time, but results may have been different at lower temperatures. An experiment was conducted on temperature-related stress for the storage of live tuatua (*Paphies donacina*), which found that mortalities were higher at 0°C compared to 4°C (Summers *et al.,* 1996). As a closely related species from the same genus as toheroa, this is a highly informative factor for future transportation endeavours. Increased temperature increases metabolic activity, and decreased temperature lowers metabolic activity (Weber *et al.,* 2008). Furthermore, it has been well documented that the transport time of shellfish can be significantly extended by reducing the metabolic rate (Wingerter *et al.,* 2013). Extremes in the upper and lower range will cease metabolic activity, causing declined health, diminished growth, and mortality (Xiao *et al.,* 2014). Therefore, determining the ideal temperature during transit for toheroa could result in metabolic stasis, thus, reducing the stress response and sustaining physiological health (Weber *et al.,* 2008).

The quantitative findings from this experiment indicate that both sand and aerated water could serve as sound transportation methods. However, from a practical viewpoint going forward, I believe the most effective method for transportation is within sand. In large-scale operations transporting toheroa in water could be more complicated to implement as it would require water aeration, temperature control, and could cause problems due to water sloshing around during transit. In contrast, the sand treatment would only require temperature control. If stored in sand, fluctuating or ambient temperatures are less likely to become an issue as this medium likely buffers naturally occurring environmental and climatic variations.

Additionally, transportation in sand is probably less stressful to toheroa as it more accurately mimics their desired niche and ability to remain burrowed.

The analysis of the successional burrowing steps shows that there was only a small difference from pre-transport to post-transport between foot initiation and full burrowing (Water = 0.53 s, Sand = 2.17 s). In contrast, the time from trial entry to complete burrowing had a much larger difference (Water = 48.08 s, Sand = 57.17 s). This suggests that handling, harvesting, and transportation mostly affect the underlying physiological response to burrowing rather than cause an impairment to the actual burrowing process. All six steps of the burrowing succession as described by Kondo and Stace (1995) were observed (Figure 50).

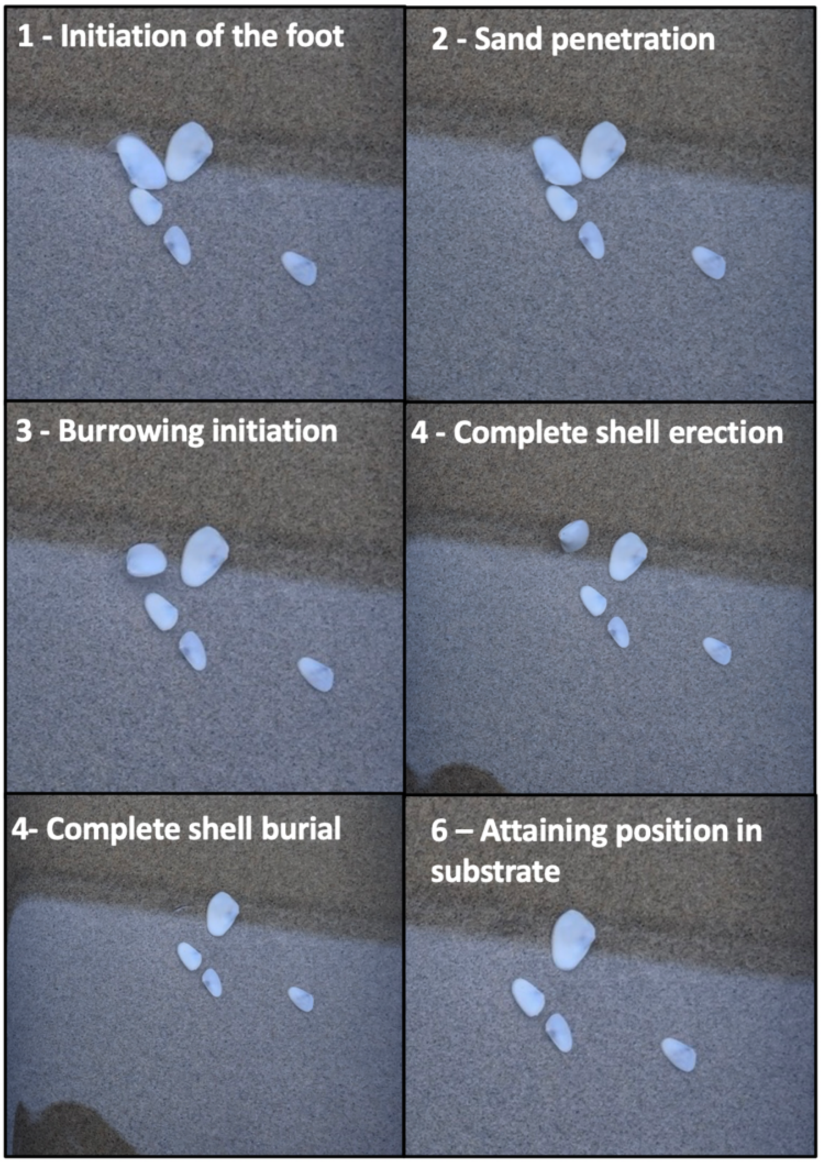


Figure 50: Example of the six successional burrowing steps for toheroa as described by Kondo and Stace (1995).

5.5 Limitations and future recommendations

This research successfully determined how stress from mechanical harvesting and inadequate transportation can induce negative effects on burrowing behaviour and have adverse physiological effects. However, it did not cover other potentially fundamental factors. Current literature all leads to temperature as a huge stress-inducing factor during transit, in future experiments, different levels of potentially 0°C, 4°C, and 22°C could be implemented to assess the effects on metabolic processes, mortality, and growth post-harvest. Additionally, trials could be run for toheroa of different size classes, such as 5mm, 10 mm, 15 mm, and 20 mm. Also, mortality rates could be assessed after transportation for freshly settled larvae that are only 2 mm in length. For example, St-Onge *et al.* (2007) studied the burrowing behaviour of recently transported juvenile softshell clams (5 – 20 mm) (*Mya arenaria*). They found that larger individuals had more difficulty being successfully relocated after transportation. This suggests that older bivalves may have a stronger negative reaction to environmental change, which could indicate that transportation in sand is best for toheroa from larger cohorts as it mimics their natural environment. Another stress-inducing factor that is known to affect bivalves is reduced salinity, both burrowing and siphon activity are noted to be significantly reduced (Domínguez *et al.,* 2020). For example, three different clam species (*Ruditapes decussatus, Ruditapes philippinarum,* and *Venerupis corrugata*) from Cambados Spain displayed reduced burrowing ability and feeding regimes following lowered salinity (salinity ≤15) (Woodin *et al.,* 2020). An observation made during experimentation was that when the overlaying water was disturbed, it appeared to initiate burrowing. Oscillatory flow over the sand surface likely simulates water movement in the swash zone, which prompts the innate survival instincts of burrowing behaviour (Yamashita *et al.,* 1997). This could mean that further research could be conducted on the effect of flow velocity during holding, transportation, and especially any potential hatchery operations.

5.6 Conclusion

The key takeaway from this research was the effect that handling and harvesting have on juvenile toheroa. For future aquaculture applications, developing efficient and low-impact strategies for wild harvest will be crucial for ensuring that toheroa maintain physiological condition through to reseeding and ongrowing in hatcheries.

Additionally, the damp cotton cloth treatment was highly inefficient and should not be implemented in future. However, further research into other materials with better ventilation, such as hessian, could be explored. The results from this experiment indicate that both sand and aerated seawater could serve as sound transportation methods. However, I believe the most effective method of transportation will be within sand. For large-scale operations, sand is likely to be less stressful as toheroa will not be subject to drastic habitat change. Additionally, the facilitation of transportation procedures is likely easier and more attainable with sand.

6 Chapter 6 – General discussion

6.1 Summary

6.1.1 Pilot surveys

In Chapter 2 of my thesis, I undertook pilot surveys on Ripiro Beach to investigate spatial distributions of juvenile toheroa recruitment regarding littoral zonation and vertical stratification in the sediment. This Chapter aimed to establish a new methodology that can be optimised for sampling spat. Prior to this research, current literature and Māori lore placed juvenile spat on the upper littoral zone between the dunes and high tide. Additionally, there was no information regarding the burrowing depth of juvenile toheroa. When plots were excavated to different depths (0-2 cm, 2-5 cm, and 5-10 cm), upwards of 90% of the sampled population was contained within the top 2 cm. Sediment depth had a significant negative effect on density, with an abrupt decrease in abundance with increasing depth. Inversely, sediment depth had a positive effect on shell size. In contrast to traditional knowledge, the hypothesis that juveniles are limited to the upper high tide was not supported by my results. Juvenile toheroa were distributed along the entire littoral width of the beach (high-tide to low-tide), with two distinct peaks of high density on either side of the mid-tide.

Surveying is often laborious, especially on beaches such as Ripiro that have wide littoral widths. In addition, sieving sand can be time-consuming when collecting buckets of water requires walking over 100 m. Therefore, optimising sampling techniques that require minimal sand quantities but still capture the entire juvenile population is beneficial. These pilot surveys achieved this, we now know juveniles predominantly inhabit the top 5 cm, and only larger adults were observed at depths greater than 5 cm. Prior to these surveys, sampling techniques would have likely been conducted on the upper littoral. However, we now know that juveniles are not limited to the high tide and dunes, so subsequent survey design should include systematic transects that cover the entire littoral zone. I believe my study successfully established a new sampling technique optimised for juvenile toheroa spat. This research has broader applications for conservation and monitoring programmes of juvenile recruitment. Additionally, these findings can be used to assess and quantify populations for future aquaculture ventures.

6.1.2 Spatial and temporal distributions

In Chapter 3 of my thesis, I aimed to understand how post-settlement juvenile toheroa are distributed spatially and temporally on Ripiro Beach. I utilised the findings from Chapter 2 in order to optimise sampling techniques that target juvenile toheroa spat. I wanted to explore the hypothesis further regarding juvenile distribution on the upper littoral. I wanted to investigate if, like adults, juvenile abundance is stream-associated. To do this, I implemented a systematic transect survey design with sediment depth optimised to 0-5 cm. Additionally, the beach was categorised into two different habitats; streams and non-streams.

The results from this study indicated that newly settled toheroa spat have highly variable distributions along the littoral zone and are not limited to the high tide. Juveniles from the same cohort often formed aggregated concentrations around the same location on the transect, and increasing shell size was typically associated with higher littoral zonation. In February, small recruits ≤5 mm had the most variable distributions, typically with two well-defined peaks of high density just above or below the mid-tide mark on stream habitats. However, over time, abundances decreased and distributions changed. From February to May, juvenile littoral distribution appeared to recede and become aggregated on the mid to high intertidal. This is likely attributed to the end of the major spawning season, bottleneck mortality, and passive transport or active habitat selection.

The non-stream habitat had lower abundances, lower frequencies of larger toheroa, and lower littoral zonation. Upper reaches on stream outlets provide thermal refuge (cooler temperatures) and ample substrate saturation, these favourable conditions could result in higher abundances and lower mortality (Cope, 2018). Non-stream habitats would be subject to desiccation, especially on the upper littoral. The mechanisms driving distribution patterns still need to be defined. However, tidal deposits in the swash zone are likely the primary reason for settlement along the intertidal zone. Freshly settled recruits less than 5 mm are probably unable to secure themselves within the substrate, frequently being resuspended and deposited via passive transport due to wave action. Factors affecting toheroa spawning and recruitment are largely unknown. However, climatic conditions such as oceanic temperature and global warming are probably the driving forces affecting recruitment abundance and mortality. I believe this research successfully filled knowledge gaps regarding the distribution and abundance of juvenile toheroa recruitment. The survey methodology developed in this chapter can be utilised in future conservation practices and population estimates.

6.1.3 Population estimates

In Chapter 4 of my thesis, I estimated the total population of juvenile toheroa on Ripiro Beach based on the data collected in Chapter 3. This Chapter aimed to estimate how the population is distributed temporally (February and May), spatially (streams Vs non-streams), and by size (0-5 mm, 5-10 mm, 10-15 mm, and >15 mm). It is widely unknown whether the failed recovery of toheroa populations is due to a lack of recruitment or mortality. These estimations hoped to inform discussions around the ethics and viability of implementing toheroa in the aquaculture industry.

Over time, distributional shifts in abundance, cohort assemblages, and habitats were observed. Even using a conservative estimate, February's total population was estimated at 587.58 (± 188.17) million compared to 31.51 (± 14.92) million in May. Overall abundance loss was ≥ 93 %. Additionally, the dominant size cohort shifted from 0-5 mm in February, to 5-10 mm in May. This likely indicates the end of the major spawning season, growth, and mortality. Furthermore, there was a slight abundance shift towards stream habitats from non-stream habitats, and low abundances of larger cohorts on non-stream habitats was observed (no toheroa > 15 mm). However, it is unknown whether this is due to active habitat selection or differential mortality due to unsuitable environmental conditions. Even though the estimates might hold a margin of error, the substantial population reduction over time indicates significant mortality rates of juvenile toheroa during the early growth period. These findings show that a lack of juvenile recruitment is not the driving factor for the continued decline of toheroa populations. The reasons for mortality are unknown, but catchment modification, climate, and desiccation on unsuitable substrates are likely the primary contributors.

I believe the estimates produced from the model I created show there is viability for aquaculture applications in the future. However, there is sensitivity around parameters such as spat size and harvest time. From an ethical perspective, harvesting smaller spat sizes will have smaller ecological impacts but likely have greater challenges when facilitating hatchery operations. Based on the results from this study, the optimal harvesting time is late February. However, due to the limited dataset and unknown annual recruitment variation, there is no certainty behind this claim. Toheroa from the 5-10 mm cohort will likely have the best ratio between ecological impact and aquaculture success. Further research is required to establish a cost-effective, low-impact strategy that maintains high hatchery success rates. In order to better comprehend juvenile abundance, it would be valuable to attain annual recruitment patterns encompassing the entire season and survey a broader area of the beach. Regular stock assessments are the only way to ensure the natural regenerative capacity of the resource is not exploited.

6.1.4 Handling and transportation

In Chapter 5 of my thesis, I investigated different methods of transporting live toheroa by utilising burrowing behaviour as a quantitative indicator for transport-related stress. Three different treatments were chosen, aerated seawater, damp cotton cloth, and freshly collected sand. Time taken to burrow was video recorded for both pre-transport and post-transport analysis. Additionally, to assess whether prolonged exposure to stress impaired burrowing ability, it was broken down into three successional steps; foot initiation, shell erection, and complete burrowing. This experiment aimed to mimic real-world applications wherein juvenile toheroa would be harvested and transported to hatcheries.

A fundamental observation from this experiment was that pre-transport burrowing times were faster than post-transport burrowing times for both the sand and water treatments, indicating that mechanical harvesting and handling can have a greater stress response than actual transportation. There appeared to be minimal difference in the time between successional steps. The most significant change was the time taken to begin burrowing upon trial entry. These observations suggest that harvesting and handling stress caused a delayed physiological response to burrowing rather than an impairment to burrowing ability. The results clearly showed that the damp cotton cloth was highly unsuitable. No toheroa from this treatment burrowed within the five-minute time frame post-transport.

Quantitatively, with both pre-transport and post-transport times taken into account, there was limited reason to claim that either water or sand treatments were superior to each other. Nevertheless, the sand treatment was identified as the most practical method for large-scale applications. This was decided upon because it is relatively easy to facilitate, likely acts as an efficient buffer to temperature fluctuations, and minimises stress as it mimics natural habitat conditions. Future research should investigate how temperature affects mortality and metabolic activity (Anacleto *et al.,* 2013; Summers *et al.,* 1996; Weber *et al.,* 2008) and whether transport and harvesting have differential effects on larvae and different size cohorts (St-Onge *et al.*, 2007).

6.2 Aquaculture applications

If the population estimates produced in this thesis truly reflect toheroa recruitment dynamics on Ripiro Beach, then I believe aquaculture is a viable option. The distribution patterns defined in Chapters 2 and 3 can be used to establish effective surveying and harvesting techniques. We now know that excavating the top 2 cm of the surface will capture upwards of 90 % of the juvenile population, with the 0-5 cm margin encompassing the entirety whilst excluding larger adults. Additionally, harvesting can be conducted along the entire littoral width. However, zonation around the intertidal and upper intertidal are the most prolific. Because juveniles were found in high densities on non-stream habitats in February, harvesting can be conducted without compromising adult beds. In future, a key factor will be defining the optimal harvest size. Ecologically, larvae and small spat less than 5 mm would be ideal as they appear in large quantities. However, there may be greater challenges in facilitating hatchery-reared toheroa of this size. From a commercial perspective, larger spat will require less cultivation and have shorter aquaculture durations. In order to optimise maximum production and sustainability yield, further research is required regarding seasonal recruitment variation. With regard to future hatchery operations, it will be essential that adequate harvesting and transportation protocols are developed that minimise handling stress to ensure physiological health.

Aside from the conservation and commercial perspective, aquaculture production can also have significant socioeconomic benefits. Globally, clam harvesting supports a significant amount of jobs and creates industry in coastal areas, contributing a sustainable source for local development (da Costa *et al.,* 2020). Aquaculture boosts economic growth and enhances food production (Theuerkauf *et al.,* 2019). From a cultural and ethical perspective, as I am not a resident of the region, nor a member of local iwi or hapū, it is not my decision to make whether toheroa aquaculture should be implemented. The purpose of my research was to better understand the dynamics of post-settlement juvenile toheroa and to provide information that could be used to inform discussions around recruitment and the viability of aquaculture for these communities.

6.3 Limitations and future recommendations

The research conducted in this thesis has established a fundamental groundwork for the distribution dynamics of post-settlement juvenile toheroa. However, further research is required to assess whether these distribution patterns are representative of the entire beach and comparable to other seasons. Surveying the entirety of Ripiro Beach in one day is an impossible task due to the area (both length and width) and incoming tide. Ideally, a large team would conduct fieldwork over a succession of days during spring tides to optimise sampling ability. In future, the width of stream bed habitats should be defined by placing multiple transects perpendicular to the shore across stream outlets (Figure 51). Additionally, in regards to aquaculture, non-stream habitats should be the primary focus for surveying as this area is where harvesting would be conducted. A comprehensive approach should be administered where monthly sampling occurs from November to May to encompass the entire recruitment season. The transects in my survey only covered a 14.7 km stretch of the 72 km beach. In future, to investigate whether distribution is consistent, systematic sampling should occur from Maunganui Bluff in the North to Poutō Peninsula in the south. For example, it has been proposed before that prevailing longshore currents are a driving mechanism for juvenile distribution on exposed sandy beaches (Dugan & McLachlan, 1999). For Ripiro Beach, southern swells drive longshore drift to the North, but is also known to sometimes switch to southeast (Cope, 2018). Strong nearshore currents could define where dense juvenile toheroa deposits occur.

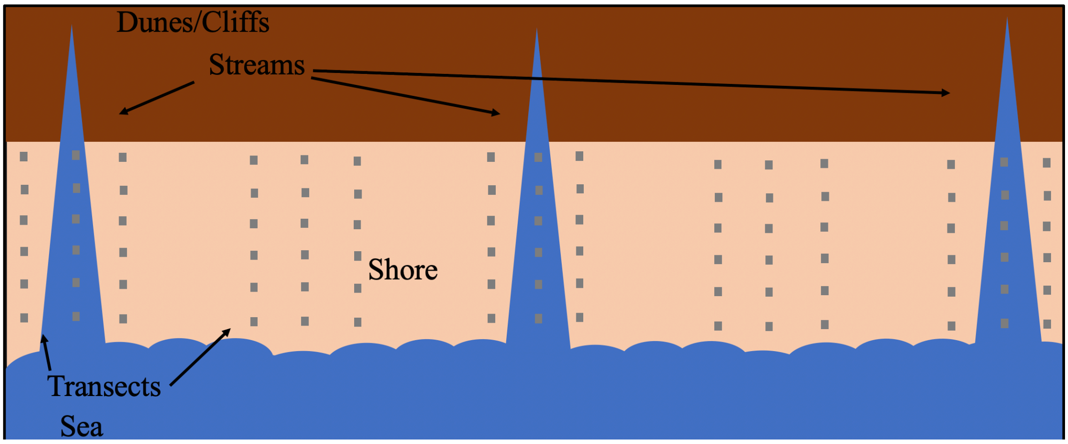
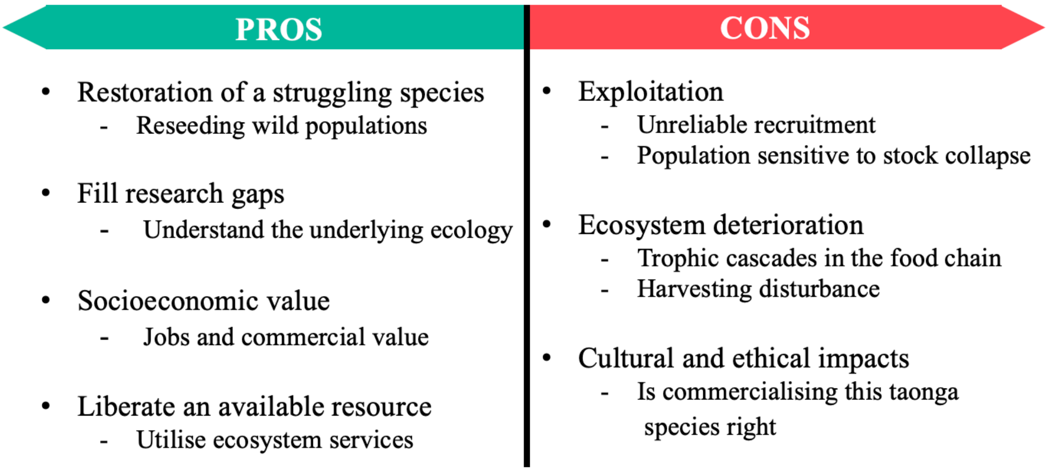


Figure 51: Schematic example of survey design for Ripiro Beach.

Because bottleneck mortality appears to occur during the early growth period, from a conservation perspective, there is a great need to understand the underlying ecology of toheroa. Toheroa have been protected for more than 40 years; given that recruitment is not the limiting factor, local environmental factors must be responsible for the continued decline. A primary focus of future research should be annual variation in recruitment and factors affecting spawning patterns and success. As discussed in Chapter 3, rising temperature plays a crucial role in mortality (Williams *et al.,* 2013b), larvae growth (Gadomski *et al.,* 2015), and spawning (onset and duration) (Redfearn, 1974). Population enhancement with hatchery-reared spat on Ripiro Beach can only be implemented once ideal toheroa habitat requirements are defined. The high mortality rates indicate some obstacle, either biotic or abiotic, which is hindering toheroa recovery. A possible line of research could be how habitat modification in the catchment has affected stream water quality and volume. Reduced and diverted stream flow could restrict the shore area containing favourable environmental conditions. In conjunction with global warming, agricultural runoff can alter biogeochemical cycling due to increased sedimentation and nutrient loading (primarily urea (nitrogen)) (Bechmann & Stålnacke, 2019). For example, in 2001, mass mortality of toheroa beds on Ripiro Beach occurred via smothering and anoxia from high toxic algal bloom concentrations (TAB) (Williams *et al.,* 2013b). Thousands of stressed toheroa surfaced from the sediment and were unable to close their valves, leaving them vulnerable to desiccation and predation (Akroyd *et al.,* 2002).

Food abundance is also thought to significantly influence spawning patterns and mortality (Redfearn, 1974). Food availability and quality reduction could create a bottleneck effect and limit the habitat's carrying capacity. For example, in Hiroshima Bay, Japan, Yamamoto (2020) found that low nutrient loading (specifically phosphorus) lead to an inadequate abundance of phytoplankton, reduced food availability generated poor culture conditions resulting in decreased population sizes. In addition, there have been various other factors implicated with toheroa population decline, including, but not limited to; vehicle traffic, predation (Redfearn, 1974), land de-vegetation and afforestation (Smale *et al.,* 1996), fertiliser and pesticides (Akroyd *et al.,* 2002), and illegal harvesting (Akroyd *et al.,* 2008). However, the inability to isolate any one inhibitory factor could mean that the failed recovery is due to the cumulative effects of all the aforementioned variables (Thrush *et al.,* 2021).

Globally, inconsistent recruitment supply and annual variation have presented major challenges to sustainability for bivalve aquaculture (da Costa *et al.,* 2020). Hatcheries established on the foundation of wild-harvested juveniles are entirely reliant on recruitment, and the scope for increased productivity yield is limited (Hair *et al.,* 2002). The exploitation of juvenile populations could have severe ecological impacts, complete stock collapse or trophic cascades from the disruption of food chains due to the removal of prey from higher trophic-level avian and pelagic predators (Hair *et al.,* 2002). Increasingly, farmers have moved towards closed-loop production to avoid the drawbacks of wild-sourced spat (Little *et al.,* 2016). Advances in larval culturing techniques within hatcheries have facilitated the ability for increased production capacity and artificial breeding, subsequently reducing reliance on natural seed sources (Hair *et al.,* 2002). Ecologically, closing the toheroa life cycle within hatchery settings would prevent ecosystem deterioration and exploitation of wild populations. Development of spawning induction, larval rearing, and culturing techniques through to post-settlement (30 mm) has been achieved by Redfearn (1982), Mandeno (1999), Smith (2003) and Gadomski *et al.* (2015). Full toheroa life cycle was supposably achieved in the 1980s at the Mahanga Bay shellfish hatchery in Wellington, but commercial development of toheroa for aquaculture was not pursued (Ross *et al.,* 2018a and references therein). Testing the viability of aquaculture for new clam species has been successful before, Castillo-Durán *et al.* (2016) took adult clams (*Chionista fluctifraga*) from commercial fishery grounds and facilitated conditioning, spawning induction, larvae cultivation, and spat nursing within a hatchery. They achieved a 95 % survival post-field cultivation and had superior growth rates and condition index compared to natural conditions. However, there are often major drawbacks when developing spawning induction and spat production, and the benefits of closed-loop aquaculture often do not always exceed the cost (Nakada, 2008). For example, it took 32 years to complete the life cycle of the Pacific bluefin tuna (*Thunnus orientalis*) in controlled settings (Hair *et al.,* 2002). The potential pros and cons for toheroa aquaculture have been summarised in Figure 52.



PROS

- Restoration of a struggling species
  - Reseeding wild populations
- Fill research gaps
  - Understand the underlying ecology
- Socioeconomic value
  - Jobs and commercial value
- Liberate an available resource
  - Utilise ecosystem services

CONS

- Exploitation
  - Unreliable recruitment
  - Population sensitive to stock collapse
- Ecosystem deterioration
  - Trophic cascades in the food chain
  - Harvesting disturbance
- Cultural and ethical impacts
  - Is commercialising this taonga species right

Figure 52: Pros and Cons table for implementing toheroa into the aquaculture industry.

6.4 Conclusion

The ecology reviewed here fills knowledge gaps regarding the distribution dynamics of post-settlement juvenile toheroa on Ripiro Beach. The surveys conducted in this thesis definitively show that juvenile toheroa exhibit far more variable distributions than previously theorised. I believe this research has successfully optimised sampling techniques that target juvenile toheroa. Recruitment patterns may be subject to vary, but the findings here show that lack of recruitment is not the limiting factor inhibiting toheroa recovery. The research in my thesis serves as a sound precursor for where future toheroa research should be directed. From a conservation perspective, it is paramount that we define the underlying ecology of toheroa habitats to determine the root cause of population decline and mortality. Human existence relies heavily on ecosystem services to feed the world, and toheroa aquaculture represents a restoration opportunity that could enhance natural populations and generate significant commercial and socioeconomic value. I believe that hatchery-reared restoration and aquaculture facilitation could hold the future for toheroa conservation.

References

Akroyd, J. A. M., Walshe, K. A., & Millar, R. B. (2002). Abundance, distribution, and size structure of toheroa (*Paphies ventricosa*) at Ripiro Beach, Dargaville, Northland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *36*(3), 547-553.

Akroyd, J., Walshe, K., Manly, B., Te Tuhi, J., Searle, B., & Searle, R. (2008). Distribution and abundance of toheroa (*Paphies ventricosa*) on Dargaville and Muriwai Beaches, 2006-07. *New Zealand Fisheries Assessment Report*, *29*, 28.

Alfaro, A. C., McArdle, B., & Jeffs, A. G. (2010). Temporal patterns of arrival of beachcast green-lipped mussel (Perna canaliculus) spat harvested for aquaculture in New Zealand and its relationship with hydrodynamic and meteorological conditions. *Aquaculture*, *302*(3-4), 208-218.

Alfaro, A. C., Nguyen, T. V., Venter, L., Ericson, J. A., Sharma, S., Ragg, N. L., & Mundy, C. (2021). The effects of live transport on metabolism and stress responses of abalone (Haliotis iris). *Metabolites*, *11*(11), 748.

Allen, D. C., & Vaughn, C. C. (2009). Burrowing behavior of freshwater mussels in experimentally manipulated communities. *Journal of the North American Benthological Society*, *28*(1), 93-100.

Anacleto, P., Maulvault, A. L., Barrento, S., Mendes, R., Nunes, M. L., Rosa, R., & Marques, A. (2013). Physiological responses to depuration and transport of native and exotic clams at different temperatures. *Aquaculture*, *408*, 136-146.

Andresen, H., Strasser, M., & van der Meer, J. (2014). Estimation of density-dependent mortality of juvenile bivalves in the Wadden Sea. *Plos one*, *9*(8), e102491.

Armonies, W., & Hellwig-Armonies, M. (1992). Passive settlement of Macoma balthica spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. *Netherlands Journal of Sea Research*, *29*(4), 371-378.

Arntz, W. E., & Tarazona, J. (1990). Effects of El Niño 1982-83 on benthos, fish and fisheries off the South American Pacific coast. *Elsevier oceanography series*, *52*, 323-360.

Asadi, M. A., Iranawati, F., & Andini, A. W. (2018). Ecology of bivalves in the intertidal area of Gili Ketapang Island, East Java, Indonesia. *Aquaculture, Aquarium, Conservation & Legislation*, *11*(1), 55-65.

Barton, B. A., & Iwama, G. K. (1991). Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. *Annual Review of fish diseases*, *1*, 3-26.

Basti, D., Bricknell, I., Hoyt, K., Chang, E. S., Halteman, W., & Bouchard, D. (2010). Factors affecting post-capture survivability of lobster Homarus americanus. *Diseases of aquatic organisms*, *90*(2), 153-166.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of animal ecology*, *78*(4), 699-714.

Bechmann, M., & Stålnacke, P. (2019). Agricultural nitrogen and phosphorus pollution in surface waters. In *Oxford Research Encyclopedia of Environmental Science*.

Beentjes, M. P. (2010a). *Toheroa survey of Bluecliffs Beach, 2009, and review of historical surveys* (p. 42). Wellington: Ministry of Fisheries.

Beentjes, M. P. (2010b). *Toheroa survey of Oreti Beach, 2009, and review of historical surveys*. Ministry of Fisheries.

Bennion, M., Ross, P. M., Lane, H. S., & McDonald, I. R. (2022). Bacterial composition in the toheroa (Paphies ventricosa), a threatened surf clam from Aotearoa (New Zealand). *Marine Biology*, *169*(3), 1-9.

Berchez, F. A. S., Ghilardi-Lopes, N. P., Correia, M. D., Sovierzoski, H. H., Pedrini, A. D. G., Ursi, S., ... & Brotto, D. S. (2016). Marine and coastal environmental education in the context of global climate changes-synthesis and subsidies for ReBentos (Coastal Benthic Habitats Monitoring Network). *Brazilian Journal of Oceanography*, *64*, 137-156.

Björndal, T., Lane, D. E., & Weintraub, A. (2004). Operational research models and the management of fisheries and aquaculture: A review. *European Journal of Operational Research*, *156*(3), 533-540.

Blundon, J. A., & Kennedy, V. S. (1982). Refuges for infaunal bivalves from blue crab, Callinectes sapidus (Rathbun), predation in Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, *65*(1), 67-81.

Broekhuizen, N., Plew, D. R., Pinkerton, M. H., & Gall, M. G. (2021). Sea temperature rise over the period 2002–2020 in Pelorus Sound, New Zealand–with possible implications for the aquaculture industry. *New Zealand Journal of Marine and Freshwater Research*, *55*(1), 46-64.

Brunton, P. M. (1978). Toheroa predation by black-backed gulls on Dargaville beach, North Auckland, New Zealand. *Notornis*, *25*(2), 128-140.

Caddy, J. F., Defeo, D., & Defeo, O. (2003). *Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources* (Vol. 448). Food & Agriculture Org..

Calixto, E. S., Santos, D. F. B., Lange, D., Galdiano, M. S., & Rahman, I. U. (2020). Aquaculture in Brazil and worldwide: overview and perspectives. *Journal of Environmental Analysis and Progress*, *5*(1), 098-107.

Carella, F., Feist, S. W., Bignell, J. P., & De Vico, G. (2015). Comparative pathology in bivalves: Aetiological agents and disease processes. *Journal of invertebrate pathology*, *131*, 107-120.

Cassie, R. M. (1951). A molluscan population with an unusual size frequency-distribution. *Nature*, *167*(4242), 284-285.

Cassie, R. M. (1955). Population studies on the toheroa, Amphidesma ventricosum Gray (Eulamellibranchiata). *Marine and Freshwater Research*, *6*(3), 348-391.

Castillo-Durán, A., Hoyos-Chairez, F., Arreola-Lizárraga, J. A., Martínez-Córdova, L., & Chávez-Villalba, J. (2016). Larval and post-larval growth, spat production and off-bottom cultivation of the smooth venus clam Chionista fluctifraga. *Aquaculture Research*, *47*(9), 2851-2860.

Champion, P. D., & Reeves, P. (2008). *Factors causing dune ephemeral wetlands to be vulnerable to weed invasion*. Pub. Team, Department of Conservation.

Christophersen, G., Román, G., Gallagher, J., & Magnesen, T. (2008). Post-transport recovery of cultured scallop (Pecten maximus) spat, juveniles and adults. *Aquaculture International*, *16*(2), 171-185.

Clements, J. C., & Hunt, H. L. (2014). Influence of sediment acidification and water flow on sediment acceptance and dispersal of juvenile soft-shell clams (Mya arenaria L.). *Journal of experimental marine biology and ecology*, *453*, 62-69.

Cook, S. D. C. (2010). *New Zealand coastal marine invertebrates*. Canterbury University Press.

Cope, J. (2018). *The modification of toheroa habitat by streams on Ripiro Beach* (Doctoral dissertation, The University of Waikato).

Coster, J. (1989). Dates from the dunes: A sequence for the Aupouri Peninsula, Northland, New Zealand. *New Zealand Journal of Archaeology*, *11*, 51-75.

Cummings, V., Hewitt, J., Halliday, J., & Mackay, G. (2007). Optimizing the success of Austrovenus stutchburyi restoration: Preliminary investigations in a New Zealand estuary. *Journal of Shellfish Research*, *26*(1), 89-100.

Cummings, V. J., Thrush, S. F., Hewitt, J. E., & Turner, S. J. (1998). The influence of the pinnid bivalve Atrina zelandica (Gray) on benthic macroinvertebrate communities in soft-sediment habitats. *Journal of Experimental Marine Biology and Ecology*, *228*(2), 227-240.

da Costa, F., Cerviño-Otero, A., Iglesias, Ó., Cruz, A., & Guévélou, E. (2020). Hatchery culture of European clam species (family Veneridae). *Aquaculture International*, *28*(4), 1675-1708.

Daily, G. C., & Matson, P. A. (2008). Ecosystem services: From theory to implementation. *Proceedings of the national academy of sciences*, *105*(28), 9455-9456.

Davis, L. E., & Schreck, C. B. (1997). The energetic response to handling stress in juvenile coho salmon. *Transactions of the American Fisheries Society*, *126*(2), 248-258.

del Próo, S. A. G., Palau, L. C., Pérez, J. B., Laguna, J. C., & Fragoso, R. H. (2003). Effects of the El Niño event on the recruitment of benthic invertebrates in Bahía Tortugas, Baja California Sur. *Geofisica internacional*, *42*(3), 429-438.

Domínguez, R., Vázquez, E., Woodin, S. A., Wethey, D. S., Peteiro, L. G., Macho, G., & Olabarria, C. (2020). Sublethal responses of four commercially important bivalves to low salinity. *Ecological Indicators*, *111*, 106031.

Druehl, L. D. (1967). Vertical distributions of some benthic marine algae in a British Columbia inlet, as related to some environmental factors. *Journal of the Fisheries Board of Canada*, *24*(1), 33-46.

Dugan, J. E., & McLachlan, A. (1999). An assessment of longshore movement in Donax serra Röding (Bivalvia: Donacidae) on an exposed sandy beach. *Journal of Experimental Marine Biology and Ecology*, *234*(1), 111-124.

Dyer, K. R., Christie, M. C., & Wright, E. W. (2000). The classification of intertidal mudflats. *Continental Shelf Research*, *20*(10-11), 1039-1060.

Ellers, O. (1995a). Behavioral control of swash-riding in the clam Donax variabilis. *The Biological Bulletin*, *189*(2), 120-127.

Ellers, O. (1995b). Form and motion of Donax variabilis in flow. *The Biological Bulletin*, *189*(2), 138-147.

Ellis, E. C. (2015). Ecology in an anthropogenic biosphere. *Ecological Monographs*, *85*(3), 287-331.

Erasito, C., Prasad, R., Southgate, P. C., & Kishore, P. (2022). Optimizing community-based pearl oyster (Pinctada margaritifera) spat collection strategies in the Fiji Islands. *Aquaculture Reports*, *26*, 101288.

Farnsworth, M. C., Male, A. J. R., & Russell, I. (1975). FORESTRY AND FARMING-A PRACTICAL EXAMPLE. In *Proceedings of the New Zealand Grassland Association* (pp. 32-37).

Finke, D. L., & Snyder, W. E. (2008). Niche partitioning increases resource exploitation by diverse communities. *Science*, *321*(5895), 1488-1490.

Ford, S. E., Kraeuter, J. N., Barber, R. D., & Mathis, G. (2002). Aquaculture-associated factors in QPX disease of hard clams: density and seed source. *Aquaculture*, *208*(1-2), 23-38.

Frankic, A., & Hershner, C. (2003). Sustainable aquaculture: developing the promise of aquaculture. *Aquaculture international*, *11*(6), 517-530.

Froehlich, H. E., Smith, A., Gentry, R. R., & Halpern, B. S. (2017). Offshore aquaculture: I know it when I see it. *Frontiers in Marine Science*, *4*, 154.

Froese, R., & Kesner-Reyes, K. (2002). Impact of fishing on the abundance of marine species. *ICES CM*, *50*, 12.

Futter, J. M. (2011). *An investigation into the murihiku toheroa (Paphies ventricosa): matauranga, monitoring and management* (Doctoral dissertation, University of Otago).

Gadomski, K. L. (2017). *Reproduction and larval ecology of the toheroa, Paphies ventricosa, from Oreti Beach, Southland, New Zealand* (Doctoral dissertation, University of Otago).

Gadomski, K., Moller, H., Beentjes, M., & Lamare, M. (2015). Embryonic and larval development of the New Zealand bivalve Paphies ventricosa Gray, 1843 (Veneroida: Mesodesmatidae) at a range of temperatures. *Journal of Molluscan Studies*, *81*(3), 356-364.

Gallardi, D. (2014). Effects of bivalve aquaculture on the environment and their possible mitigation: a review. *Fisheries and Aquaculture Journal*, *5*(3).

Gopal, T. S., Rao, C. V. N., Perigreen, P. A., & Govindan, T. K. (1985). Studies on the Transportation of Live Clams. *Fishery Technology*, *22*(1).

Gould, A. J., Needham, E. W., & Knauer, J. E. N. S. (2012). Make it count: maximising the stocking density of juvenile fluted giant clams (Tridacna squamosa Lamarck) during simulated live transportation. *Asian Fisheries Science*, *25*(1), 75-84.

Greenway, J. P. C. (1969). Population surveys of toheroa (Mollusca: Eulamellffiranchiata) on Northland Beaches, 1962–67. *New Zealand journal of marine and freshwater research*, *3*(2), 318-338.

Gulland, J. A. (1983). *Stock Assessment: Why?*. Training Department, Southeast Asian Fisheries Development Center.

Haddon, M., Wear, R. G., & Packer, H. A. (1987). Depth and density of burial by the bivalve Paphies ventricosa as refuges from predation by the crab Ovalipes catharus. *Marine Biology*, *94*(1), 25-30.

Hair, C., Bell, J., & Doherty, P. (2002). The use of wild-caught juveniles in coastal aquaculture and its application to coral reef fishes. *Responsible marine aquaculture*, 327-353.

Hamilton, A. (1908). *Fishing and sea-foods of the ancient Maori* (No. 2). J. Mackay, Government printer.

Harley, C. D., & Helmuth, B. S. (2003). Local-and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnology and Oceanography*, *48*(4), 1498-1508.

Hayward, B. W., & Records, N. (1975). Additional Archaeological Sites from Maunganui Bluff.

Heslinga, G. A., Perron, F. E., & Orak, O. (1984). Mass culture of giant clams (F. Tridacnidae) in Palau. *Aquaculture*, *39*(1-4), 197-215.

Hiddink, J. G., & Wolff, W. J. (2002). Changes in distribution and decrease in numbers during migration of the bivalve Macoma balthica. *Marine Ecology Progress Series*, *233*, 117-130.

Hobday, A. J., Tegner, M. J., & Haaker, P. L. (2000). Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Reviews in Fish Biology and Fisheries*, *10*(4), 493-514.

Hughes, R. N. (1970). Population dynamics of the bivalve Scrobicularia plana (Da Costa) on an intertidal mud-flat in North Wales. *The Journal of Animal Ecology*, 333-356.

Klein, G. D. (1985). Intertidal flats and intertidal sand bodies. In *Coastal sedimentary environments* (pp. 187-224). Springer, New York, NY.

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., ... & Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *science*, *293*(5530), 629-637.

Jeffs, A. G., Delorme, N. J., Stanley, J., Zamora, L. N., & Sim-Smith, C. (2018). Composition of beachcast material containing green-lipped mussel (Perna canaliculus) seed harvested for aquaculture in New Zealand. *Aquaculture*, *488*, 30-38.

Jennings, S. (2004). The ecosystem approach to fishery management. *Marine Ecology Progress Series*, *274*, 279-282.

Kondo, Y., & Stace, G. (1995). Burrowing ability and life position of Toheroa (Paphies ventricosa: Mesodesmatidae), an unusually large, deep-burrowing ocean beach bivalve endemic to New Zealand. *VenUs (japanese journal of Malacology)*, *54*(1), 67-76.

Konisky, R., Grizzle, R. E., & Ward, K. M. (2011). Restoring Native Oysters in Great Bay Estuary, NH (2011).

Kranz, P. M. (1974). The anastrophic burial of bivalves and its paleoecological significance. *The Journal of Geology*, *82*(2), 237-265.

Little, D. C., Newton, R. W., & Beveridge, M. C. M. (2016). Aquaculture: a rapidly growing and significant source of sustainable food? Status, transitions and potential. *Proceedings of the Nutrition Society*, *75*(3), 274-286.

Lotze, H. K. (2004). Repetitive history of resource depletion and mismanagement. *Marine Ecology Progress Series*, *274*, 282-285.

Luttikhuizen, P. C., Drent, J., Van Delden, W., & Piersma, T. (2003). Spatially structured genetic variation in a broadcast spawning bivalve: quantitative vs. molecular traits. *Journal of Evolutionary Biology*, *16*(2), 260-272.

Lytle, L. A. (2009). Measuring the food environment: state of the science. *American journal of preventive medicine*, *36*(4), S134-S144.

Mandeno, M. (1999). *Gonadal Cycle and Spawning Induction in Toheroa (Paphies Ventricosa) from Southern New Zealand: A Thesis Submitted for the Degree of Master of Science at the University of Otago, Dunedin, New Zealand* (Doctoral dissertation, University of Otago).

Manzi, J. J., Hadley, N. H., & Maddox, M. B. (1986). Seed clam, Mercenaria mercenaria, culture in an experimental-scale upflow nursery system. *Aquaculture*, *54*(4), 301-311.

Marin, M. G., Moschino, V., Meneghetti, F., & Ros, L. D. (2005). Effects of mechanical stress in under-sized clams, Tapes philippinarum: a laboratory approach. *Aquaculture International*, *13*(1), 75-88.

Martin, R. E., Carter, E. P., & Davis, L. M. (2000). *Marine and freshwater products handbook*. CRC Press.

Marsden, I. D. (2002). Recruitment in the swash zone–temporal variations in juvenile recruitment of an exposed sand beach surf clam. *Hydrobiologia*, *477*(1), 47-57.

McCay, D. P. F., Gibson, M., & Cobb, J. S. (2003). Scaling restoration of American lobsters: combined demographic and discounting model for an exploited species. *Marine Ecology Progress Series*, *264*, 177-196.

McEwan, A. J., Dobson-Waitere, A. R., & Shima, J. S. (2020). Comparing traditional and modern methods of kākahi translocation: implications for ecological restoration. *New Zealand Journal of Marine and Freshwater Research*, *54*(1), 102-114.

Ministry for the Environment. (2017). Oceanic sea surface temperature, 1993–2016. https://data.mfe.govt.nz/table/89406-oceanic-sea-surface-temperature-19932016/

Miskelly, C. M. (2016). Legal protection of New Zealand's indigenous aquatic fauna–an historical review. *Tuhinga*, *27*, 81-115.

Morrison, M., & Parkinson, D. (2008). Distribution and abundance of toheroa (Paphies ventricosa) on Ninety Mile Beach, 2006. *New Zealand Fisheries Assessment Report*, *26*, 27.

Murton, B. (2006). 'Toheroa Wars': Cultural politics and everyday resistance on a northern New Zealand beach. *New Zealand Geographer*, *62*(1), 25-38.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, *423*(6937), 280-283.

Nakada, M. (2008). Capture-based aquaculture of yellowtail. *Capture-based aquaculture. Global overview. FAO Fisheries Technical Paper*, *508*, 199-215.

Nascimento-Schulze, J. C., Bean, T. P., Houston, R. D., Santos, E. M., Sanders, M. B., Lewis, C., & Ellis, R. P. (2021). Optimizing hatchery practices for genetic improvement of marine bivalves. *Reviews in Aquaculture*, *13*(4), 2289-2304.

Newcombe, E., Sciascia, P., Heasman, K., Spinks, A., Poutama, M., Smith, H., & Sinner, J. (2015). *Towards revitalisation of toheroa in the Horowhenua* (No. 24). Manaaki Taha Moana Research Report.

Nguyen, T. V., Ragg, N. L., Alfaro, A. C., & Zamora, L. N. (2020). Physiological stress associated with mechanical harvesting and transport of cultured mussels (Perna canaliculus): A metabolomics approach. *Aquaculture*, *529*, 735657.

Nickell, T. D., & Moore, P. G. (1992). The behavioural ecology of epibenthic scavenging invertebrates in the Clyde Sea area: laboratory experiments on attractions to bait in moving water, underwater TV observation in situ and general conclusions. *Journal of Experimental Marine Biology and Ecology*, *159*(1), 15-35.

Philippart, C. J., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadée, G. C., & Dekker, R. (2003). Climate-related changes in recruitment of the bivalve Macoma balthica. *Limnology and Oceanography*, *48*(6), 2171-2185.

Porter, J., Costanza, R., Sandhu, H., Sigsgaard, L., & Wratten, S. (2009). The value of producing food, energy, and ecosystem services within an agro-ecosystem. *AMBIO: A Journal of the Human Environment*, *38*(4), 186-193.

Prosser, D. J., Jordan, T. E., Nagel, J. L., Seitz, R. D., Weller, D. E., & Whigham, D. F. (2018). Impacts of coastal land use and shoreline armoring on estuarine ecosystems: an introduction to a special issue. *Estuaries and Coasts*, *41*(1), 2-18.

Raimondi, P. T. (1988). Rock type affects settlement, recruitment, and zonation of the barnacle Chthamalus anisopoma Pilsbury. *Journal of Experimental Marine Biology and Ecology*, *123*(3), 253-267.

Rapson, A. M. (1952). The toheroa, Amphidesma ventricosum Gray (Eulamellibranchiata), development and growth. *Marine and Freshwater Research*, *3*(2), 170-198.

Rapson, A. M. (1954). Feeding and Control of Toheroa (Amphidesma ventricosum Gray)(Eulamellibranchiata) Populations in New Zealand. *Marine and Freshwater Research*, *5*(3), 486-512.

Redfearn, P. (1974). Biology and distribution of the toheroa Paphies (Mesodesma) ventricosa (Gray). *Fisheries Research Division, New Zealand Ministry of Agriculture and Fisheries*, *21*.

Redfearn, P. (1982). Larval shell development of the toheroa, Paphies ventricosa (Gray, 1843)(Mactracea: Mesodesmatidae). *New Zealand Journal of Marine and Freshwater Research*, *16*(3-4), 241-252.

Rehman, S., Gora, A. H., Ahmad, I., & Rasool, S. I. (2017). Stress in aquaculture hatcheries: source, impact and mitigation. *International Journal of Current Microbiology and Applied Sciences*, *6*(10), 3030-3045.

Ripley, B. J., & Caswell, H. (2008). Contributions of growth, stasis, and reproduction to fitness in brooding and broadcast spawning marine bivalves. *Population ecology*, *50*(2), 207-214.

Roberts, R. D., Keys, E. F., Prendeville, G., & Pilditch, C. A. (2007). Viability of abalone (Haliotis iris) stock enhancement by release of hatchery-reared seed in Marlborough, New Zealand. *Journal of Shellfish Research*, *26*(3), 697-703.

Rocha, C. P., Cabral, H. N., Marques, J. C., & Gonçalves, A. M. (2022). A Global Overview of Aquaculture Food Production with a Focus on the Activity's Development in Transitional Systems—The Case Study of a South European Country (Portugal). *Journal of Marine Science and Engineering*, *10*(3), 417.

Roebeling, P. C., Van Grieken, M. E., Webster, A. J., Biggs, J., & Thorburn, P. (2009). Cost-effective water quality improvement in linked terrestrial and marine ecosystems: a spatial environmental–economic modelling approach. *Marine and Freshwater Research*, *60*(11), 1150-1158.

Ross, P. M., Beentjes, M. P., Cope, J., De Lange, W. P., McFadgen, B. G., Redfearn, P., ... & Williams, J. R. (2018a). The biology, ecology and history of toheroa (Paphies ventricosa): a review of scientific, local and customary knowledge. *New Zealand journal of marine and freshwater research*, *52*(2), 196-231.

Ross, P. M., Knox, M. A., Smith, S., Smith, H., Williams, J., & Hogg, I. D. (2018b). Historical translocations by Māori may explain the distribution and genetic structure of a threatened surf clam in Aotearoa (New Zealand). *Scientific Reports*, *8*(1), 1-8.

Ross, P. M., Pande, A., Jones, J. B., Cope, J., & Flowers, G. (2017). First detection of gas bubble disease and Rickettsia-like organisms in Paphies ventricosa, a New Zealand surf clam. *Journal of fish diseases*, *41*(1), 187-190.

Schiel, D. R., Lilley, S. A., South, P. M., & Coggins, J. H. (2016). Decadal changes in sea surface temperature, wave forces and intertidal structure in New Zealand. *Marine Ecology Progress Series*, *548*, 77-95.

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Cardona, A. (2012). Fiji: an open-source platform for biological-image analysis. *Nature Methods*, *9*(7), 676–682. doi:10.1038/nmeth.2019

Schlacher, T. A., Thompson, L., & Walker, S. J. (2008). Mortalities caused by off-road vehicles (ORVs) to a key member of sandy beach assemblages, the surf clam Donax deltoides. *Hydrobiologia*, *610*(1), 345-350.

Sheaves, M. (2009). Consequences of ecological connectivity: the coastal ecosystem mosaic. *Marine Ecology Progress Series*, *391*, 107-115.

Sheppard, N., Pitt, K. A., & Schlacher, T. A. (2009). Sub-lethal effects of off-road vehicles (ORVs) on surf clams on sandy beaches. *Journal of Experimental Marine Biology and Ecology*, *380*(1-2), 113-118.

Shinde, T. A., Dhangar, Y., Patil, L. N., & Patil, S. P. (2020). To study the effect of finishing chemicals on physical and chemical properties in terry towel. *Man-Made Textiles in India*, *48*(5).

Shumway, S. E., Davis, C., Downey, R., Karney, R., Kraeuter, J., Parsons, J., ... & Wikfors, G. (2003). Shellfish aquaculture–in praise of sustainable economies and environments. *World aquaculture*, *34*(4), 8-10.

Shumway, S. E., Scott, T. M., & Shick, J. M. (1983). The effects of anoxia and hydrogen sulphide on survival, activity and metabolic rate in the coot clam, Mulinia lateralis (Say). *Journal of Experimental Marine Biology and Ecology*, *71*(2), 135-146.

Sidwell, N. J. (2002). *The toheroa, Paphies ventricosa, the feeding and diet of, with morphology notes* (Doctoral dissertation, University of Otago).

Smaal, A. C., Ferreira, J. G., Grant, J., Petersen, J. K., & Strand, Ø. (2019). *Goods and services of marine bivalves* (p. 591). Springer Nature.

Smale, M. C., Hall, G. M. J., & Gardner, R. O. (1996). *Monitoring condition of sand dune kanuka forest at Woodhill*. Wellington,, New Zealand: Department of Conservation.

Smith, S. (2003). *The reproduction and recruitment of toheroa (Paphies ventricosa)* (Doctoral dissertation, University of Auckland).

Snedecor, G. W., & Cochran, W. G. (1989). Statistical methods, 8thEdn. *Ames: Iowa State Univ. Press Iowa*, *54*, 71-82.

South, P. M., Floerl, O., & Jeffs, A. G. (2020a). Magnitude and timing of seed losses in mussel (Perna canaliculus) aquaculture. *Aquaculture*, *515*, 734528.

South, P. M., Quirino, M. N., LaDiega, C., & Delorme, N. J. (2020b). Emersion and relative humidity control resettlement success of juvenile marine mussels. *Aquaculture*, *529*, 735675.

Stace, G. (1991). The elusive toheroa. *New Zealand Geographic*, *9*, 18-34.

Stanley, S. M. (1973). Effects of competition on rates of evolution, with special reference to bivalve mollusks and mammals. *Systematic Zoology*, *22*(4), 486-506.

Stephenson, T. A., & Stephenson, A. (1961). Life between tide-marks in North America: Vancouver Island, I. *The Journal of Ecology*, 1-29.

Stickney, R. R., & McVey, J. P. (Eds.). (2002). *Responsible marine aquaculture*. CABI.

St-Onge, P., Miron, G., & Moreau, G. (2007). Burrowing behaviour of the softshell clam (Mya arenaria) following erosion and transport. *Journal of Experimental Marine Biology and Ecology*, *340*(1), 103-111.

Street, R. J. (1971). *Studies on toheroa at Te Waewae Bay, Southland*. Marine Department.

Summers, G., Wong, R. J., & Rogers, M. L. (1996). Effect of storage temperature on stress levels in live clams (Paphies donacina; tuatua). *Journal of Aquatic Food Product Technology*, *5*(1), 7-23.

Supono, S., Dunphy, B., & Jeffs, A. (2020). Retention of green-lipped mussel spat: the roles of body size and nutritional condition. *Aquaculture*, *520*, 735017.

Sutton, P. J., & Bowen, M. (2019). Ocean temperature change around New Zealand over the last 36 years. *New Zealand Journal of Marine and Freshwater Research*, *53*(3), 305-326.

Symonds, J. E., Clarke, S. M., King, N., Walker, S. P., Blanchard, B., Sutherland, D., ... & Dodds, K. G. (2019). Developing successful breeding programs for New Zealand aquaculture: a perspective on progress and future genomic opportunities. *Frontiers in genetics*, *10*, 27.

Tal, Y., Schreier, H. J., Sowers, K. R., Stubblefield, J. D., Place, A. R., & Zohar, Y. (2009). Environmentally sustainable land-based marine aquaculture. *Aquaculture*, *286*(1-2), 28-35.

Tallis, H., Ferdana, Z., & Gray, E. (2008). Linking terrestrial and marine conservation planning and threats analysis. *Conservation Biology*, *22*(1), 120-130.

Taylor, G. F. (2013). Management of Sand Beaches for the Protection of Shellfish Resources.

Theuerkauf, S. J., Morris Jr, J. A., Waters, T. J., Wickliffe, L. C., Alleway, H. K., & Jones, R. C. (2019). A global spatial analysis reveals where marine aquaculture can benefit nature and people. *PLoS One*, *14*(10), e0222282.

Thompson, P. L., Rayfield, B., & Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, *40*(1), 98-108.

Thrush, S. F., Hewitt, J. E., Gibbs, M., Lundquist, C., & Norkko, A. (2006). Functional role of large organisms in intertidal communities: community effects and ecosystem function. *Ecosystems*, *9*(6), 1029-1040.

Thrush, S. F., Hewitt, J. E., Gladstone-Gallagher, R. V., Savage, C., Lundquist, C., O'Meara, T., ... & Pilditch, C. (2021). Cumulative stressors reduce the self-regulating capacity of coastal ecosystems. *Ecological Applications*, *31*(1), e02223.

Trego-Hall, T. P., Te Awhitu, L., & Mikahere-Hall, A. (2020). The politics of Toheroa soup: A pūkōrero about whānau and me. *Ata: Journal of Psychotherapy Aotearoa New Zealand*, *23*(2), 113-122.

Underwood, A. J., & Fairweather, P. (1989). Supply-side ecology and benthic marine assemblages. *Trends in Ecology & Evolution*, *4*(1), 16-20.

Vallyon, L. M. D. (2020). *Birds vs. Clams: Assessing the impacts of South Island pied oystercatcher predation on Toheroa at Ripiro Beach, New Zealand* (Doctoral dissertation, The University of Waikato).

van Gils, J. A., Kraan, C., Dekinga, A., Koolhaas, A., Drent, J., de Goeij, P., & Piersma, T. (2009). Reversed optimality and predictive ecology: burrowing depth forecasts population change in a bivalve. *Biology letters*, *5*(1), 5-8.

Velez, C., Figueira, E., Soares, A. M., & Freitas, R. (2016). Combined effects of seawater acidification and salinity changes in Ruditapes philippinarum. *Aquatic Toxicology*, *176*, 141-150.

Wasson, K., Gossard, D. J., Gardner, L., Hain, P. R., Zabin, C. J., Fork, S., ... & Hughes, B. B. (2020). A scientific framework for conservation aquaculture: a case study of oyster restoration in central California. *Biological Conservation*, *250*, 108745.

Weber, K., Sturmer, L., Hoover, E., & Baker, S. (2008). The role of water temperature in hard clam aquaculture. *EDIS*, *2008*(1).

Williams, J. (2004). *E pakihi hakinga a kai: An examination of pre-contact resource management practice in Southern Te Wai Pounamu* (Doctoral dissertation).

Williams, J. R., Ferguson, H., & Tuck, I. D. (2013a). *Distribution and abundance of toheroa (Paphies ventricosa) and tuatua (P. subtriangulata) at Ninety Mile Beach in 2010 and Dargaville Beach in 2011*. Ministry for Primary Industries.

Williams, J. R., Sim-Smith, C., & Paterson, C. (2013b). *Review of factors affecting the abundance of toheroa (Paphies ventricosa)*. Wellington: Ministry for Primary Industries.

Wingerter, K., Mujica, B., & Miller-Morgan, T. (2013). Development of live shellfish export capacity in Oregon.

Woodin, S. A., Wethey, D. S., Olabarria, C., Vázquez, E., Domínguez, R., Macho, G., & Peteiro, L. (2020). Behavioral responses of three venerid bivalves to fluctuating salinity stress. *Journal of Experimental Marine Biology and Ecology*, *522*, 151256.

Xiao, B. C., Li, E. C., Du, Z. Y., Jiang, R. L., Chen, L. Q., & Yu, N. (2014). Effects of temperature and salinity on metabolic rate of the Asiatic clam Corbicula fluminea (Müller, 1774). *SpringerPlus*, *3*(1), 1-9.

Yamamoto, T. (2020). Modeling bottom-up and top-down controls on the low recruitment success of oyster larvae in Hiroshima Bay, Japan. *Aquaculture*, *529*, 735564.

Yamashita, T., Wada, A., Matsuoka, G., Yano, K., & Akeda, S. (1997). Experimental Study on the Behavior of Bivalves by Oscillatory Flow. In *Coastal Engineering 1996* (pp. 4353-4363).

Ye, Y., Cochrane, K., Bianchi, G., Willmann, R., Majkowski, J., Tandstad, M., & Carocci, F. (2013). Rebuilding global fisheries: the World Summit Goal, costs and benefits. *Fish and Fisheries*, *14*(2), 174-185.

Yongqiang, C. H. E. N., Shaofang, L. I., Hongmei, L., Pin, T., & Yilin, C. H. E. N. (2019, August). Application of intelligent technology in animal husbandry and aquaculture industry. In *2019 14th International Conference on Computer Science & Education (ICCSE)* (pp. 335-339). IEEE.

Table 17: Size cohort (mm) distribution of juvenile toheroa spat in February on the Baylys Beach transect.

Size cohort (mm) Baylys February				
Plots	0-4.9	5-9.9	10-14.9	>15
1 (low tide)	24	6	0	1
2	40	5	1	0
3	57	5	3	0
4	67	8	0	0
5	32	26	17	7
6	133	6	0	0
7	201	8	0	0
8	131	4	0	0
9	26	2	1	0
10	66	6	0	0
11	122	33	0	0
12	117	125	8	4
13	3	17	6	0
14	0	0	1	0
15	2	3	0	0
16 (high tide)	0	1	1	0
Mean	63.81	15.94	2.38	0.75
SD	60.36	30.48	4.56	1.95
SE	15.09	7.62	1.14	0.49

Table 18: Size cohort (mm) distribution of juvenile toheroa spat in February on Maramoenui transect.

Size cohort (mm) - Maramoenui February				
Plot	0-4.9	5-9.9	10-14.9	>15
1 (low tide)	26	3	0	2
2	27	3	1	5
3	41	5	0	0
4	152	12	0	0
5	126	9	0	0
6	70	7	0	0
7	64	7	0	0
8	59	8	0	1
9	51	23	0	2
10	104	74	13	8
11	189	98	7	3
12	15	7	0	0
13 (high tide)	0	0	0	0
Mean	71.08	19.69	1.62	1.62
SD	56.44	30.34	3.93	2.47
SE	15.65	8.42	1.09	0.68

Table 19: Size cohort (mm) distribution of juvenile toheroa spat in May on Maramoenui transect.

	Size cohort (mm)			
Plot	0-4.9	5-9.9	10-14.9	>15
1 (low tide)	1	0	0	0
2	2	0	0	0
3	3	1	0	0
4	1	0	0	0
5	0	0	0	0
6	0	0	0	0
7	1	0	0	1
8	0	0	1	1
9	1	5	10	0
10	0	3	2	1
11	0	0	0	1
12	0	0	0	0
13 (high tide)	0	0	0	0
Mean	0.69	0.69	1	0.31
SD	0.95	1.55	2.77	0.48
SE	0.27	0.45	0.8	0.14

Table 20: Size cohort (mm) distribution of juvenile toheroa spat in February on non-stream habitat in February transect.

	Size cohort (mm)			
Transect (meters)	0-4.9	5-9.9	10-14.9	>15
1 (low tide)	10	1	0	0
2	15	0	0	0
3	34	6	0	1
4	147	3	0	0
5	73	29	0	1
6	52	29	0	0
7	39	23	3	0
8	12	7	2	0
9	10	3	0	0
10	0	0	0	0
11 (high tide)	0	0	0	0
Mean	35.64	9.18	0.45	0.18
SD	43.5	11.78	1.04	0.4
SE	13.11	3.55	0.31	0.12

Table 21: Size cohort (mm) distribution of juvenile toheroa spat in May on non-stream habitat in May transect.

	Size cohort (mm)			
Plot	0-5	5-10	10-15	>15
1 (low tide)	0	1	0	0
2	0	0	0	0
3	3	1	0	0
4	0	8	0	0
5	0	3	1	0
6	0	0	0	0
7 (high tide)	0	0	0	0
Mean	0.43	1.86	0.14	-
SD	1.13	2.91	0.38	-
SE	0.43	1.1	0.14	-

Table 22: Size cohort (mm) distribution of juvenile toheroa spat in May on the Island transect.

	Size cohort (mm) island			
Plot	0-4.9	5-9.9	10-14.9	>15
1 (low tide)	6	6	4	0
2	0	1	0	0
3	0	2	0	0
4	0	0	0	0
5	2	1	0	0
6 (high tide)	1	0	1	0
Mean	1.5	1.67	0.83	-
SD	2.35	2.25	1.6	-
SE	0.96	0.92	0.65	-

Table 23: Size cohort (mm) distribution of juvenile toheroa spat in May on Mahuta Gap transect.

	Size cohort (mm) Mahuta			
Plot	0-4.9	5-9.9	10-14.9	15-20
1 (low tide)	3	0	0	0
2	1	1	0	0
3	3	0	0	0
4	1	1	0	0
5	1	0	0	0
6	6	15	3	1
7	13	28	17	4
8	1	27	18	1
9	0	2	4	0
10	0	6	5	0
11	0	2	0	0
12 (high tide)	0	0	0	0
Mean	2.42	6.83	3.92	0.5
SD	3.78	10.55	6.6	1.17
SE	1.09	3.04	1.9	0.34

Table 24: Size cohort distribution of all sampled toheroa from the five plots on the adult bed excavation. (*n*=109)

Shell Length (mm)	Plot 1		Plot 2		Plot 3		Plot 4		Plot 5	
	0-5cm	5-10cm	0-5cm	5-10cm	0-5cm	5-10cm	0-5cm	5-10cm	0-5cm	5-10cm
0-4.9			0							
5-9.9	1		5		1		1			
10-14.9	4				2					
15-19.9	4						4		1	
20.24.9	3		2		6				3	
25-29.9	1		1						5	
30-34.9					1					
35-39.9	1								1	
40-44.9			1	1				1		
45-49.9		1	0							
50-54.9		1	0							
55-59.9		1	0			1				
60-64.9		2	2	2		2		1	1	2
65-69.9		4		5		1		7		8
70-74.9		2		1	1	2		2		
75-79.9		5				1				2
80-84.9		1								
85-89.9								1		