The modification of toheroa habitat by streams on Ripiro Beach

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JANE COPE

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“*We leave something of ourselves behind when we leave a place, we stay there, even though we go away. And there are things in us that we can find again only by going back there*”

– Pascal Mercier, Night train to London

Abstract

Habitat modification and loss are key factors driving the global extinction and displacement of species. The scale and consequences of habitat loss are relatively well understood in terrestrial environments, but in marine ecosystems, and particularly soft sediment ecosystems, this is not the case. The characteristics which determine the suitability of soft sediment habitats are often subtle, due to the apparent homogeneity of sandy environments. This can make it difficult to detect habitat change in the first place let alone understand ecological consequences. Subtle differences in habitat quality are even harder to detect on dynamic surf beaches which are controlled by the interactions between the wave climate and the beach sands, and experience frequent and large changes. The exposed surf beaches of northern New Zealand, are home to toheroa (*Paphies ventricosa*), an endemic surf clam and New Zealand's most protected shell fish species. Over the course of the 20th century, toheroa were harvested to the point of collapse resulting in the closure of an important cultural, recreational and commercial fishery. Despite more than 40 years of protection, toheroa populations have failed to recover with populations in most locations continuing to decline.

In northern New Zealand toheroa distribution is strongly associated with the small streams which flow across the toheroa beaches. A reduction in the flow of fresh water to the beach via these streams has been suggested as one possible factor which may be preventing the recovery of toheroa. However, little is known about the characteristics of the habitat, and the mechanism driving this toheroa-stream relationship has not received specific attention. The objective of this research was to better understand the effect of streams on beach habitat in the hope of determining the drivers of toheroa distribution. Specifically, I investigated how sediment type, topography, water table depth and sediment temperatures varied across exposed intertidal sediments adjacent to and away from streams. Sampling took place at four sites along Ripiro Beach during the summer, the season when toheroa are most susceptible to thermal stress and streams are thought to provide some protection from dissipation and heat stress. Grainsize distributions from the sampled sediment cores were processed using a Malvern Mastersizer 3000 laser

diffractometer (Malvern, UK). The surface elevation and sediment temperature profiles of the subaerial beach was measured using a theodolite CDN pro accurate waterproof thermometers (Model DTW450L). Temperatures were measured at five sediment depths (2cm, 4cm, 7.5cm, 10.5cm, 20.5cm) throughout the sampling period.

The effect of the streams on the grain size distribution of intertidal sediments appeared to be limited to the high tide, where the proportion of fine sediments was highest in stream adjacent sediments. Greater variations in grain size occurred along the beach, but the greatest difference in sediment sizes occurred when contrasting current day beach grain size distributions with sediment data collected in 1974. Beach sediments from 2017 contained 26661% time more medium sediment indicating the beach is now much coaster than it was 44 years ago. However, as no time series is available for sediment composition at Ripiro it is uncertain whether this change in beach make up is indicative of year-to-year variation or a long term trend. Beach topography varied consistently in the vicinity of streams. The elevation and slope of the beach face was lowest in the path of streams. Along the upper beach, low elevation in the path of the stream lead to the formation of deep bowl like features. As a result of this topography, adjacent to the stream, the water table remained close to the sediment surface throughout the sampling period (< 20 cm), in contrast to point’s away from the stream where the water table was below the sampling depth.

The hypothesis that streams would provide a thermal refuge for toheroa was one of the key questions of this thesis. What I found was that stream driven difference in sediment temperatures were only apparent in the upper intestinal, the area occupied by juvenile toheroa when they first recruit to the beach. Temperatures away from streams were significantly higher (> 3.5 °C) than stream adjacent sediments. However, in the middle intestinal, the area occupied by adult toheroa, the seep face exerted a greater influence on sediment temperatures than the stream and temperatures were no different regardless of stream proximity. The findings of this study suggest that the toheroa-stream relationship is not a direct response to the presence of freshwater, but rather is driven by the modification of the intertidal sediments by the streams. The increased erosion in these areas reduces

the distance between the sediment surface and the water table, increasing the moisture content of the sediments. Additionally, the formation of the basin like depressions in the upper intertidal may act to aggregate spat and juvenile toheroa through the effect of this topography on the beach swash regime. At mid-tide areas adjacent to streams, the depth of the water table was such that adult toheroa are likely to be either fully or partially immersed throughout the low tide. Away from streams, the water table is beyond the burrowing depth of toheroa. For both juveniles and adults, stream associated areas may provide important protection against desiccation, through increasing moisture content of the sediments and for juveniles through reduced sediment temperatures.

Evidently, streams do modify beach habitat in a way that makes it inhabitable for toheroa. Just not in the way that was anticipated. This study has increased our knowledge of beach characteristics that provide good toheroa habitat. Further research is required to test these hypotheses and better understand the effects of climate and terrestrial land use on beach state and therefore the suitability of the beach for toheroa.

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Table of Contents

List of Figures

List of Tables

Chapter 1

General Introduction

1.1 Introduction

In conjunction with climate change, habitat modification and loss is a key factor driving the global extinction and displacement of species (Mantyka-pringle *et al.*, 2012). Habitat loss occurs when an environment undergoes changes so great that it can no longer sustain the original species which inhabited it (Sodhi & Ehrlich, 2010). In terrestrial systems, for example rain forests and wetlands, habitat loss is well understood and has been well documented (*sensu* Mantyka-pringle *et al.*, 2012). The effect of habitat loss within marine environments is best understood in coastal systems, which support high levels of productivity or biodiversity, including rocky reefs and coral reefs (Diaz & Rosenberg, 2008; Halpern *et al.*, 2008; Munday, 2004). Within soft sediment environments, the subtle differences that determine or alter habitat suitability are less evident, largely due to the infaunal position of the organisms, and relative homogeneity of the environment. Along sandy coastlines, estuaries have been the focus of many studies due to their high levels of productivity, recreational value and easy accessibility (Thrush *et al.*, 2013). Subsequently, the effects of factors like grain size or sedimentation on biological communities is well understood (Thrush *et al.*, 2004). By contrast, sandy beaches, and surf beaches in particular are poorly studied and knowledge of the subtleties that influence beach habitat is limited. Over the course of the last century, one of the greatest observed changes has been the decline in surf clam populations, much of which has been driven by unsustainable human harvesting. However, the failure of many of these fisheries to recover is unexplained (McLachlan *et al.*, 1996). Consequently, attention is turning to changes in habitat as a possible explanation for the current status of surf clams.

1.1.1 Surf clams worldwide

Surf clams are infaunal marine bivalves that live within or immediately behind the surf zone, or across the intertidal zone of sandy beaches (Cranfield *et al.*, 1994). Prior to the undergoing taxonomic restructure (Bieler *et al.*, 2014), most, if not all, surf clams belong to the order *Veneridae*, which was considered the largest order of marine bivalves, comprised of more than 680 species (Gaspar *et al.*, 2012). The accessibility of surf clams for human harvest has made them an important part of many cultural and recreational fisheries, past and present. The commercial harvest of surf clams began during the early 1900's, and today they are considered part of a high value bivalve fishery, despite accounting for less than 1% of all marine organisms harvested for food each year (Gaspar *et al.*, 2012).

Globally, many surf clam fisheries are experiencing a decline in stocks, with others having already collapsed (McLachlan *et al.*, 1996). For most, if not all of the fisheries, this downturn has occurred despite efforts to manage the fishery by way of protected areas, open seasons, quota and size limits and restrictions on the methods or mechanisms used for harvest (Aburto & Stotz, 2013; Chu, 2009; Wang, 1995). Anthropogenic factors attributed to the decline in clam numbers include both legal and illegal overfishing and habitat degradation. Fluctuating recruitment, the recovery of predator populations and low genetic diversity are examples of natural causes which are believed to be adversely effecting populations (Donrung *et al.*, 2011; McLachlan *et al.*, 1996). Mass mortality events are common amongst surf clams, and are believed to be driven by storm events, changes in sea temperature, parasitic infestations and algal blooms (Ortega *et al.*, 2012; Williams *et al.*, 2013b).

1.1.2 Surf clams in New Zealand

In New Zealand, the commercial surf clam fishery is built around seven species (Cranfield *et al.*, 1994), all of which occur sub tidally within the surf zone. In pre-European New Zealand, pipi (*Paphies australis*), tuatua (*Paphies subtriangulata*) cockles (*Austrovenus stutchburyi)* and toheroa (*Paphies ventricosa*) were an important food source for Maori (Wehi *et al.*, 2013) and were easily accessible along the intertidal zone of sandy beaches and estuaries. Today, tuatua and cockles continue to be an important part of cultural and recreational fisheries, but the harvesting of toheroa is prohibited, except under individually issued cultural permits (Ross *et al.*, 2017a). Toheroa are the only New Zealand shellfish which are managed this way, and can therefore be considered to be one of New Zealand's most protected marine organisms (Ross *et al.*, 2017a).

1.1.3 Toheroa

Toheroa are endemic to New Zealand and are closely related to pipi, tuatua, and southern tuatua (*P. donacina*). During the first half of the 20th century, substantial toheroa populations were found in northern New Zealand at Ripiro, Ninety Mile and Muruwai Beaches, with minor populations recorded elsewhere (Mitimiti, Spirits Bay, Tom Bowling Bay, Tokerau, Te Arai, Whangape, Pollok, Piha, Ohope and Opotiki). Toheroa were also abundant on the Kapiti-Horowhenua coast (Himatangi, Foxton, Waiterere, Hokio and Otaki) (Cassie, 1951; Redfearn, 1974; Street, 1971), with other populations occurring as far as Southland (Oreti and Blue Cliff (Te Waewae)) (Figure 1).

Toheroa are the largest clam found in New Zealand. Previously, Northland toheroa appear to have reached sizes of up to 180 mm, but present day adults rarely exceed 100mm (Cook, 2010; Williams *et al.*, 2013a; P. Ross, personal communication). By contrast, Southland toheroa commonly grow to 100– 145 mm (Beentjes, 2010b, 2010a). Toheroa reproduce by broadcast-spawning, with peaks occurring around the time of full and new moons (Smith, 2003). Under favourable conditions, northern toheroa can spawn year round under (B. Searle, personal communication) but the main spawning event occurs in early spring with other notable events in autumn and winter (Redfearn 1974; Smith 2003). After releasing their gametes into the seawater where external fertilisation takes place, larval development occurs at sea and lasts approximately three weeks (Redfearn, 1982). Based on this larval duration and the lunar cycle, it is estimated that larvae reach the shore on the neap tide. Here, they are progressively carried towards the spring high water mark on successive tides, where they metamorphose into juvenile toheroa (spat) with a length at settlement of 2 mm or less (Redfearn 1974). In Northland, juvenile toheroa are most abundant in the sediments adjacent to the streams which flow onto the beach (Smith, 2003). As the toheroa grow, they migrate down towards the mid-tide region of the beach, where the adult beds are established. Early observations describe single cohort beds (Redfearn, 1974), however during this research, juveniles were frequently observed adjacent to and within adult beds in the region of the mid-tide. As with the juveniles, the largest and densest adult beds occur near streams, but they do occur the length of the beach (Akroyd *et al.*, 2002; Williams *et al.*, 2013a). Toheroa appear to be unique in this regard, with no mention in the literature of other clams exhibiting a strong relationship with streams. The biology and ecology of toheroa has been thoroughly reviewed by (Ross *et al.*, 2017a) (Supporting publications: Publication 1).

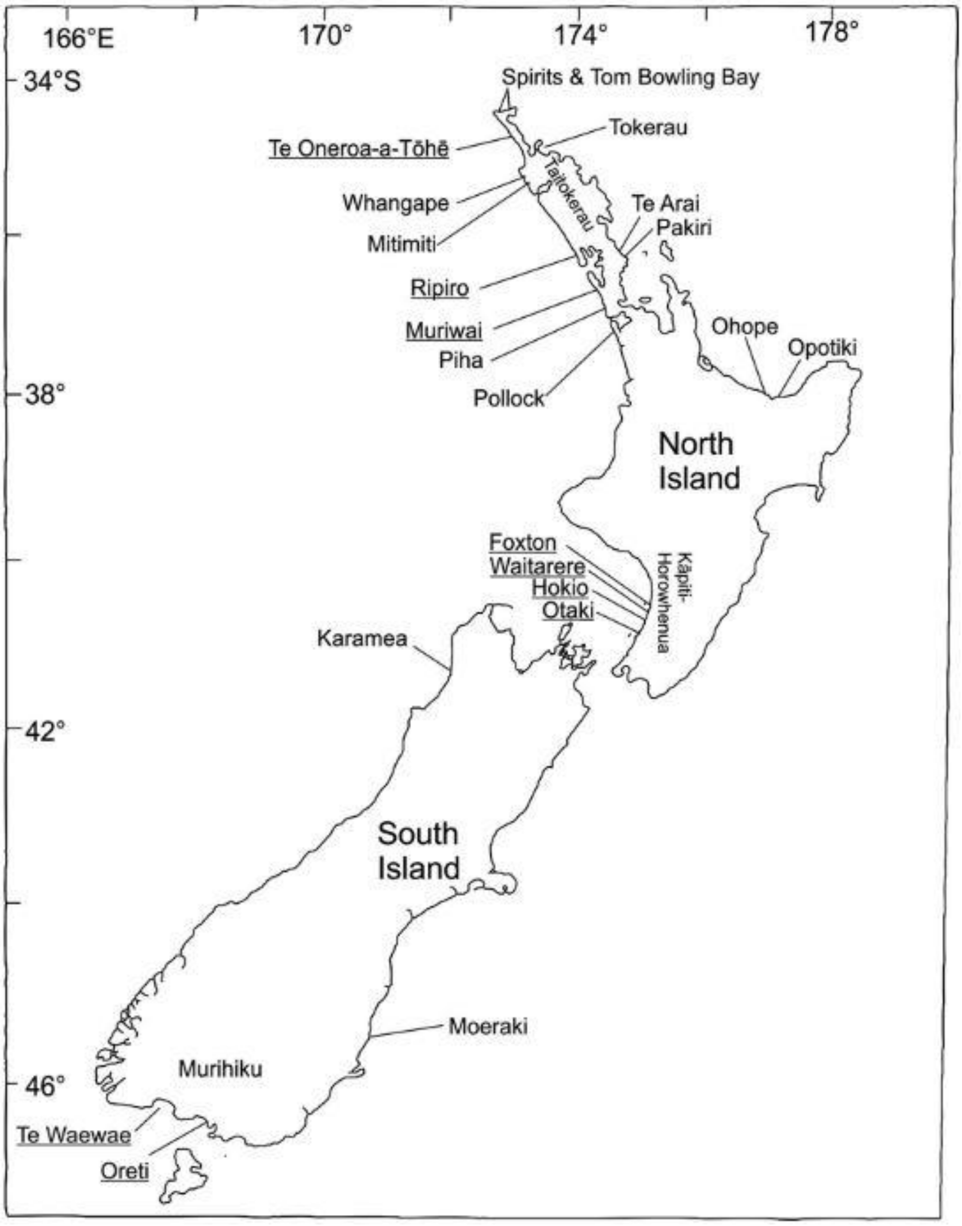

Figure 1: Distribution of toheroa (*Paphies ventricosa*) in New Zealand. Major populations are underlined. Figure reproduced from Redfearn (1974) and Ross et al. (2017a).

Toheroa were an important food source for Māori prior to their discovery by European New Zealanders in the late 1800’s (Murton, 2006 and references therein; Redfearn, 1974) Thereafter, they gained rapid popularity amongst European settlers, developing into an important commercial fishery, much of which was exported as canned toheroa (Williams *et al.*, 2013b). Canneries were established along Ripiro and Ninety Mile Beaches, with intermittent operations at Muruwai, Kapiti-Horowhenua and Southland toheroa (Williams *et al.*, 2013b). Toheroa were not exempt from the population fluctuations reported in other clam species (Arntz *et al.*, 1988; Brown & McLachlan, 2010; Coe, 1955; Fiori *et al.*, 2004; McLachlan *et al.*, 1996), but harvesting continued with limited intervention to encourage the sustainability of the fishery. Concerns soon developed that the combined harvest of the commercial fishery and the largely unregulated recreational fishery were depleting the resource (Murton, 2006). Fisheries regulations were introduced incrementally from 1913 (Miskelly, 2016; Murton, 2006), but ultimately failed to halt the decline of the fishery. By the mid-1900s toheroa populations declined to levels where their harvest was no longer viable (Murton, 2006; Redfearn, 1974; Stace, 1991). All commercial harvest ceased by 1969 and regional recreational fishery closures occurred between 1971 and 1980 (Williams, Sim-Smith, et al., 2013). Since that time, toheroa harvesting has been restricted to customary take by Māori (Miskelly, 2016).

Despite more than 40 years of protection, toheroa populations have failed to recover with many continuing to decline (Williams *et al.*, 2013b). Where post-exploitation populations have failed to recover, continued overharvesting as well as a range of other threats including off-road vehicles, pollution, coastal engineering and coastal development have been implicated (Heasman *et al.*, 2012; McLachlan *et al.*, 1996). The factors considered most likely to be preventing the toheroa recovery have been reviewed by Williams *et al.* (2013b), and include climate and weather, food availability, vehicle activity, water quality and changes to adjacent land use. The introduction of exotic forestry (*Pinus radiata*) into beach catchments has been blamed for a reduction in the volume of fresh water flowing to the beach, causing numerous streams along Northlands beaches to dry up (Williams *et al.*, 2013b). Because of the strong relationship between toheroa and streams, the decline in the flow of fresh water is seen as a possible contributor to the continued decline of toheroa. It is hypothesised that changes to the beach resulting from this reduced flow may be altering the suitability or availability of habitat that is most suitable for toheroa (Williams *et al.*, 2013b).

1.1.4 Coastal research

Changes in the way in which land adjacent to a coast is utilised are easily identified. However, the effects and ecological consequences of these changes are often difficult to discern. On coastlines dominated by plantation forestry there are reports of reduced water levels in dune lakes and the disappearance of coastal streams (Williams *et al.*, 2013b). Unfortunately, very little is known about the potential consequences of reduced freshwater flows on coastal ecosystems, as most research is focused on understanding the consequence of inputs into the system. Additionally, both *beach science* and ecological studies within sandy beach ecosystems are largely underrepresented in scientific literature (Nel *et al.*, 2014). Our understanding of the interplay between hydrology and ecology is undoubtedly diminished by the strong disconnect between these two disciplines which often operate independently from each other despite a shared interest in coastal processes.

1.1.5 Coastal research in New Zealand

In New Zealand’s more remote regions, the regional councils initiate much of the environmental research. Consequently, monitoring has been focused on the east coast where populations are greatest. Where monitoring has been conducted on the west coast, it is largely confined to stretches of coast associated with larger communities or tourism, for example Auckland’s west coast beaches and Ninety Mile Beach. In Northland, the west coast is sparsely inhabited and the availability of information reflects this. For example, the beach profile at Muriwai, on Auckland’s West coast, has been surveyed four times a year for the last 33 years (Boyle, 2016). By contrast, the beach profile at Ahipara, on the Northland West coast was surveyed three times over a 12 year period (Tonkin & Taylor Ltd, 2014). Consequently, there is limited information available describing the current environmental conditions along Northlands toheroa beaches, and historical reference points are limited. Much of the environmentally orientated information available for Ripiro Beach has been a result of work undertaken by early toheroa researchers (Cassie, 1955; Redfearn, 1974), prompted by the demise and imminent collapse of the fishery. Since its collapse, research into the environmental conditions of the beach have been limited. This explains why the golden era of toheroa research was limited to the period between 1950 and 1970.

In northern New Zealand, one of the most striking features of the distribution of toheroa is their close association with streams (Akroyd *et al.*, 2002; Cassie, 1955; Rapson, 1954; Redfearn, 1974). This association has been repeatedly noted in fisheries and scientific literature dating back to 1955 with the largest, densest toheroa beds often reported in stream adjacent areas. Despite this, the mechanics of the stream-toheroa relationship have never been thoroughly investigated. It is uncertain whether this distribution is indicative of active selection by toheroa, passive placement driven by conditions associated with the environment or differential survival. Streams are presumed to either provide or improve beach habitat for occupation by toheroa, but the differences in environmental parameters adjacent to and away from streams have never been quantified. From a global perspective, the modification of the intertidal regions by fluvial processes is under researched, particularly along exposed beaches that experience large tides and swash regimes. On less exposed beaches, freshwater inputs are often the result of seeps, and effect salinity, temperature and nutrients concentrations (Befus *et al.*, 2013; Dale & Miller, 2007; Miller & Ullman, 2004; Vandenbohede & Lebbe, 2011) which in turn influence the distribution of shell-less invertebrates with differing tolerance levels. In the absence of this environmental knowledge, and with a poor understanding of what constitutes good toheroa habitat, it is difficult to know what is driving the relationship, or whether the environment is undergoing changes, which may alter habitat suitability for toheroa.

1.1.6 Beaches

Beaches are physically controlled systems. The underlying geology (Jackson *et al.*, 2005) and interactions between the sand and wave climate give rise to a continuum of beach morphodynamic types, ranging from dissipative to reflective through various intermediate stages (Wright & Short, 1984b), or states as referred to herein. Dissipative beaches are synonymous with exposed coastlines where waves break off shore and much of the energy is dissipated by the time the swash reaches the beach. These beaches are wide (macro tidal), flat and are comprised of fine sands. By contrast, reflective beaches are characterised by waves, which surge or break on the beach. These beaches tend to be narrow and steep with their sediments made up of coarser grains (Nordstrom, 1977). The state of a beach has a direct effect on ecology. Richness, abundance and the composition of biological communities is influenced by beach state, with dissipative beaches generally more habitable than reflective ones (McLachlan, 1990, 1996). This difference in habitability is a function water table height, swash climate and sediment transport which varies between beach states. The moisture content of intertidal sediments is also an important factor which will influence the distribution of organisms across the intertidal zone (Brown & McLachlan, 2010; Cassie, 1951; Salvat, 1967).

1.1.7 Research gaps

The streams that flow onto Ripiro Beach have the potential to modify sediment moisture content both along and across the shore. In addition to moisture, streams may alter the temperature and salinity of intertidal sediments (Befus *et al.*, 2013; Dale & Miller, 2007; Miller & Ullman, 2004; Vandenbohede & Lebbe, 2011), as well as the grain size distribution of the sediments and beach topography, as a consequence of higher erosion (Atherton *et al.*, 2001; Oh & Dean, 1995). As mentioned above, the mechanisms driving the toheroa-stream relationship are unknown. It may be driven by differential mortality or the physical delivery of toheroa or habitat selection based on any number of environmental parameters. Without an understanding of what makes for good toheroa habitat, it is difficult to assess whether habitat loss or degradation is an explanation for the continued demise of toheroa.

1.1.8 Purpose of the research

The purpose of my research is to better understand the mechanisms behind the observed toheroa-stream associations. I want to understand why toheroa beds near streams are larger, denser and more stable over time. I want to understand how streams modify the habitability of high-energy surf beaches. To achieve this, my research focuses on describing the physical parameters of the beach environment adjacent to and away from streams. Specifically, I evaluate the effect of streams on sediment grain sizes, beach morphology and thermal regimes. This research is conducted in habitat occupied by juvenile (upper intertidal) and adult toheroa (mid intertidal).

Chapter 2 provides a summary description of study sites, and provides rational for the selection of Ripiro Beach as the study site.

In **Chapter 3,** I investigate whether streams alter the grain size distribution of intertidal sediments. I also examine grain size distributions at a larger scale along 32 km of Ripiro Beach, and then address questions about long-term change in sediment characteristics by comparing contemporary sediment structure to historical data. I test the hypothesis that stream adjacent sediments will differ from sediments away from streams on account of either the introduction of fine terrestrially derived sediments, or alternatively the erosion of fine beach as a consequence of moisture facilitated erosion. The implications of these features on habitat suitability for juvenile and adult toheroa are also discussed.

In **Chapter 4** I investigate the effect of streams on beach topography to the hypothesis that beach morphology in the vicinity of streams could act to aggregate toheroa or their food, in much the same way as beach cusps act as aggregation points in the swash zone (Chelazzi & Vannini, 2013; McLachlan & Hesp, 1984). Specifically, I investigate beach slope and elevation near streams. The implications of these features on habitat suitability for juvenile and adult toheroa are also discussed.

In **Chapter 5,** I look at the effect of streams on thermal regimes in the sediments of Ripiro Beach. Heat exposure is a major stressor for intertidal organisms (Macho *et al.*, 2016; McQuaid & Scherman, 1988), and it is hypothesised that streams may provide a temperature refuge for toheroa thereby increasing their survival and abundance in these areas.

1.2 Permits and ethics

Toheroa are the only protected bivalve species in New Zealand. Commercially and recreational harvesting is prohibited and customary harvest is only allowed when permitted and in accordance with tikanga Māori. The level of protection afforded to toheroa is so great that even the disturbance of toheroa beds in not allowed. My supervisor, Dr. Ross worked Te Uri o Hau prior to commencement of this research and developed a plan to operate under a customary permit. However, when it came time to begin my research, despite the project having full support of the iwi, a customary permit could not be obtained. There was not sufficient time to obtain a special permit from the Ministry for Primary Industries. Consequently, my thesis proposal was reworked and research designed so that I could investigate toheroa habitat without disturbing or collecting toheroa themselves. However, over the course of this project I have been fortunate to spend time with kaitiaki on Northland beaches and was able to get hands on experience with toheroa in accordance with tikanga Maori. I also participated in a routine stock assessment for toheroa on Oreti beach, Southland. These opportunities have proved invaluable and provide additional knowledge to draw on when discussing my observations and data. A special issue permit was obtained in the later stages of the research for the limited collection of diseased toheroa. These findings are presented in a separate paper included in the appendices of this thesis (Ross et al. 2017).

Chapter 2

Study Location – Ripiro Beach

2.1 Ripiro beach and its relevance to toheroa

Ripiro Beach has been the epicentre of all things toheroa going back to at least the late 1800s (P. Ross, personal communication). Of all these toheroa beaches, Ripiro has always been noted as the most productive. Ripiro Beach was the site of the first and longest running toheroa cannery operation, and was the only beach where more than one cannery operated concurrently, with up to four existing at one time. It was also the site of conflict between Maori and the NZ government around the management of toheroa (Murton, 2006). Today, Ripiro Beach continues to support the largest remaining toheroa population in New Zealand, and is the only beach in the North Island where significant numbers of toheroa can still be found. The position of the beds along the beach are variable, with a higher abundance to the North of the beach in some years (Williams *et al.*, 2013a) and to the south in others (Akroyd *et al.*, 2002). However, the largest toheroa and most abundant beds have been found along the central and southern sections of beach between Chases Gorge (Baylys Beach) and Glinks Gully (Akroyd *et al.*, 2002; Greenway, 1969).

During a 2011 survey by Williams *et al.* (2013a), 45 toheroa beds were found along Ripiro Beach, with a population estimated at approximately 75.6 million individuals. In contrast, a similar survey along Ninety Mile beach found only 38 individual toheroa, and estimated the population in this location to be only 2.4 million. Toheroa recruitment is good along Ripiro, and juveniles (<15 mm) are the most abundant size class (Williams *et al.*, 2013a). This decrease in abundance with increasing size is anticipated, as a consequence of natural mortality, but the extent of decline over time and the failure for toheroa to recover following protection is unexpected and unexplained (Morrison & Parkinson, 2008b; Williams *et al.*, 2013a). Inconsistency and developments in sampling methodologies over time have resulted in differing population estimates, making direct comparisons with early estimates potentially erroneous and unreliable (Akroyd *et al.*, 2002). Historical estimates do however provide a reference point for stock abundance, and have been reviewed by Heasman, Keeley, & Sinner (2012).

2.2 Physical description of Ripiro Beach

Ripiro Beach, also known locally as Dargaville Beach and formerly as North Kaipara Beach, is a dissipative mesotidal beach (Redfearn, 1974) located on the west coast of Northland, New Zealand. At 82 km long, it is New Zealand’ s longest drivable beach, and a recognised national road (Kaipara District Council, 2014). The beach is oriented in a North West direction, stretching from Kaipara North Head (Pouto peninsular) in the south to Maunganui Bluff in the north. Sediments are mostly fine (125-250µm) (approximately 98%) and comprised of quarts and feldspar (Rapson, 1952; Redfearn, 1974; Schofield, 1970), though titanium magnetite is also present throughout. The coastline is exposed to the Tasman Sea and subject to continuous wave action, with waves ranging between 1.5 – 2.5 meters and a wave period of 6 to 8 seconds (Gorman *et al.*, 2003). It has a semidiurnal tidal regime and a maximum tidal range of 2.9 meters. Seawater salinities range from 35 – 35.5‰ and the sea surface temperature (SST) ranges between 14°C and 22°C (Kerr, 2005). Longshore drift is largely to the North, driven by swell coming from the Southern Ocean, but can switch to south east (Hamill & Ballance, 1985; Schofield, 1970). During erosive periods associated with heavy wave action, sand is moved to offshore bars (Kerr, 2005).

The beach undergoes extensive periods of erosion and accretion, with substantial changes in volume occurring. Based on the disappearance of known landmarks, locals have estimated the beach has accreted by approximately 8 meters over the course of 60 years; however, this has never been quantified and may be an exaggeration. During 2016 and 2017, the beach underwent a period of extensive erosion, during which time, remnants of ancient forest were exposed, but not the aforementioned landmarks. At shorter time frames, changes in height of ±1 meter have been observed in a single tidal cycle (Redfearn, 1974). Although again unquantified, the erosion that occurred during 2016 and 2017 was extreme according to locals, exposing large rock shelves, boulder fields and petrified kauri forests. These obstacles made sampling challenging, as access to several parts of the beach was restricted to low tide when one could drive below the hazards.

The beach is backed by sandstone cliffs between Maunganui Bluff and Kopowai (Figure 2). During periods of accretion, dunes can form in front of the cliffs and in the gullies around the streams. South of Kopowai, the cliffs turn inland, and there is an intervening region of parabolic sand dunes that widen from the north to the South (Redfearn, 1974; Williams *et al.*, 2013b)

Figure 2: Example of sandstone cliffs along Ripiro beach between Maunganui Bluff and Kopowai.

Extensive efforts have been made along this beach to replace introduced marram grass (*Ammophila*) (Cockayne, 1909) with sand tussocks, including *Spinifex* and pingao (*Ficinia spiralis*, previously known as *Desmoschoenus spiralis*). In mātauranga Māori, pingao and spinifex are believed to be the nursery habitat for toheroa, and the restoration of these dune grasses is seen as a key component in restoring toheroa (Ross et al, 2017, J. Te Tuhi and B.Young personal communication). In addition, dune restoration acts to stabilize the beach, reducing erosion by facilitating beach accretion (Gómez-Pina *et al.*, 2002; Nordstrom *et al.*, 2000). The southern areas of the beach, towards the Pouto peninsular, is renowned for its multiple dune lakes, many of which are now incorporated into farmland or near forestry blocks (McKelvey, 1999) as a consequence of land conversion.

2.3 Adjacent land use

In contrast to Ninety Mile and Murawi beaches, where much of the catchment has been converted into exotic *Pinus radiata* forestry, much of the Ripiro catchment has been converted to crop and pasture, with some dairy and a small area of forestry, largely confined to a small block between Glinks Gulley and Third streams and Pouto Peninsula (the northern head of the Kaipara and southern reach of Ripiro Beach) (McKelvey, 1999). There are local accounts of water being pumped from coastal bores to farms on the escarpment that could have an impact on the flow of water onto the beach, but at present, forestry is largely blamed for a reduction in the volume of water reaching the beach and flowing across it as streams (Ross *et al.*, 2017a).

2.4 Streams

The shallow streams that flow from the cliffs or gullies onto the sand are a distinctive feature of Ripiro Beach, and toheroa beds are present at every stream. The association between toheroa and streams was first noted by Rapson (1952), with subsequent researchers confirming a higher abundance of toheroa in stream and seep areas compared to dry sections of beach (Ross *et al.*, 2017a; Smith, 2003; Williams *et al.*, 2013a; Williams *et al.*, 2013b). Williams et al. (2013) compared topographic maps from 1940 and 2002 (LINZ 1:50000 series) and concluded that the number of streams flowing onto the beach at Ripiro had reduced from 15 to nine over a 62 year period. This reduction in water flow onto the beach is purported to be impacting toheroa populations (Williams *et al.*, 2013b). However, the 2002 map rendering may have missed two major streams to the South of Glinks Gully that are still in existence to this day, and as such, the comparison of topographic maps may not provide an accurate reflection of the number of streams actually flowing onto Ripiro Beach.

The maximum depth of streams on Ripiro Beach is approximately 5cm, located at the interface between the land and the beach, with streams becoming shallower (<2 cm) to the point of being a sheen as they flow across the beach with the receding tide. Initially the streams remain connected to the line of the ebbing tide, but at varying points and rates, they separate and the surface flow dissipates and retreats towards the upper beach (Figure 3). Although the exact mechanics of this are unknown, observations seem to indicate that evaporation (through solar radiation and increasing sediment temperatures) is a likely driver although tidal action and hydraulic gradients may influence this retreat to some extent.

Figure 3: An example of the change in stream flow over the course of a low tide at Chases Gorge, Ripiro Beach. As the tide recedes, the streams begin to flow across the intertidal beach, remaining connected to the swash front until the point of the seep face (top). Over the course of the low tide, surface flow associated with the stream dissipates and retreats toward the upper beach (bottom).

2.5 Site selection criteria

The objective of this thesis is to assess the effect of streams on the physical and geochemical characteristics of the beach, by comparing and contrasting properties of the beach within or adjacent to streams, with areas away from streams. To achieve this objective, the following criteria were used in the selection of sites for this study:

- The presence of a stream flowing onto the beach;
- Evidence of a large and dense toheroa bed in the vicinity of the stream;
- Accessibility. Severe erosion in the months prior to sampling had exposed large rock shelves and boulder fields, restricting vehicular access past them to the lowest points of the tide. This, coupled with high seas and the issuing of a tsunami warning for the area of coastline, meant that only sites in the more accessible central region of the beach were sampled.

2.6 Study sites

Five sites were selected using the above criteria for the current study along a 31 km stretch of Ripiro beach (Figure 4). They were as follows:

- **Kelly's**, the northernmost sampling site (35°55'29.8"S 173°43'04.7"E) located between the seaside townships of Omamari and Bayley's Beach (Figure 5 - 7);
- **Chases Gorge,** located immediately to the South of Baylys Beach (35°57'16.9"S 173°44'42.6"E). Chases Gorge was the only populated location used in this study (Figure 8 - 9);
- **Mahuta Gap** (Mahuta) (36°00'12.9"S 173°47'18.5"E) (Figure 10 - 11);
- **Kopowai** (36°02'24.0"S 173°49'12.9"E) (Figure 12 - 14), located between Baylys Beach and Glinks Gully; and
- **Third Stream,** the southernmost research site (36°09'18.5"S 173°55'05.2"E) located within what was formerly the Meredith Brothers toheroa harvesting concession area and was once a once bountiful toheroa harvesting area (Redfearn, 1974) (Figure 15 - 17).

The sites selected are typical of the numerous streams that run on to the beach. Localised anthropogenic pressures to which they are subjected may vary due to their proximity to settlements and beach access (harvesting, vehicle effects) and adjacent land use (water quality, water abstraction).

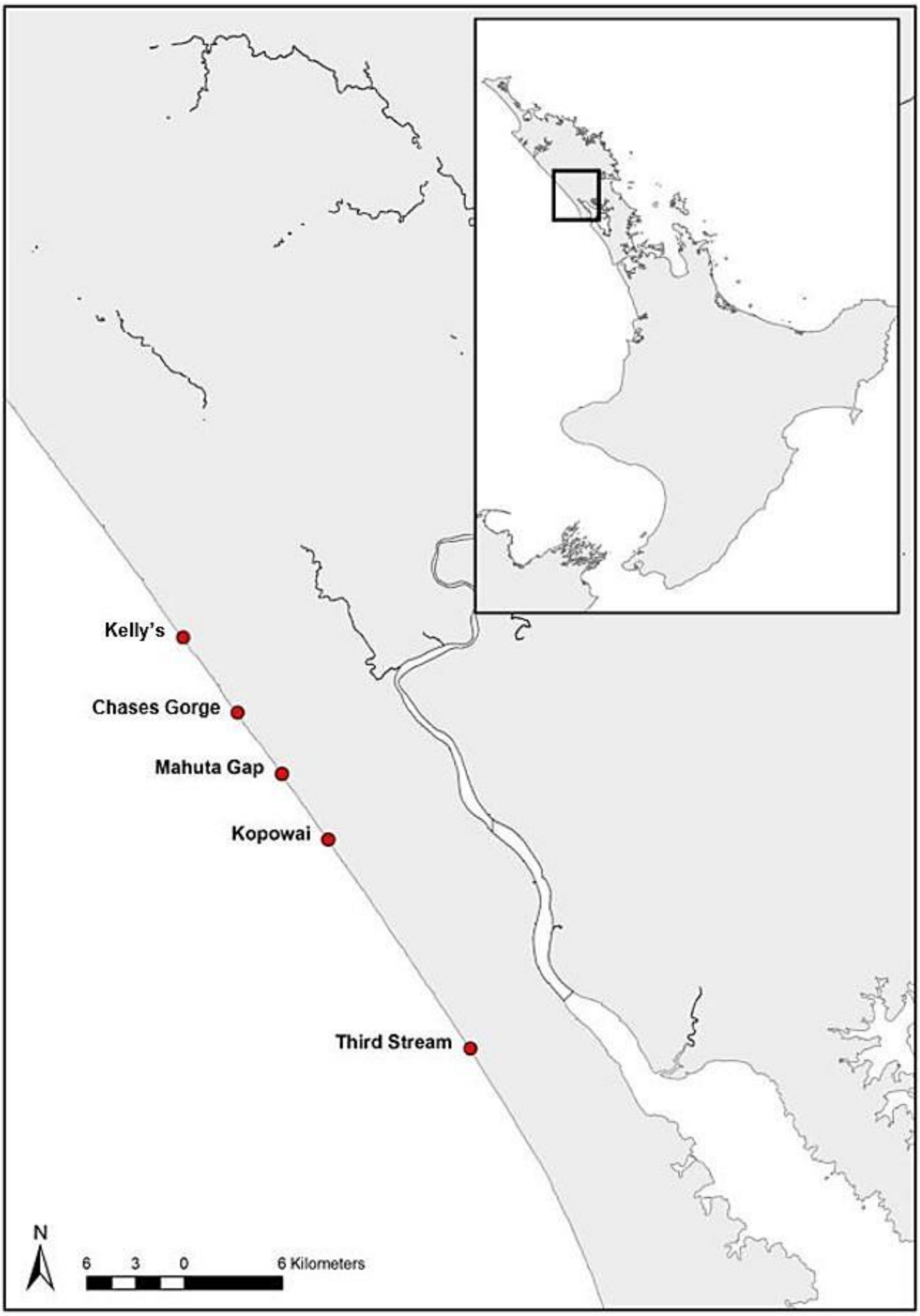

Figure 4: Sample sites along Ripiro Beach, located on the west coast of Northland, New Zealand.

2.6.1 Kelly's

Figure 5: Aerial view of the sampling site at Kelly's (arrow). Small pockets of native bush remain, but much of the adjacent land has been converted to pasture. Sourced from the LINZ Data Service and licensed by Northland Regional Council for re-use under the Creative Commons Attribution 3.0 New Zealand licence.

Figure 6: View from the north to the south of Ripiro Beach, across the sample site at Kelly's (circled). (Photograph reproduced with permission of Phil Ross, © 2018).

Figure 7: View from the south of Kelly's stream towards the north. The vehicle marks the point of the stream across the beach. (Photograph reproduced with permission of Phil Ross, © 2018).

2.6.2 Chases Gorge

Figure 8: Aerial view of the sampling site at Chases Gorge (arrow). Baylys Beach lies to the north of the stream and is the largest settlement along Ripiro Beach. Much of the land to the south is pastoral. Sourced from the LINZ Data Service and licensed by Northland Regional Council for re-use under the Creative Commons Attribution 3.0 New Zealand licence.

Figure 9: The incoming swash at Chases Gorge extending beyond the line of the high tide in stream regions. (Photograph reproduced with permission of Phil Ross, © 2018).

2.6.3 Mahuta Gap

Figure 10: Aerial view of the sampling site at Mahuta Gap (arrow). Much of the adjacent land has been converted to pasture. Sourced from the LINZ Data Service and licensed by Northland Regional Council for re-use under the Creative Commons Attribution 3.0 New Zealand licence.

Figure 11: Looking up the stream towards the hills from below mid-tide. The stream is little more than 1 cm deep at this point. (Photograph reproduced with permission of Jacintha Forde, © 2018).

2.6.4 Kopawai

Figure 12: Aerial view of the sampling site at Kopowai (arrow). Much of the adjacent land has been converted to pasture. Sourced from the LINZ Data Service and licensed by Northland Regional Council for re-use under the Creative Commons Attribution 3.0 New Zealand licence.

Figure 13: Looking towards the north along Ripiro Beach, over the stream flowing onto the beach at Kopawai. (Photograph reproduced with permission of Phil Ross, © 2018).

Figure 14: Looking southward over the stream flowing onto Ripiro Beach at Kopawai. (Photograph reproduced with permission of Phil Ross, © 2018).

2.6.5 Third Stream

Figure 15: Aerial view of the sampling site at Third Stream (arrow). An intervening region of parabolic dunes lies between the beach and the sandstone cliffs. Much of the adjacent land has been converted to pasture. Sourced from the LINZ Data Service and licensed by Northland Regional Council for re-use under the Creative Commons Attribution 3.0 New Zealand licence.

Figure 16: Looking south over the intertidal stream at Third Stream. (Photograph reproduced with permission of Phil Ross, © 2018).

Figure 17: Looking landward across the intertidal zone and the sheen remnants of the stream at Third stream. (Photograph reproduced with permission of Phil Ross, © 2018).

Chapter 3

Spatial and temporal grain size distributions of Ripiro beach

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3.1 Introduction

The distribution of sediment grain sizes across a coastline can influence the distribution and species of inhabiting organisms, resulting from species adaptation to, or preferences for particular sediment compositions (Fiori & Carcedo, 2015; McLachlan, 1996). Along beaches, grain size provides an indication of the wave climate, which may also alter a species' ability to survive or compete at a given location. However, these two parameters are largely synonymous, working in conjunction with each other to influence organism distribution.

A sandy beach is a dynamic environment shaped by the interaction between wave climate and grain size (Brown & McLachlan, 2010; Masselink & Short, 1993; Wright & Short, 1984b). Sand particles along these types of beaches range in size from very fine (64 µm) to very coarse (200 µm). Grain size provides an indication of the sediment source, wave energy and the hydraulic mechanisms that sort and transport sediments from, to and within the system (Folk, 1966; Komar, 1998; Nordstrom, 1977). Consequently, grain size varies spatially and temporally along beaches, reflecting differential deposition and erosion, seasonal variability in wave climate and the decay in longshore drift (Gallagher *et al.*, 2016; Otvos Jr, 1965). In spite of this known variability, beaches are often characterised based on an average of only a small number of sediment samples (Prodger *et al.*, 2017), and thus may not give an accurate reflection of the wider system.

The entrainment and transporting of sediments into, within or from a system is a function of hydrodynamic energy and grain size (Masselink & Short, 1993; Short & Wright, 1983), with finer fractions requiring less energy to be suspended and transported than coarser ones. In addition, particle size has an indirect influence on sediment porosity, owing to its effect on sediment sorting (McLachlan & Turner, 1994; McLean & Kirk, 1969). Sorting effects the hydraulic conductivity and capillary forces of the sediments , and the extent to which interstitial moisture can be held in sediments above the water table (Folk, 1966; Mason & Coates, 2001). Grain size also influences permeability of the beach, which is the main determinant of beach slope (Masch & Denny, 1966; McLean & Kirk, 1969). Thus the relationship between grain size and beach slope has been well studied (Bascom, 1951; Reis & Gama, 2010). A significant change in porosity, permeability and hydraulic conductivity occurs in grain sizes larger than >200 µm (Wieser, 1959). Changes in grain size, and subsequently slope, are often indicative of a change in beach state.

Beaches are described according to their state, a classification that takes into account sand particle size and wave energy (wave height / wave velocity) (Masselink & Short, 1993; McLachlan *et al.*, 1995; Short & Wright, 1983). These variables act together to produce a continuum of states from dissipative to reflective, through several intermediate stages (Masselink & Short, 1993; Short & Wright, 1983). Dissipative beaches occur along exposed coastlines, where they are subject to high wave energy, much of which is dissipated across the surf zone producing long slow swash regimes. These beaches consist of fine sand (<200 µm) and are wide and gently sloping. At the opposite end of the spectrum, reflective beaches have coarser sediments and steeper gradients. On these beaches, little energy is lost from the waves before they break and surge up the beach, thus much of the energy is reflected back out to sea. On a dissipative beach, an increase in grain size can indicate a move towards an intermediate state. The wave climate along exposed coasts often causes beaches to rapidly alternate between dissipative and intermediate states, with seasonal changes not uncommon (Short & Jackson, 2013; Wright & Short, 1984b). Furthermore, grainsize distributions along the shoreline are variable.

Both grain size and beach state are ecologically important. Changes in sediment size can have a direct effect on the burrowing ability of intertidal organisms, and variations in grain size on a beach can influence bed dynamics along the shore and the vertical position of beach fauna across the shore (Fiori & Carcedo, 2015; McLachlan, 1996; McLachlan *et al.*, 1995; Rhoads, 1974; Tallqvist, 2001). Additionally, the diversity, abundance and biomass of intertidal organisms, including clams, are known to decrease linearly with a shift from dissipative to reflective states (McLachlan, 1990, 1996; McLachlan & Turner, 1994; Olivier, 1971), in part due to the accompanying shift from benign to harsh swash conditions (McLachlan & Dorvlo, 2005). Changes in slope can also alter the drainage (i.e. permeability and porosity) of the beach, subsequently influencing the width and position of the seep face on the shore, and the depth of the water table below the sediment surface (Horn, 2002). Sediment moisture acts to protect intertidal organisms from desiccation during prolonged periods of exposure (Bally, 1983; Salvat, 1967), and has previously been identified as a possible driver of toheroa distribution along the shore (Redfearn, 1974; Williams *et al.*, 2013b). The effects of the beach slope on swash regimes, and subsequent ecological implications is discussed further in Chapter 4.

Toheroa are known to occur along beaches with wide shallow gradients usually backed by sand dunes or cliffs, with fine uniform sand of an average grain size ranging between 21 - 33 µm (Rapson, 1952). Along Ripiro Beach, the largest and most abundant toheroa beds have been associated with streams, which aligns with sediment moisture as a factor determining distribution. In 1974, Ripiro beach was described as being a fine sand beach, due to the high proportion of fine sediments (98%) (Redfearn, 1974), however there has been little detailed research into the current sedimentary environment of the beach, and in particular the sediment structure in the vicinity of streams is unclear.

This research will determine whether the distribution of toheroa beds along Ripiro Beach may be driven by sediment size, in addition to whether the sediment profile of Ripiro Beach has changed since the 1970s assessment. Initially it will look at specific habitats to see whether streams have an effect on grain size, therefore resulting in more preferable locations for toheroa, or whether sediments might account for long shore distributions. Additionally, current sediment composition along the beach is compared to that published in 1974 to determine whether grain size may explain the long shore distribution of toheroa beds or account for changes in population over time.

3.2 Methods

Sediment samples were collected from three sites along Ripiro Beach in December 2017. Sites are known locally as Kelly's, Kopowai and Third Stream (Figure 18 - 19). Site selection and descriptions of study sites is detailed in Chapter 2 above.

3.2.1 Sample collection

At each site, three transects were established perpendicular to the shoreline. One transect was positioned immediately adjacent to the stream and the other two were positioned approximately 100 m either side of the stream (non-stream) (Figure 20). Along each transect, sediment samples were taken at points hereafter referred to as high (H), mid (M) and low (L) points. The high point marked the position of the most recent high tide and determined the uppermost sampling point for each transect. Tidal height is highly variable from day to day, being influenced by swell, atmospheric pressure and lunar phase. Mid and low sampling positions were determined by the position of toheroa beds. Mid sampling positions were positioned immediately above (landward) the main toheroa bed as indicated by the position of toheroa siphon holes. Low positions were positioned immediately below (seaward) the bed. Mid and low positions were selected above and below the bed to minimise disturbance to the toheroa. In addition to harvesting, the disturbance of toheroa beds without a permit is an offence. Consequently, environmental parameters were measured as close to the bed as possible, acknowledging that they may not be an indication of conditions within the bed. Grain size distributions within the bed may also be modified because of bioturbation. Due to siphon holes indicating the location of toheroa often only visible in the sediment approximately one hour after the ebb tide has passed over the bed, the tide was often well below the low sampling point before points could be marked and sampling could begin. Non-stream (NS) sampling points were positioned at equivalent tidal height to stream adjacent sampling positions.

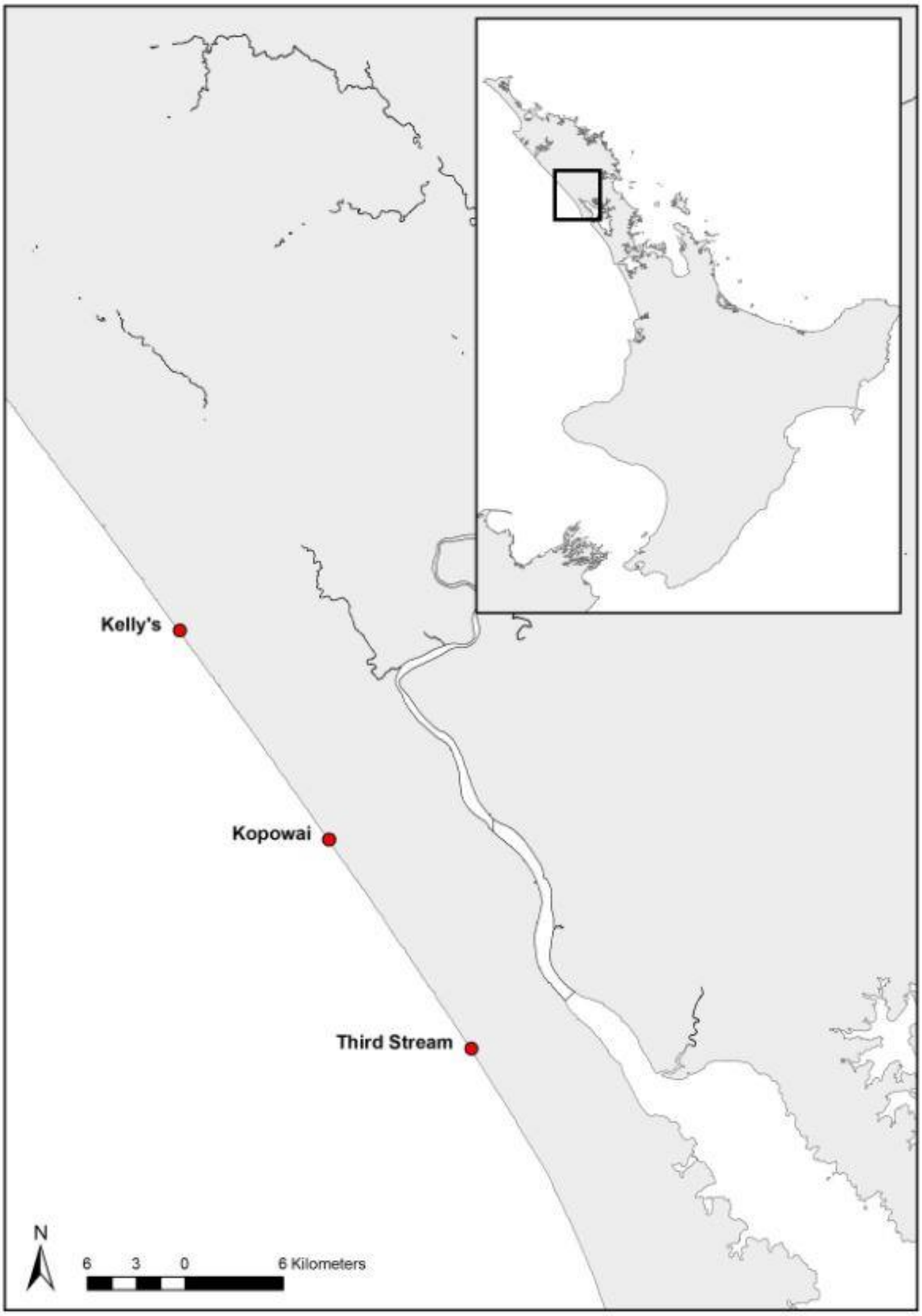

Figure 18: Sediment cores were collected from three points along Ripiro Beach, Dargaville for grain size analysis.

Figure 19: At each site, sediment cores were collected from nine points across the beach, representing the high tide (high) and upper (mid) and lower (low) edges of the toheroa bed at mid-tide. These points were sampled immediately adjacent to the stream, and 100 m to the North and South.

Sediment samples were collected with a 26mm diameter corer to a depth of 10 cm. Samples were randomly collected in triplicate within 1m^2 of the point. Although grain size analysis can be conducted on surficial sediments (Nordstrom, 1977) core samples provide a better representation of toheroa habitat and are recommended by a previous similar study (Masselink *et al.*, 2007). The integrity of the cores was maintained by wrapping them in tinfoil and freezing them for subsequent subsampling. Subsampling for analysis was achieved by shaving slithers of sediment from the length of each core using a knife, until there was a sufficient amount for a 5 ml sample.

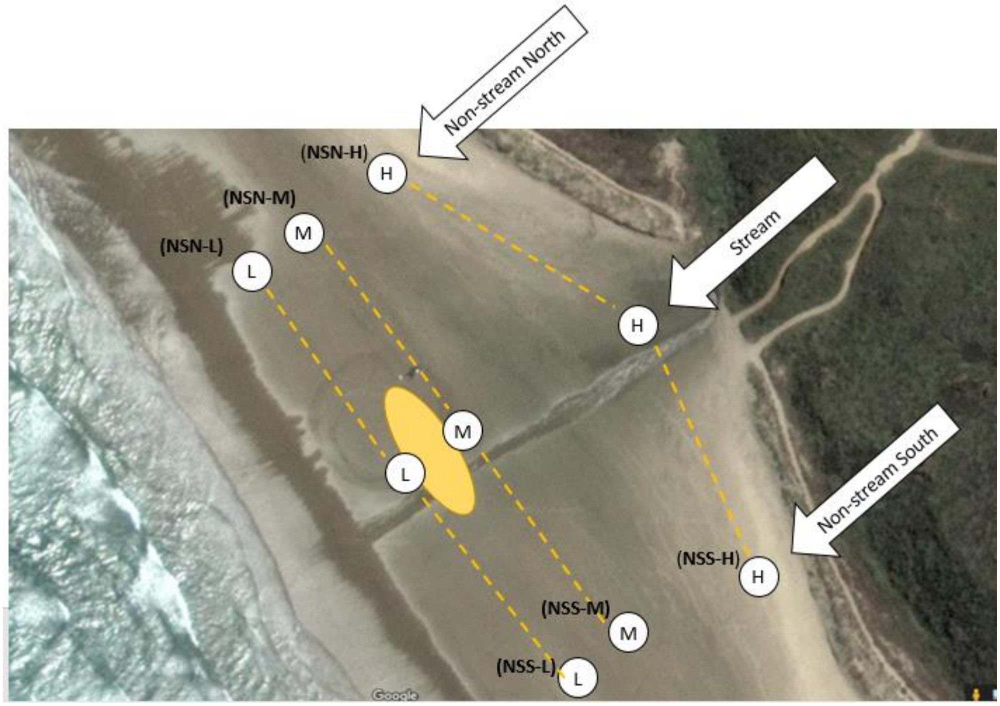

Figure 20: Annotated photo showing position of sampling locations relative to stream position and tidal height. H = high, M = Mid, L = Low. Shaded area shows position of toheroa bed.

3.2.2 Sediment digestion

Sediment samples were placed into a glass beaker and covered with a 10% hydrogen peroxide solution for seven days to dissolve any organic matter. Samples were stored in a warm (40°C) room to increase reaction times. Minor effervescing was observed during this period indicative of the reaction. Organic material in a sample can mar grainsize analysis by binding fine particles and making them appear larger. The exoskeletons of infaunal crustaceans were removed as they came to the surface. Calcium carbonate could have been dissolved from the sample, but there was concern that this could interfere with any shell derived sand fractions. After seven days, excess hydrogen peroxide was carefully siphoned off with a syringe, and sediments were treated with a second stronger hydrogen peroxide treatment (30%) for two days to accelerate the dissolution of any remaining material. Samples were kept saturated in a weak (10%) hydrogen peroxide solution until analysis.

3.2.3 Grain size analysis

Saturated sediments were sized using a Malvern Mastersizer 3000 laser diffractometer (Malvern, UK), at the University of Waikato, Hamilton. Since sediments were still saturated, they were not treated with Calgon, often is used to disperse grains bound together during drying. Sediments were processed in accordance with the manufacturer’s instructions using a predefined program for “marine sediments”, configured by a trained laboratory technician. Under this setting, the refractive index is set to 1.5, the absorption index to 0.2 and the dispersant refractive index to 1.33

3.2.4 Statistical analysis of sediments (granulometric analysis)

A sample average was calculated in Microsoft Excel using the decimal proportions for each size class from the triplicate samples output from the Malvern analysis. These were entered into GRADISTAT (Version 8.0), a grain size distribution and statistics package (Blott & Pye, 2001) where sample mean, median, mode(s), standard deviation (sorting), skewness and kurtosis and proportional representation of size classes (by volume) was calculated. These were derived from Folk and Ward (1957) equations, with size class classifications consistent with the Wentworth scale (Wentworth, 1922).

3.3 Results

3.3.1 Statistical analysis of sediments (granulometric analysis)

The unconsolidated sediments sampled at Ripiro Beach ranged in size from 105 µm (very fine) to 500 µm (coarse), the proportion of which varied between samples. Very fine and coarse grains were present in most samples, but only accounted for a small proportion of the total volume (<1% and <2% respectively), with fine and medium sediments making up the rest (Table 1) (Figure 21).

At Kelly's, the average grain sizes for each sampled point ($n = 9$) ranged between 243.5 µm to 290.9 µm, with the median ranging from 243.5 µm to 290.3 µm. With the exception of the sample taken from the stream at high tide, more than 50% of the volume in each sample was comprised of sediments 250 µm – 420 µm, and can therefore be described as being "medium sand" following the Wentworth scale (Blott & Pye, 2001). The sample from the stream contained mostly (> 50 %) "Fine" (125 µm – 249 µm) sediments. At Kopowai and Third streams, the mean grain sizes for each sample ranged from 217.2 µm - 235.7 µm and 218.9 µm - 250.7 µm respectively. Medians ranged from 217.7 µm - 290.3 µm and 219.3 µm - 251.1 µm. Sediments 125 µm – 249 µm accounted for the largest proportion of the sample at both sites, and are therefore classified as "Fine" (Table 1) (Figure 22).

Across all sites, the sorting of each sampled point ranged from 1.3 – 1.4 (σ) making sediments 'well sorted' according to the classification of Folk & Ward (1957). Sorting, measured by the standard deviation, measures uniformity of the grains within the sample (Hatch & Choate, 1929), providing an indication of the range of size classes within the sediment and the effectiveness of the hydrodynamic environment in sorting grains of different sizes (Folk, 1966). Skewness, a measure of the asymmetry of frequency distribution curve and kurtosis, a measure of the normality of the distribution measured < 0 and 0.9 – 1.0 respectively across all samples, thus they can be described as symmetrical (Folk & Ward (1957). All samples were unimodal. At Kelly's the primary mode was 275 µm, with Kopowai and Third streams 230 µm (Appendix A, Appendix B).

Table 1: Proportion (%) of each sediment size class within each sediment sample, and the total proportion of sediments in each size classification (very fine (VF), fine (F), medium (M), coarse(C) composition for each sampling point across all sampled sites. At each site, grain size analysis was conducted on sediments to the north and south of the stream and adjacent to it, at the high tide and above and below the main toheroa bed. (n= 3 sediment samples per point).

	Size classification		Very fine (VF)		Fine (F)				Medium (M)				Coarse (C)	VF	F	M	C
	Size class (µm)		88	105	125	149	177	210	250	300	350	420	500	Total proportion (%)			
Kelly’s	**North**	**High**	0	0.1	1.4	5.6	12.3	20.6	24.3	17.7	12.4	5	0.6	0.1	39.9	59.4	0.6
		Mid	0	0.1	1.6	6.6	15	24.2	25.9	16	8.3	2.2	0.2	0.1	47.4	52.4	0.2
		Low	0	0	1	5.2	13.3	23.9	27.2	17.5	9.4	2.4	0.2	0	43.4	56.5	0.2
	Stream	**High**	0	0.5	3.6	9.7	16.9	22.8	22.6	13.9	7.7	2.2	0.2	0.5	53	46.4	0.2
		Mid	0	0	0.8	4.3	11.3	21.4	26.3	18.9	12.2	4.2	0.5	0	37.8	61.6	0.5
		Low	0	0	0.3	2.3	7.8	18.3	26.1	21.4	16.1	6.7	1.2	0	28.7	70.3	1.2
	South	**High**	0	0.1	1.7	5.9	11.9	19.2	22.6	17.1	13.2	6.3	1.9	0.1	38.7	59.2	1.9
		Mid	0	0	0.9	4.5	11.3	20.7	25.4	18.6	12.7	4.8	1	0	37.4	61.5	1
		Low	0	0	0.7	3.7	9.5	18.3	23.9	19.2	15.3	7.2	2.1	0	32.2	65.6	2.2
Kopowai	**North**	**High**	0	0.6	4.2	11.4	19.4	24.7	22.2	11.7	5	0.9	0	0.6	59.7	39.8	0
		Mid	0	0.3	3.4	11	20.7	27.1	23.2	10.8	3.4	0.2	0	0.3	62.2	37.6	0
		Low	0	0.3	3.3	11	20.9	27.4	23.2	10.6	3.2	0.2	0	0.3	62.6	37.2	0
	Stream	**High**	0	0.5	3.8	10.9	19.2	24.9	22.5	11.9	5.1	1	0.1	0.5	58.8	40.5	0.1
		Mid	0	0.2	2.9	10.6	20.9	27.9	23.7	10.7	3.1	0	0	0.2	62.3	37.5	0
		Low	0	0.2	2.6	9.7	19.5	27.1	24.3	11.9	4.2	0.6	0	0.2	58.9	41	0
	South	**High**	0.1	1.1	6.1	14.8	22.7	25.2	19.3	8.2	2.4	0.1	0	1.2	68.8	30	0
		Mid	0	0.3	3.9	12.9	23.7	28.4	21.1	7.9	1.7	0	0	0.3	68.9	30.7	0
		Low	0	0.1	2.3	9.1	19.5	27.9	25	11.9	3.9	0.4	0	0.1	58.8	41.2	0
Third	**North**	**High**	0	0.5	3.9	10.9	18.8	24.3	22.3	12.2	5.6	1.3	0.1	0.5	57.9	41.4	0.1
		Mid	0	0.4	4.1	12.6	22.5	27.2	21.4	8.9	2.5	0.3	0	0.4	66.4	33.1	0
		Low	0	0.4	4.1	12.7	22.8	27.6	21.4	8.7	2.2	0.1	0	0.4	67.2	32.4	0
	Stream	**High**	0.1	0.9	5.7	14.3	22.6	25.4	19.7	8.4	2.5	0.3	0	1	68	30.9	0
		Mid	0	0.4	3.8	11.8	21.3	26.9	22.3	10	3.2	0.4	0	0.4	63.8	35.9	0
		Low	0	0.3	3	9.7	18.1	24.7	23.1	12.8	6.2	1.8	0.3	0.3	55.5	43.9	0.3
	South	**High**	0	0.6	3.8	9.7	16.4	21.9	21.9	13.8	8.4	2.9	0.5	0.6	51.8	47	0.5
		Mid	0	0.3	3.2	9.5	17.3	23.8	23.2	13.6	7	1.8	0.2	0.3	53.8	45.6	0.2
		Low	0	0.2	2.6	8.2	15.6	22.7	23.6	15	8.8	2.8	0.4	0.2	49.1	50.2	0.4

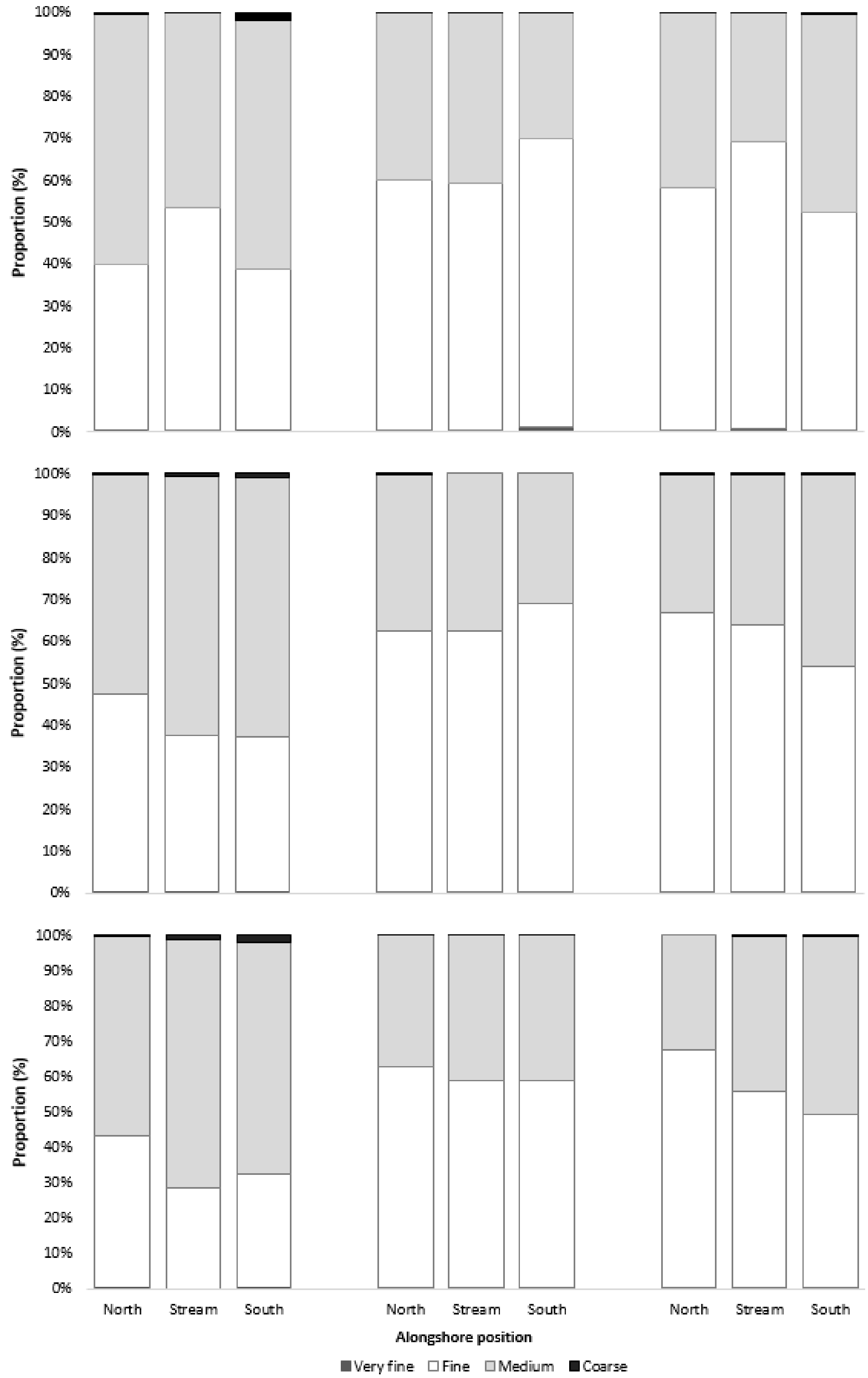

Figure 21: Proportional representation of each sediment size classification (very fine: dark grey, fine: white, medium: light grey and coarse: black) from each sample. Size classes are based on the Wentworth scale.

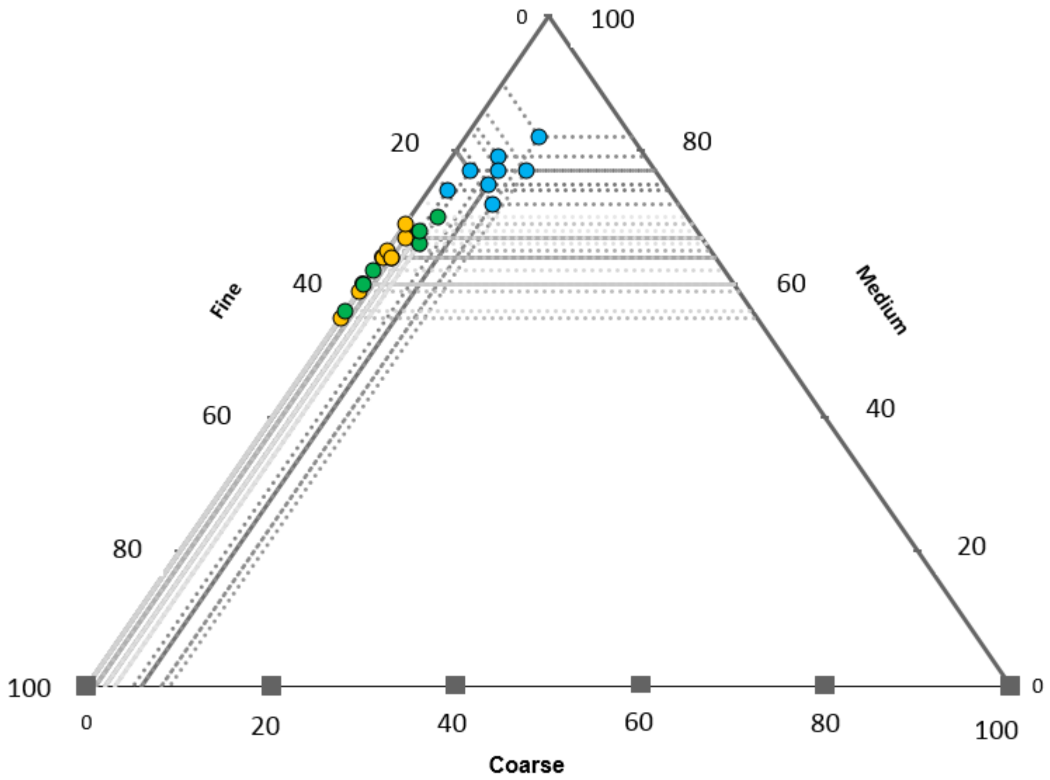

Figure 22: Ternary diagram displaying the proportional distribution of the predominant size classes (fine-medium-coarse) in each sample by site (Kelly's (blue dots), Kopowai (yellow dots) and Third streams (green dots)).

3.3.2 Stream and non-stream sediment comparisons.

At Kelly's and Third streams, the proportion of fine sediments in the stream at the high tide was higher than at the non-stream points either side (Kelly's: north 19.4%, stream 30.6%, south 19.7% | Third Stream: north 34.1%, stream 43.7%, south 30.6%). At Kopowai, the stream had 10% fewer fine sediments than the non-stream southern sample and 0.1% more than the non-stream northern sample (Kopowai: north 35.6%, stream 34.4%, south 44.8%). At the mid sampling point, there was <1% difference in the proportion of fine sediments in the stream and the sample from the north or south. At the sampling points, the proportion of fine sediments in each sample decreased from the north to the south. At all points, changes in the proportion of fine sediments resulted in the opposite occurrence of medium sediments.

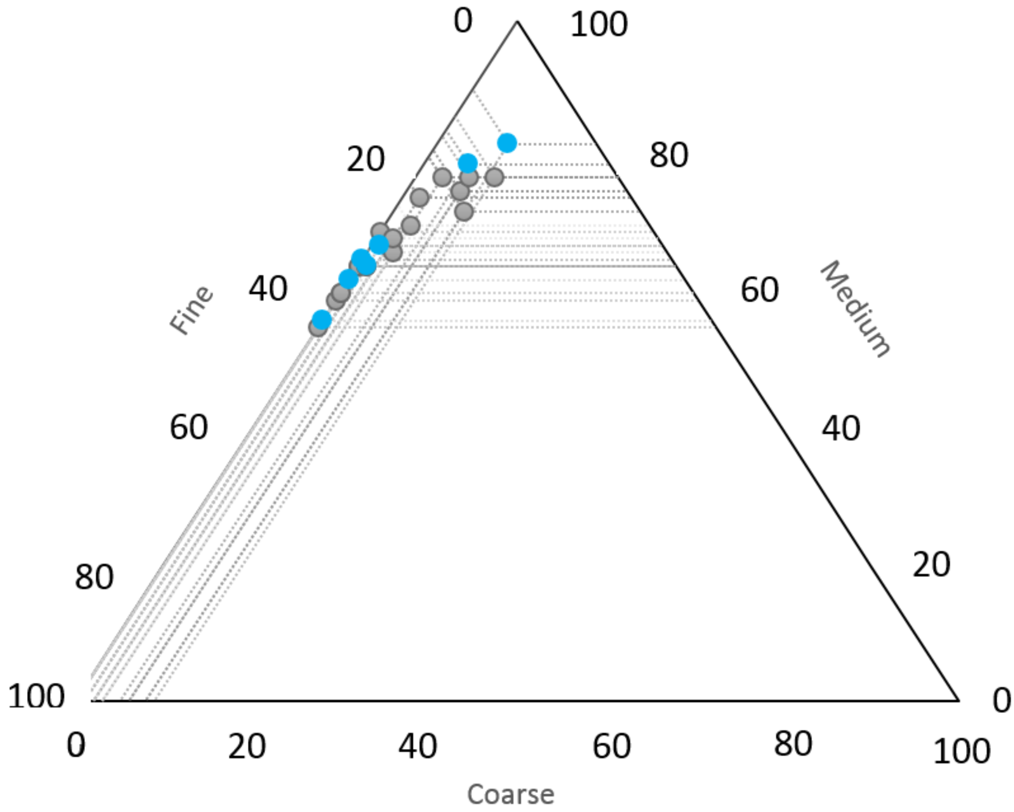

Figure 23: Ternary diagram displaying the proportional distribution of the predominant size classes (fine-medium-coarse) in each sample from the high, mid and low sampling points adjacent to (blue dots) and away (grey dots) from the stream).

3.3.3 Comparison between historical and current

In 1974, Redfearn described the average sediment sample from Ripiro beach as being comprised of 98.1% fine sediments, 1.7% very fine sediments and 0.2% medium sediments. There were no coarse fractions. In 2017, fine sediments accounted for 54% of the beach wide average, with medium sediments contributing 45%. Very fine and coarse sediments represented <0.5% of the sample respectively. This represents a 45% decrease in fine sediments and a 26661% increase in medium sediments from 1974. Very fine sediments have decreased 81%, and there has been no change in the proportion of coarse sediments.

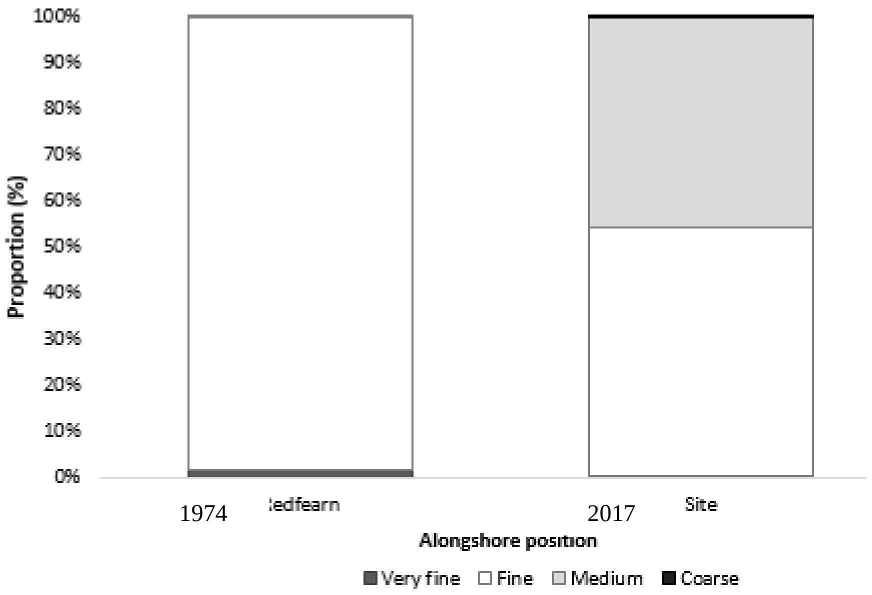

Figure 24: Grain size distribution at Ripiro Beach in 1974 versus 2017 showing the decrease in proportion of fine sediments and the increase in medium sediments.

3.4 Discussion

3.4.1 Environment

Toheroa have long been associated with fine sandy beaches, sometimes described as dissipative (Smith, 2003; Williams *et al.*, 2013b). The results of the grain size analysis presented in this study indicate that although still dominated by fine sand, in its current state, Ripiro Beach exhibits a marked change from the beach described by Redfearn in 1974, with a notable shift toward coarser sediments. The proportion of fine sediments increases towards the central and southern region of the beach, an area that has always supported notable toheroa beds. There is no evidence of this longshore gradient at a site-specific scale, where sediments along the mid-tide region were uniform adjacent to and away from the stream. However, there is evidence to suggest that along the upper reaches of the beach, sediments in the vicinity of streams may have a higher proportion of fine sediments. Grain size and beach state play an important role in the structuring of intertidal communities, and so changes to either parameter is likely to have an effect on toheroa populations. This study provides no evidence of timeframes over which this change is occurring. Exposed beaches can undergo seasonal shifts in state, which would indicate a temporary change; however, change can also occur over longer periods and even be permanent. A long term or permanent shift may explain why toheroa have failed to recover, whereas shorter-term fluctuations may explain the “boom and bust” years reported in the toheroa fishery, also typical of other surf clams.

Since it was first described in 1955, Ripiro beach has always been referred to as a “fine sandy beach” (Cassie, 1951; Redfearn, 1974; Schofield, 1970; Smith, 2003; Williams *et al.*, 2013a), and at times described as dissipative (Smith, 2003). Based on data collected in this study and the definitions supplied by Folk and Ward (1957), Ripiro Beach could still be classed as a fine sand beach, suggesting the beach is in a similar state to that of 50 years ago. However, despite still being classified as fine, a comparison of current and historical sediment distributions shows that proportional contribution of each of the size classes represented in the samples has changed dramatically since 1974. Fifty-three years ago, fine sediments accounted for 98% of a typical beach sample in contrast to the 54% at present. In addition to a marked increase in the proportion of medium sediments

(45%) and a subsequent reduction in fine sediments (45%); there has also been an introduction of a coarse fraction which was notably absent from the historical data. Descriptive classifications may therefore have the capacity to be misleading, causing the proportional contributions of each size class to be overlooked and changes to the composition to be missed.

In this study, the unimodality of the sediment samples and their sorting (well-sorted) indicate that at each of the sites, and across the wider beach, beach sediments are from a single source, having been present in the system for a similar period of time (Folk, 1966; Nordstrom, 1977; Okeyode & Jibiri, 2012) This suggests that, rather than an influx of coarser (medium) sediments into the system, the change may be as a consequence of a loss of fine fractions. Such coarsening is often symptomatic of erosive events (Masselink *et al.*, 2007), such as those which have occurred at the beach throughout the sampling for the current study. Erosion can operate on different time scales depending on the cause. In Southland, the interruption of sediment supply to Bluecliffs, a known toheroa beach, resulted in a permanent loss of sand from the system until only the underlying gravel and boulders remained (Beentjes *et al.*, 2006). More commonly, erosion is the result of a change in wave climate and is therefore temporary. Such changes often occur mid-summer and are accompanied by a shift in beach state, from dissipative to intermediate (Davis Jr & Fox, 1972; McLachlan, 1990; Prodger *et al.*, 2017). Because wave period and height were not quantified at the time of sampling, the current state of the beach cannot be determined. However, with the majority of sediments in the sample >200 µm, it is possible that the beach may be in an intermediate state (Cassie, 1955; Morrison & Parkinson, 2008a).

In spite of the beach wide average grain size suggesting Ripiro beach was fine sand dominated, the sediment at Kelly’s, the northernmost site in the study, consisted primarily of medium-grained sand. This may be indicative of differential erosion occurring along the beach, with the southward transportation of the fine eroded sediments a consequence of selective entrainment, which reflects the direction of the long shore drift (Abuodha, 2003; Allen, 1981; Bryant, 1982; MacCarthy, 1931). Along Ripiro Beach longshore drift can switch from a south–east to north-west direction depending on angle and approach of the waves (Hamill & Ballance, 1985; Schofield, 1970). The erosion of the dunes along the central and southern extent of the beach may also have contributed to an increase in the proportion of fine sediments. Dune sediments are finer than beach sediments (Schoeman & Richardson, 2002; Schofield, 1970); this enables them to be transported away from the system by the wind, in much the same way that smaller particles are more readily transported by current.

In this study, the proportion of fine sediments appear to increase near streams at the upper beach. This may be a result of the increased moisture content of the sediments in these regions causing fine sediments to adhere to them thus halting or slowing their transport from the system. Along Ripiro Beach, stream adjacent sediments at the upper reaches of the beach appear to have higher moisture content than sediments away from the beach as indicated by more cohesive sediments, which were darker in colour and damp to the touch (Figure 25). With only a small proportional increase in fine sediments, and with sediments across the beach being similarly sorted, it is unlikely that the observed moisture increase is a function of the sediments themselves. Rather, the moisture may be an indication of topographic features of the beach, with low lying areas of the beach attributed to higher moisture content (Redfearn, 1974). Along the mid and low tide, moist sediments extended the length of the beach running parallel to the shore, indicating the position of the seep face. The relative homogeneity in sediment size and the absence of any sediment patterns specific to the stream in this region of the beach suggests that marine processes dominate this region of beach. This is consistent with the unpublished work of Eberhardt (1988) and reflects previously observed sediment distribution patterns along non-stream beaches (Prodger *et al.*, 2017).

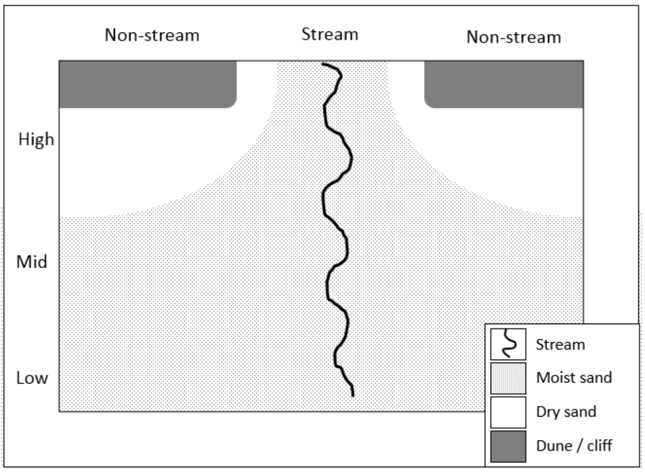

Figure 25: In the vicinity of streams, sediment moisture content of stream adjacent sediments along the upper beaches appears to increase. Along the mid and low region of the beach moisture content increases in response to the seep face that flows along the beach parallel to the shore.

3.4.2 Implications for toheroa

Large fluctuations in abundance are common for surf clam species due to variability in recruitment success (Arntz *et al.*, 1988; Brown & McLachlan, 2010; Coe, 1955; De Villiers, 1975; Fiori *et al.*, 2004; Fiori & Carcedo, 2015; McLachlan, 1996). Toheroa are no different, with large fluctuations in populations recorded during the periods of commercial harvesting and since (Beentjes, 2010b, 2010a; Williams *et al.*, 2013b). Although the toheroa fishery had already collapsed and closed by 1974 when Redfearn published his grain size analysis, the beds he described were 4ha, covering an area considerably larger than the beds today (Redfearn, 1974). It may therefore be possible, that the observed increase in medium-grained sediments and a decrease in fine sediment will be adversely affecting toheroa communities. If this coarsening is part of a long-term change, it may explain some of the continued decline seen in toheroa populations. If part of a short term change, it may be possible that short term switches between dissipative and reflective beach states account for the observed population fluctuations with boom years coinciding with a beach high in fine sediments (potentially dissipative state) and bust years during coarsening (potentially intermediate states). It is possible that toheroa can recruit to both dissipative and intermediate beaches, but may only thrive in areas where sediment grain size provides optimum conditions. Larger populations to the South of the beach where sediments were finer, would support this hypothesis, however the disturbance of the bed was prohibited at the time of sampling, due to a lack of permit.

Coarsening of sediments has an adverse effect on intertidal communities, with species richness and abundance decreasing linearly with the accompanying shift from a reflective to intermediate state (McLachlan, 1990). Increasing grain size can directly affect burial capabilities of clams, with some species able to bury in a wider range of sediment sizes than others (De la Huz *et al.*, 2002; Fiori & Carcedo, 2015; Nel *et al.*, 2001). In these instances, adults appear to be more affected than juveniles are. By failing to bury, exposed toheroa face risk of desiccation or predation on intertidal sediments. Alternatively, they face being washed back to sea, where predation by stingrays and other durophagous or opportunistic fish can occur (Cassie, 1955; B. Searle, personal communication). Based on observation, toheroa along Ripiro Beach appear to be able to bury, provided they are immersed in the swash. However, the sediment preferences of toheroa are unknown, and there is a possibility that they may be affected by changes in grain size. When increasing grain size is accompanied by a change in slope, it is possible that toheroa are exposed to increased risk of desiccation and heat stress as a consequence of lowering moisture content of the sediments. This is discussed in subsequent chapters.

Long shore drift is attributed to the transportation of spat along the beach (Taylor, 2013). It is therefore possible that the shifts in the directions of the drift along the coastline may explain why in some years, beds are more abundant to the North of the beach than to the South (Akroyd *et al.*, 2002; Williams *et al.*, 2013b). However, more often, the large and high density toheroa beds occur along the central and southern region of the beach (Akroyd *et al.*, 2002). Whilst the transportation of spat by longshore drift may provide some explanation of this distribution, this study indicates that the southern region of beach (Kopowai and Third) has a higher proportion of fine sediments, which toheroa have been associated with in the past. Therefore, it may be possible that the long shore distribution patterns are a reflection of habitat quality given the importance of physical elements structuring beach communities (McLachlan, 1996).

The high abundance of juvenile toheroa near streams may reflect the increased proportion of fine sediments. Although previous studies have found that burial ability of juvenile surf clams is less affected by grain size than that of adults, making them more tolerant of reflective conditions, (Alexander *et al.*, 1993; De la Huz *et al.*, 2002), spat have been observed to have an association with fine sediments which weakens as they grow (Lastra & McLachlan, 1996). This could facilitate the migration of juveniles from the upper beach towards the mid-tide as they grow (Redfearn, 1974). With little difference in sediment sizes adjacent to and away from the stream at mid-tide, grain size is unlikely to explain the toheroa-stream association amongst adults. This suggest that the toheroa distribution may reflect large-scale habitat characteristics (i.e. distribution along the shore) rather than to small-scale variability (i.e. adjacent to and away from streams)

Although grain size is known to influence the distribution of intertidal organisms, including surf clams (Arruda & Amaral, 2003; Fiori & Carcedo, 2015; Jansson, 1967), there is limited data available on the sediment size distributions along Ripiro Beach. With only a small number of inhabitants living along the coast, environmental monitoring efforts appear to be focused on more densely populated areas, and the beach is largely data deficient. What limited data there is is largely the result of toheroa related research. With limited grain size data available since that published by Refearn (1974), data can only be compared, but the temporal and spatial scales over which the observed changes in grain size are occurring cannot be determined.

In this study, sediments were treated with hydrogen peroxide to break down aggregated particles, prior to using a Malvern Mastersizer to size the sediments in the samples. Laser sizer technology is underpinned by Mie theory, in which particle size is determined by the way light interacts (reflects, absorbs) with the particles. This behaviour is affected by grain colour. The “marine sediments” setting, recommended by the University of Waikato sediments technician is calibrated for light coloured beach sediments, which are different to those from the west coast that contain varying proportions (mostly less than 10%, but up to 30%) of fine grained titanium magnitide (black sand) (Schofield, 1970). Whilst laser technology may be effective in sizing either black or white particles, it may not be an accurate way of sizing mixed colour samples. Consequently, the settings used may not accurately reflect particle sizes along Ripiro Beach. Unfortunately, the small sample volume meant that a more suitable setting could not be configured, as there were no superfluous samples that could be experimentally processed for this purpose.

In addition to this, methods utilised by Redfearn (1974) for sorting and sizing sediments for his study were unpublished, and there is no indication as to whether sediments were pre-treated. Given the period in which he undertook his study, it is most likely that he used a sieving or settling method. The effectiveness of these methods in titanomagnetite-rich sediments has been discussed in detail by Robinson *et al.* (2003). In this paper, the authors suggest that settling rates can be erroneous unless the correct corrections are applied. They also found that sieving produced a higher proportion of fine sediments in the same samples than settling, which could explain the high proportion of fine sediments in this previous assessment. Both assessments of grain size at Ripiro Beach may therefore be slightly erroneous, which would affect the accuracy of the comparison between sets. However, whilst this margin of error may exist, and must be interpreted with caution, the very large extent of the differences in proportions of grain size between assessments suggests that a change has more than likely occurred it is just the exact magnitude of this change cannot be calculated.

To improve the accuracy of this study, it may have been preferable to process the samples by the sieving method, which would have produced results comparable to those of the previous study. This would have required larger samples and more processing time. In order to gain a more comprehensive understanding of grain size distributions at this site, and perhaps elucidate any seasonal shifts in state, a seasonal component to sampling should be added to future studies, in addition to the inclusion of wave height and period, which would enable beach state to be estimated. It would also be desirable to incorporate small-scale toheroa abundance monitoring concurrently or alternatively to include this environmental evaluation into the stock assessment studies when these are undertaken.

Chapter 4

Modification of beach topography by streams

4.1 Introduction

The effects of topography on the distribution and biodiversity of organisms is most evident in terrestrial systems where large-scale topographic features often dominate the landscape. In such environments, physical factors such as elevation, aspect and slope influence temperature, sunlight, rainfall and drainage; which in turn drive the distribution of organisms in accordance with the physiological requirements and tolerances of individual species (Dachnowski, 1911; Daubenmire, 1943). Similar patterns have been observed in the marine environment, for example, in the rocky intertidal some organisms are restricted to rock pools or crevices where they have continual access to water. Others inhabit the more shaded faces of rocks as this reduces rates of desiccation, while plants and animals that are more resilient to desiccation may occupy the unshaded top surfaces of rocks (Chappuis *et al.*, 2014; Southward, 1958). Similarly, on subtidal rocky reefs, the distribution of species is determined by factors such as depth and slope (Baker, 1909; Cárdenas *et al.*, 2012). In marine soft sediment ecosystems, particularly along the face of dissipative beaches, topographic features are not as prominent and the beach surface can appear homogenous, despite the presence of subtle but important relief features (Wright *et al.*, 1979). Despite a uniform appearance, the slope of a beach can vary along the shore, and this can have an important influence on community structure and the distribution of biodiversity (McLachlan, 1990, 1996; McLachlan & Dorvlo, 2005; Schlacher & Thompson, 2013; Stephen, 1930).

The morphology of a beach is controlled by the physical environment, with the beach face a consequence of complex interactions between grain size and wave height (Bascom, 1951; Emery & Gale, 1951; Wright & Short, 1984a). As a result of the temporal variability in swell and wave height, the beach face is highly dynamic, and can exhibit strong storm and seasonal profiles (Gallagher *et al.*, 2016; Otvos Jr, 1965; Short & Jackson, 2013). The slope of the beach is determined by the difference in elevation between the upper and lower reaches of the littoral zone, and is influenced by the width of the beach. Steep gradients occur along coarse-grained reflective beaches, which are subject to waves that break across the intertidal zone. Shallow gradients are synonymous with the dissipative and intermediate beaches, which often occur along exposed coastlines and are characterised by fine sands and waves that break offshore. The interaction between slope and wave climate determines the swash regime of the beach, which when combined with the height of the water table influences accretion and erosion of the beach face, sediment stability and tidal exposure time (Horn *et al.*, 1999; Oh & Dean, 1995; Short & Jackson, 2013). Consequently, both swash dynamics and moisture content, associated with the water table, have been attributed to the distribution of organisms across the intertidal zone (Bally, 1983; McArdle & McLachlan, 1992; Salvat, 1967).

For intertidal organisms, the episodic inundation by the tide and swash and the subsequent exposure to atmospheric conditions is a primary stressor. Some organisms are only able to feed during tidal inundation; but all organisms are vulnerable to thermal stress and desiccation when the tide is out (Andersom, 1978; Ansell *et al.*, 1981; Macho *et al.*, 2016). Organisms that occupy the upper intertidal zone, such as juvenile toheroa, are most at risk of experiencing exposure related stress because the inundation of these areas can be short and infrequent, with periods of exposure lasting anywhere from hours to weeks depending on shore position, tide and weather regimes. The risk of exposure is reduced in a seaward direction as sediments undergo more frequent wetting and the physical environment facilitates increased retention of sediment moisture, through the interactions of slope and grainsize. This moisture gradient may influence the distribution of organisms across the intertidal zone, and has been described by Salvat (1967).

For some organisms, the availability of terrestrially derived water may act as a buffer against salinity, desiccation and exposure related stress (Befus *et al.*, 2013 and references therein). As discussed in Chapter 1, the association between toheroa and streams is well known. However, the mechanisms which drive this association has yet to be satisfactorily explained (Ross *et al.*, 2017a). It is possible that streams alter sediment characteristics or thermal properties of the beach habitat and this may explain the distribution of toheroa. These hypotheses are investigated in chapters 3 and 5 respectively. Another hypothesis that is yet to be investigated is that the toheroa-stream association is a function of the beach topography.

It has been suggested that shallow basins may form in areas where streams cross the toheroa beaches. A gentler gradient or shallow depressions could facilitate increased toheroa abundances through a number of processes (Smith, 2003). For example, this topography may aggregate juvenile and adult toheroa, it may increase inundation and therefore increase available feeding time, it may increase the delivery of food, or it may reduce the distance between the sediment surface and the water table. While the hypothesis that topography influences toheroa distribution is plausible, there has been limited investigation into beach topography surrounding streams or toheroa beds in order to validate this theory.

Before attempting to assign causation to the stream-toheroa association and determine whether it is indeed a function of topography, an essential first step in this investigation was to ascertain the topography of Ripiro Beach near streams. To achieve this, sections of beach between mid and high tide were surveyed to determine whether streams were characterised by topographic depressions that have the potential to act as aggregation or settlement points for toheroa at different life stages. The slope of the beach face in the stream path was also compared with that of the adjacent beach in order to understand how swash regimes may alter inundation time or influence distribution of toheroa.

4.2 Methods

Topographic surveys were conducted at Chases Gorge, Mahuta Gap, Kopawai and Third streams on a single low tide during December 2017 (Figure 26). A detailed description of Ripiro Beach and these study sites is provided in Chapter 2.

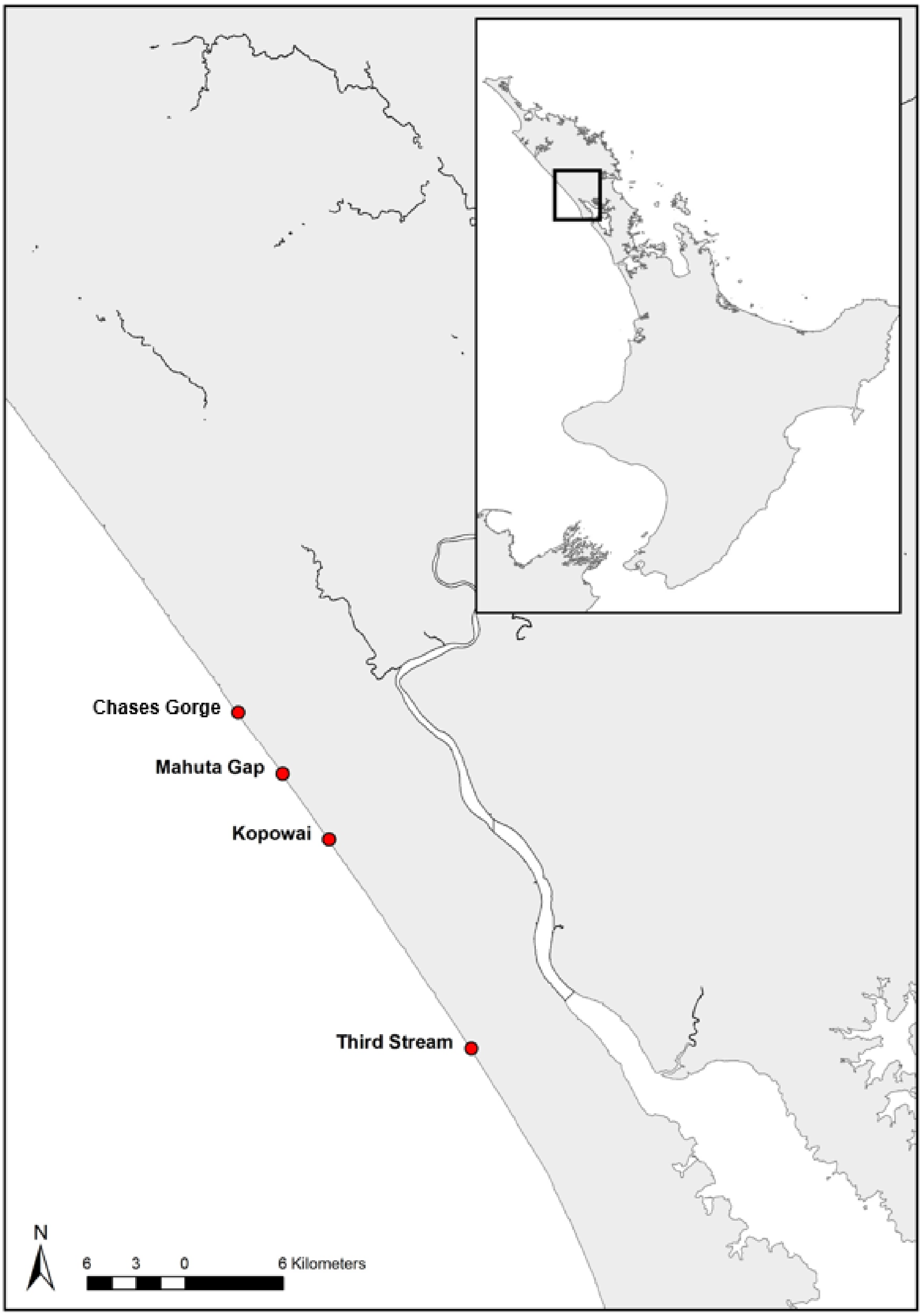

Figure 26: Sample sites along Ripiro Beach, located on the west coast of Northland, New Zealand.

4.2.1 Sampling

A surveyor's theodolite was used to measure surface elevation across a section of subaerial beach. At each site, three 100m transects were established parallel to the shoreline. The first at the high tide line, a second immediately landward of the toheroa bed in the vicinity of mid-tide, and a third transect below the toheroa bed. The position of the toheroa bed across the shoreline, and the position of the wrack line determined the distance between mid and high transects. The distance between the low and mid transects was determined by the dimensions of the bed at each site. The stream intersected each transect at its mid-point (Figure 27). Eleven elevation measurements were taken along each transect, each approximately 10 meters apart. Elevation was measured relative to a fixed (zero) point provided by the total station, located immediately adjacent to the stream above the high tide line.

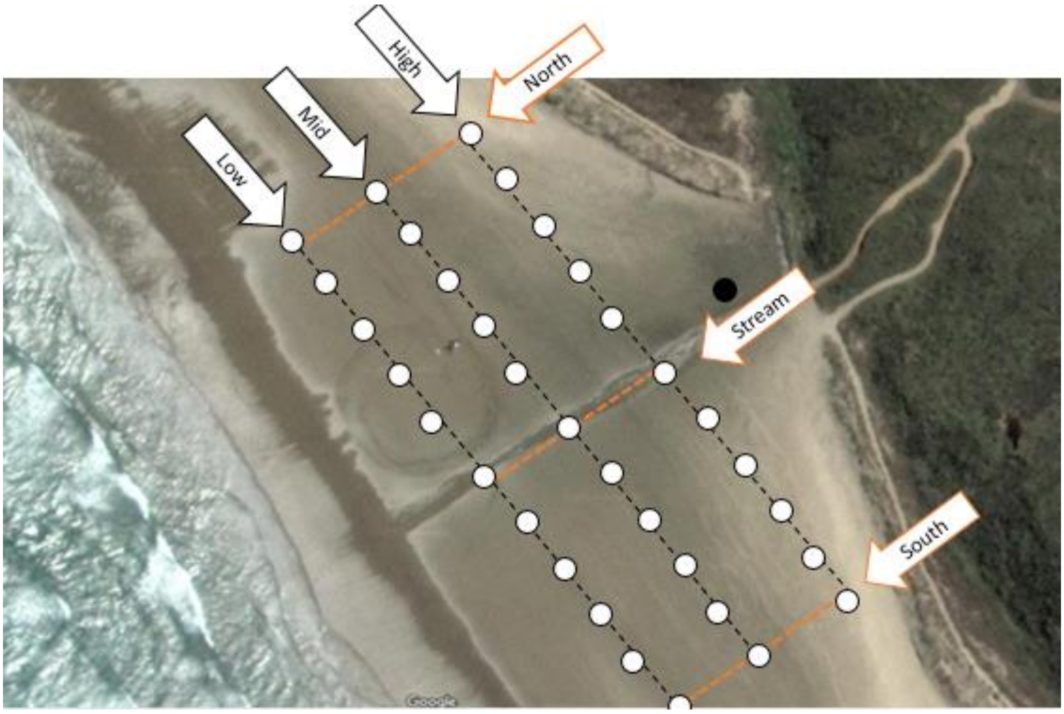

Figure 27: Topographic survey points at four survey locations on Ripiro Beach. At each site three horizontal transects parallel to the shoreline were surveyed (black dashed line). Transects were positioned at the high tide mark (as indicated by the high tide rack line) while mid and low transects were positioned immediately above and below the main toheroa bed. Beach profiles (vertical) were generated within the stream and to the north and south by using corresponding points from each transect (orange dashed line). Across shore, surface elevation was recorded relative to a fixed point (black circle).

The eleven elevation points along each transect were used to plot the long shore (horizontal) profiles of each site, for the purpose of identifying whether topographic depressions occurred in the vicinity of steams, that could act as aggregation points for toheroa. Three cross-shore (vertical) profiles were then generated from the elevation points for each site. One within the path of the stream and one to the north and one to the south. These profiles provided slopes for the mid (between low and mid transects) and upper (between mid and high transects) beach adjacent to streams, in the area where toheroa beds occur, and away from the streams, where they do not.

4.2.2 Analysis

Profiles for each site were plotted in Microsoft Excel using the elevation coordinate (z) and the x and y coordinates respectively. To generate cross-shore profiles, the distance between points across the shore (low – mid, mid – high) was calculated with the Pythagorean Theorem using the following equation:

$$a^2 + b^2 = c^2$$

where *c* is the hypotenuse and *a* and *b* the other two sides of the triangle.

The slope of the mid (low to mid points) and upper (mid to upper points) reaches was calculated using the following:

$$m = \frac{(y2 - y1)}{(x2 - x1)}$$

where *m* is the slope, *y* is the elevation and *x* the distance. The numbers *1* and *2* indicate the measurement points.

Along shore profiles were plotted using the elevation (*z*) coordinate for each point along each respective transect (high, mid, low).

4.3 Results

4.3.1 Slope

Beach slope across all surveyed areas was generally less than 2° (Table 2). Upper beach region was mostly steeper than mid beach region (Mean slope gradients: Upper beach = 1.8 ± 0.1°, Mid beach = 1.4 ± 0.1°). The difference in gradient between mid an upper beaches was greatest at Mahuta (Mid beach = 1.4 ± 0.1° , Upper beach = 2.2 ± 0.4°). At the other sites the upper beach was steeper than the mid beach by between 0.2 – 0.9°. Across both mid and upper regions, the beach gradient was lower within the stream than away from the stream to the north or south (Figure 28). Differences in slope gradient between stream and adjacent areas were lower across the mid regions (0.1° – 0.7°) of the beach than in the upper intertidal (0.3° – 1.5°).

Table 2: Slope characteristics across the mid (between low and mid transects) and upper (between mid and high transects) regions of the shore at four locations on Ripiro beach adjacent to the stream, and to the North and South of the stream. Bold text indicates shallowest gradient for each tidal height.

Location	Transect Position	Degrees (°)		Grade (%)		Ratio (1 :)	
		Mid	Upper	Mid	Upper	Mid	Upper
Chases	**North**	1.58	1.96	2.75	3.43	36	29
	Stream	**0.88**	**1.16**	**1.54**	**2.03**	**65**	**49**
	South	1.28	1.48	2.24	2.58	45	39
Mahuta	**North**	1.51	2.41	2.63	4.21	38	24
	Stream	**1.25**	**1.32**	**2.18**	**2.31**	**46**	**43**
	South	1.38	2.79	2.40	4.88	42	20
Kopowai	**North**	1.50	2.14	2.61	3.73	38	27
	Stream	**1.22**	**1.46**	**2.13**	**2.55**	**47**	**39**
	South	1.76	1.99	3.08	3.47	32	29
Third	**North**	1.79	1.50	3.12	2.62	32	38
	Stream	**1.15**	**1.14**	**2.00**	**1.98**	**50**	**50**
	South	1.49	1.95	2.60	3.41	38	29

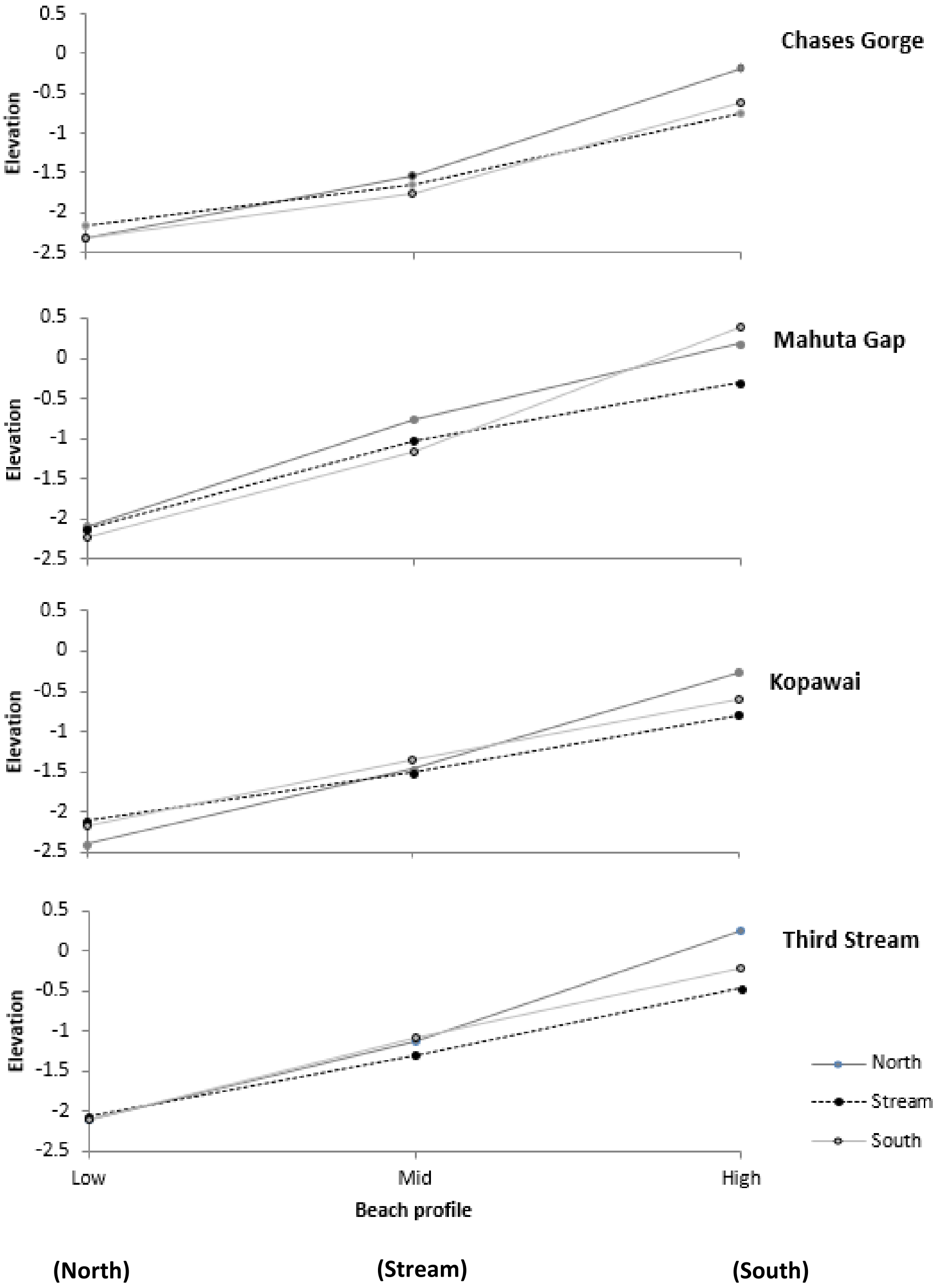

Figure 28: Slope profiles across Ripiro Beach in four locations from low to mid and mid to high. Low and mid points are determined by the position of the main toheroa bed across the shoreline with the mid-point directly landward of the bed and low seaward of the bed.

4.3.2 Elevation

Upper beach transect: At all sites, surface elevation along the upper beach (high transect) increased away from the streams (Figure 29). The greatest difference in elevation between stream and non-stream areas was recorded at Mahuta where the stream surface was 77.6 cm lower than the beach face at the southern end of the transect (Table 3). Across the other transects the difference in height between stream and non-stream areas ranged between 13.4 cm – 71.5 cm with the beach face adjacent to streams always lower. The beach face to the north of the streams surveyed was generally more elevated than the southern beach face, with the average difference between these points 59.3 ± 4.1 cm and 40.1 ± 12.9 cm respectively.

Mid beach transect: Along the mid transect, beach elevation decreased in a southward direction at all sites except Third Stream. The greatest difference in elevation between stream and non-stream points occurred at Mahuta, where the stream was 26.5 cm lower than the northern point, and 30.3cm higher than the southern. At Third Stream, the stream was 19.7 cm lower than the points approximately 50 m to the North and South.

Lower beach transect: Along the low transects at Chases, Kopowai and Third, the stream was higher in elevation than both the northern and southern most points. At Mahuta, the stream was 1.5cm lower than northern point, but 11.5cm higher than southern point (Table 3).

Table 3: Differences in elevation (cm) between the stream and northern and southern most points of the transect along high, mid and low transects for each surveyed site. Bold negative values denote lower elevations within the stream areas.

		North elevation vs stream elevation (cm)	South elevation vs stream elevation (cm)
Chases Gorge	High	**-54.8**	**-13.4**
	Mid	**-11.9**	10.5
	Low	16	15.2
Mahuta Gap	High	**-56.8**	**-77.6**
	Mid	**-26.5**	30.2
	Low	-1.5	11.5
Kopawai	High	**-27.0**	**-20.2**
	Mid	**-5.2**	**-15.9**
	Low	22.0	4.8
Third	High	**-71.5**	24.3
	Mid	**-17.7**	**-21.7**
	Low	4.7	3.6

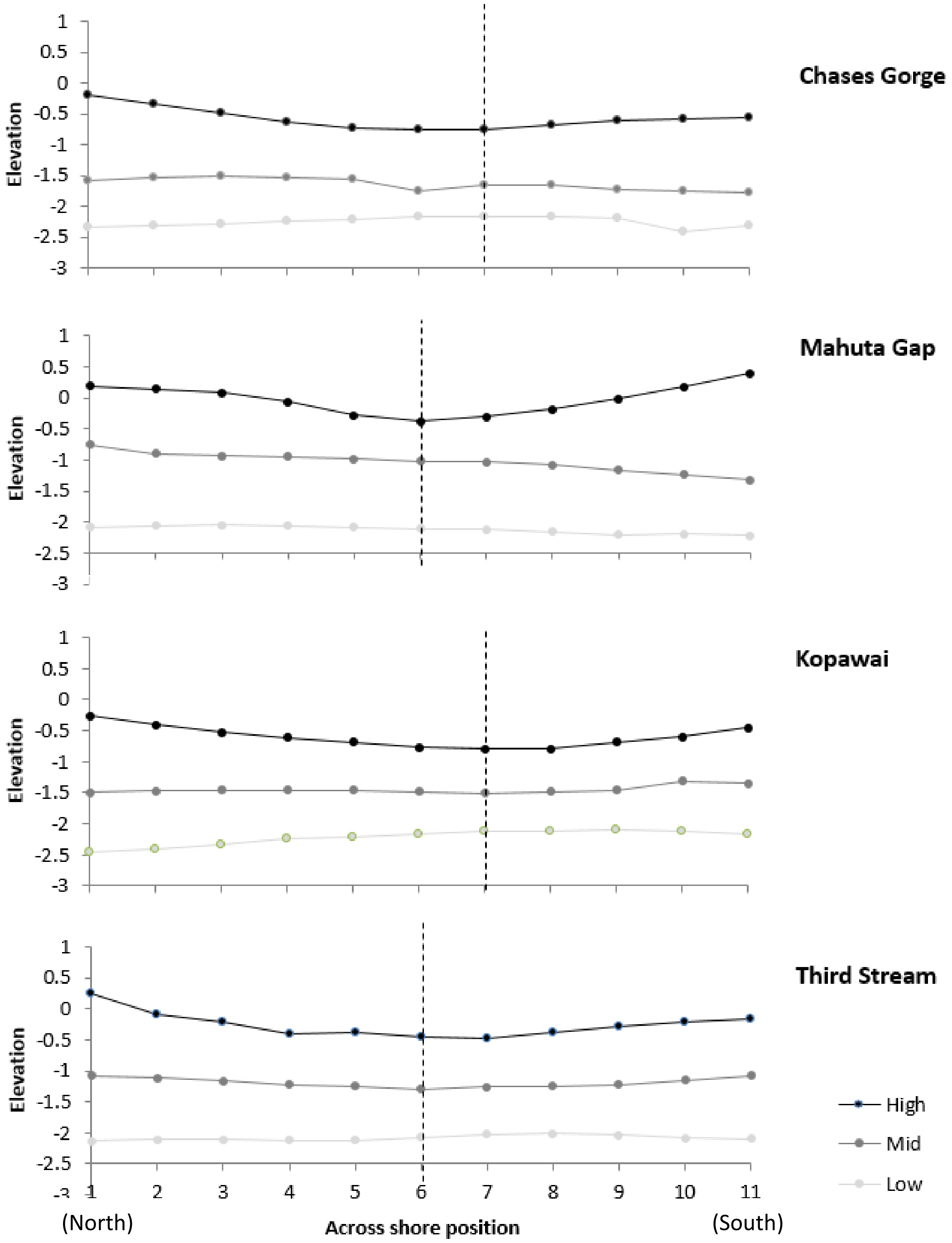

Figure 29: Along shore profiles at three positions across the exposed intertidal zone (high tide ("high), above (mid) and below (low) the toheroa bed). Topographic depressions near the streams (vertical dotted line) were evident along the high tide mark (black). Elevation (meters) is measured relative to a fixed point within the stream and above the high tide mark.

4.4 Discussion

These data show that Ripiro Beach is a very gently sloping beach, increasing in steepness from mid to upper intertidal, a feature characteristic of exposed beaches (King *et al.*, 2006). Both slope and elevation were variable along the beach but were consistently lower adjacent to streams, possibly because of increased sediment instability associated with these features. The lower elevation of these areas was most evident at the upper beach, particularly at the high tide line, an area of high juvenile toheroa recruitment. This results in the formation of a bowl-like beach surface in stream adjacent areas at the upper reaches of the beach. This basin-like topography is less evident at mid-tide, where the adult toheroa beds are established. These topographic features may have important ecological consequences for toheroa, that may go somewhere towards explaining their association with streams. In addition to acting as aggregation points for spat, juveniles and food, the gentler slope and lower elevation can increase inundation time, thus increasing feeding time and reducing exposure stress. Lower elevation may also reduce distance between sediment surface and ground water, which may be an important factor in protection against desiccation.

The beaches that occur along exposed coastlines are characterised by wide, apparently featureless intertidal zones with gentle slopes (Komar, 1998; Masselink *et al.*, 2007; Masselink & Kroon, 2009; Wright & Short, 1984b). Visually, Ripiro beach is consistent with these descriptions, with this study quantifying the gradient of the beach slope. The profile of the beach was consistent with that of exposed beaches, with a flat mid-tide region becoming steeper towards the upper beach (King *et al.*, 2006), reflecting the differences in the way wet and dry sediments accrete and erode. Whilst waves and swash action are important for transportation of sediments, the saturation level of the sediments is of greater influence (Bryant, 1985; Grant, 1948).

In this study, the higher elevation and steeper beach face away from the streams was most evident along the high tide region and is a likely indication of a lower sediment moisture content in non-stream sediments. Under normal conditions (i.e. non-storm events), dry beaches accrete as the up rushing swash infiltrates through the sediments, depositing entrained particles and reducing the volume of backrush and subsequent removal of sediment from the beach in the process. By contrast, the low permeability of saturated sediments results in a stronger backwash, as a large volume of the uprush is returned as backwash facilitating the removal of sediments from the system and in so doing, flattening the beach (Komar, 1998; Oh & Dean, 1995). Erosion in stream areas at the upper beach is likely to be exacerbated as swash from the elevated adjacent beach face preferentially flows into low-lying areas, rather than back down the beach face, increasing both volume and duration of the backrush in these areas. Reduced differences in elevation between stream and non-stream areas of the beach at mid-tide is likely to be the result of increased moisture content in non-stream sediments, either as a result of the seep face or due to regular waterlogging of the sand by more frequent swash (Brown & McLachlan, 2010; Salvat, 1967). Erosion may be greater along some streams on account of a higher moisture content, which may explain the variability in slope and elevation between streams. The concave upper shore profile exhibited in stream areas, is indicative of erosion, with convex profiles a sign of accretion (Bird & Lewis, 2014).

The source of the moisture content in stream adjacent sediment is uncertain. It may be the result of sub surface flow associated with the stream or could be a seep associated with the water table of the beach. While the accretion of sediments away from the stream increases the distance between the sediment surface and the water table, erosion adjacent to the stream would reduce this distance. A feedback loop may become established in this circumstance, with a reduction in distance to the water table increasing the moisture content of the sediment, and thus driving increasing erosion, further reducing the water table depth.

The abundance of both adults and juvenile toheroa is highest in stream areas despite these areas being subject to greater sediment instability and erosion, with recruitment greatest along streams with a gentle slope (Smith, 2003). The increased volume of swash to these areas may concentrate spat and juvenile numbers, with the low elevation of the upper beach facilitating aggregation. This basin-like topography may not directly explain the distribution of adult toheroa however, as it is less pronounced at mid-tide, and adult beds are reported to occur away from streams, with some beds migrating along the shore (Akroyd *et al.*, 2002; Ross *et al.*, 2017a; Williams *et al.*, 2013b; B. Searle, personal communication). A reason for this reduced variation in elevation may be attributed to an increase in the moisture content of the sediments along the beach as a consequence of the seep face. Rather than being confined to the stream area, this would drive erosive processes the length of the beach. Furthermore, the swash dynamics resulting from the upper beach topography may increase the volume of phytoplankton and surf diatoms travelling through the mid-tide area, and thus increase the food available for toheroa positioned adjacent to streams. In addition to increased food availability, feeding time may be prolonged in these areas as the low permeability of the saturated sediments and gentle slope of the beach allow the swash to extend higher up the beach and at a slower rate (Schoeman & Richardson, 2002). This slower swash movement, coupled with longer inundation time may also enable toheroa to gain better purchase in the sediments, reducing the number of animals washed out to sea with the swash. This has been proven to be the case in *Donax serra*, a small intertidal surf clam occurring on exposed beaches along the South African coastline (Donn Jr *et al.*, 1986; Laudien, 2002; McLachlan & Hesp, 1984; Schoeman & Richardson, 2002). The increased moisture content of the sediments in stream areas may also be important for reducing desiccation in buried animals during exposed periods and reducing heat stress.

The current study has shown that both elevation and slope are contributing factors to beach topography in stream adjacent areas on dissipative beaches. This leads to the formation of low-lying basins along the upper beach as a consequence of increased erosion in these areas. These depressions may act as important aggregation points for spat and juvenile toheroa transported to the upper beach by the swash, thus accounting for the high abundance in these regions (Smith, 2003). The lower elevation of stream areas may also channel a higher volume of swash along these parts of the beach, increasing inundation time, food concentration and prolonging feeding opportunities for toheroa. Additionally, the lower elevation of these stream areas may reduce the distance between the sediment surface and the water table, explaining the increased moisture content of the sediments. Increased moisture content could have important implications for all toheroa life stages, by buffering sediment temperatures and providing protection against desiccation.

Chapter 5

The effect of streams on the temperature of intertidal sediments and the ecological implications for toheroa

5.1 Introduction

Along the sandy beaches of exposed coastlines, the intertidal zone, also known as the littoral zone, is a harsh and unforgiving environment. Inhabiting a habitat that is in equal measures part marine and part terrestrial, intertidal organisms are adapted to survive these alternating periods of inundation by the tide and subsequent exposure to atmospheric conditions and its associated stressors. (McLachlan *et al.*, 1993). Physiological stress can occur when environmental conditions fall outside the optimal range for which a species has evolved and this may limit its performance, survival and reproduction (Cairns, 2014). Environmental stressors, for example pollution or salinity can either be acute or chronic, depending on the duration and the frequency of exposure (Elliott, 1982). Acute stressors are those that an organism is exposed to for short periods of time, whilst chronic stressors are defined as a constant or recurring exposure that may cause a prolonged physiological response (Elliott, 1982). Both acute and chronic stressors can have severe negative effects on an organism's health, compromising its scope for growth, feeding, reproduction, mortality and susceptibility to disease (sensu Macho *et al.,* 2016). The level of risk is dependent on the specific tolerance of an organism (Brierley & Kingsford, 2009), which is a reflection of the organisms physiological adaptations, for example colour, protective coating, external membrane, sweating in mammals.

By inhabiting in the intertidal zone, organisms benefit from reduced competition with subtidal taxa and reduced exposure to exclusively subtidal marine predators, for example, stingrays or fish. The trade off to these benefits of intertidal living is an increased exposure to atmospheric conditions and associated stressors, of which desiccation and overheating are among the greatest threats (Befus *et al.*, 2013; Broekhuysen, 1940; Finke *et al.*, 2007). Most organisms are adapted to a temperature range within which optimum performance is achieved at intermediate temperatures (Martin & Huey, 2008). Thermal stress can occur when an organism is exposed to higher or lower temperatures than is optimal, which may disrupt homeostatic processes by altering the performance of various physiological pathways with the potential for both sub lethal and lethal consequences (Andersom, 1978; Compton *et al.*, 2007). Although performance can be adversely affected by temperatures both above or below an optimum range, higher temperatures typically have a greater negative effect (Martin & Huey, 2008). While intertidal organisms are adapted to these environmental conditions, they may still be vulnerable to extreme events such as unusually high atmospheric temperatures, extreme tides or severe weather systems, which may result in prolonged periods of exposure.

Organisms that occupy the upper reaches of the littoral zone experience the shortest inundation time. At the extremes of the intertidal zone, organisms may only be inundated during spring tides or storms. Consequently, these organisms are most at risk of experiencing heat related stress as they can spend hours, days or weeks exposed to temperatures at the limits of their optimal ranges, especially during the summer when daytime temperatures are high. Thermal stress brought about by overheating and desiccation is thus one of the major physical hazards to be overcome by intertidal organisms (Broekhuysen, 1940; Brown & McLachlan, 2010; Finke *et al.*, 2007; Foster, 1971; Macho *et al.*, 2016).

Along the rocky shore, the physiological adaptations of organisms, coupled with the availability of shade and moisture, enable organisms to survive periods of exposure on the hard substrate (Foster, 1971; Harley & Helmuth, 2003; Tomanek & Helmuth, 2002). In soft sediment ecosystems, the risk of overheating decreases with burial depth and proximity to the shoreline (Johnson, 1965; Salvat, 1967; Tallqvist, 2001; Wilson & Elkaim, 1991). Despite the protection of the sediments, intertidal organisms are nonetheless subjected to reoccurring temperature changes associated with alternating periods of tidal inundation and exposure as well as daily diurnal cycles (Johnson, 1965). These temperature fluctuations may be buffered by streams, which could also maintain lower temperatures (Befus *et al.*, 2013; Dale & Miller, 2007; Miller & Ullman, 2004), thus providing some thermal refuge. This modification of the habitat could explain the reported toheroa-stream associations. Consequently, thermal stress has been suggested as a factor that may be influencing the fine scale distribution of toheroa along Northland beaches (Williams *et al.*, 2013b).

Along Ripiro Beach, toheroa are often associated with streams. Juvenile toheroa are most abundant at the upper reaches of the beach (Rapson, 1952; Smith, 2003), where they are buried in the surface sediments (Kondo *et al.*, 1995), and adults are found deeper below the surface (Kondo *et al.*, 1995) in the region of the mid-tide. Although numerous streams still flow into the beach at Ripiro, there is both documented and anecdotal evidence to indicate that flow of water to Ripiro Beach has decreased over time to the point where some streams no longer flow (Williams et al. 2013). Therefore, it has been suggested that reduced freshwater flow may be diminishing the availability of habitat suitable for toheroa.

However, of the studies to investigate this hypothesis, the majority have been conducted in estuaries or at sheltered beaches (Befus *et al.*, 2013; Dale & Miller, 2007; Li *et al.*, 2006; Miller & Ullman, 2004), the physical environment of which are quite unlike that of exposed coastal beaches. This type of study has not been undertaken on exposed high-energy coastlines, presumably due to the challenges of conducting experiments along beaches with large swash regimes and near continuous high swell conditions. Differences in the physical environment may contribute to thermal regimes, making it inappropriate to make inferences about one environment from experiments conducted in another (Harrison & Phizacklea, 1987). Consequently, there is insufficient information available to determine the plausibility of the hypothesis that streams provide a thermal refuge to toheroa.

As an initial step towards investigating the thermal refuge hypothesis, and understanding the possible role of decreasing freshwater inputs in the continued decline of toheroa, this study aimed to determine how sediment temperatures on Ripiro Beach vary with proximity to streams. This will provide an understanding of whether the thermal refugia hypothesis is plausible, and in so doing, inform future ecological studies investigating toheroa-stream associations.

5.2 Methods

Ripiro Beach lies between 35°77’ and 36°39’ south and experiences a sub-tropical temperate climate, partly modified by the extensive surrounding ocean. Northland has New Zealand’s highest average annual temperature, due to warm humid summers, and mild wet winters. Temperatures can exceed 30 °C during January and February, the hottest months of the year. Winter temperatures range between 14 °C and 20 °C (Chappell, 2014) (Figure 30).

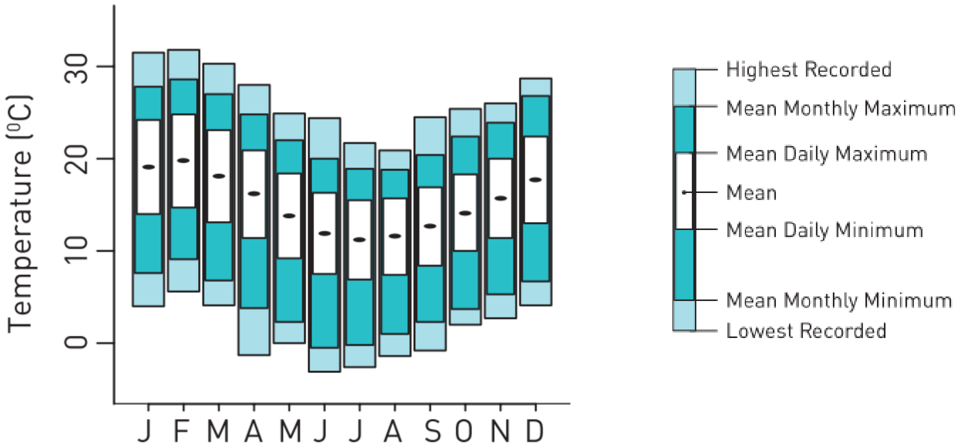

Figure 30: Mean, maximum, and minimum monthly temperature for Dargaville, a town close to Ripiro Beach, and the location of the nearest weather station. (Chappell, 2014).

Seasonal changes in sea surface temperature lag six to eight-weeks behind land surface temperatures. February and August are the warmest (mean = 21 °C) and coolest (mean = 16 °C) months with respect to sea temperatures. Precipitation occurs year round, although heaviest in winter, and the region regularly experiences two to three week long fine, dry spells in summer. The prevailing winds are from the southwest, but during the summer months the region can experience storms associated with the remnants of tropical cyclones and sub-tropical low pressure systems (Chappell, 2014).

In this study, four sites were sampled during the outgoing tide over four consecutive days (6 – 9 December 2016) a week prior to the spring tide. Temperatures were above average, but the weather was unsettled, varying between rain and fine conditions (Figure 31). Temperature and rainfall levels for

Dargaville were above average in the month leading up to sampling (AccueWeather, 2016), although base river flows were low leading into December (Northland Regional Council, 2016). (Appendix C)

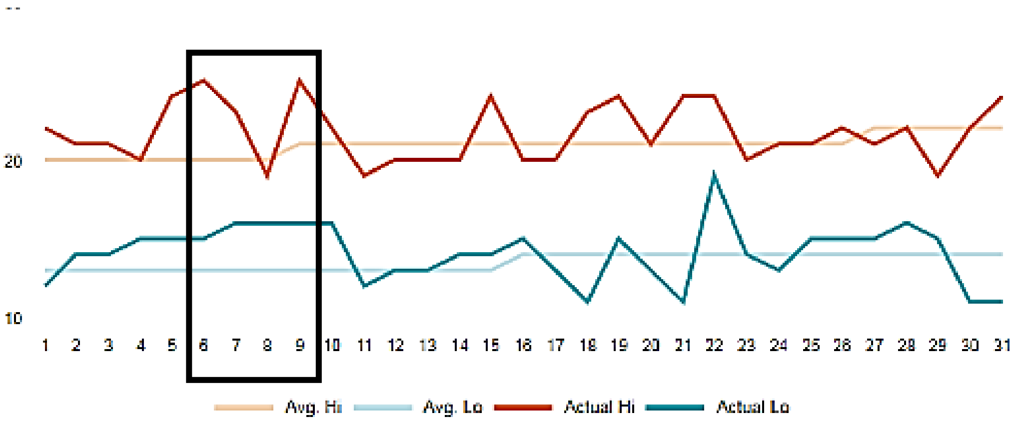

Figure 31: Maximum (red) and minimum (blue) temperatures (°C) recorded at Dargaville in December 2016. The black box indicates the sampling period. Historical temperature data sourced from www.accuweather.com.

5.2.1 Study sites

Sediment temperature, the depth of the water table below the sediment surface and salinity were measured at Kelly's, Mahuta Gap, Kopowai and Third Stream (Figure 32) on consecutive days between the 6th and 9th of December 2016. Descriptions of sites can be found in Chapter 2.

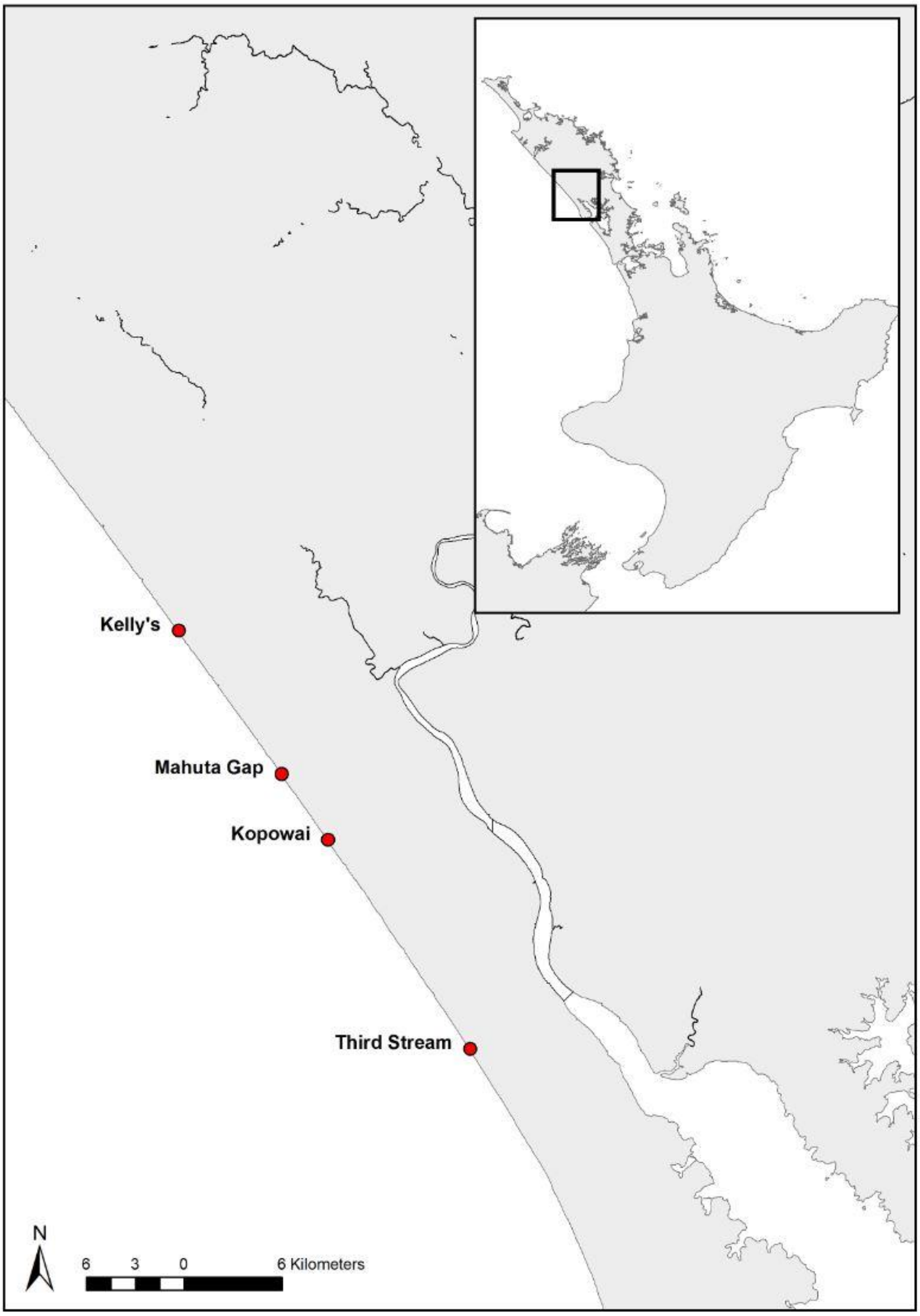

Figure 32: Map of Ripiro Beach indicating the locations of the four streams where sampling was conducted.

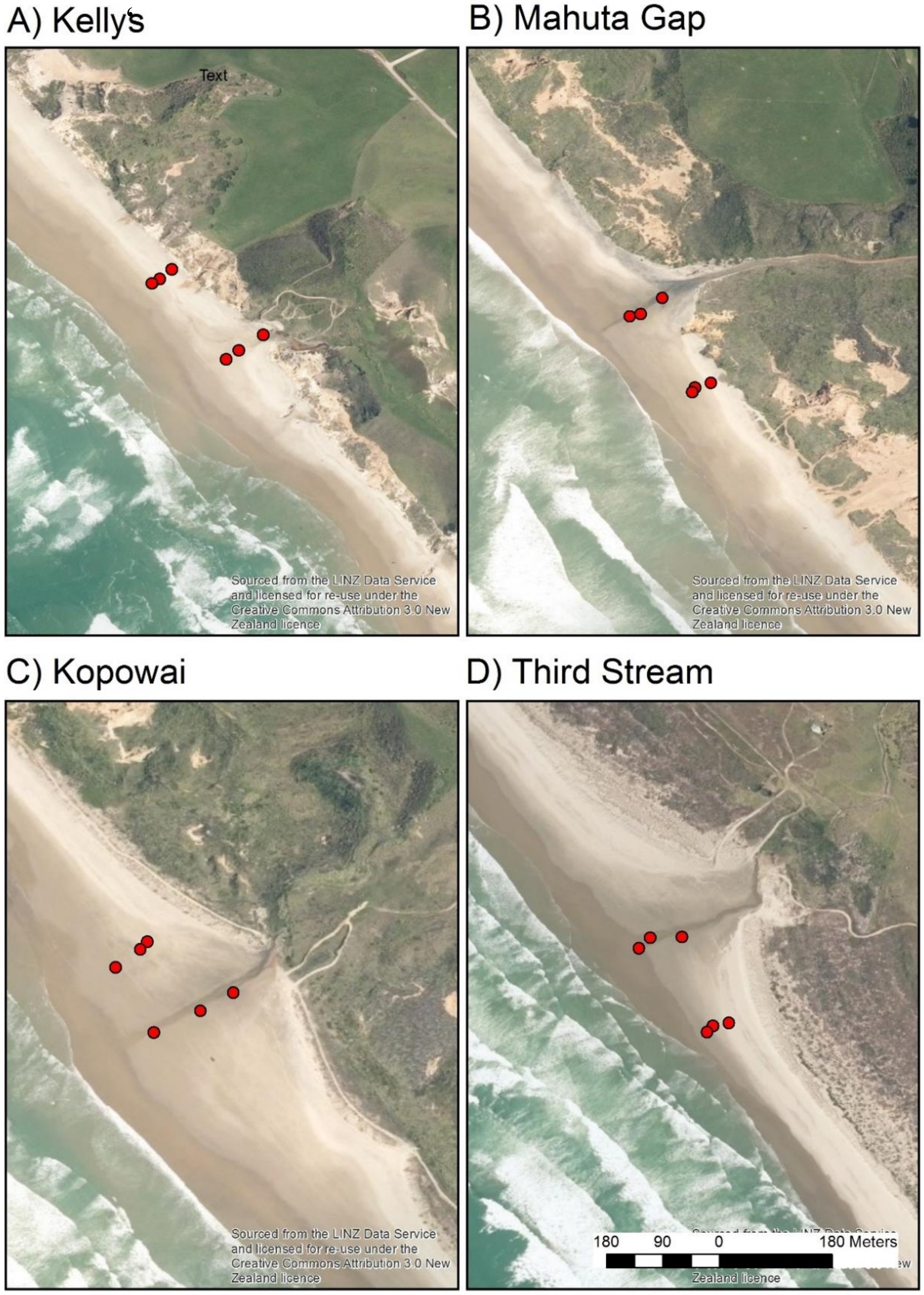

Figure 33: At each of the four sites, the temperature of the exposed sediments, the depth of the water table below the sediment surface and the salinity of the pore water was monitored at nine points across the beach. These points were positioned adjacent to (stream (S)) and away from the stream (non-stream (NS)) at the high tide (High) and the upper (Mid) and lower (Low) edges of the toheroa bed at mid-tide.

5.2.2 Methodology

At each site, two transects were established perpendicular to the shoreline. One transect was positioned immediately adjacent to the stream (stream) and the other at a distance of approximately 100 m from the stream (non-stream), in order to determine the effect of streams on sediment temperatures. Along each transect, sediment temperatures were measured at positions hereafter referred to as high (H), mid (M) and low (L) points. The high point marked the position of the previous high tide, determining the uppermost sampling point for each transect. The position of the tide varied by up to 70 m between days depending on the weather and lunar phases. Mid and low sampling positions were determined by the position of the toheroa bed at the site. The mid transect was positioned immediately above the main toheroa bed (as indicated by the position of siphon holes in the sediment). The Low transect was positioned immediately below the bed. Mid and low positions were selected above and below the bed to minimise disturbance to the toheroa. Because siphon holes often only begin to become visible in the sediment approximately one hour after the ebb tide has passed over the bed, the tide was often well below the low point, before sampling points could be marked and sampling could begin. Non-stream sampling stations were positioned at equivalent tidal height to stream adjacent sampling positions (Figure 34).

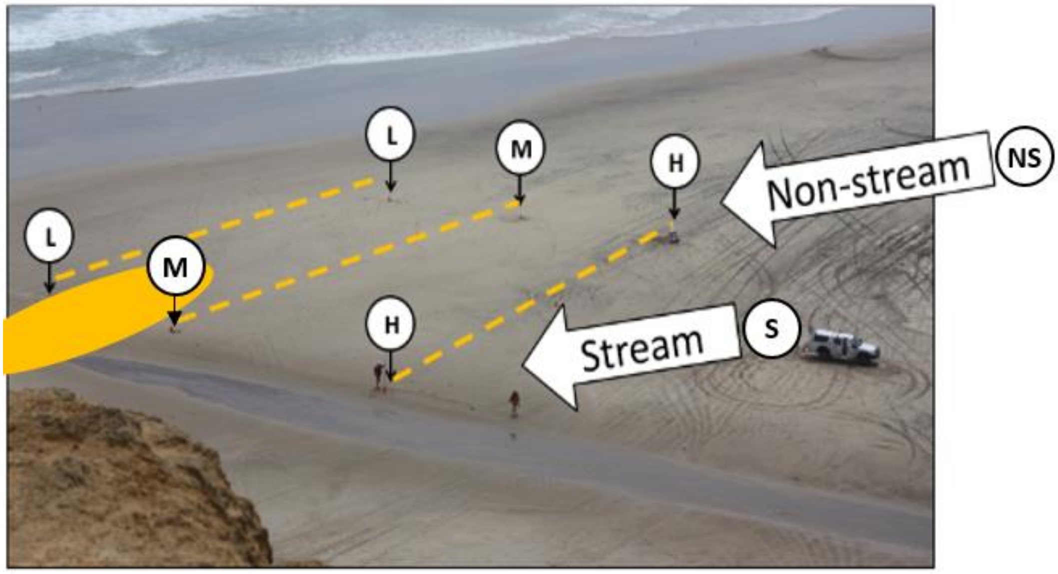

Figure 34: Annotated photograph showing the position of sampling points adjacent to (stream (S)) and away from (non-stream (NS)) the stream at the high tide (H), and above (mid) and below (low) the main toheroa bed solid yellow) at mid-tide.

Each point was sampled sequentially, moving in a clockwise direction starting at the stream adjacent high point (S-H) and ending at the high point away from the stream (NS-H). At each site, all points were sampled an equal number of times, beginning from the time that all sampling points could be established until the low sampling station was inundated by the rising tide. Due to variations in tidal exposure periods, the total number of sampling rounds varied between sites (between 5 to 8), as did sampling duration and time of sampling (Table 4). During each sampling event, sediment temperature, pore water salinity and the distance from surface to water table were measured using methodology defined below. Pore water salinity and depth of the water table were measured to determine whether the sediment moisture content mentioned in previous chapters was associated with the stream or the beach ground water system.

Table 4: Sampling times for each site in relation to high and low tides.

Site	**Kelly's**	**Mahuta Gap**	**Kopowai**	**Third Stream**
Date	08 December	07 December	09 December	06 December
Time (start-end)	10:02 - 11:36	09:04 - 12:50	11:14 - 14:07	07:20 - 11:33
Duration	90 min	225 minutes	170 minutes	240 minutes
Sample rounds	5	8	8	7
Tide times (low–high)	11:34 -18:00	10:41 - 17:09	12:34 - 18:57	09:53 -16:20

5.2.2.1 Sediment temperature

Sediment temperature was measured using a number of CDN pro accurate waterproof thermometers (Model DTW450L) (accuracy: 1.1 °C, resolution: 0.1 °C). Thermometers were calibrated daily in accordance with the manufacturer's instructions. Specially constructed thermometer stands allowed for the simultaneous measurement of sediment temperatures at depths of 2 cm, 4 cm, 7.5 cm 10.5 cm and 20.5 cm (Figure 35). Using four stands and 20 thermometers, four replicate measurements were taken at each depth simultaneously. Upon insertion into the sediments, each thermometer was activated and allowed to stabilize for at least five seconds before temperatures were recorded. Thermometers were marked to ensure that they measured the same depth throughout the study. The distance between the sampling points varied across the beach, and therefore the time that elapsed between measurements varied, because of the time taken to move between them. For each sampling event, the thermometers were inserted into fresh sediment, avoiding the holes left from previous sampling efforts. This ensured that temperatures were measured in the sediments not exposed to the air and ambient conditions.

Figure 35: A custom-built thermometer stand allowed for the simultaneous measurement of sediment temperatures at depths of 2 cm, 4 cm, 7. 5cm 10.5 cm and 20.5 cm below the beach surface.

5.2.2.2 Groundwater

In the context of coastal systems, the term “groundwater” refers to the water within the interstitial spaces of sediments (pore water), and is derived from both marine and terrestrial sources (Mulligan & Charette, 2009). Much of this water is contained in subterranean aquifers, at pressures below atmospheric pressure (Horn, 2002). The water table marks the surface of the aquifer and represents a point of differential pressure, where pressure changes to the ambient (Horn *et al.*, 1999). Above the water table, interstitial moisture content is maintained through capillary rise. In this study, reference is made to the depth of the water table below the sediment surface. However, it is more accurately the depth to which the effects of capillary rise are observed. Because the streams that flow across Ripiro Beach are ephemeral, the depth and salinity of the pore water was used to ascertain the extent of the streams influence across the littoral zone in the absence of surface flow. It also served as an indication rather than a measure of the moisture content within the sediment. To measure these parameters at each sampling point, a sampling well constructed from a 25 cm length of 5cm diameter PVC pipe, was inserted into the exposed intertidal sediment to a depth of 20 cm. To measure these parameters. Holes were drilled 5 cm above the base of the well in order to facilitate the flow of water through the well, and screened to prevent infilling by the sediments (Figure 36).

The depth of the water table was measured using a hollow graduated tube. One end of the tube was lowered into the well, whilst blowing on the other end until water bubbles could be heard indicating that the surface of water had been reached. The distance from the water surface to the top of the well was measured with the tube. The height of well above the sediment surface (5 cm) was then subtracted to give the depth of the water table below the sediment surface.

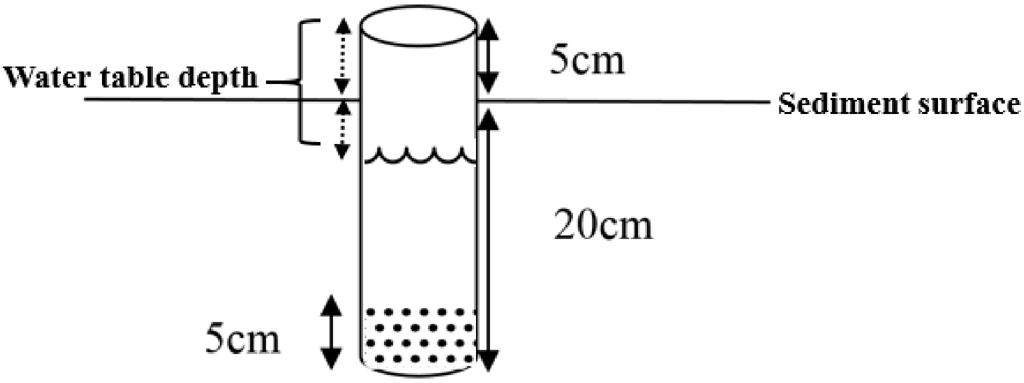

Figure 36: Sampling wells were constructed using 25cm long screened PVC pipes which were inserted 20 cm into the sediment. The wells enabled pore water salinity to be measured in addition to water table depth. The depth of the water table was measured relative to the sediment surface by subtracting the height of the well above the sediment surface from the depth of the water from the top of the well.

5.2.3 Data analysis

Visual examination of the data was performed in Excel 2016 (Microsoft) in order to identify any trends and/or patterns. All statistical analysis was performed in SPSS Statistics for Windows Version 24 (IBM Corp. Armonk, New York). Significance was taken as $\alpha < 0.05$ for all analyses.

5.2.3.1 The effects of depth and shore position on mean temperature

In order to examine whether there were any differences between temperatures at different depths, at different shore positions (i.e. NS-H vs S-H) and whether there were any interactions between depth and shore position on the temperature, a two-way ANOVA was performed. Independent variables were position (six levels) and depth (five levels) with temperature (°C) as the dependant variable.

Simple main effects were tested for each site, including those without significant interaction effects to determine the points of significant difference ($p < 0.05$) (between depths per point, between points per depth). For sites without significant interaction effects, main effects were tested. Samples were balanced (Kelly’s: $n = 5$, Mahuta Gap = 8, Kopowai: $n = 8$, Third Stream: $n = 7$) and residual analysis was performed to ensure the assumptions for ANOVA were met. Outliers were identified as being greater than three box-lengths from the edge of the box in a boxplot (the equivalent of 3 standard deviations) (Statistics, 2015). Prior to analysis, normality was assessed with a Shapiro-Wilk's normality test for each cell of the design, and homogeneity of variances was assessed by Levene's test. If outliers were found the datasheets were checked to ensure their presence was not the result of data entry errors. Thereafter, t-tests were run to compare sample round means with and without the outliers. As there were no significant differences ($p < 0.05$) outlying values were left in the dataset. Shapiro-Wilk tests of normality on the standardised residuals identified a low number of violations to the assumption of normality at Kelly’s and Mahuta (Kelly’s: Non-stream (mid) 2 cm $p = 0.016$, Stream (Low) 20.5 cm $p = 0.009$; Mahuta: Stream (Low) 2 cm $p = 0.008$). A *reflect and square root transformation* was used to reduce non-normality at Kopowai (5 violations / 17% of the dataset) but failed normalise data from Kelly’s, Mahuta and Third streams (other transformation methods (LOG+ 1, Natural Log (LN), Square root) were also unsuccessful (McDonald, 2009). The residuals from Third Stream were intractably heterogeneous with 76.6% of the data violating the normality assumption. Efforts to transform the data at this site compounded the problem. Since ANOVA is tolerant to some deviation to this assumption if samples are balanced, the data from Kelly’s, Mahuta and Third streams was not transformed (Statistics, 2015). In forcing the ANOVA, it was noted that subsequent analysis would be conservative with an increased likelihood of a Type II error. The assumption of homogeneity of variances was violated for all sites ($p = 0.000$).

5.2.3.2 Temperature over time

Two one-way ANOVA were performed to test the difference between stream and non-stream temperatures at the start and end of sampling respectively. The independent factor was *point* (six levels) with the dependant variables *start temperature* and *end temperature* respectively. Samples were balanced ($n = 4$) and residual analysis was performed to ensure the assumptions for ANOVA were met, as described above.

Assessing differences between corresponding stream and non-stream points (for example NS-H and S-H) and those immediately adjacent to each other across the shore (for example S-M vs. S-L and S-M vs. S-H) were considered important in order to test the hypothesis that sediment temperature adjacent to the stream would be cooler or slower to change. Paired residuals with no significant difference ($p > 0.05$) at the start and end of sampling could therefore be assumed to increase in temperature at a similar rate over the course of the day. Whilst a two-way repeated measures ANOVA would have enabled a comparison of changes between points over time, the sampling intervals were not fixed and varied between points and rounds as described above. Had sampling intervals been fixed, this analysis would have enabled comparison of temperature at equal points throughout sampling. Instead, we looked the difference in temperatures between first and last sample rounds as a gauge of rate of temperature change.

5.3 Results

5.3.1 Water table depth and salinity

The water table remained within 20 cm of the sediment surface in all stream adjacent wells and in two NS-L wells (Kopowai and Third Stream) throughout the entire sampling period (Figure 37). Wells at the other non-stream sampling positions were dry, indicating that the water table was below the well depth of 20 cm. The depth of the water table fluctuated over the monitoring period, but the general trend was for water table depth increasing during the ebbing period of the tide. On the incoming tide, the response varied across the shore and between sites. At Mahuta, the water table rose rapidly at S-H, slowly at S-M with little change observed at S-L. At Kopowai, the water table continued to drop at S-H and S-M, with S-L fluctuating. At Third Stream, the water table rose at S-H and continued to fall at S-M and S-L. Water table depth decreases in both NS-L wells were only seen in the last sample round when the wells were inundated by the swash.

Pore water salinity was highly variable between stream adjacent wells and across sites, ranging from 0.00 (± 0) ‰ to 33.3 (± 0.5) ‰, remaining below the average seawater concentrations for the region (35‰). In the S-H wells at Kelly's and Kopowai salinity remained at 0‰ throughout sampling. At Kelly's and Third, there was <5‰ difference in salinity between low and mid wells. This increased to 10‰ at Mahuta and approximately 15‰ at Kopowai. Salinity increased in a seaward direction across the sampling points at Mahuta and Kopowai. At Kelly's, the lowest salinity was recorded in the high well (0.00 ± 0‰), and the highest salinity in the mid well (33.3 ± 0.5‰). The highest salinity at Third Stream was recorded in the high well (11.6 ± 0.3‰) and the lowest in the mid (2.4 ± 0.5‰) (Table 5). Salinity could only be measured at NS-L at Kopowai and Third stream. In both of these wells, salinity was greater than that in the stream adjacent wells.

Table 5: Pore water salinity (‰) could only be measured if the water table was within the depth of sampling. At points adjacent to the stream, water was brackish, indicating the presence of the intertidal saline circulation cell (ISC). Low salinity (0‰) suggests a direct influence of fresh water. Low salinity is indicative of the edges of the saline cell where freshwater and saline water mix.

Site	Across shore height	Along shore position	
		Non-stream	Stream
		Mean ± SE (‰)	Mean ± SE (‰)
Kelly's	High	-	0 ± 0
	Mid	-	33.3 ± 0.5
	Low	-	27.8 ± 0.5
Mahuta	High	-	14.9 ± 0.1
	Mid	-	24.1 ± 0.1
	Low	-	34.3 ± 0.4
Kopowai	High	-	0 ± 0
	Mid	-	6.3 ± 0.5
	Low	29.0 ± 0.8	24.8 ± 0.6
Third	High	-	11.6 ± 0.3
	Mid	-	2.4 ± 0.5
	Low	21.7 ± 0.8	7.2 ± 0.7

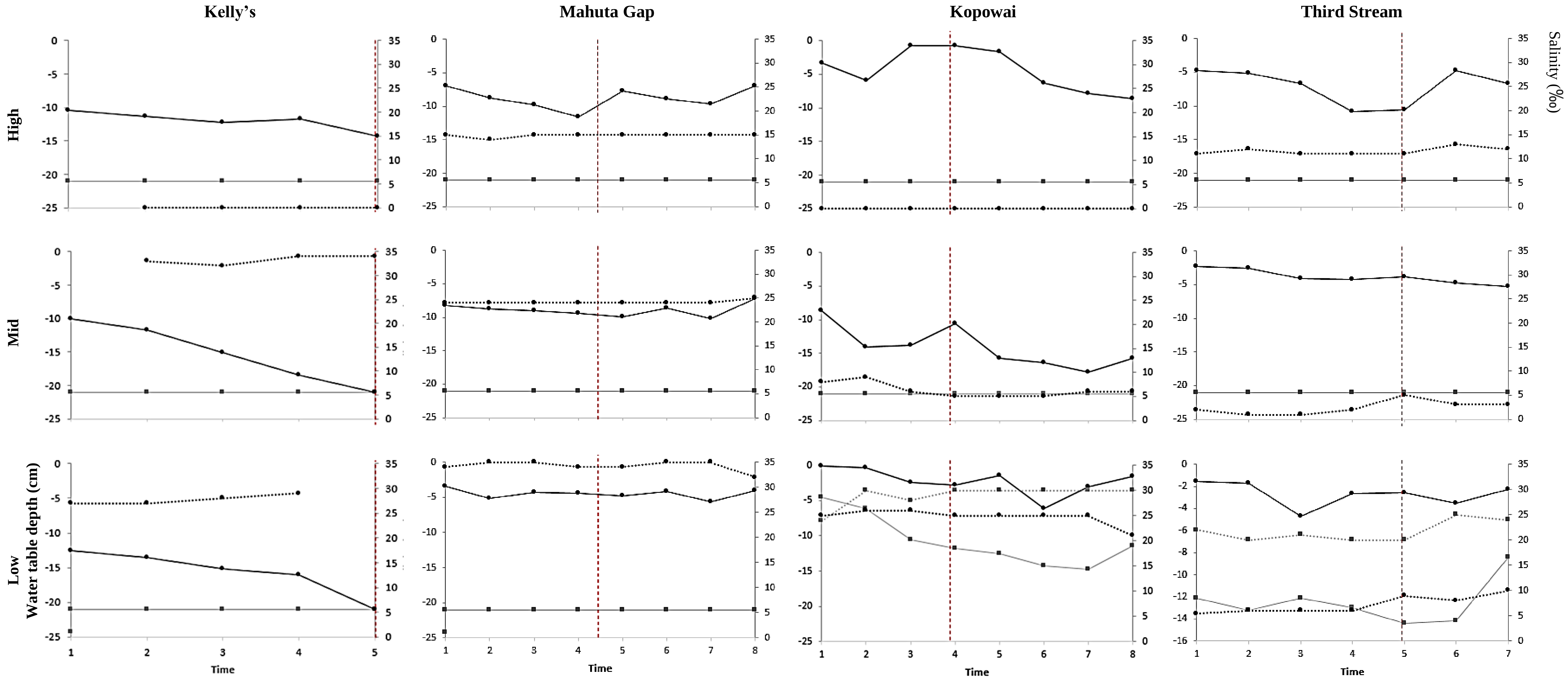

Figure 37: Salinity (dotted line) and the depth of the water table depth (cm) below the sediment surface (solid line) was measured in sampling wells adjacent to (grey) and away from the stream (black) at three tidal heights (high, mid and low) throughout the sampling period (time). Both salinity and water table depth could only be measured if the water table was within measurement range (<20cm below the surface). Vertical dotted line indicates timing of low tide relative to the sampling period

5.3.2 Temperature

Temperatures decreased and were more stable with increasing depth. The exception to this was at Kelly’s where temperatures at NS-H increased with depth (Figure 38). For all sites, temperatures at 2 cm below the surface ranged from 19.8 ± 0.1 °C (Kelly’s S-L) to 30.5 ± 0.5 °C (Kopowai NS-H). At 20.5 cm, temperatures ranged between 18.1 ± 0.1 °C (Third Stream S-L) and 21.8 ± 0.1 (Kelly’s NS-H) (Table 6).

The largest differences in temperature between stream and non-stream locations occurred at the high tide sampling points where temperatures away from the stream were higher at all depths (Figure 39). At 2 cm deep, NS-H temperatures were significantly higher than S-H ($p < 0.05$) at all sites except for Kelly’s, with temperature differences ranging between 2.0 ± 0.7 °C (Kopowai) and 3.5 ± 0.8 °C (Third). At 4 cm, temperature differences ranges between 0.7 ± 0.1 °C (Kelly’s) and 2.4 ± 0.8 °C (Third) and were significant ($p < 0.05$) for all sites. Below this, NS-H temperatures were still higher than S-H, but were only significantly higher (p <0.05) at Kelly’s and Mahuta (Appendix D). At the mid and low sampling points, temperatures adjacent to and away from the stream were not significantly different ($p > 0.05$) (Table 6). However, temperatures at the mid points at Kelly’s, Mahuta and Kopowai were on average slightly warmer in stream adjacent sediments (<1 °C) than those away from the stream. Similar non-significant differences were recorded at the low points, with temperatures slightly warmer away from the stream at Kelly’s, Kopowai and Third.

Across the beach, between low and high, the largest temperature differences occurred between NS-H and NS-M. At Kelly’s and Mahuta these differences were significant for all depths ($p < 0.05$), whilst at Kopowai and third Stream they were limited to the 2 cm sampling depth. Adjacent to the stream, temperatures between high and mid, and mid and low were similar (<0.8 °C), with little significant variation between them (Appendix E).

At Kelly’s ($F_{(20,\ 570)} = 9.903$, $p < 0.001$) and Kopowai ($F_{(20,\ 930)} = 1.825$, $p < 0.015$), the results from the two-way ANOVA indicated a significant interaction between shore position and depth (point*depth) on sediment temperatures. At Mahuta and Third there was no interaction effect, with both depth and shore position having a significant effect on temperatures (Appendix F).

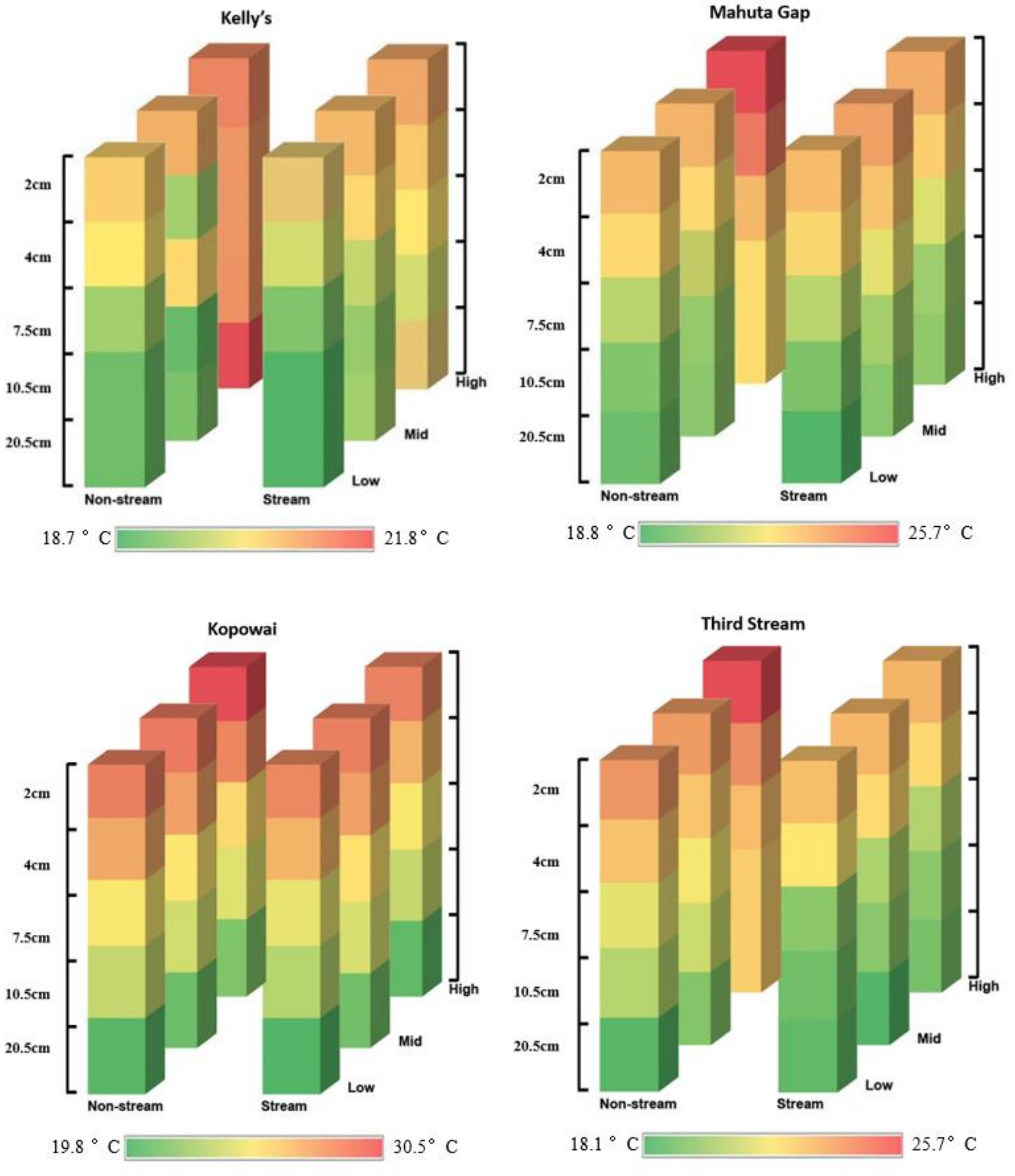

Figure 38: Average temperatures at each depth (2 cm, 4 cm, 7.5 cm, 10.5, 20.5 cm) for each point adjacent to (stream) and away from the stream (non-stream) at high, mid and low points. Temperature scale varies for each site.

Table 6: Average temperature with standard error (SE) for each depth (2 cm, 4 cm, 7.5 cm, 10.5 cm, 20.5 cm) along stream and non-stream transects at high tide (high) and above (mid) and below (low) the main toheroa bed at mid-tide. The highest temperature in a stream versus non-stream comparison are in bold.

		Kelly's		**Mahuta Gap**		**Kopowai**		**Third Stream**	
Position	Depth	Non-stream	Stream	Non-stream	Stream	Non-Stream	Stream	Non-stream	Stream
High	2 cm	**21.0 ± 0.1**	20.5 ± 0.1	**25.7 ± 0.4***	23.2 ± 0.2	**30.5 ± 0.5***	28.4 ± 0.3	**25.7 ± 0.9***	22.2 ± 0.8
	4 cm	**20.7 ± 0.1***	20.1 ± 0.1	**24.5 ± 0.4***	22.3 ± 0.3	**28.3 ± 0.4***	26.7 ± 0.3	**23.3 ± 0.8***	21.0 ± 0.7
	7 cm	**20.7 ± 0.1***	19.6 ± 0.1	**22.9 ± 0.3***	21.3 ± 0.3	**25.5 ± 0.3**	24.7 ± 0.3	**21.8 ± 0.6**	19.6 ± 0.5
	10 cm	**20.8 ± 0.1***	19.4 ± 0.1	**22.0 ± 0.3***	20.5 ± 0.2	**24.0 ± 0.2**	23.3 ± 0.2	**21.3 ± 0.4**	19.2 ± 0.4
	20 cm	**21.8 ± 0.1***	19.8 ± 0	**21.2 ± 0.3***	19.9 ± 0.2	**21.3 ± 0.1**	20.3 ± 0.1	**21.3 ± 0.1**	18.9 ± 0.1
Mid	2 cm	**20.4 ± 0.1**	20.3 ± 0.2	23.0 ± 0.3	**23.5 ± 0.2**	**28.8 ± 0.3**	28.6 ± 0.4	**22.9 ± 0.7**	22.1 ± 0.8
	4 cm	19.8 ± 0.1	**19.9 ± 0.1**	22.1 ± 0.3	**22.6 ± 0.3**	27.3 ± 0.3	27.3 ± 0.3	**21.6 ± 0.6**	20.8 ± 0.7
	7 cm	19.2 ± 0.1	**19.3 ± 0.1**	21.2 ± 0.3	**21.4 ± 0.3**	25.1 ± 0.2	**25.2 ± 0.3**	**20.3 ± 0.5**	19.5 ± 0.5
	10 cm	18.8 ± 0.1	**19.1 ± 0.1**	20.4 ± 0.2	**20.6 ± 0.2**	23.7 ± 0.2	**23.9 ± 0.2**	**19.9 ± 0.4**	19.1 ± 0.4
	20 cm	18.9 ± 0	**19.2 ± 0**	**19.8 ± 0.2**	19.7 ± 0.2	20.6 ± 0.1	**20.8 ± 0.1**	**19.1 ± 0.1**	18.4 ± 0.1
Low	2 cm	**20.0 ± 0.1**	19.8 ± 0.1	**22.9 ± 0.2**	22.8 ± 0.2	**28.6 ± 0.4**	28.2 ± 0.3	**23.0 ± 0.7**	21.7 ± 0.8
	4 cm	**19.6 ± 0.1**	19.4 ± 0.1	22.1 ± 0.2	22.1 ± 0.2	**27.1 ± 0.4**	26.7 ± 0.3	**21.6 ± 0.6**	20.5 ± 0.7
	7 cm	**19.2 ± 0.1**	19.0 ± 0.1	20.9 ± 0.2	20.9 ± 0.3	**24.7 ± 0.3**	24.3 ± 0.2	**20.1 ± 0.5**	19.1 ± 0.5
	10 cm	**18.9 ± 0.1**	18.7 ± 0.1	**20.2 ± 0.2**	20.1 ± 0.2	**23.3 ± 0.2**	22.9 ± 0.2	**19.6 ± 0.4**	18.8 ± 0.3
	20 cm	**18.9 ± 0**	18.7 ± 0	**19.3 ± 0.2**	18.8 ± 0.3	**20.0 ± 0.1**	19.8 ± 0.1	**18.5 ± 0.1**	18.1 ± 0.1s

* denotes statistical significance at the 0.05 level

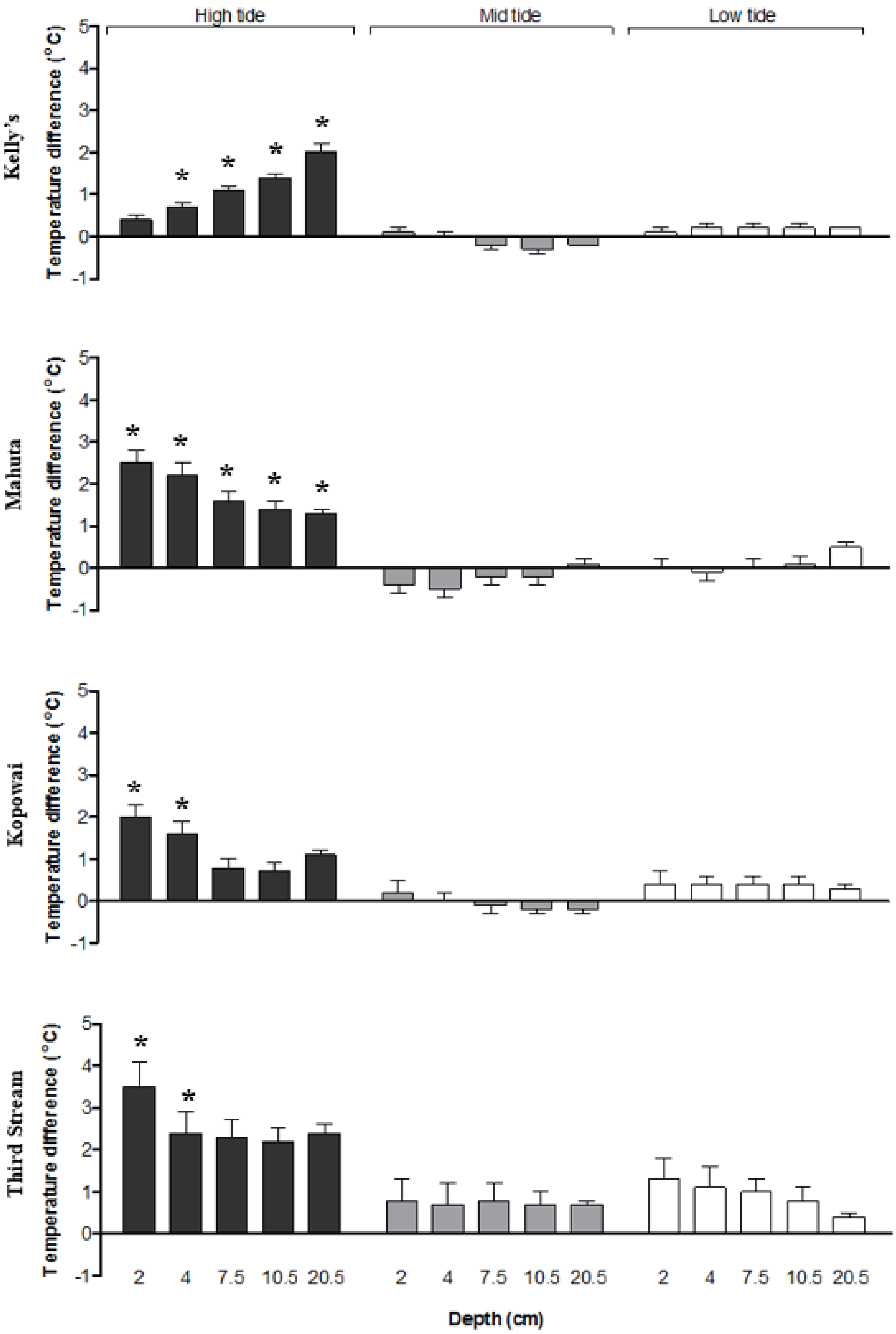

Figure 39: Difference in mean temperature along stream and non-stream transects at high tide (high), immediately shoreward of the main toheroa bed (mid) and directly seaward of the bed (Low) at each sampling site (Chases Gorge, Mahuta Gap, Kopowai, Third Stream). Error bars ± *SE*.

*** denotes statistical significance at the 0.05 level**

5.3.2.1 Temp over time

Temperatures at NS-H increased more rapidly than elsewhere across the beach. At the high points of Kelly’s, Mahuta and Third streams, non-stream temperatures were significantly higher (*p* <0.05) than the corresponding stream temperatures in the first sampling round (start) for most depths. The greatest difference was observed at Kelly’s where the NS-H temperature (22.5±0.1 °C) was 2.7 °C higher than the S-H temperature (19.8±0.1 °C) at 20.5 cm in the first round of sampling. Over the course of sampling, the temperature difference decreased as NS sediments underwent a cooling period. NS-H was 1.8 °C warmer than S-H (*p* <0.05) on the last sample round, and was the only significant difference in end temperature at Kelly’s. At Mahuta and Third Stream, NS temperatures increased more rapidly than stream temperatures resulting in a greater temperature difference throughout the day. The largest increase in absolute temperature occurred at Third Stream, where NS-H (2 cm) temperature rose 12.5±1.1 °C over a four hour period whilst S-H increased by 9.9±0.2 °C.

In the last sampling round, NS temperatures were significantly higher than S-H at all depths. The largest difference in temperature was 3.9 °C (Third Stream, 2 cm). At Kopowai, temperatures adjacent to (S-H) and away from the stream (NS-H) were similar (*p* >0.05) at the start of sampling, but NS-H temperatures increased rapidly over the sample period and were significantly warmer (*p* <0.05) than S-H temperatures at the end of sampling, at most depths (Figure 40) (Bold denotes the mean difference is significant at the .05 level.

Appendix G). At the mid and low points, there was no significant difference (*p* >0.05) in start and end temperatures adjacent to and away from the streams. Across all points and sites, temperatures at 2 cm deep increased between 0.8 °C and 12.5 °C over the sample period, with the greatest increases occurring at NS-H. The extent of the temperature increase decreased with depth, but at 10.5 cm, increases of up to 5.4 °C over the course of sampling were recorded.

5.3.2.2 Temperatures between sites (temperature range)

Sediment temperatures varied between sites. The lowest maximum temperature was recorded at Kelly's, which had lower average temperatures for each sampling position and each depth than the corresponding positions at the other sites. Temperatures at this site ranged from 18.7 ± 0 °C to 21.0 ± 0.1 °C. The highest temperature was recorded at Kopowai where temperatures ranged from 19.8 ± 0.1 °C - 30.5 ± °C.

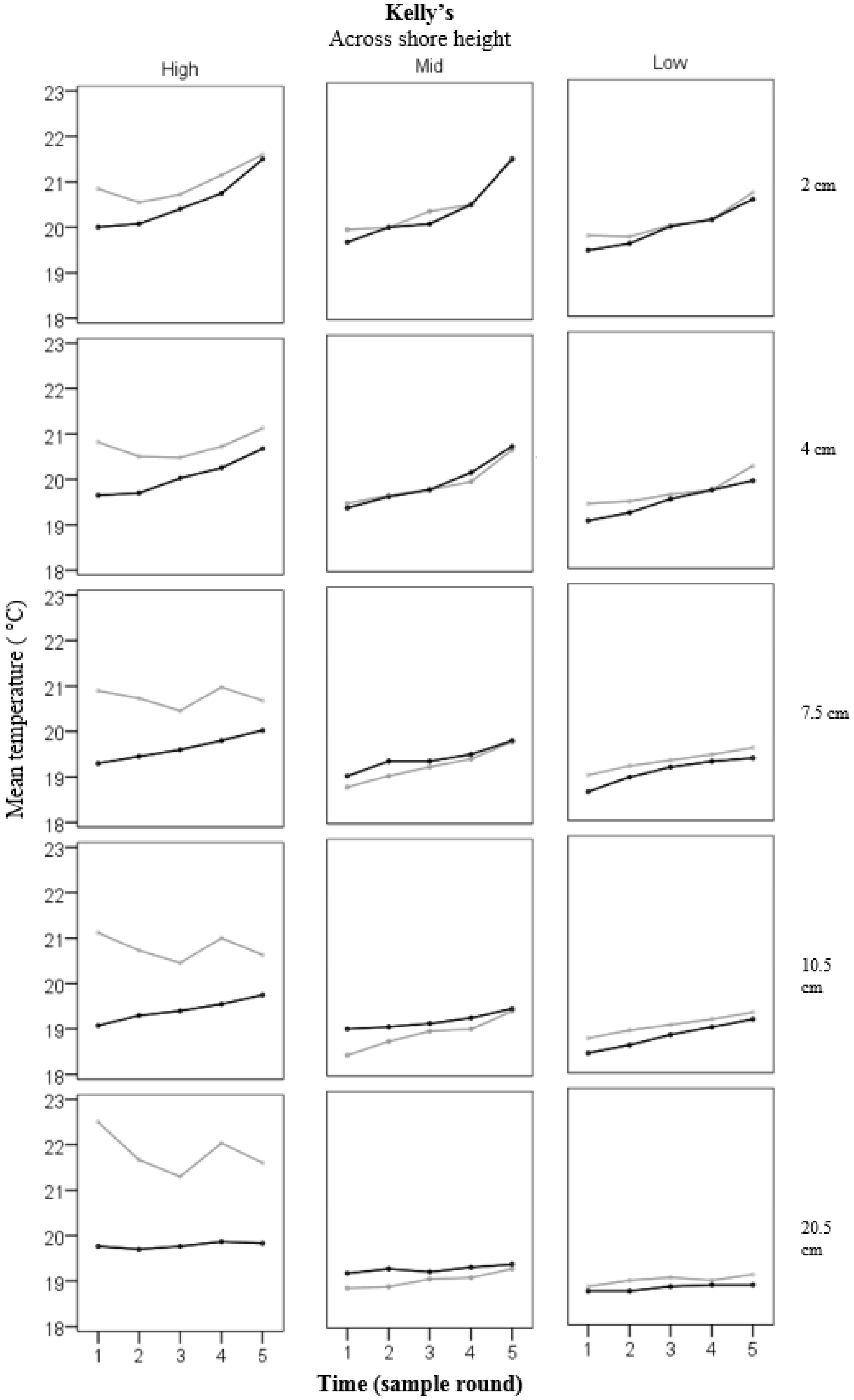

Figure 40: Kelly's - Changes in sediment temperature at stream (black) and non-stream (grey) points, for each sampling round. Sediment temperature was recorded at five depths (2 cm, 4 cm, 7.5 cm, 10.5 cm, 20.5 cm) at the high tide (high) and shoreward (mid) and seaward (low) of the adult toheroa bed.

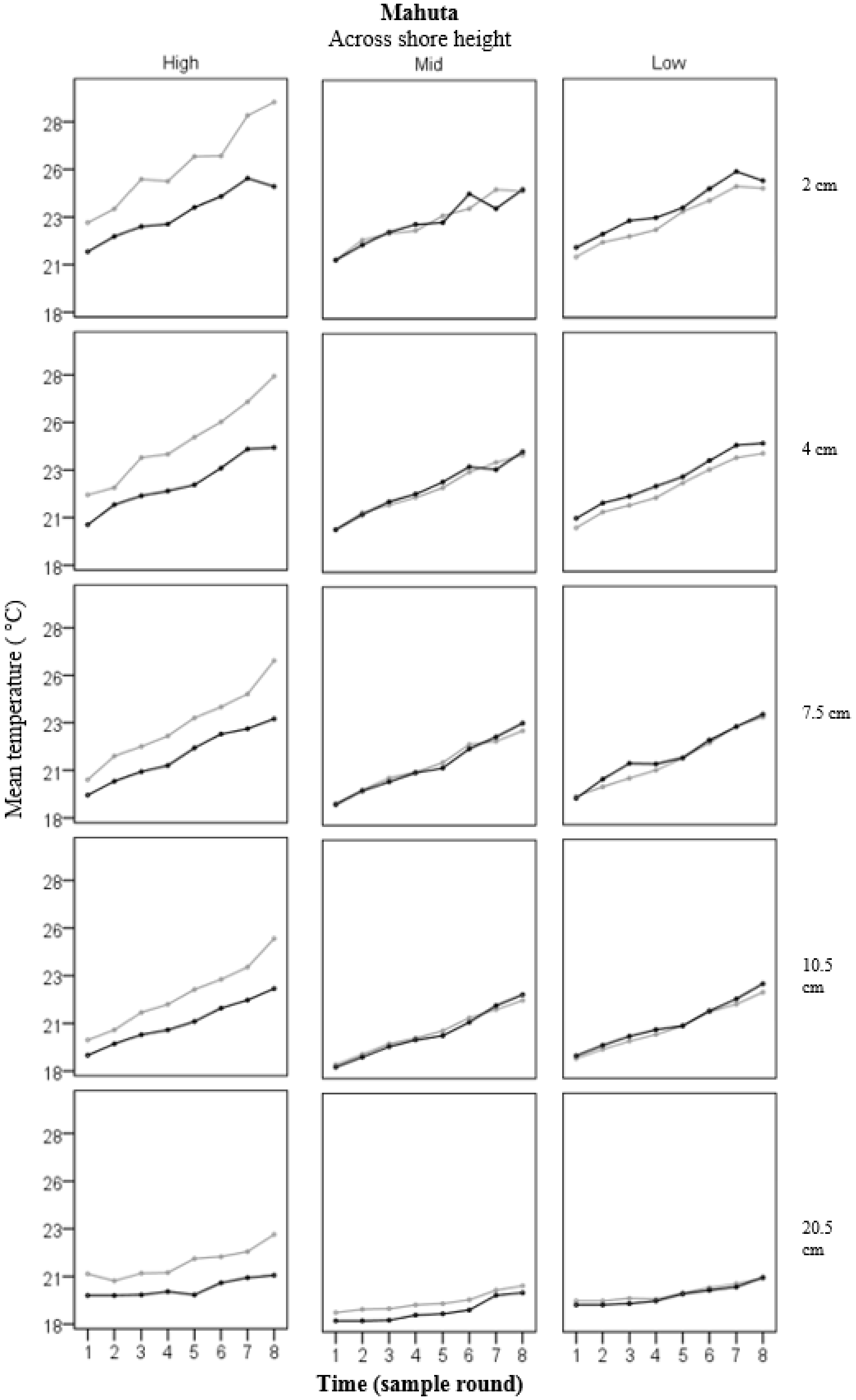

Figure 41: Mahuta - Kelly's - Changes in sediment temperature at stream (black) and non-stream (grey) points, for each sampling round. Sediment temperature was recorded at five depths (2 cm, 4 cm, 7.5 cm, 10.5 cm, 20.5 cm) at the high tide (high) and shoreward (mid) and seaward (low) of the adult toheroa bed.

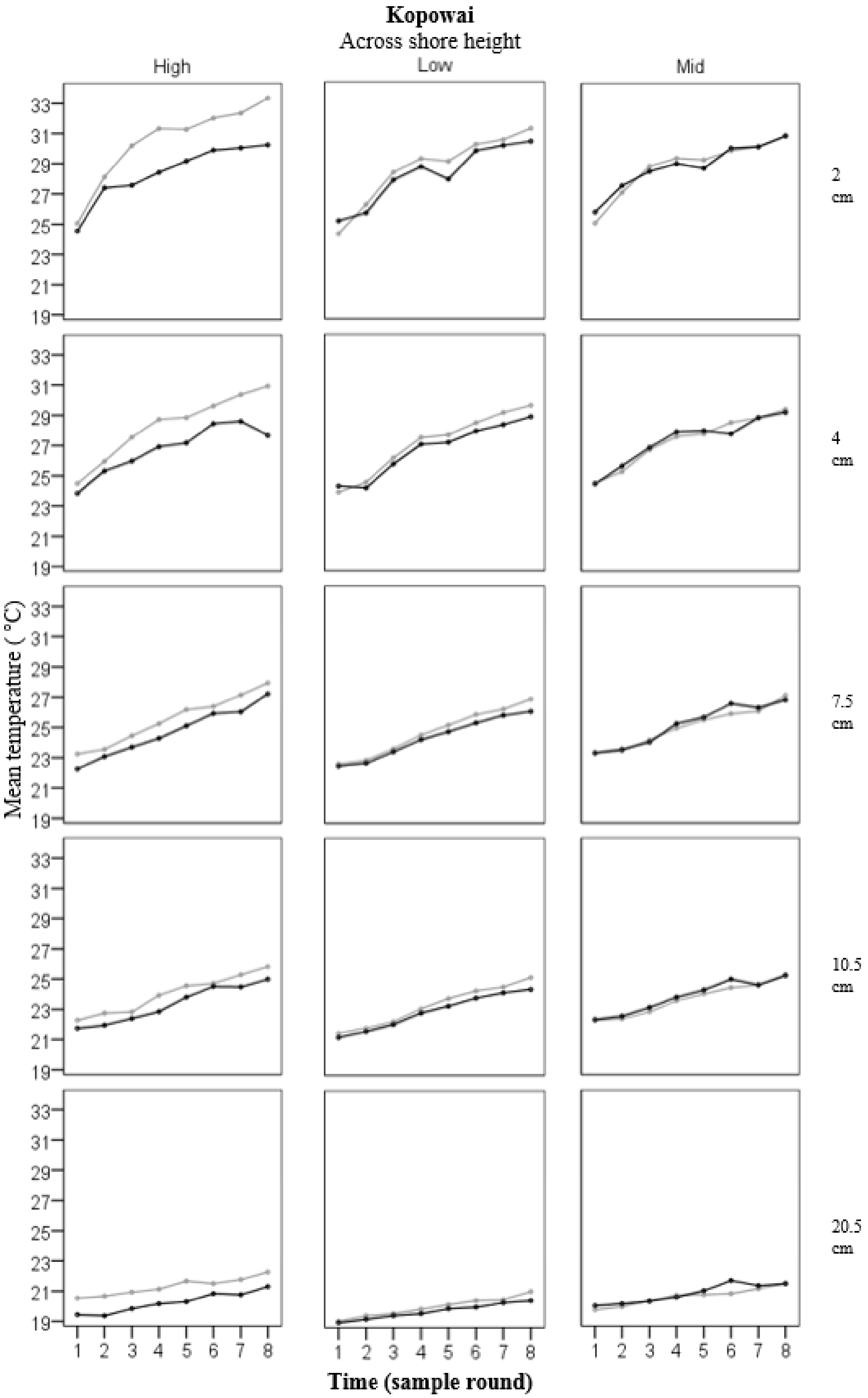

Figure 42: Kopowai - Kelly's - Changes in sediment temperature at stream (black) and non-stream (grey) points, for each sampling round. Sediment temperature was recorded at five depths (2 cm, 4 cm, 7.5 cm, 10.5 cm, 20.5 cm) at the high tide (high) and shoreward (mid) and seaward (low) of the adult toheroa bed.

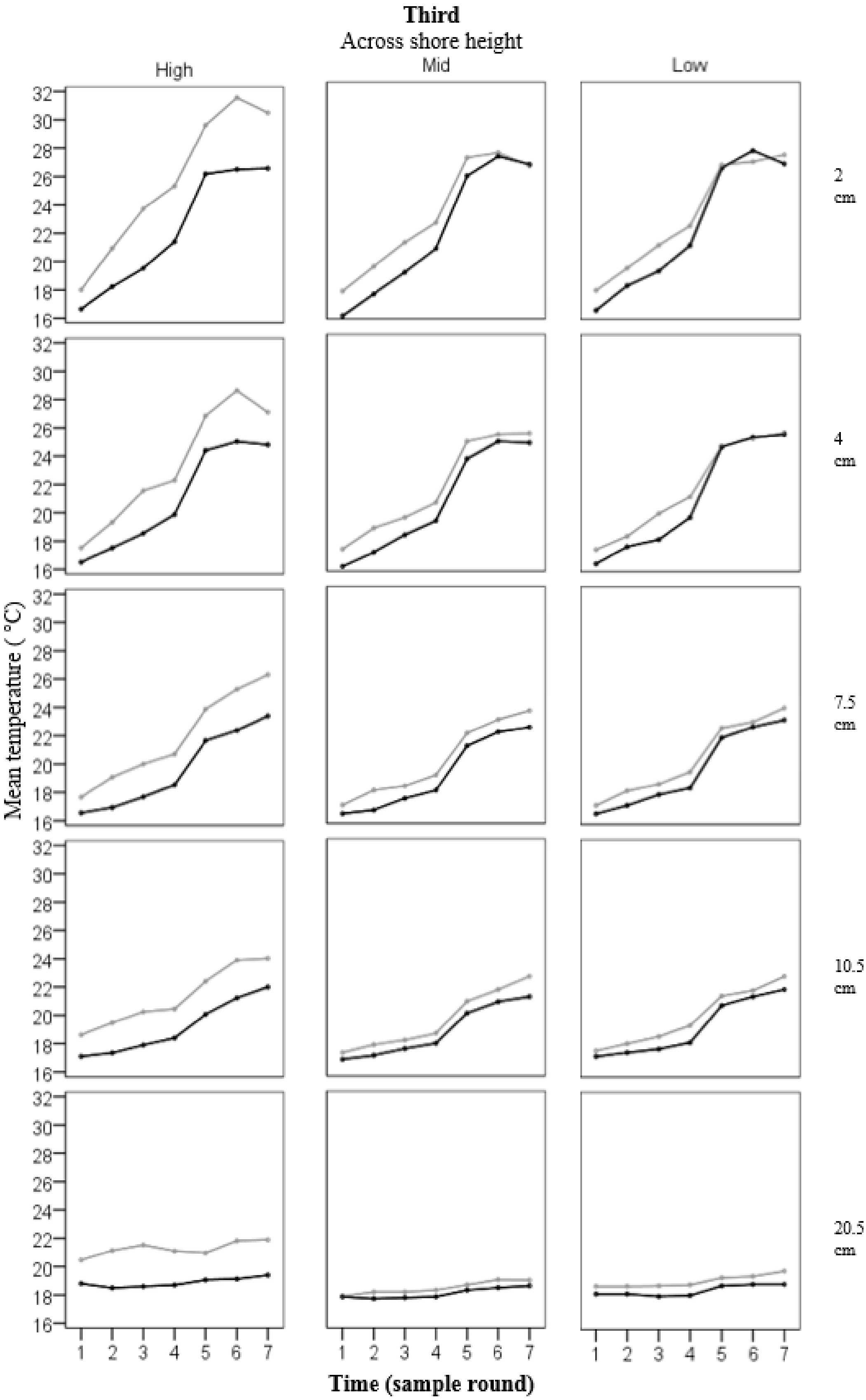

Figure 43: Third Stream - Changes in sediment temperature at stream (black) and non-stream (grey) points, for each sampling round. Sediment temperature was recorded at five depths (2 cm, 4 cm, 7.5 cm, 10.5 cm, 20.5 cm) at the high tide (high) and shoreward (mid) and seaward (low) of the adult toheroa bed.

5.4 Discussion

The temperature data collected in this study provides strong evidence that streams may provide a thermal refuge for shallow burying juvenile toheroa inhabiting the upper intertidal regions of Ripiro Beach (Beentjes, 2010a; Redfearn, 1974; Smith, 2003; Williams *et al.*, 2013b). Along the upper section of beach, sediment temperatures away from streams (NS) increased by up to 12.5 °C during the sampling period and were up to 3.5 ± 0.8 °C warmer than stream adjacent sediments (S). Had sampling been undertaken either during the hottest part of the day, or in January or February, which are the hottest months, differences between stream (S) and non-stream (NS) points, are likely to have been even greater. In the mid intertidal, where adult toheroa beds are typically found, temperature differences between S and NS points were less evident, suggesting that sediment temperature is not the driver for the toheroa-stream association for adult toheroa. Instead, this association may be driven by the depth of the water table below the sediment surface, which in stream adjacent sediments, seldom dropped below the depth to which one could expect adult toheroa to bury. This suggests that at stream locations, buried adult toheroa are likely to be fully or partially submerged during low tide. It is likely to play an important role in protecting buried toheroa from desiccation.

Prior to this experiment, it was assumed that the streams would have a direct influence on the temperature of sediments across the intertidal zone. However, over the course of sampling, the surface flow of water associated with the streams retreated towards the high tide region of the beach, leaving intertidal sediments exposed. Within the sampling wells, the water table in stream adjacent sediments was below the sediment surface throughout much of the sampling period, indicating that pore water had a greater influence on interstitial moisture content. That the salinity of the pore water was less than that of the regions seawater (35‰) is evidence of freshwater inputs throughout. Although not limited to the high wells, fresh water exerted greater influence on the pore water at the upper beach, with greater marine influences in the mid and low wells. Despite differing salinities, and dissipated surface flow, there was little difference in sediment temperatures adjacent to the streams. This indicates that in stream-associated areas, sediment temperatures are influenced by pore water, regardless of its source.

Interestingly, sediment temperatures at the mid and low points away from the stream were similar to those adjacent to the stream despite the water table being below the sampled depths. At these points the sediments were still damp, likely due to the effects of capillary rise (discussed in Chapter 3), as was evident by the dark colour and cohesive characteristics of the sediment. This indicates that rather than flowing or pooling water, it may be moisture content that determines sediment temperatures.

Moisture is the primary driver of temperatures within the exposed sediments of the intertidal zone, altering the ability of sediment to conduct or transfer heat (thermal conductivity) (Abu-Hamdeh, 2003; Wilson, 1983). Thermal conductivity increases with moisture, slowing the rate at which heat is lost or gained. In dry sediments, low thermal conductivity leads to rapid fluctuations, with heat lost or gained depending on conditions (Wilson, 1983). Rather than simply being a function of exposure time, sediment properties (i.e. grain size, mineralogy) (Campbell, 1985; Harrison & Phizacklea, 1987); and beach topography (i.e. slope and elevation) influence the moisture content of intertidal sediments through their effect on permeability and porosity which influence drainage rates and depth of the water table below the sediment surface, in addition to the extent of the seep face (Horn *et al.*, 1999). Since these are not homogenous across the beach face, exposed sediments undergo differential heating rates resulting in a thermally diverse surface (Befus *et al.*, 2013; Heiss *et al.*, 2015; Ricklefs & Vanselow, 2012).

The visible increase in the moisture content of stream adjacent sediments along the upper beach was introduced in previous chapters. In Chapter 4, it was suggested that the water table might be closer to the sediment surface along the path of the stream than away from the stream, as evidenced by the lower elevation and gentle gradient of the beach face in this region. This study confirms this hypothesis, establishing that in stream adjacent sediments, pooling water was present within 20 cm of the sediment surface at all times, but never at the surface. This pooling water, coupled with the saline influence in the water at numerous wells suggests that the increased sediment moisture content in the path of the stream is likely to be a result of the water table being closer to the sediment surface. The shallower position of the water table being a consequence of the higher erosion of stream sediments, with freshwater seeps, rather than the stream water itself directly influencing the upper regions (Figure 44).

The extent of the freshwater influence on pore water salinity could not be determined, due to water in the NS wells being below sampling depth. However, salinity in the two NS-L wells was higher than the three stream adjacent wells, suggesting that salinity may be lower closer to the stream. Pore water salinity across the intertidal zone was variable, consistent with the findings by Miller and Ullman (2004). The effect of higher salinity concentrations in the mid and low sampling wells point towards the presence of the intertidal saline cell (ISC). This is a tidally driven region of brackish water (0.5‰ - 35‰) within the beach, which recharges as seawater infiltrates unsaturated sediments during the incoming tide (Charbonnier *et al.*, 2013; Lebbe, 1999). The upper and lower edges of the cell are lower in salinity, marking the points where they meet and mix with fresh water, either flowing into the beach system through seeps (or streams) or flowing from the system by way of subterranean discharge (SGD) (Charbonnier *et al.*, 2013; Dale & Miller, 2007). The height of both the ISC and the water table are influenced by a range of complex interactions between freshwater inputs, coastal forcings and drainage rates, which are further influenced by the effects of the tide, lunar cycles (Befus *et al.*, 2013; Emami, 2016; Li *et al.*, 2006; Mulligan & Charette, 2009).

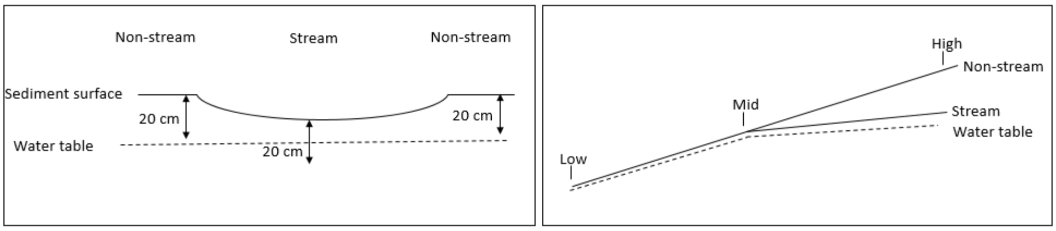

Figure 44: Schematic of water table relative to sediment surface adjacent to and way from streams.

The effects of the shallow water table on sediment temperatures was most pronounced along the upper reaches of the beach (high), where sediments away from the stream were significantly warmer than those at the stream. Both points would have experienced a similar exposure period, but the topography of the beach (detailed in Chapter 4) away from the stream facilitated more rapid drying and was higher above the water table. As the interstitial water is replaced by air, the heating capacity is lowered, expediting increases in temperature in the drying sediments (Harrison, 1985). This process explains why temperatures away from the stream were already significantly higher at the start of sampling, and why they increased at an accelerated rate. The increased rate facilitated a larger absolute change over the same duration, which is likely to have been even greater during the height of summer.

Whilst temperatures adjacent to the stream were slower to change, their rate of change was comparable with those at the mid and low points along the beach, which provide further evidence of the effects of higher heat capacity associated with the moist sediments (Harrison, 1985). Adjacent to the stream, temperature was taken at depths, which were within the water table, whereas away from the stream the water table was deeper than the sampled depths, albeit that sediments were still moist, as a likely consequence of capillary rise. In spite of this difference in moisture content, temperatures between NS-M and S-M, and NS-L and S-L were not significantly different. At the top of the beach, sediments near NS-H were visibly drier, being lighter in colour and freer moving. This point experienced the most rapid changes in temperature, suggesting that a threshold may exist whereby once a certain moisture level is exceeded, accelerated changes may occur.

Whether temperatures in the sediments away from the stream are able to reach this tipping point during the hotter months or during periods when the water table is lower remains unknown. As such, there was insufficient evidence to suggest that the proximity of the water table to the sediment surface in stream-associated areas has any effect on sediment temperatures of the mid intertidal region. A combination of summer time mortality events (Williams *et al.*, 2013b) (Williams *et al.*, 2013b) (Williams *et al.*, 2013b) and the recent discovery of gas bubble disease in Northern toheroa populations (Ross *et al.*, 2017b) (Supporting publications: Publication 2) suggests that streams may not provide guaranteed refugia, and the animals are still subject to thermal stress.

5.4.1 Implications for toheroa

Both geographic distribution and across shore position reflect the environmental tolerances of an organism (Compton *et al.*, 2007; Khoo & Chin, 1980; Stillman & Somero, 1996; Williams *et al.*, 2003). Given the broad extent of their distribution from Northland to Southland, and across much of the littoral zone, toheroa are thought to have a broad thermal tolerance, consistent with that of many temperate species (Compton *et al.*, 2007; Ross *et al.*, 2017a). However, to date, only larval tolerances and the temperature requirements for reproduction have received any significant attention (Gadomski *et al.*, 2015; Rapson, 1952; Smith, 2003) leaving a large knowledge gap for post settlement stages.

On sandy beaches, burial provides organisms with a refuge from surficial heat stress during periods of exposure, with cooler temperatures deeper in the sediments. Toheroa are thought to bury deeper than any of the other members of the *Paphies* genus (Kondo *et al.*, 1995), possibly due to them being the only species that permentantly occupies the mid to low intertidal zone. The depth to which they bury is largely regarded as a function of size, with large adults buried deeper than juveniles are. Kondo *et al.* (1995) found that at Muruwai beach, to the south of Ripiro, juveniles buried to depths approximately five times and adults to 1.7 times their shell length, which is comparable with observations of toheroa along Ripiro Beach. During summer of 2016 and 2017, mid-sized adults (*c.*70 mm) at Ripiro were observed buried approximately 10cm below the sediment surface. This contrasts with observations from Oreti Beach in Southland where larger toheroa (10-12 cm) were positioned much closer to the sediment surface (~50 mm) at the same time of year (J. Cope. Unpublished data). Overheating is unlikely to be a significant issue for Southland toheroa and this regional difference in burial depth may indicate that burial depth is influenced by climate and may merit future investigation.

Fluctuations in temperature do not need to be large to have biologically significant consequences. Peck *et al.* (2004) found that minor increases could turn sub lethal temperatures into lethal ones. Research into global warming has found that a 2 °C temperature rise could trigger extinction events, with many animals unable adapt to and survive rapid environmental change (Khoo & Chin, 1980). With temperatures in surficial sediments of the upper beach, an area associated with thermally sensitive spat and juveniles, rising by 12.5 °C away from the stream under warm but not peak summer conditions, this size class is most at risk of heat stress. In addition to high temperatures, living in the top 5cm of sediment exposes them to highly variable temperature regimes (Johnson, 1965; Williams *et al.*, 2003). Evidence of spat along the upper reaches of the beach is verified using the *bucket test* (Smith 2003), in which recently settled toheroa float to the surface as a bucket of water is poured onto the sand. While this test verifies absence or presence of toheroa, it provides no measure of animal health or mortality.

The cooler sediments associated with streams are therefore likely to provide a thermal refuge for young toheroa, opening up important habit in the upper reaches which otherwise would not be available and increasing juvenile toheroa survival rates. Another intertidal surf clam species from a marginally lower latitude (42°N) has been seen to exhibit thermal stress symptoms at temperatures higher than their optimal (Macho *et al.*, 2016). While this species is likely to be adapted to a lower optimal range and the temperatures in question are lower than those seen in this investigation, it is likely that toheroa may suffer from a similar effect with super-optimal temperature exposure. In the case of toheroa at Ripiro, a thermal refuge is likely to have strong seasonal relevance, playing a more important role in summer than winter, with temperatures expected to rise beyond those of this study in the height of summer (January and February). During the cooler, wet winters, when surficial temperatures are likely to be lower and more homogenous across the beach face, increased survivorship of spat and juveniles away from the stream may be possible. Although under dry conditions, sediments adjacent to the stream may be warmer, it is unlikely that temperatures away from the stream would reach lower tolerance levels for toheroa in Northland.

Across the mid intertidal, an area associated with the main adult toheroa beds, the effect of streams on sediment temperature was less apparent, with the seep face having a greater influence on temperatures resulting in little variation in temperature along the beach face. During stock assessments, adult beds have consistently been found along the beach away from streams (Akroyd *et al.*, 2002; Williams *et al.*, 2013b), indicating that survival under non-stream conditions is common. The number of beds reported away from the stream exceed the number of streams and stream associated beds along the beach. Although the evidence is only anecdotal, it has been suggested that these non-stream beds may be transitory, moving along the shoreline until they encounter stable beds associated with the streams (Ross *et al.*, 2017a). In the absence of data to suggest otherwise, this cannot be refuted. However, it may be that transitional beds are only able to survive away from the streams during cooler periods, such as those under which the sampling is done. In the height of summer, sediment temperatures away from the stream could increase (as discussed above) to the point that any alongshore movement of these beds is driven by either the preferential selection of cooler sediments or a higher water table associated with stream areas.

The higher water table associated with streams may be important for preventing desiccation (Redfearn, 1974). In this study, the depth of the water table below the surface of stream adjacent sediments was similar to the depth at which toheroa in the main bed could be expected to bury, suggesting larger toheroa in the main bed would be either partially or fully submersed for much if not all of the low tide. Although I was unable to find reference to this in the literature, it is suggested that clams buried in fish tanks do not retract their foot into their shell (M. Patterson, personal communication), behaviour which would support the requirement for partial submergence in order to keep the extended foot moist. Reported mass mortality events are often attributed with prolonged periods of summer time exposure, but as such, there is no indication of the depth of the water table below the sediment surface, which could be a contributing factor.

A higher water table may also inhibit rapid and potentially large temperature changes which occur within the sediments either during exposure to ambient conditions or with inundation of the swash as cooler seawater infiltrates through heated sediments (Wilson, 1983). The recent discovery of gas bubble disease in northern toheroa, suggests that toheroa are experiencing temperatures sufficiently high for oxygen to come out of solution in their tissues (Ross et al. 2017). Although gas bubble disease can be induced by pressure changes, there are no reports of it occurring in Southland or Kapiti-Horowhenua toheroa, suggesting that gas bubble disease is likely to be temperature driven. Although worse in the summer, the bubbles found on toheroa shells during the winter are a likely indication that the animals are subject to year round thermal stress, which may reach lethal levels during the summer months.

In addition to mass mortality events and thermally induced disease, slower growth rates and weaker, potentially thinner, shells (Mackenzie *et al.*, 2014) may be further indication that Northland toheroa are being subjected to thermal stress. The growth rates of northern toheroa is slower than Southland toheroa (M.P Beentjes, In review), and shells are smaller and thinner than those which were once encountered along the beach. This could be evidence of speciation, changes in environmental conditions or the result of gene expression making offspring more susceptible to thermal stress. All would require further testing to elucidate.

Reports of lowering water tables associated with increasing plantation forestry in the area (Cromarty & Scott, 1996; McKelvey, 1999) coupled with growing knowledge of hydrological demands and water use efficiency of plantation species is sufficient to suggest that changes in land use may be reducing water inputs into coastal systems (Fahey, 1994). Furthermore, during this research, it emerged that water was being diverted from bores on beach adjacent farms to dairy farms on the escarpment above. Although unquantified or verified, such practices could lead to huge losses of water from the system, which could have a direct effect on sediment moisture and temperatures within the intertidal zone, which in turn could have subsequent effects on toheroa populations.

This study provides evidence to suggest that the presence of streams could create habitat for and increase survival of the early life stages of toheroa along the upper beach during the hot summer months. The associated damp sediments may also protect shallow buried juveniles from desiccation. This potential protection against desiccation is more evident in the region of mid-tide, where adult beds are established. At this elevation, the seep face exerts a greater influence on sediment temperatures than the stream, as is evident by the more homogenous temperatures along the beach. The cool temperatures away from the stream may facilitate the survival of adults in non-stream beds. However, in stream regions, the water table is closer to the sediment surface supporting partial or full submergence of adult toheroa during much of the exposed tide. This may have greater relevance for animals during the summer months, and might explain the movement of the transitory beds along the shoreline.

A better understanding of the environmental conditions which toheroa are exposed to when living in beds away from streams may strengthen the evidence to support the hypothesis that the stream association exhibited by toheroa is driven by the proximity to the water table, with partial submergence during exposed periods protecting toheroa against desiccation. A seasonal component to future investigations could establish whether transitory beds are more prevalent during the winter months than summer months, when the risk of thermal stress and desiccation is lowered, enabling toheroa to survive conditions away from the streams. During the hotter summer months, stream regions may increase in importance due to the higher water table. Redfearn (1974) suggested that when away from streams, adult toheroa occupied low-lying regions of the beach where the water table was closer to the surface. This study suggests that stream areas meet these criteria for the same reasons. To better understand the significance of sediment temperatures, research into the thermal tolerances of all toheroa life stages is required. The monitoring of sediment temperatures over the course of a summer, including during high-risk periods (off shore winds, neap tides) would provide researchers with a better indication of the range of temperatures to which toheroa are exposed. A longer sampling period may also assist in establishing whether increases in sediment temperatures are solely a response to seasonal changes or whether changes in the flow of freshwater onto the beach also have a role.

Chapter 6

Ecological implications for toheroa

6.1 Goals and a synthesis of findings

In this thesis, I set out to address some of the major uncertainties around what constitutes good toheroa habitat and the potential role of habitat loss or modification in preventing the recovery of toheroa. Specifically, I sought to better understand the relationship between toheroa beds and the numerous small streams that flow onto west coast beaches in northern New Zealand. As discussed throughout this thesis, large and stable toheroa beds are often found near streams, yet the mechanism driving this association is unknown. One possibility is that these streams modify beach habitat in a way that makes it more suitable for toheroa occupation. If this is the case, then activities that modify the flow of streams to beaches will potentially degrade the quality or availability of toheroa habitat. Therefore, I set out to investigate how streams flowing onto Ripiro Beach modify the intertidal zone, an area occupied by both juvenile and adult toheroa. To achieve this, my research looked at how sediment grain sizes, beach topography and sediment temperatures varied adjacent to and away from streams, between high and mid-tide regions. The selection of these tidal heights was driven by their biological relevance, with the high tide region of the beach commonly associated with spat and juvenile toheroa, and the mid-tide with adult beds (Redfearn, 1974; Smith, 2003). In the paragraphs below, I summarise the key findings of my research and then pull this new knowledge together to consider possible implications for the state of toheroa populations.

6.1.1 The effect of streams on sediment grain size

In chapter three, I set out to investigate the effect of streams on the size distribution of beach sediments. I also tested for differences in grain size distributions along 31 km of Ripiro Beach, and compared present day sediment size structure with historical data to address questions about possible long-term change at Northland beaches.

I found that the effect of streams on the composition of intertidal sediments appeared to be limited to the high tide, where the proportion of fine sediments was marginally higher adjacent to streams. No differences were evident in the middle intertidal. However, changes in size distributions were evident at larger spatial scales. To the north of the study area, sediments were predominantly medium grained (250 – 499 µm), while sediments in the southern stretches of Ripiro Beach were more dominated by fine grain sediments (125 – 249 µm). The southern region of the beach has always been noted as supporting better toheroa beds than the north and it is possible this is on account of these differences in grain size. Perhaps the most interesting result from this piece of research did not relate to streams at all and was the finding that Ripiro beach sediments appear to have changed over time. In contrast to 1974, the current state of the beach shows strong evidence of coarsening. Where medium-grained sediments previously accounted for 0.2% of the average sample, medium sediments now represent 45% of the sample.

6.1.2 The effect of streams on beach topography

In chapter four I set out to investigate the effect of streams on beach topography to test the hypothesis that beach morphology near streams could act to aggregate toheroa or their food. To achieve this, I measured beach slope and elevation in and away from the streams.

What I found was that along the upper intertidal, beach face elevation decreased in the vicinity of streams leading to the formation of basin like depressions in stream areas. This lowering of the beach face is a consequence of increased rates of erosion resulting from the reduced permeability and porosity of the sediments on account of the increased moisture content. In the mid intertidal, it appeared that the seep face exerted a greater influence on the beach face than the stream, resulting in a more a more homogenous beach with little along shore variation in elevation. Because of these erosion patterns, the gradient of the beach slope in the path of the stream was lower than the adjacent beach, where greater permeability and porosity facilitated the accretion of sediments leading to the development of a steeper slope. The resultant topography has potential consequences for the transport, feeding and survival of toheroa and is discussed below.

6.1.3 Temperature

In chapter five I set out investigate the effect of streams on the thermal regimes of intertidal sediments at Ripiro Beach. Heat exposure is a major stressor for intertidal organisms (Macho *et al.*, 2016; McQuaid & Scherman, 1988), and it was hypothesised that streams could provide a temperature refuge for toheroa, thereby increasing their survival and abundance in these areas. I also explored the effects of topography on sediment moisture content, particularly the distance from the beach surface to the water table. In addition to terrestrially derived water, the depth of the water table would potentially influence temperature and the risk of desiccation, as moisture content is an important driver of sediment temperatures. The salinity of pore water was also measured to determine the source (terrestrial vs. marine) of the water which toheroa are exposed to.

I found that within stream adjacent areas, the water table remained close to the sediment surface throughout the sampling period at all tidal heights, in contrast to areas away from the stream where the water table was mostly deeper than the sampling depth and the depth to which toheroa bury. The salinity of the pore water in stream adjacent sediments reflected both freshwater and marine inputs, indicating that rather than being a solely function of the stream, the moisture present in the sediment of toheroa beds may be associated with the beach groundwater system, and in particular the intertidal saline cell (ISC). Freshwater inputs were greatest at, but not limited to, the upper beach, with highly variable salinity concentrations in the region of the adult toheroa beds at the mid-tide.

Interstitial moisture acted as a greater control on sediment temperatures than either the stream or the water table. In both damp and saturated sediments, sediment moisture slowed the rate at which temperatures increased and consequently sediments were cooler. By contrast, temperatures in dry sediments increased rapidly, attaining higher temperatures and in so doing, undergoing greater increases in absolute temperature over the same sampling duration. This contrast in heating was only evident along the upper beach, where temperatures in the dry sediment away from the stream (NS-H) were significantly higher than elsewhere across the beach. Sediments influenced by either the stream or the seep face were similar, with no significant difference apparent, despite differing moisture contents and moisture sources. The temperature of the sediments in the dry upper intertidal (NS-H) increased more rapidly than either the moist or the saturated sediments across the rest of the beach.

6.2 Discussion

Absent from the toheroa literature available prior to this study was any description of the streams with which toheroa beds are associated, including any mention of the important fact that these streams are ephemeral. The streams, which flow to Ripiro Beach through gullies in the adjacent land, begin to flow across the intertidal sediments as the tide recedes, sometime remaining connected to the tidal front to the region of the low tide. Over the course of the low tide, the connection to the sea breaks as the surface flow associated with the stream begins to dissipate and retreat, sometimes as far back as the upper beach (Figure 3). The rate and extent to which this occurs is variable. The mechanics of the stream flow was beyond the scope of this research, but based on observations it appears that the depth of the water table below the sediment surface and the ambient and sediment temperatures may be influencing factors. As the water table lowers with the falling tide, and the permeability of the sediments increases, surface flow may begin to percolate through the sand. The loss of surface flow may be accelerated with evaporation, which increases with increasing ambient and sediment temperatures. Temperatures are influenced by ambient conditions, time of the day and seasonal climatic differences. Over the course of sampling, the surface flow associated with the streams was often confined to the beach above the adult toheroa beds. This raised the question of what constitutes a stream, whether these streams that I was studying were in fact streams and whether it was actually the stream influencing the association with toheroa.

Based on the findings of my three research chapters detailed above I would suggest that it is more the indirect effects of the stream, rather than just the input of freshwater, that generates good toheroa habitat. Stream flow onto Ripiro Beach results in an increase in the moisture content of the sediments, particularly towards the upper region of the beach, which would otherwise be dry. The increased moisture content causes higher rates of erosion near these streams, which reduces the distance from the beach surface to the water table and altering the swash climate along these sections of the beach, in addition to altering the thermal regimes of the exposed intertidal sediments (Figure 44). By so doing, it both creates and improves habitat suitability for toheroa.

For juvenile toheroa at the upper beach, the increased erosion leads to the formation of basin like depression which may act to aggregate spat and juveniles, potentially explaining their higher abundance in stream adjacent areas (Smith, 2003). Furthermore, the high moisture content of the sediments reduces the rate at which temperatures increase in the exposed intertidal sediments, resulting in significantly cooler areas of the beach compared to areas away from the streams. Lower temperatures and high moisture content may reduce thermal stress and desiccation, thus increasing survival of juveniles. Additionally, the reduced permeability of stream-associated sediments, coupled with a gentler beach slope, causes the uprush from the swash to extend well beyond the height of the high tide, which could provide spat deposited at the spring high water mark with periods of inundation between the spring tides. This modification of the swash regime may also provide spat with greater feeding opportunities due to increased inundation time and a slower rate of uprush.

Because the bottleneck in Northland toheroa populations appears to be the survival of adults rather than juveniles (Ross et al. 2018), from a management perspective there is great interest in gaining and understanding of the habitat requirements of adult toheroa. Adults are the size classes that have failed to recover despite efforts at protecting them. Unlike the juveniles which appear to be passively aggregated by the effects of topography, adult toheroa are potentially more active in their selection of habitat, with both individual toheroa and entire beds recorded moving along the beach. This suggests that for the adult size class, the toheroa-stream association may be a result of preferential selection of habitat rather than passive transport or differential mortality.

The thermal refuge hypothesis may only hold true for adult toheroa so far as the buffering of temperatures is concerned, rather than the cooling of sediments. At the mid-tide, the influence of the seep results in similar temperatures along the beach, regardless of the proximity to the stream. Instead, the association between adult toheroa and the stream may be driven by the close proximity of the water table to the sediment surface. In stream areas, the depth of the water table below the sediment surface is such that buried adults may be partially or fully submersed throughout the entire tidal cycle. This may protect buried toheroa from rapid changes in temperature that would otherwise occur when the cool incoming tide infiltrated through the heated exposed sediments (Wilson, 1983). Even in damp sediments, toheroa may experience large increases in temperature over the course of a day time low tide. It is unknown what effect such increases have on toheroa, but the recent discovery of gas bubble disease in Ripiro Beach toheroa provides evidence to suggest that rapid temperature changes may affect toheroa health (Ross *et al.*, 2017b). In addition to buffering temperatures, submersion in the water table may protect toheroa from desiccation, which may be especially important if toheroa leave their foot extended for anchoring purposes when buried (as anecdotal evidence suggests their congener (*Paphies substriangulata*) does (M. Patterson, personal communication). Toheroa may attain further benefit from living in these areas by a possible increase in food concentrations and prolonged feeding opportunities resulting from the greater volumes of backrush to these areas, albeit at the cost of higher rates of erosion.

The depth of the water table relative to the beach face will vary in both time and space and its value to toheroa as a habitat modifier may vary as well. The association between toheroa and streams may of greater importance during the hot dry summer months, when the water table away from the streams is too deep below the sediment surface to be accessible to toheroa. The height of the water table is determined by the volume of water flowing into and from the aquifer, and is further modified by complex interactions between coastal marine hydrodynamic forcings, lunar cycles and terrestrially derived water inputs (Barlow, 2003; Li *et al.*, 2006; Raubenheimer *et al.*, 1999; Robinson *et al.*, 2007). Terrestrial water inputs can undergo seasonal changes associated with changes in rainfall and evaporation and possibly effected by the abstraction of water from coastal aquifers. During winter, higher rainfall within the catchment combined with lower evaporation rates and less demand for water abstraction could result in a higher water table. Additionally, the distance to the water table, which may be of greater biological relevance, could be reduced by increased rates of erosion accompanying winter storm events (Oh & Dean, 1995). Coupled with cooler ambient temperatures, the combined effect of these changes may enable toheroa to move away from stream areas during the cooler months, drawing them back to the streams in the summer months.

The contrast between the bed dynamics reported in the literature (Akroyd *et al.*, 2002; Greenway, 1969; Rapson, 1952; Redfearn, 1974; Williams *et al.*, 2013a) and my observations over two summers spent at Ripiro Beach supports my hypothesis that the importance of streams varies with season. Even though I spent many weeks on Ripiro Beach over the summers of 2015/16 and 2016/17, I only observed one toheroa bed away from a stream. I saw no evidence of the single or multi cohort transitional beds reported in published in fisheries assessments or by other researchers (Rapson, 1952; Redfearn, 1974). Interestingly, none of these studies had been conducted during the summer period, presumably to avoid working on toheroa during the busy summer season. To me, these seasonal differences in the observed distribution of toheroa suggests that during the cooler months, toheroa beds may form away from stream locations, with the animals then aggregating near streams during the summer months due to preferential conditions. Although this seasonal behaviour may reduce their vulnerability to desiccation during summer, it also potentially makes them more vulnerable to illegal harvesting during the busy summer holiday season. Toheroa aggregated around the stream are easily found and harvested. During winter or during spring tides when the water table is closer to the sediment surface, toheroa may be more vulnerable to vehicular damage if the depth to which they bury is in some way influenced by the need to attain partial or full immersion by the water table. This hypothesis, like the others described above would require additional research for corroboration.

In addition to the short term changes discussed previously, a long term lowering of the water table can be effected by changing land use (Cromarty & Scott, 1996; McKelvey, 1999), with exotic forestry already implicated in the reduction of stream flow to the beach (Williams *et al.*, 2013b). Rather than just affecting the height of the water table, lower volumes or rates of freshwater flow onto the beach has the potential to decrease the area of the beach face being eroded, thereby reducing available habitat for toheroa. Additionally, decades of extensive efforts to restore the Ripiro Beach dunes with native dune grasses may also have had some effect on water table levels. Unlike introduced dune species, for example, marram (*Ammophila*) which raise the height of the water table, the native dune grasses *Spinifex* and pingao (*Ficinia spiralis*, previously *Desmoschoenus spiralis*) lower the water table (de Lange & Jenks, 2007; International Global Change Institute, n.d), facilitating the accretion of the beach face and the development of dune systems. In doing so, the beach is able to provide greater protection to the human communities and their infrastructure occupying the shoreline, buffering them against storms and large waves. This desire for more stable sand dunes prompted the planting of introduced marram grasses in the early 1900's (Cockayne, 1909), in response to the erosion caused by the clearance of coastal forest and bush. Coastal aquifers and sandy beaches along the New Zealand coastline have no doubt undergone changes because of these activities, which have further been compromised by the conversion of many coastal watersheds to pasture and exotic forestry. Unfortunately, it is plausible that efforts to restore natural function to these systems may have come at a cost for toheroa, by increasing the distance to the water table. Further investigation is required to better understand the consequences of different dune planting regimes and their influences on beach ecology.

In its current state, there is little evidence to suggest that dune restoration has stabilised Ripiro beach given the high rates of erosion in reported in recent years. Increases may be a consequence of shifts in the direction of the prevailing winds from South West to West as suggested by local experts (B. Searle, personal communication). This change in wind direction, could account for high proportion of fine sediments aggregated towards the southern end of the beach, with the angle of the wave approach to the shoreline driving longshore drift in a southerly direction. Based on my understanding of sediment transport in coastal environments, flow in this direction would result in a net export of sediments from the system, as sediment inputs into the system are blocked by Maunganui Bluff to the north of the beach, resulting in a coarsening of the beach. In the opposite direction, a northern longshore drift would supply finer sediments from the Kaipara Harbour into the system. The high proportion of fine sediments on the beach in 1974 may be indicative of a southward longshore drift, the opposite of today. Changes is prevailing wind and swell directions driven by larger scale weather processes may alter sediment characteristics and habitat suitability.

A coarsening of sediments, if accompanied by a change wave climate, can be indicative of a shift in the morphodynamic state of the beach. On exposed beaches, such shifts between dissipative and intermediate states have strong seasonal cycles (Gallagher *et al.*, 2016; Otvos Jr, 1965) and have been found to impact the abundance and densities of intertidal organisms (McArdle & McLachlan, 1992; McLachlan, 1990). Increases in grain size result in steeper beaches with narrower seep faces and lower water tables. If toheroa distributions are associated with higher water tables, then the boom and bust years reposted by the toheroa fishery could be connected to fluctuations in beach state. Such fluctuations in population abundance have also been reported in other intertidal clam species worldwide (Arntz *et al.*, 1988; Brown & McLachlan, 2010; Coe, 1955; De Villiers, 1975; Fiori *et al.*, 2004). Like toheroa, they face similar threats of changing land use and climatic patterns. Without understanding the specifics of what constitutes good habitat for toheroa, or other surf clam, it is difficult to ascertain whether anything can be done to protect or restore populations.

6.3 Future research

This study provides evidence to suggest that the depth of the water table below the sediment surface may be an important mechanism driving the association between toheroa and stream regions. To verify this, it is recommended that future studies look to explore seasonal variation in water table depth and the position of toheroa beds. An important component of this would be monitoring areas where toheroa are present, in addition to areas from which they are absent. Such sampling will also provide an indication of the seasonal differences in the association between toheroa and streams. To ascertain whether toheroa populations are influenced by changes in beach state, it may be necessary to extend the sampling duration over multiple years to capture the frequency of the changes. This would require that methods similar to those used by (Wright & Short, 1984b) be followed, which includes the monitoring of wave climate and grain size. By including the beach profiles, future research can identify whether changes in grain size is accompanied by changes in beach slope, or whether beach slope and the height of the beach face above the water table may be influenced by dune restoration efforts.

Our current knowledge of beach state and sediment characteristics at Ripiro Beach is derived from two data points. This study and the figures reported by Redfearn in 1974. Beach profile data collected at Muruwai beach by the Auckland Regional Council (Tonkin & Taylor Ltd, 2014) may provide insight into historical changes in beach state for the west coast in general, and more specifically whether long-term changes are likely to have reduced the carrying capacity of the toheroa beaches.

The loss of habitat is a global challenge to the preservation of biodiversity (Mantyka-pringle *et al.*, 2012) with habitat preservation and restoration and major tool in the fight against the decline and disappearance of species. However, in many cases we do not have a good understanding about what constitutes the essential components of a species' habitat making it difficult to implement novel or targeted restoration effort. For toheroa, I approached this thesis thinking that the freshwater derived from streams was the important aspect of this habitat. However, at the completion of this thesis I now believe that streams are fundamental in creating and maintaining the habitat, by way of facilitating erosion, but that it is access to the water table, which is potentially most important. Although additional research is required to verify my hypotheses detailed in this thesis, the potential management actions that could be taken based on this newfound knowledge are different to those that might have been considered prior to my research. Knowledge of the mechanisms that drive species-habitat relationships is key. Without it, restoration efforts may be misguided or ineffective.

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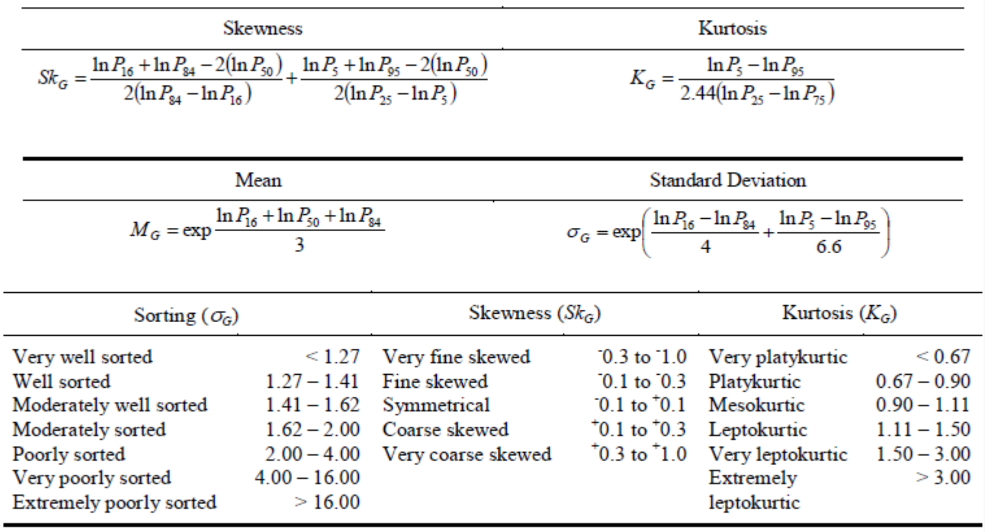
Appendices

Appendix A. Grain size classifications

Folk and Ward (1957) equations and classifications for sediment samples

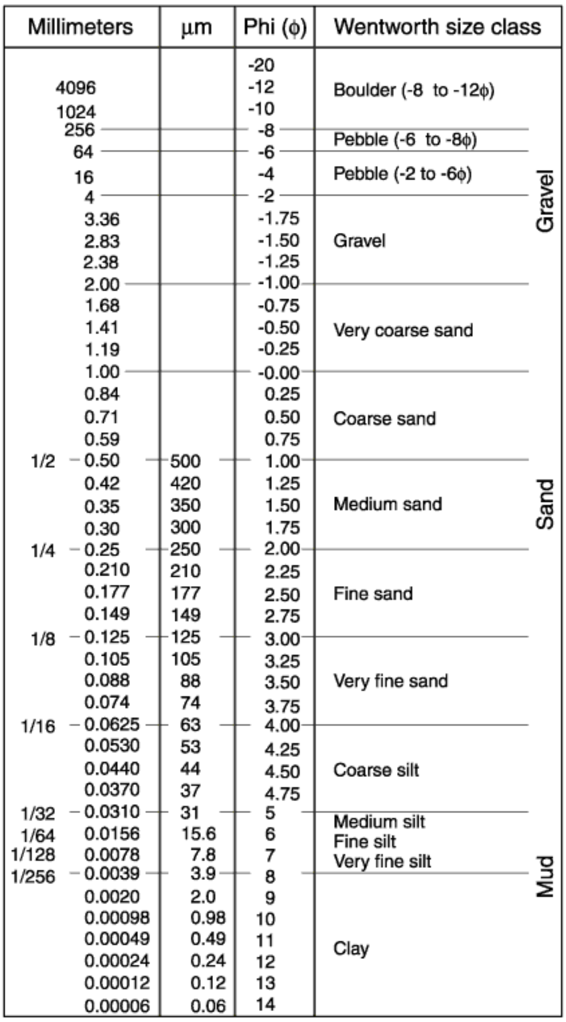


Skewness	Kurtosis
$Sk_G = \frac{\ln P_{16} + \ln P_{84} - 2(\ln P_{50})}{2(\ln P_{84} - \ln P_{16})} + \frac{\ln P_5 + \ln P_{95} - 2(\ln P_{50})}{2(\ln P_{25} - \ln P_5)}$	$K_G = \frac{\ln P_5 - \ln P_{95}}{2.44(\ln P_{25} - \ln P_{75})}$

Mean	Standard Deviation
$M_G = \exp\frac{\ln P_{16} + \ln P_{50} + \ln P_{84}}{3}$	$\sigma_G = \exp\left(\frac{\ln P_{16} - \ln P_{84}}{4} + \frac{\ln P_5 - \ln P_{95}}{6.6}\right)$

Sorting (σ_G)		Skewness (Sk_G)		Kurtosis (K_G)	
Very well sorted	< 1.27	Very fine skewed	$^{-}0.3$ to $^{-}1.0$	Very platykurtic	< 0.67
Well sorted	1.27 – 1.41	Fine skewed	$^{-}0.1$ to $^{-}0.3$	Platykurtic	0.67 – 0.90
Moderately well sorted	1.41 – 1.62	Symmetrical	$^{-}0.1$ to $^{+}0.1$	Mesokurtic	0.90 – 1.11
Moderately sorted	1.62 – 2.00	Coarse skewed	$^{+}0.1$ to $^{+}0.3$	Leptokurtic	1.11 – 1.50
Poorly sorted	2.00 – 4.00	Very coarse skewed	$^{+}0.3$ to $^{+}1.0$	Very leptokurtic	1.50 – 3.00
Very poorly sorted	4.00 – 16.00			Extremely leptokurtic	> 3.00
Extremely poorly sorted	> 16.00				

Udden-Wentworth grain size classess used in the classification of sediments



Millimeters		µm	Phi (ϕ)	Wentworth size class	
			-20		
	4096		-12	Boulder (-8 to -12ϕ)	
	1024		-10		
	256		-8	Pebble (-6 to -8ϕ)	
	64		-6		
	16		-4	Pebble (-2 to -6ϕ)	
	4		-2		Gravel
	3.36		-1.75		
	2.83		-1.50	Gravel	
	2.38		-1.25		
	2.00		-1.00		
	1.68		-0.75		
	1.41		-0.50	Very coarse sand	
	1.19		-0.25		
	1.00		-0.00		
	0.84		0.25		
	0.71		0.50	Coarse sand	
	0.59		0.75		
1/2	0.50	500	1.00		
	0.42	420	1.25		
	0.35	350	1.50	Medium sand	Sand
	0.30	300	1.75		
1/4	0.25	250	2.00		
	0.210	210	2.25		
	0.177	177	2.50	Fine sand	
	0.149	149	2.75		
1/8	0.125	125	3.00		
	0.105	105	3.25		
	0.088	88	3.50	Very fine sand	
	0.074	74	3.75		
1/16	0.0625	63	4.00		
	0.0530	53	4.25		
	0.0440	44	4.50	Coarse silt	
	0.0370	37	4.75		
1/32	0.0310	31	5	Medium silt	
1/64	0.0156	15.6	6	Fine silt	
1/128	0.0078	7.8	7	Very fine silt	
1/256	0.0039	3.9	8		Mud
	0.0020	2.0	9		
	0.00098	0.98	10		
	0.00049	0.49	11	Clay	
	0.00024	0.24	12		
	0.00012	0.12	13		
	0.00006	0.06	14		

Appendix B. GRADISTAT grainsize analysis output summary

			Sample type	Textural Group	Mean	Sorting	Skewness	Kurtosis	Mean	Sorting	Skewness	Kurtosis	Mode
High	**Kelly's**	**North**	Unimodal, Well Sorted	Sand	268.9	1.3	0	1	Medium Sand	Well Sorted	Symmetrical	Mesokurtic	275
		Stream	Unimodal, Well Sorted	Sand	243.5	1.3	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		High	Unimodal, Well Sorted	Sand	273.8	1.4	0	1	Medium Sand	Well Sorted	Symmetrical	Mesokurtic	275
	Kopowai	**North**	Unimodal, Well Sorted	Sand	232.6	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		Stream	Unimodal, Well Sorted	Sand	234.3	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		High	Unimodal, Well Sorted	Sand	217.2	1.3	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
	Third	**North**	Unimodal, Well Sorted	Sand	235.7	1.3	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		Stream	Unimodal, Well Sorted	Sand	218.9	1.3	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		High	Unimodal, Well Sorted	Sand	245.4	1.4	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
Mid	**Kelly's**	**North**	Unimodal, Well Sorted	Sand	253.9	1.3	0	1	Medium Sand	Well Sorted	Symmetrical	Mesokurtic	275
		Stream	Unimodal, Well Sorted	Sand	272.2	1.3	0	0.9	Medium Sand	Well Sorted	Symmetrical	Mesokurtic	275
		High	Unimodal, Well Sorted	Sand	274.3	1.3	0	1	Medium Sand	Well Sorted	Symmetrical	Mesokurtic	275
	Kopowai	**North**	Unimodal, Well Sorted	Sand	230.4	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		Stream	Unimodal, Well Sorted	Sand	230.8	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		High	Unimodal, VWell sorted	Sand	222.3	1.3	0	0.9	Fine Sand	VWell Sorted	Symmetrical	Mesokurtic	230
	Third	**North**	Unimodal, Well Sorted	Sand	224.5	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		Stream	Unimodal, Well Sorted	Sand	228.2	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		High	Unimodal, Well Sorted	Sand	242.8	1.3	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
Low	**Kelly's**	**North**	Unimodal, Well Sorted	Sand	260.6	1.3	0	1	Medium Sand	Well Sorted	Symmetrical	Mesokurtic	275
		Stream	Unimodal, Well Sorted	Sand	290.9	1.3	0	1	Medium Sand	Symmetrical	Symmetrical	Mesokurtic	275
		High	Unimodal, Well Sorted	Sand	287.5	1.3	0	1	Medium Sand	Symmetrical	Symmetrical	Mesokurtic	275
	Kopowai	**North**	Unimodal, Well Sorted	Sand	230	1.3	0	0.9	Fine Sand	Symmetrical	Symmetrical	Mesokurtic	230
		Stream	Unimodal, Well Sorted	Sand	235.4	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		High	Unimodal, Well Sorted	Sand	235.7	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
	Third	**North**	Unimodal, Well Sorted	Sand	223.8	1.3	0	0.9	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		Stream	Unimodal, Well Sorted	Sand	240.7	1.3	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230
		High	Unimodal, Well Sorted	Sand	250.7	1.3	0	1	Fine Sand	Well Sorted	Symmetrical	Mesokurtic	230

Appendix C. Baylys Beach weather history for period 6 – 9 December 2016

Weather conditions leading up to, and at the time of, sediment temperature sampling at Third Stream, Mahuta Gap, Kelly’s and Kopowai (6 – 9 December 2016)

Sourced from: https://www.worldweatheronline.com/baylys-beach-weather-history/nz.aspx

6 December 2016 - Third Stream was sampled between 07:20 and 11:33

Time	**00:00**	**03:00**	**06:00**	**09:00**	**12:00**	**15:00**
Weather	☁	☁	☁	🌤	☀	☀
Temperature	15°C	15°C	15°C	17°C	23°C	21°C
Feels like	15°C	15°C	15°C	17°C	25°C	21°C
Wind	6 mph NNW	7 mph N	11 mph N	11 mph NNW	13 mph NNW	13 mph NNW
Cloud cover	100%	83%	100%	95%	100%	100%
Precipitation	0.5mm	5.4mm	5.0mm	1.1mm	0.2mm	0.4mm
Pressure	1014mb	1012	1011	1011	1010	1009

8 December 2016 – Kelly’s was sampled between 10:02 - 11:36)

Time	**00:00**	**03:00**	**06:00**	**09:00**	**12:00**	**15:00**
Weather	🌧	🌧	🌧	🌧	🌧	🌧
Temperature	15°C	15°C	15°C	17°C	23°C	21°C
Feels like	15°C	15°C	15°C	17°C	25°C	21°C
Wind	6 mph NNW	7 mph N	11 mph N	11 mph NNW	13 mph NNW	13 mph NNW
Cloud cover	100%	83%	100%	95%	100%	100%
Precipitation	0.5mm	5.4mm	5.0mm	1.1mm	0.2mm	0.4mm
Pressure	1014mb	1012mb	1011mb	1011mb	1010mb	1009mb

7 December 2016 - Mahuta was sampled between 09:04 – 12:50

Time	**00:00**	**03:00**	**06:00**	**09:00**	**12:00**	**15:00**
Weather	☁	☁	☁	🌤	☀	☀
Temperature	12°C	11°C	15°C	23°C	24°C	23°C
Feels like	12°C	11°C	15°C	25°C	26°C	25°C
Wind	3 mph N	3 mph NNE	4 mph NNE	10 mph N	14 mph N	13 mph N
Cloud cover	8%	12%	26%	52%	4%	10%
Precipitation	0mm	0mm	0mm	0mm	0mm	0mm
Pressure	1020mb	1018mb	1018mb	1019mb	1017mb	1015mb

9 December 2016 - Kopowai was sampled between 11:14 – 14:07

Time	**00:00**	**03:00**	**06:00**	**09:00**	**12:00**	**15:00**
Weather	🌧	☁	☁	🌦	🌧	🌦
Temperature	17°C	16°C	16°C	21°C	23°C	23°C
Feels like	17°C	16°C	16°C	21°C	25°C	25°C
Wind	mph NNW	7 mph N	11 mph N	11 mph NNW	13 mph NNW	13 mph NNW
Cloud cover	100%	83%	100%	95%	100%	100%
Precipitation	0.5mm	5.4mm	5.0mm	1.1mm	0.2mm	0.4mm
Pressure	1014mb	1012	1011	1011	1010	1009

Appendix D: Alongshore differences in temperature (°C)

Simple pairwise comparisons for the temperature differences (°C) between stream and non-stream points per depth and by tidal height

		Kelly's		**Mahuta**		**Kopowai**		**Third**	
		Difference (°C)	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**
High	**2cm**	0.4 ± 0.1	**0.06**	2.5 ± 0.3	**0.00**	2 ± 0.7	**0.00**	3.5 ± 0.8	**0.00**
	4cm	0.7 ± 0.1	**0.00**	2.2 ± 0.3	**0.00**	1.6 ± 0.4	**0.00**	2.4 ± 0.8	**0.04**
	7.5cm	1.1 ± 0.1	0.00	1.6 ± 0.3	0.00	0.8 ± 0.0	0.90	2.3 ± 0.8	0.06
	10.5cm	1.4 ± 0.1	0.00	1.4 ± 0.3	0.00	0.7 ± 0.0	1.00	2.2 ± 0.8	0.09
	20.5cm	2 ± 0.1	**0.00**	1.4 ± 0.3	**0.00**	1.1 ± 0.1	**0.70**	2.4 ± 0.8	**0.03**
Mid	**2cm**	0.1 ± 0.1	1.00	-0.5 ± 0.3	1.00	0 ± 0.2	1.00	0.8 ± 0.8	1.00
	4cm	0 ± 0.1	1.00	-0.5 ± 0.3	1.00	0 ± 0.1	1.00	0.7 ± 0.8	1.00
	7.5cm	-0.2 ± 0.1	1.00	-0.2 ± 0.3	1.00	-0.1 ± 0.1	1.00	0.8 ± 0.8	1.00
	10.5cm	-0.3 ± 0.1	0.98	0.1 ± 0.3	1.00	-0.2 ± 0.1	1.00	0.7 ± 0.8	1.00
	20.5cm	-0.2 ± 0.1	1.00	0.1 ± 0.3	1.00	-0.2 ± 0.1	1.00	0.7 ± 0.8	1.00
Low	**2cm**	0.1 ± 0.1	1.00	0 ± 0.3	1.00	0.4 ± 0.4	1.00	1.3 ± 0.8	1.00
	4cm	0.2 ± 0.1	1.00	-0.1 ± 0.3	1.00	0.4 ± 0.3	1.00	1.1 ± 0.8	1.00
	7.5cm	0.2 ± 0.1	1.00	0 ± 0.3	1.00	0.4 ± 0.2	1.00	1 ± 0.8	1.00
	10.5cm	0.2 ± 0.1	1.00	0.5 ± 0.3	1.00	0.4 ± 0.2	1.00	0.8 ± 0.8	1.00
	20.5cm	0.2 ± 0.1	1.00	0.5 ± 0.3	1.00	0.3 ± 0.1	1.00	0.4 ± 0.8	1.00

Bold denotes the mean difference is significant at the .05 level.

Appendix E: Cross shore differences in temperature (°C)

Simple pairwise comparisons for the temperature differences (°C) between high and mid, and mid and low points along stream and non-stream transects.

			Kelly's		**Mahuta**		**Kopowai**		**Third**	
		Depth	**Difference (°C)**	**Std.Error**	**Difference (°C)**	**Std.Error**	**Difference (°C)**	**Std.Error**	**Difference (°C)**	**Std.Error**
Non Stream	**High-mid**	**2cm**	**-0.6**	0.1	**-2.8**	0.3	**-1.7**	0.8	**-2.7**	0.8
		4cm	**-0.9**	0.1	**-2.4**	0.3	-1.0	0.4	-1.8	0.8
		7.5cm	**-1.6**	0.1	**-1.7**	0.3	-0.5	0.3	-1.6	0.8
		10.5cm	**-2.0**	0.1	**-1.6**	0.3	0.4	0.2	-1.4	0.8
		20.5cm	**-2.9**	0.1	**-1.4**	0.3	-0.7	0.0	-2.2	0.8
	Mid - Low	**2cm**	0.4	0.1	0.0	0.3	0.0	0.1	-0.1	0.8
		4cm	0.2	0.1	0.0	0.3	0.0	0.1	0.0	0.8
		7.5cm	-0.1	0.1	0.3	0.3	-0.1	0.1	0.2	0.8
		10.5cm	-0.1	0.1	0.3	0.3	-0.1	0.1	0.3	0.8
		20.5cm	0.1	0.1	0.5	0.3	-0.1	0.1	0.6	0.8
Stream	**High-mid**	**2cm**	-0.3	0.1	0.3	0.3	-0.4	2.1	-0.1	0.8
		4cm	-0.2	0.1	0.3	0.3	-0.6	1.6	-0.1	0.8
		7.5cm	-0.3	0.1	0.1	0.3	-0.5	1.3	-0.1	0.8
		10.5cm	-0.3	0.1	-0.2	0.3	-0.5	0.6	0.0	0.8
		20.5cm	**-0.6**	0.1	-0.2	0.3	-0.6	0.0	-0.5	0.8
	Mid - Low	**2cm**	0.4	0.1	0.6	0.3	0.6	0.0	0.3	0.8
		4cm	**0.5**	0.1	0.5	0.3	0.6	0.0	0.3	0.8
		7.5cm	0.3	0.1	0.5	0.3	0.9	0.0	0.4	0.8
		10.5cm	0.4	0.1	0.1	0.3	1.0	0.0	0.3	0.8
		20.5cm	**0.5**	0.1	0.8	0.3	1.1	0.0	0.3	0.8

Bold denotes the mean difference is significant at the .05 level

Appendix F. Sediment temperature comparisons

Two-way ANOVA comparing the mean sediment temperature (°C) at six points across the beach (adjacent to (stream) and away from the stream (non-stream) at the high tide (high) and at the mid-tide, above (mid) and below (low) the toheroa bed at five depths (2cm, 4cm, 7.5cm, 10.5cm, 20.5cm). Significant p-values indicated in bold at $\alpha = 0.05$.

		Type III SS	***df***	***MS***	***F***	***Sig.***
Kelly's	**Point**	231.763	5	46.353	209.361	**.000**
	Depth	79.596	4	19.899	89.878	**.000**
	Point * Depth	43.850	20	2.192	9.903	**.000**
Kopowai	**Point**	8.181	5	1.636	20.100	**.000**
	Depth	232.097	4	58.024	712.837	**.000**
	Point * Depth	2.971	20	0.149	1.825	**.015**
Mahuta	**Point**	576.570	5	115.314	63.397	**.000**
	Depth	1701.943	4	425.486	233.922	**.000**
	Point * Depth	33.604	20	1.680	.924	.556
Third	**Point**	812.316	5	162.463	19.178	**.000**
	Depth	1651.160	4	412.790	48.727	**.000**
	Point * Depth	41.373	20	2.069	.244	1.000

Bold denotes the mean difference is significant at the .05 level.

Appendix G: Sediment temperature changes (°C) over sampling period

Sediment temperatures at the start and end of sampling, including absolute change in temperature Δ (°C) and proportional change % Δ (°C)

Kelly's

		Non-stream				Stream			
		Start temp (°C)	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**	**Start temp (°C)**	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**
High	**2cm**	20.9 ± 0.1	21.6 ± 0.1	0.8 ± 0.2	3.6	20 ± 0.1	21.5 ± 0.1	1.5 ± 0.1	7.5
	4cm	20.8 ± 0.3	21.1 ± 0.3	0.3 ± 0.1	1.4	19.7 ± 0.2	20.7 ± 0.2	1 ± 0	5.2
	7.5cm	20.9 ± 0.2	20.7 ± 0.2	-0.2 ± 0.1	-1.1	19.3 ± 0.2	20 ± 0.2	0.7 ± 0	3.8
	10.5cm	21.1 ± 0.3	20.6 ± 0.2	-0.5 ± 0.1	-2.4	19.1 ± 0.2	19.8 ± 0.2	0.7 ± 0.1	3.5
	20.5cm	22.5 ± 0.1	21.6 ± 0.1	-0.9 ± 0.1	-4	19.8 ± 0.1	19.8 ± 0.1	0.1 ± 0.1	0.3
Mid	**2cm**	19.9 ± 0.1	21.5 ± 0.1	1.6 ± 0.2	7.9	19.6 ± 0.2	21.4 ± 0.1	1.8 ± 0.2	9.3
	4cm	19.4 ± 0.2	20.6 ± 0.2	1.2 ± 0	6.1	19.3 ± 0.2	20.7 ± 0.3	1.4 ± 0.2	7
	7.5cm	18.7 ± 0.2	19.7 ± 0.2	1 ± 0	5.3	19 ± 0.3	19.7 ± 0.2	0.8 ± 0.1	4.1
	10.5cm	18.4 ± 0.2	19.3 ± 0.2	1 ± 0	5.3	18.9 ± 0.1	19.4 ± 0.2	0.5 ± 0.2	2.4
	20.5cm	18.8 ± 0	19.2 ± 0	0.4 ± 0	2.3	19.1 ± 0	19.3 ± 0	0.2 ± 0	1
Low	**2cm**	19.7 ± 0.1	20.6 ± 0.1	1 ± 0.1	4.8	19.4 ± 0.2	20.5 ± 0.1	1.1 ± 0.1	5.8
	4cm	19.3 ± 0.2	20.2 ± 0.2	0.8 ± 0.1	4.3	19 ± 0.3	19.8 ± 0.2	0.9 ± 0	4.6
	7.5cm	18.9 ± 0.2	19.5 ± 0.2	0.6 ± 0	3.2	18.5 ± 0.2	19.3 ± 0.2	0.8 ± 0.1	4
	10.5cm	18.7 ± 0.2	19.2 ± 0.2	0.6 ± 0	3.1	18.3 ± 0.2	19.1 ± 0.3	0.8 ± 0.1	4.1
	20.5cm	18.7 ± 0	19 ± 0	0.3 ± 0	1.4	18.6 ± 0	18.8 ± 0	0.1 ± 0	0.7

Sediment temperatures at the start and end of sampling, including absolute change in temperature Δ (°C) and proportional change % Δ (°C)

Mahuta

		Non-stream				**Stream**			
		Start temp (°C)	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**	**Start temp (°C)**	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**
High	**2cm**	22.7 ± 0.2	29 ± 0.6	6.3 ± 0.8	27.9	21.2 ± 0.1	24.6 ± 0.1	3.4 0.2	16.2
	4cm	21.7 ± 0.1	27.9 ± 0.6	6.2 ± 0.4	28.7	20.1 ± 0.3	24.2 ± 0.2	4.1 0.1	20.1
	7.5cm	20 ± 0.2	26.3 ± 0.5	6.3 ± 0.4	31.4	19.2 ± 0.2	23.2 ± 0.2	4 0	20.8
	10.5cm	19.6 ± 0.3	25 ± 0.4	5.3 ± 0.3	27.1	18.8 ± 0.2	22.3 ± 0.2	3.5 0.1	18.6
	20.5cm	20.7 ± 0.1	24.1 ± 1.4	3.4 ± 1.4	16.4	19.7 ± 0.2	21.4 ± 0.8	1.7 0.7	8.8
Mid	**2cm**	20.9 ± 0.1	24.5 ± 0.2	3.6 ± 0.1	17.2	21.4 ± 0.1	24.9 ± 0.1	3.5 0.1	16.3
	4cm	20 ± 0.3	23.9 ± 0.5	3.9 ± 0.2	19.5	20.5 ± 0.2	24.5 ± 0.2	3.9 0.1	19.1
	7.5cm	19.2 ± 0.3	23.4 ± 0	4.2 ± 0.3	21.6	19.1 ± 0.2	23.5 ± 0.2	4.4 0.3	23
	10.5cm	18.8 ± 0.2	22.3 ± 0.3	3.5 ± 0	18.5	18.9 ± 0.2	22.7 ± 0.1	3.8 0	19.9
	20.5cm	19.5 ± 0.2	21.4 ± 0.8	1.9 ± 0.7	9.5	19.4 ± 0.3	21.4 ± 0.8	2 0.6	10.3
Low	**2cm**	20.9 ± 0.1	24.5 ± 0.2	3.6 ± 0.1	17.3	20.8 ± 0.2	24.5 ± 0.1	3.7 0.2	17.8
	4cm	20 ± 0	23.9 ± 0.1	3.9 ± 0.2	19.5	20 ± 0.2	24.1 ± 0.3	4.1 0.2	20.5
	7.5cm	18.9 ± 0.1	22.7 ± 0.2	3.8 ± 0.3	20.1	18.8 ± 0.2	23.1 ± 0.2	4.3 0.2	22.7
	10.5cm	18.5 ± 0.2	21.9 ± 0.2	3.4 ± 0.4	18.3	18.4 ± 0.2	22.2 ± 0.3	3.8 0.1	20.7
	20.5cm	19 ± 0.2	20.9 ± 0.7	1.9 ± 0.5	10.2	18.6 ± 0.3	20.8 ± 1	2.2 0.8	11.9

Sediment temperatures at the start and end of sampling, including absolute change in temperature Δ (°C) and proportional change % Δ (°C)

Kopowai

		Non-stream				Stream			
		Start temp (°C)	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**	**Start temp (°C)**	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**
High	**2cm**	25.1 ± 0.1	33.4 ± 0.2	8.3 ± 0.1	33.1	24.6 ± 0.4	30.3 ± 0.5	5.7 ± 0.2	23.2
	4cm	24.5 ± 0.2	30.9 ± 0.2	6.4 ± 0.3	26.2	23.9 ± 0.3	27.7 ± 0.8	3.8 ± 0.6	16
	7.5cm	23.3 ± 0.2	28 ± 0.3	4.7 ± 0.2	20.2	22.3 ± 0.4	27.2 ± 0.7	5 ± 0.5	22.4
	10.5cm	22.3 ± 0.2	25.8 ± 0.2	3.6 ± 0.1	15.9	21.8 ± 0.4	25 ± 0.2	3.2 ± 0.5	14.8
	20.5cm	20.5 ± 0.1	22.3 ± 0.1	1.7 ± 0.1	8.4	19.4 ± 0	21.3 ± 0.1	1.9 ± 0.1	9.6
Mid	**2cm**	25.1 ± 0.1	30.8 ± 0.4	5.8 ± 0.3	22.9	25.8 ± 0.1	30.8 ± 0.2	5 ± 0.3	19.4
	4cm	24.5 ± 0.2	29.4 ± 0.2	4.9 ± 0	19.9	24.5 ± 0.2	29.2 ± 0.1	4.7 ± 0.2	19.3
	7.5cm	23.3 ± 0.2	27.1 ± 0.3	3.8 ± 0.3	16.4	23.3 ± 0.2	26.8 ± 0.1	3.5 ± 0.3	15
	10.5cm	22.3 ± 0.2	25.2 ± 0.1	2.9 ± 0.2	13	22.3 ± 0.2	25.3 ± 0.1	2.9 ± 0.2	13.1
	20.5cm	19.8 ± 0	21.5 ± 0.1	1.7 ± 0.1	8.8	20 ± 0	21.5 ± 0	1.5 ± 0	7.3
Low	**2cm**	24.3 ± 0.3	31.3 ± 0.2	7 ± 0.4	28.6	25.2 ± 0.1	30.4 ± 0.2	5.3 ± 0.3	20.9
	4cm	23.9 ± 0.2	29.6 ±	5.7 ± 0.2	24	24.3 ± 0.2	28.9 ± 0.2	4.6 ± 0.1	18.8
	7.5cm	22.6 ± 0.2	26.9 ± 0.2	4.3 ± 0.2	18.9	22.5 ± 0.2	26.1 ± 0.1	3.6 ± 0.1	16
	10.5cm	21.5 ± 0.3	25.1 ± 0.1	3.7 ± 0.3	17.1	21.2 ± 0.2	24.4 ± 0.1	3.2 ± 0.1	15
	20.5cm	18.8 ± 0.2	21.1 ± 0.1	2.3 ± 0.2	12.3	19 ± 0	20.5 ± 0.1	1.5 ± 0	7.7

Sediment temperatures at the start and end of sampling, including absolute change in temperature Δ (°C) and proportional change % Δ (°C)

Third Stream

		Non-stream				**Stream**			
		Start temp (°C)	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**	**Start temp (°C)**	**End temp (°C)**	**Δ (°C)**	**% Δ (°C)**
High	**2cm**	18 ± 0.6	30.5 ± 0.7	12.5 ± 1.1	69.4	16.7 ± 0.1	26.6 ± 0.3	9.9 ± 0.2	59.6
	4cm	17.5 ± 0.5	27.1 ± 1	9 ± 1.2	54.6	16.5 ± 0.1	24.8 ± 0.4	8.3 ± 0.4	50.3
	7.5cm	17.7 ± 0.6	26.3 ± 0.9	8 ± 1.3	49	16.6 ± 0.2	23.4 ± 0.5	6.9 ± 0.3	41.4
	10.5cm	18.6 ± 0.6	24 ± 0.1	5.4 ± 0.5	29	17.1 ± 0.2	22 ± 0.2	4.9 ± 0.1	28.7
	20.5cm	20.5 ± 0.4	21.9 ± 0.1	1.4 ± 0.4	7	18.8 ± 0.2	19.4 ± 0.1	0.6 ± 0.3	3.2
Mid	**2cm**	17.7 ± 0.2	27.2 ± 0.2	9.5 ± 0.1	53.7	16.3 ± 0.1	26.6 ± 0.3	10.3 ± 0.3	63
	4cm	17.2 ± 0.2	25.5 ± 0.1	8.2 ± 0.1	47.8	16.2 ± 0.2	25.3 ± 0.1	9.1 ± 0.1	56.1
	7.5cm	17 ± 0.2	23.9 ± 0.3	6.9 ± 0.3	40.3	16.4 ± 0.2	23 ± 0.3	6.6 ± 0.1	40.2
	10.5cm	17.5 ± 0.2	22.7 ± 0.3	5.2 ± 0.1	29.9	17.1 ± 0.3	21.8 ± 0.2	4.7 ± 0.2	27.5
	20.5cm	18.7 ± 0.1	19.8 ± 0.1	1.1 ± 0.2	5.7	18.2 ± 0.1	18.8 ± 0.2	0.7 ± 0.3	3.7
Low	**2cm**	17.6 ± 0.2	26.5 ± 0.3	8.8 ± 0.2	50.1	15.9 ± 0.1	26.5 ± 0.2	10.7 ± 0.3	67.1
	4cm	17.2 ± 0.2	25.4 ± 0.2	8.2 ± 0.2	47.3	16 ± 0.2	24.7 ± 0.3	8.7 ± 0.2	54.4
	7.5cm	17 ± 0.2	23.6 ± 0.3	6.7 ± 0.3	39.2	16.4 ± 0.2	22.4 ± 0.3	6.1 ± 0.2	37.2
	10.5cm	17.3 ± 0.2	22.7 ± 0.3	5.4 ± 0.2	30.9	16.8 ± 0.2	21.2 ± 0.3	4.4 ± 0.1	26.2
	20.5cm	17.9 ± 0.2	19 ± 0	1.1 ± 0.2	6.3	21.4 ± 3.5	18.6 ± 0.1	-2.7 ± 3.5	-12.7

Appendix H: Two one-way ANOVA stream vs non-stream temperature differences

Two-way ANOVA comparing stream and non-stream sediment temperatures (°C) at the start and end of sampling

		Kelly's				**Mahuta**				**Kopowai**				**Third Stream**			
		Start		**End**		**Start**		**End**		**Start**		**End**		**Start**		**End**	
		Difference (°C)	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**	**Difference (°C)**	**p value**
High	**2cm**	0.9 ± 0.2	**0.01**	0.1 ± 0.1	0.96	1.5 ± 0.2	**0**	4.4 ± 0.4	**0**	0.5 ± 0.3	0.62	3.1 ± 0.4	**0**	1.4 ± 0.4	**0.03**	3.9 ± 0.5	**0**
	4cm	1.2 ± 0.3	**0.02**	0.4 ± 0.4	0.79	1.6 ± 0.3	**0**	3.8 ± 0.5	**0**	0.6 ± 0.3	0.36	3.3 ± 0.5	**0**	1 ± 0.4	0.13	2.3 ± 0.6	**0.02**
	7.5cm	1.6 ± 0.3	**0**	0.6 ± 0.3	0.3	0.8 ± 0.3	0.19	3.1 ± 0.4	**0**	1 ± 0.4	0.1	0.7 ± 0.5	0.69	1.1 ± 0.5	0.21	2.9 ± 0.7	**0.01**
	10.5cm	2.1 ± 0.3	**0**	0.9 ± 0.3	0.09	0.8 ± 0.3	0.21	2.6 ± 0.4	**0**	0.5 ± 0.3	0.65	0.9 ± 0.2	**0.01**	1.5 ± 0.5	**0.04**	2 ± 0.4	**0**
	20.5cm	2.7 ± 0.1	**0**	1.8 ± 0.1	**0**	1.1 ± 0.1	**0**	2.1 ± 0.2	**0**	1.1 ± 0.1	**0**	1 ± 0.1	**0**	1.7 ± 0.3	**0**	2.5 ± 0.2	**0**
Mid	**2cm**	0.3 ± 0.2	0.78	0 ± 0.1	1	1.5 ± 0.2	**0**	4.4 ± 0.4	**0**	0.5 ± 0.3	0.62	3.1 ± 0.4	**0**	1.4 ± 0.4	**0.02**	0.6 ± 0.5	0.82
	4cm	0.1 ± 0.3	1	-0.1 ± 0.4	1	-0.5 ± 0.3	0.64	-0.5 ± 0.5	0.91	0.1 ± 0.3	1	0.2 ± 0.5	1	1 ± 0.4	0.14	0.1 ± 0.6	1
	7.5cm	-0.2 ± 0.3	0.96	0 ± 0.3	1	0.1 ± 0.3	1	-0.1 ± 0.4	1	0 ± 0.4	1	0.3 ± 0.5	0.99	0.6 ± 0.5	0.78	0.9 ± 0.7	0.82
	10.5cm	-0.6 ± 0.3	0.47	-0.1 ± 0.3	1	-0.1 ± 0.3	1	-0.4 ± 0.4	0.81	-0.1 ± 0.3	1	-0.1 ± 0.2	1	0.4 ± 0.5	0.95	0.9 ± 0.4	0.14
	20.5cm	-0.3 ± 0.1	**0**	-0.1 ± 0.1	0.83	0.2 ± 0.1	0.72	0 ± 0.2	1	-0.3 ± 0.1	**0.01**	0 ± 0.1	1	0.5 ± 0.3	0.58	1 ± 0.2	**0**
Low	**2cm**	0.3 ± 0.2	0.64	0.1 ± 0.1	0.8	0 ± 0.2	1	-0.1 ± 0.4	1	-0.8 ± 0.3	0.12	0.9 ± 0.4	0.31	1.8 ± 0.4	**0**	-0.1 ± 0.5	1
	4cm	0.4 ± 0.3	0.86	0.3 ± 0.4	0.94	0 ± 0.3	1	-0.2 ± 0.5	1	-0.4 ± 0.3	0.8	0.8 ± 0.5	0.67	1.2 ± 0.4	**0.05**	0.7 ± 0.6	0.89
	7.5cm	0.4 ± 0.3	0.81	0.2 ± 0.3	0.97	0.1 ± 0.3	1	-0.4 ± 0.4	0.9	0.1 ± 0.4	1	0.8 ± 0.5	0.57	0.6 ± 0.5	0.78	1.2 ± 0.7	0.56
	10.5cm	0.3 ± 0.3	0.9	0.2 ± 0.3	1	0.1 ± 0.3	1	-0.3 ± 0.4	0.96	0.3 ± 0.3	0.96	0.8 ± 0.2	**0.02**	0.5 ± 0.5	0.9	1.4 ± 0.4	**0.01**
	20.5cm	0.1 ± 0.1	0.69	0.2 ± 0.1	0.11	0.5 ± 0.1	**0.05**	0.4 ± 0.2	0.32	0.1 ± 0.1	0.64	0.6 ± 0.1	**0**	0 ± 0.3	1	0.4 ± 0.2	0.3

Bold denotes the mean difference is significant at the .05 level.

Supporting publications

Publication 1

Ross, P., Beentjes, M., Cope, J., de Lange, W., McFadgen, B., Redfearn, P., Searle, B., Skerrett, M., Smith, H., & Smith, S. (2017a). 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*, 1-36.

Publication 2

Ross, P., Pande, A., Jones, J., Cope, J., & Flowers, G. (2017b). First detection of gas bubble disease and Rickettsia‐like organisms in Paphies ventricosa, a New Zealand surf clam. *Journal of Fish Diseases*.

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The biology, ecology and history of toheroa (*Paphies ventricosa*): a review of scientific, local and customary knowledge

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RESEARCH ARTICLE

The biology, ecology and history of toheroa (*Paphies ventricosa*): a review of scientific, local and customary knowledge

P. M. Ross[a], M. P. Beentjes[b], J. Cope[a], W. P. de Lange[a], B. G. McFadgen[c], P. Redfearn[a], B. Searle[a], M. Skerrett[d], H. Smith[e], S. Smith[f], J. Te Tuhi[g], J. Tamihana[h] and J. R. Williams[i]

[a]University of Waikato, Environmental Research Institute, Tauranga, New Zealand; [b]NIWA, Dunedin, New Zealand; [c]Victoria University of Wellington, School of Māori Studies, Wellington, New Zealand; [d]Te Rūnanga o Waihōpai, Ngai Tāhu, New Zealand; [e]Te Rangitāwhia Whakatupu Mātauranga Ltd, Wellington, New Zealand; [f]Triplefin Environmental Consulting, Napier, New Zealand; [g]Te Popoto Hapu of Ngāpuhi, Te Kopuru, New Zealand; [h]Ngāti Huia Hapu of Ngāti Raukawa, Foxton, New Zealand; [i]NIWA, Auckland, New Zealand

ABSTRACT
Toheroa (*Paphies ventricosa*) were formerly abundant on west and south-facing New Zealand surf beaches. Harvesting of this surf clam was intense during the early to mid-1900s, and populations declined to levels where harvesting was no longer viable. Despite having now been protected for 35–45 years, toheroa have failed to recover. This paper reviews the history of human interactions with toheroa and our understanding of their ecology, with a view to identifying knowledge requirements for management and restoration. Historical and legal documents pertaining to the use of marine resources are reviewed and scientific understanding compared with customary and local knowledge. We consider the factors that may be preventing toheroa recovery and make recommendations for research into life history, habitat requirements and the ecological consequences of changing land use. Management options are suggested to address the effects of vehicle use on beaches, poaching and the failings of the customary harvest system.

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Introduction

Toheroa (*Paphies ventricosa*) are a species of large intertidal surf clam endemic to New Zealand. At the start of the twentieth century, extensive toheroa populations were present on the exposed west-facing surf beaches of Taitokerau (Northland) and the Kāpiti-Horowhenua coast, and on the south coast of Murihiku (Southland; Figure 1; Redfearn 1974). Toheroa were a staple food for Māori in these areas and began to be harvested more extensively by pakeha (New Zealanders of European descent) from the late 1800s (Redfearn 1974; Murton 2006 and references therein). The popularity of toheroa as a recreational harvest grew quickly and commercial operations were soon established, primarily for the export of canned toheroa (Williams, Sim-Smith, et al. 2013). Toheroa populations fluctuated in size as is typical of surf clams (Coe 1955; de Villiers 1974;

CONTACT P. M. Ross ✉ rossp@waikato.ac.nz

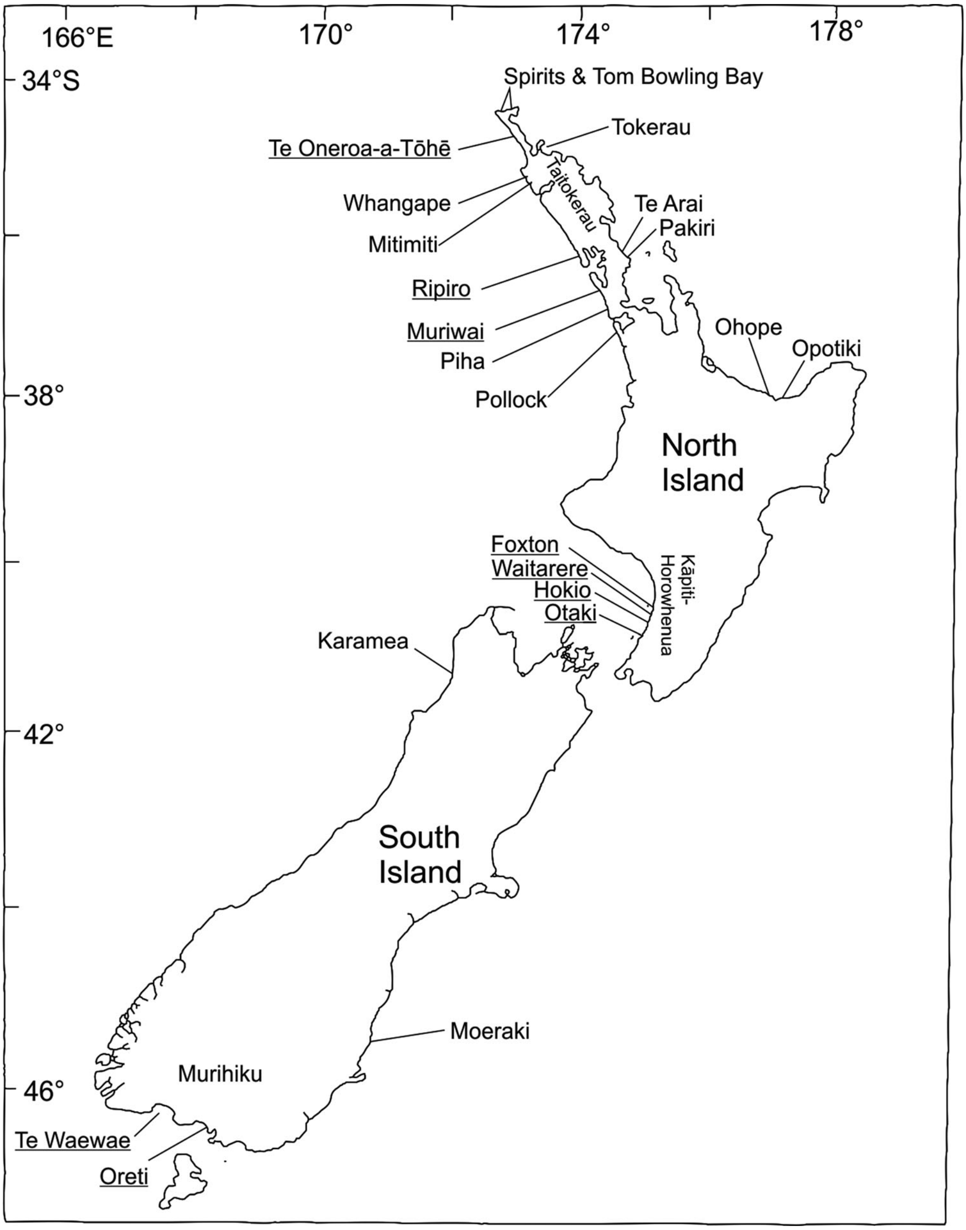

Figure 1. Distribution of toheroa (*Paphies ventricosa*) in New Zealand. Major populations are underlined. Figure reproduced from Redfearn (1974).

Arntz et al. 1988; Fiori et al. 2004; McLachlan and Brown 2006). However, concerns soon developed that the combined harvest of the commercial fishery and the largely unregulated recreational fishery were depleting the resource (Murton 2006). Fisheries regulations were introduced incrementally from 1913 (Murton 2006; Miskelly 2016), but ultimately failed to halt the decline of the fishery. By the mid-1900s toheroa populations declined to levels where their harvest was no longer viable (Redfearn 1974; Stace 1991; Murton

2006). All commercial harvest ceased by 1969 and regional recreational fishery closures occurred between 1971 and 1980 (Williams, Sim-Smith, et al. 2013). Since that time, toheroa harvesting has been restricted to customary take by Māori (for which an authorisation to take for customary purposes is required), largely for hui (meetings) or tangi (funerals), and a number of recreational open days in Murihiku, the last of which took place at Oreti Beach in 1993 (Miskelly 2016). Despite having been protected for 40+ years, toheroa populations nationwide have, for unknown reasons, failed to recover, with some populations continuing to decline (Williams, Sim-Smith, et al. 2013).

Knowledge of the biology and ecology of toheroa, and of New Zealand surf clams in general, is surprisingly limited compared to other iconic New Zealand kai moana (seafood) species. This is in spite of the cultural significance of toheroa, their status as a New Zealand culinary icon, their potential commercial value and the mystery surrounding the reasons for their collapse and lack of recovery. Systematic keyword searches in the Scopus online journal database using the terms ‘toheroa’, *Paphies ventricosa* and this species’ previous names *Amphidesma ventricosa* or *Mesodesma ventricosa* produced only 21 peer-reviewed scientific journal articles, including a 1928 summary in *Nature* of Malcolm’s (1928) work on the nutritional value of toheroa soup. By comparison, searches for the similarly iconic and recreationally and/or commercially important New Zealand kai moana species: cockles (*Chione stutchburyi* or *Austrovenus stutchburyi*); snapper (*Pagrus auratus* or *Chrysophrys auratus*); crayfish (*Jasus edwardsii*); and mussels (*Perna canaliculus*), produced 139, 562, 384 and 322 publications, respectively. These search results are not necessarily a fair indication of the research effort that has been directed at toheroa. Much of the toheroa science conducted to date relates to population surveys and stock assessment rather than ecological research. For example, 30 toheroa surveys were conducted at Oreti Beach, in Murihiku, between 1969 and 2005 (Beentjes and Gilbert 2006b). This body of stock assessment work resides largely in the grey literature in the form of reports to government agencies (Ministry for Primary Industries and its precursors) and is not easily discoverable through journal database searches. The heyday of toheroa research was the 1950s to 1970s period when researchers such as Cassie (1951, 1955), Rapson (1952, 1954) and Redfearn (1974, 1982) produced detailed accounts of toheroa natural history and developed ideas about the ecology of toheroa that remain largely unchanged today. In recent times, toheroa research has occurred only sporadically, in accordance with the interests and resources of individual researchers. There has been no coordinated national approach to acquiring knowledge that may be needed to support the restoration and management of this taonga (treasured) species.

Increasingly, Māori are able to take a leading role in the management of their rohe (territory) (Moller, Lyver, et al. 2009; Taiapa et al. 2014). Environmental restoration, particularly of ecosystems that once supported the provision of food, water and other resources to tangata whenua (people of the land – Māori), is of particular importance to Māori (Tipa and Teirney 2006; Smith et al. 2011; Taiapa et al. 2014). Ecological information, both western science and mātauranga Māori (Māori knowledge), is being sought to support restoration and management efforts for a range of species and environments (Smith et al. 2011; Robb 2014; Taiapa et al. 2014). For Taitokerau, Kāpiti-Horowhenua and Murihiku, there are aspirations that toheroa will recover to the point where they can once again be a sustainably harvested resource (customary, recreational and commercial). Some groups also hope that toheroa may one day be cultured commercially, to both assist with restoration activities and to provide new sources of revenue and employment for Māori (Newcombe et al. 2015).

Given the current level of interest in toheroa from the communities living at these beaches, the resource users and managers, and the scientific community, now is an appropriate time to consider the existing knowledge of the biology and ecology of toheroa with a view to identifying information requirements for future management and restoration. As a contribution to this process, this paper combines the knowledge of experts from a diversity of backgrounds with a view to integrating both 'western scientific' and mātauranga Māori perspectives. By taking this approach to the review of human interactions with toheroa, and by comparing our current scientific understanding of toheroa against the knowledge held by local experts, we provide a comprehensive summary of toheroa-related knowledge (and knowledge gaps) and context to the present ecological challenges and uncertainty. While the local experts, whose knowledge has been incorporated into this review, would traditionally be thought of as laypeople or amateur naturalists, in this instance many are kaitiaki (guardians) or tohunga (experts). These are formal titles or positions bestowed within Māori culture, and the practitioners are holders of a considerable body of personally acquired and intergenerationally transferred environmental knowledge. By assembling this diverse body of knowledge and identifying factors that may be preventing the recovery of toheroa and possible management actions, this review provides a resource for anyone with an interest in toheroa or their management and a starting point for future investigations into this species. This review does not attempt to replicate or extend the critical analyses of trends in toheroa population abundance and size structure that have been conducted on numerous occasions over the last 50+ years (see Beentjes and Gilbert 2006b; Williams, Sim-Smith, et al. 2013; Williams, Ferguson, et al. 2013 and references therein). This contemporary approach to fisheries research and management has been unsuccessful in informing or facilitating the restoration of toheroa and as such there is a need to understand the failings of the current management system and explore alternative approaches.

Methods

The available published and unpublished literature on toheroa was reviewed, including scientific research papers, graduate research theses and reports to the Ministry for Primary Industries (and its precursors). The task of collating and synthesising the literature was somewhat simplified by the fact that several reports, focussing on the factors that may be preventing the recovery of toheroa, have been recently produced (Heasman et al. 2012; Williams, Sim-Smith, et al. 2013). In addition to the scientific data sources traditionally examined when conducting ecological reviews of this nature, we also searched newspaper archives and legal and historical data sources, including university theses and documents pertaining to Māori use of marine resources and Treaty of Waitangi claims.

Once the available ecological literature had been reviewed, meetings were held with local experts in Taitokerau, Kāpiti-Horowhenua and Murihiku. The scientific understanding of toheroa ecology was discussed and local experts were able to provide their own perspectives. For the most part, these meetings took place on or near the toheroa beaches. Where scientific and local knowledge differed it was sometimes possible to examine toheroa beds or the surrounding environment to validate or challenge the scientific or local understanding. In other cases, scientific and local knowledge were aligned but the understanding of the mechanisms behind observations differed. In these cases, alternative observations or interpretations of observations were shared and recorded.

The early history of toheroa

Toheroa were once abundant on Te Oneroa-a-Tōhē (Ninety Mile Beach), Mitimiti, Ripiro (Dargaville / North Kaipara Beach) and Te Oneone Rangatira (Muriwai) beaches in Taitokerau, on the Kāpiti-Horowhenua coast from the Rangitikei River to Waikanae Beach, and in Murihiku at Oreti, Bluecliffs and Orepuki Beaches (Figure 1). Small populations also existed in the North Island at Spirits Bay, Tom Bowling Bay, Tokerau, Te Arai, Whangape, Pollok, Piha, Ohope, Opotiki, and in the South Island at Hampden, Waikouiti and Long Beach, although only single specimens have been found at the latter two beaches (Hoby 1933; Cassie 1955; Street 1971; Redfearn 1974). For Māori in Taitokerau, Kāpiti-Horowhenua and Murihiku, toheroa had long been a staple food (Murton 2006 and references therein). The toheroa beds on the West Coast of Taitokerau are said to have been particularly valuable, with early newspaper articles suggesting that attempts to secure the possession of these beds may have given rise to some warfare among Māori (Stallworthy 1916). Toheroa were largely dried or smoked and were probably a traded commodity (Stace 1991). Toheroa, also known in some regions as taiwhatiwhati roroa, moeone, tupehokura, roroa and tohemanga, are a taonga (treasure), a prestigious kai moana and are a desirable dish to be served at hui or tangi for coastal peoples (Murton 2006). Toheroa are linked to the Māori people through whakapapa (genealogy). They are given the same respect as the family, or tribal entity, provoking a fierce ethic of stewardship, or kaitiakitanga (Smith 2013). The provision of toheroa to visitors is also an important component of manaakitanga (the act of giving mana, or utmost respect, to another through the expression of hospitality and generosity), a tikanga (custom) that has been compromised by the mismanagement and collapse of the fishery.

The whakapapa of the toheroa is that it was held in such high esteem that it was brought to New Zealand from Hawaiki (the traditional Māori place of origin where Io, the supreme being, created the world and its first people) by the high chief Mareao who seeded toheroa on the west coast of the North Island (Wai27 1988). A second origin story recalls an incident in which a group of Te Rarawa men from Ahipara (Taitokerau) were caught poaching kukupa (New Zealand wood pigeon; *Hemiphaga novaeseelandiae*) in the Hokianga area. Forced to flee for their lives back up to Te Oneroa-a-Tōhē, they discarded all their food and equipment in order to outrun their pursuers. After many hours, famished and nearly spent, they pleaded with their chief to intercede with the spirits. Mounting a rocky outcrop and facing the beach, the chief uttered a karakia (prayer), beseeching his atua (god) to save them. Immediately a whirlwind appeared and the chief was told to continue his journey and the way would be made clear. Shortly afterwards the men noticed slit-like holes in the sand. Thinking that shellfish might be lurking beneath, they dug but found nothing. Dejected, they were at the point of giving up when the whirlwind appeared again, giving the message 'Tohe roa, tohe roa!' ('Persist a long time!'). Digging deeper, they eventually found the shellfish, eased their hunger and got home safely. In giving thanks for their narrow escape, the chief declared that the life-giving shellfish should be known as toheroa (Stace 1991).

Māori would often make hazardous expeditions, sometimes fatal, to the long beaches of the west coast of Taitokerau to collect toheroa (Stallworthy 1916, Stace 1991). These journeys were not just for the purposes of food harvest. The translocation of toheroa to new locations and their cultivation may have been common practise for Māori (J. Williams 2004, 2012). Translocations are thought to have been for the purpose of establishing new populations in areas where they could be more easily accessed. Live toheroa may have even been a traded commodity. Rakiihia Tau (Ngāi tahu), in his testimony to the Waitangi Tribunal (Wai27 1988), describes the translocation of toheroa in the South Island, stretching back at least four or five generations, to Kahurangi Point (north of Karamea) and to the beaches of Canterbury, Otago and Murihiku. New Zealand Government agencies (New Zealand Marine Department) were also involved in transplants during the 1920s and 1930s, moving thousands of toheroa between North Island beaches (New Zealand Herald 1926, 1934; Auckland Star 1930). Historical documents including newspaper and magazine articles describe how ‘many experiments have been made to transplant the toheroa to other beaches, apparently of similar nature to its native haunts’ (Samuel 1936).

The practise of translocating toheroa has persisted into more recent times. Kaitiaki have shared their knowledge of toheroa translocation from Taitokerau and Horowhenua to the eastern beaches of Taitokerau, the Bay of Plenty, Horowhenua and Hawke’s Bay (various, personal communication). Toheroa were also translocated from Bluecliffs Beach to Orepuki in Te Waewae Bay (Futter 2011). Toheroa translocation appears to have been a common practice at least up until the 1970s when the toheroa fisheries closed. This is perhaps not surprising as the translocation of toheroa, and other shellfish species including cockles (*Austrovenus stutchburyi*), scallops (*Pecten novaezelandiae*), tuatua (*Paphies australis*) and paua (*Haliotis iris*) was probably an important component of Māori marine resource management stretching back several hundred years (Wai27 1988; Williams 2004, 2012).

Despite what appears to be widespread and repeated translocation activity, it would seem that in most locations, transplanted toheroa have failed to thrive or persist. This is probably due to the specific habitat requirements of toheroa and the necessity for new populations to be sustained through self-recruitment (of pelagic larvae) when transplanted outside their natural geographical distribution. Due to the 20–40 day larval period of toheroa (Redfearn 1974, 1982; Gadomski et al. 2015), the hydrodynamic conditions resulting in the retention of larvae would be required for the necessary self-recruitment to occur (Cowen et al. 2007 and references therein). Research, incorporating genetics, archaeology and oral history, is currently underway to ascertain whether any of the present day toheroa populations result from historical transplants (Ross *unpublished data*). Should the translocation hypothesis be correct, this traditional practise may explain the peculiar geographical distribution of the toheroa which spans biogeographical boundaries and is unlike that of any other New Zealand marine organism (Figure 1; Ross et al. 2009; Shears et al. 2008).

In Taitokerau (but not in Murihiku), the story of toheroa is closely tied to that of the dune grass pingao (*Ficinia spiralis*), a New Zealand endemic sedge that grows on active sand dunes (Stace 1991; Te Tuhi & Gregory 2008). The whakapapa of pingao is that she was put on the dunes by her father, Tangaroa (the god of the sea), to nurture her whanau (family), the toheroa. The authors have heard two versions of Māori lore regarding the reproduction of toheroa. One is that toheroa spat are born in the pingao (whose seeds are shaped like toheroa spat) and in the native dune grass spinifex (*Spinifex sericeus*; also known in Te Reo Māori as matihetihe, kowharawhara, raumoa and turikakoa). The other is that spat are carried to the dunes on the foaming surf at the highest of tides and are deposited on the sand dunes and into the pingao and spinifex where they are reared within the structures of these grasses. Transportation from the dune grasses to the juvenile beds in the upper intertidal occurs in spring. The spat held by the pingao are blown onto the upper beach, while the tumbleweed-like seed heads of the spinifex transport their toheroa pēpi (babies) along the beach through the action of cross-shore winds. The spat are then washed from the tumbling seed heads as they traverse the numerous streams and seeps running down the northern beaches. These streams are where the spat settle thus explaining the stream-associated distribution of toheroa in Taitokerau. At times when the transference of spat to the beach was considered to be taking place, children were not allowed to play their game of waiwatai, in which seed heads were chased as they were blown over the sand (Rapson 1952). This tikanga provided protection for both the nursery habitat and the vulnerable early life stages of toheroa.

Traditional Māori fisheries management practices were not restricted to translocation and nursery protection (Table 1). The setting aside of reserves (rāhui) and spawning areas was something that Māori had long practised (Minister of Marine 1933; Parore 1933). There was also a cessation of harvesting during the main spawning time which was indicated by the annual flowering of kumarahou (*Pomaderris kumarahou*) and the full moon (Smith 2003). It has also been suggested that Māori may have preferentially harvested middle-sized toheroa, possibly as a consequence of processing, preservation and usage practices, leaving larger individuals in place as broodstock to sustain the resource (J. Te Tuhi, personal communication). It is possible the practise of not harvesting large toheroa may have led to some degree of inaccuracy in archaeological midden records, as small toheroa and large tuatua can be hard to differentiate without knowledge of diagnostic shell characteristics (Cassie 1955). As a consequence, the historical geographic distribution of toheroa and their importance in the diet of Māori may have been underestimated in some locations (Ross, *unpublished data*).

The recent history of toheroa

When pakeha first began taking notice of toheroa, they appeared to be so abundant as to be considered an almost inexhaustible resource (Samuel 1936). By the late nineteenth century, the pakeha residents of Taitokerau towns, such as Te Kopuru, Aratapu and Dargaville, began spending time at the toheroa beaches over summer and rapidly came to appreciate toheroa, both as a food item and as bait for fishing (Murton 2006). The first toheroa cannery was established at Mahuta Gap, Ripiro Beach, in the 1890s (Stace 1991), and before long four factories operated on that stretch of Kaipara coastline and a fifth at Te Oneroa-a-Tōhē (Figure 2; Redfearn 1974; Stace 1991). The total commercial production for Taitokerau beaches from 1928 to 1969 was typically around 20 tonnes of canned product per annum, with record production of 77 tonnes in 1940 (Figure 3; Redfearn 1974). At various times and for brief periods toheroa were also canned at Muriwai, on the Kāpiti-Horowhenua coast and at Te Waewae Bay (Williams, Sim-Smith, et al. 2013).

Table 1. Summary of factors considered to potentially be preventing the recovery of toheroa, the mechanisms by which these factors might affect toheroa recovery, possible management actions to address factors and relevant toheroa literature.

Factors that may be preventing the recovery of toheroa		Management actions to address effects			Relevant toheroa literature and research
	Possible mechanism(s)	Past	Present	Possible future options	
Climate and weather	Changes in food availability; frequency of stranding events; beach morphology, sand smothering or beach instability	–	–	Adjust customary harvest to account for environment-driven population variation	Williams, Sim-Smith, et al. (2013), Cassie (1955)
Toxic algal blooms (TAB)	Mortality via smothering and anoxia	–	–	Adjust customary harvest to account for population variation as a consequence of TAB related mortality	Williams, Sim-Smith, et al. (2013)
Disease	Mortality events; effects on health, growth or reproduction	Avoid harvesting (or survey) practises that damage unharvested animals or involve the processing of toheroa, or discarding of their waste, on the beach or near a toheroa bed	Avoid harvesting (or survey) practises that damage unharvested animals or involve the processing of toheroa, or discarding of their waste, on the beach or near a toheroa bed (not practised by all harvesters and researchers)	Adjust customary harvest to account for population variation as a consequence of disease and mortality events; Manage translocations of toheroa and other species to reduce risk of spreading disease to uninfected locations	Ross et al. (2017)
Recruitment limitation	Levels of recruitment may be insufficient to facilitate recovery of toheroa populations	Māori may have preferentially harvested middle sized toheroa leaving larger individuals in place as broodstock to sustain the resource; Tikanga around foot traffic on upper beach provided protection for both the nursery habitat and the vulnerable early life stages of toheroa; Translocation of toheroa to supplement existing populations or establish new ones;	Translocation of toheroa to supplement existing populations or establish new ones. Contemporary translocations are at present being conducted both with and without permits	Spat production and reseeding or translocation of adults where populations demonstrated to be recruit limited; Management of vehicle activity during recruitment season to maximise survival of spatfall	Newcombe et al. (2015), Williams, Ferguson, et al. (2013), Beentjes (2010a), Beentjes (2010b), Moller et al. (2009b), Williams (2004), Smith (2003), Minister of Marine (1933), Parore (1933)

(*Continued*)

Table 1. Continued.

Factors that may be preventing the recovery of toheroa		Management actions to address effects			Relevant toheroa literature and research
	Possible mechanism(s)	Past	Present	Possible future options	
		Tikanga around cessation of harvesting during main spawning periods which was indicated by the annual flowering of kumarahou (Pomaderris kumarahou) and the full moon; Use of rāhui to set aside beds and spawning areas; Commercial fishery at Ripiro transplanted large toheroa to the southern end of Pouto Peninsula, to act as a source of recruits to beds to the north			
Vehicle activity	Direct crushing, increased desiccation risk, or increased predation risk from birds, reduced stability	–	Adjustments to location of annual beach motorcycle race at Oreti to minimise impacts on toheroa	Driver education to modify behaviour and use of vehicles on beaches; Spatial and/or temporal closures of beaches to vehicles Insertion of physical barriers as a way of modifying vehicles activity	Moller et al. (2009b), Hooker and Redfearn (1998), Brunton (1978), Redfearn (1974)
Changes in land use	Changes in flow of freshwater to coast; degradation of water quality; changes in beach morphology; beach erosion and loss of habitat	–	–	Modify land use to minimise impacts on (or restore) toheroa habitat and ecology	Williams, Sim-Smith, et al. (2013), Smith (2013), Beentjes et al. (2006), Akroyd (2002)
Human harvesting	Harvesting at an unsustainable level or at levels that do not allow populations to recover; incidental mortality of non-harvested toheroa	Allocation of lease areas for commercial harvesting Minimum size, daily bag limit, harvest method, season and area restrictions for recreational fishery; Rotational harvest of toheroa	Closure of commercial and recreational fisheries; Creation of customary harvest system	Improvements to customary harvest system; Allocation of resources to improve enforcement of fisheries regulations; Education and community engagement to inform	Miskelly (2016), Akroyd et al. (2008), Smith (2013), Redfearn (1974)

		beds and 'thinning' of selected high density beds by customary fishers; Cessation of harvesting effort by customary fishers around known times of major spawning events		customary harvest, reduce illegal harvesting, and assist enforcement of regulations through peer pressure and reporting of illegal harvest	
Natural predation by birds, fish or invertebrates	Predation at an unsustainable level or at levels that do not allow populations to recover	Collection or destruction of black-backed gull (*Larus dominicanus*) eggs by locals from breeding rookeries located among cliffs above toheroa beds	–	Management of bird populations if/where links to toheroa population failure are proven	Brunton (1978)

Figure 2. (Clockwise from top left) Toheroa collected from Hokio Beach during the September open day in 1977 (EP/1077/3679/36-F. Alexander Turnbull Library (ATL)); Three women from Northland, photographed ca. 1910–1930s, shelling toheroa meat into tin cans for a toheroa cannery. Their kete (flax bags) are full of shellfish, and they are surrounded by empty shells (1/1-026522-G. ATL); Harvesting toheroa on a Northland beach, ca. 1920s–1930s (1/1-010575-G. ATL); Toheroa being dug from trenches on Muriwai Beach, 1962. (AAQT 6539, A70987. Archives New Zealand, The Department of Internal Affairs, Te Tari Taiwhenua).

The emergence of toheroa as one of 'New Zealand's great contributions to the epicurean world' had to wait until the visit of the Prince of Wales in 1921. Prince Edward asked for a second helping of toheroa soup at a banquet, a request that broke with royal protocol and was reported throughout the Empire (Stace 1991). After this event, no self-respecting New Zealand hotel was without toheroa soup on the menu, and the collecting and eating of toheroa became a national pastime (Murton 2006). Toheroa, 'a delicacy highly esteemed by the most fastidious gourmet' was considered 'a gift of nature which is a remarkable commercial asset, and although a mere shellfish, has done much to advertise the Dominion all over the world' (Samuel 1936). From the 1920s, roads improved and cars became more common, making the toheroa beaches accessible to people living further away in towns such as Auckland, Whangarei and Wellington.

The harvesting of toheroa escalated quickly and it was not long before toheroa numbers began declining (Murton 2006; Williams, Ferguson, et al. 2013). At Ripiro, there was soon friction between the various groups of toheroa harvesters including local and visiting Māori, local pakeha and those residing at beach campgrounds and settlements during the summer, hawkers who dug and sold toheroa, and the canneries (Murton 2006). At Ripiro, a reserve for 'camper' harvesting of toheroa was established in 1913. In 1915, lease areas for commercial harvesting were established. Recreational harvesting

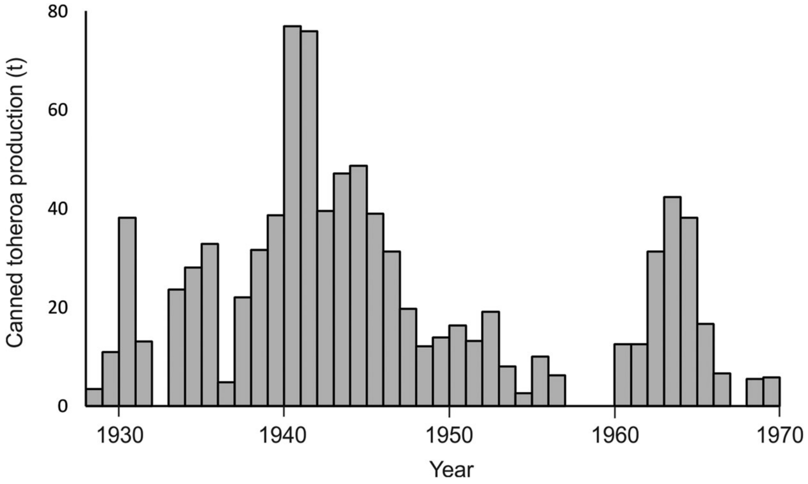

Figure 3. Total commercial production of toheroa (*Paphies ventricosa*; tonnes of canned toheroa product) from canneries at Northland Beaches (Te Oneroa-a-Tōhē, Ripiro and Te Rangatira) from 1928 to 1969. Data from Marine Department Annual records for 1928–1940 and 1943–1948 tabulated by Cassie (1955) and for 1941–1942 and 1949–1969 graphed by Redfearn (1974). Figure reproduced from Williams, Sim-Smith, et al. (2013).

regulations were first introduced in 1932 in response to dwindling numbers and mass mortality events in northern populations (Williams, Sim-Smith, et al. 2013). The Marine Department established a two-month closed season during spawning (October to November), introduced a minimum size (3 in./76 mm), banned certain digging implements for non-commercial harvesters and introduced a quota for pakeha (50 toheroa per person per day), but not Māori. A quota for Māori was introduced in 1941 (Redfearn 1974).

After commercial harvesting began, Māori expressed dismay over wasteful methods and the depletion they observed (Murton 2006). They opposed commercial toheroa digging in traditional harvesting areas and from 1915, Māori at Ripiro lobbied for the establishment of ‘Māori toheroa reserves’ (similar to the camper reserve established in 1913). However, the Chief Inspector of Fisheries (1939) commented that toheroa were a ‘national possession’ that belonged to everyone, and just because some families lived near them he did not think that they alone should be privileged. Māori requests and complaints were largely ignored as was the fact that toheroa were a traditional and staple Māori food, but ‘only relish as far as Europeans are concerned’ (Under Secretary Maori Affairs 1950). By the 1940s and 1950s it had become fashionable for urban pakeha to make the trip to the collect toheroa (Figure 2). In 1957, the occupants of 2000–3000 cars visited Glinks Gully (Ripiro) over a weekend to harvest toheroa (Auckland Star 1957). In 1966 an estimated 12,000 cars and 50,000 people visited Ripiro Beach in one weekend, harvesting an estimated 1,000,000 toheroa (Murton 2006 and references therein).

Unfortunately, there is only limited population data from the early days of the toheroa fishery (Figure 4; Williams, Ferguson, et al. 2013). No one knows how many toheroa were present on the beaches at the start of the twentieth century but it is likely that population sizes did fluctuate, as is typical for surf clams (Coe 1955;

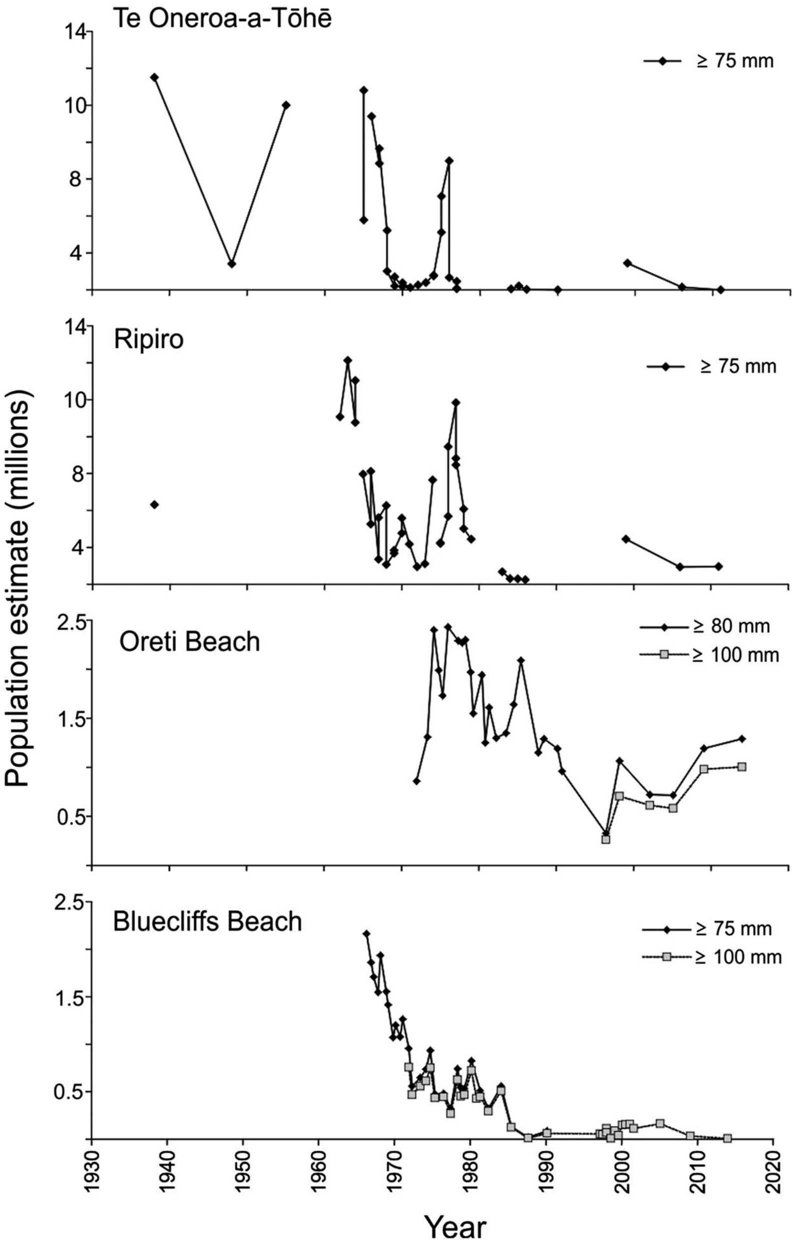

Figure 4. Population estimates of large adult toheroa (*Paphies ventricosa*) at Te Oneroa-a-Tōhē (≥75 mm; 1933–2010), Ripiro (≥ 75 mm; 1938–2011), Oreti (≥80 mm and ≥100 mm; 1972–2009) and Bluecliffs Beach (≥75 mm and ≥ 100 mm; 1966–2009) from 1930 to 2015. Figures reproduced from Williams, Ferguson, et al. (2013), Beentjes (2010a, 2010b) and Berkenbusch et al. (2015).

de Villiers 1974; Arntz et al. 1988; McLachlan et al. 1996; Fiori et al. 2004; McLachlan and Brown 2006). The commercial fishery has traditionally received much of the blame for the decline of toheroa. Based on what we now know, however, it appears likely that non-commercial harvesting was of at least equal importance in contributing to the collapse of toheroa populations. Commercial harvesting practices varied between locations (B. Searle, personal communication). At Ripiro Beach, commercial harvesting was restricted to lease areas from 1915 (Murton 2006). Accounts from those involved in the later periods of the commercial fishery indicate that individual toheroa beds were only partially harvested and the harvest limited to mid-sized toheroa (B. Searle, personal communication). Smaller toheroa were returned to the trenches from which they were dug and larger specimens either returned to the trenches or transplanted to the southern end of Pouto Peninsula, to act as a source of recruits to beds to the north (Figure 2). Similar harvesting practises were not necessarily used at other beaches. Differences in harvesting practices may to some extent explain the persistence of adult toheroa beds at Ripiro, while at Te Oneroa-a-Tōhē and the Kāpiti-Horowhenua Beaches toheroa have all but disappeared. In contrast to the commercial fishery, the recreational fishery was not managed spatially and there was no maximum size limit in place to ensure that the reproductive capacity of the beds was maintained. There are also accounts of recreational fishers following behind the commercial harvesters and ‘cleaning out’ sections of toheroa beds purposefully left undug by the canneries (B. Searle, personal communication). To manage the recreational harvest, bag limits (50 for pakeha in 1932; 80 for Māori in 1939; 20 per person regardless of ethnicity in 1950), a minimum size and seasonal harvesting restrictions were incrementally introduced (Murton 2006; Miskelly 2016). However, these regulations probably became less effective at controlling total catch as the numbers of recreational harvesters grew.

Once population surveys began in earnest in the 1960s, large fluctuations in abundances were recorded (Beentjes 2010a, 2010b; Williams, Sim-Smith, et al. 2013; Figure 4). Mass mortalities were reported at various locations in 1888, 1900, 1917, 1932, 1938, 1956–1959, 1970–1971, 2001 and 2013, contributing to this variability in biomass, as did high levels of recreational and commercial harvesting (Rapson 1954; Cassie 1955; Williams, Sim-Smith, et al. 2013). In 1955, the North Island closed season for both commercial and recreational fisheries was extended to 10 months and quotas reduced. By 1966 the total commercial harvest of toheroa had dropped to less than 10 tonnes of canned product per annum (Figure 3), and all commercial harvesting ceased in 1969. Toheroa populations continued to decline and recreational harvesting was eventually closed at Te Oneroa-a-Tōhē (1971), Muriwai (1976), Kāpiti-Horowhenua (1978) and Ripiro (1980). Oreti and Bluecliffs beaches in Murihiku were opened sporadically for harvesting from 1972, with the last open days at Bluecliffs and Oreti held in 1980 and 1993, respectively (Stace 1991; Miskelly 2016). Since the fishery closures, harvesting has been restricted to a limited take for customary purposes. Illegal harvesting of toheroa occurs at most locations (various, personal communication) but has not been quantified (Williams, Sim-Smith, et al. 2013). Despite having been protected for 40 + years, toheroa populations have, for unknown reasons, failed to recover (Williams, Ferguson, et al. 2013; Berkenbusch et al. 2015).

The biology and ecology of toheroa

Toheroa are suspension-feeding surf clams in the family Mesodesmatidae. This family also includes three other bivalves of the New Zealand endemic genus *Paphies*. These clams are pipi (*P. australis*), tuatua (*P. subtriangulata*) and the deep water or southern tuatua

(*P. donacina*). Toheroa are the largest of these four *Paphies* species, and the largest of any clam species found in New Zealand. In Murihiku, toheroa commonly grow to 100–145 mm and are sometimes recorded up to 150 mm (Beentjes 2010a, 2010b). In Taitokerau, subfossil toheroa shells commonly exceed 150 mm in length, but living specimens rarely exceed 100 mm (Cook 2010; Williams, Ferguson, et al. 2013; P. Ross, personal communication). *Paphies australis* may grow to 100 mm, *P. subtriangulata* to 80 mm and *P. donacina* to 110 mm (Cook 2010). The morphology of juvenile and adult toheroa was described by Rapson (Figure 5; 1954). Their shell is solid and ovately shaped with valves that do not completely close (Figure 6). The gaps between the valves are covered by folds of the mantle, which can appear pink in some individuals (S. Smith, personal communication). The toheroa has two long extendable siphons that protrude from the sand when feeding (Figure 5). The siphons are separate, long (relative to other *Paphies spp.*) and are highly contractile. The outer aperture of the inhalant siphon is encircled by a complex of tentacles which serve to prevent the passage of large particles into the mantle cavity (Rapson 1952). The foot is large and triangular (Figure 5) and enables the animal to burrow rapidly into the sand, with large individuals able to burrow to depths of greater than 20 cm (Kondo & Stace 1995).

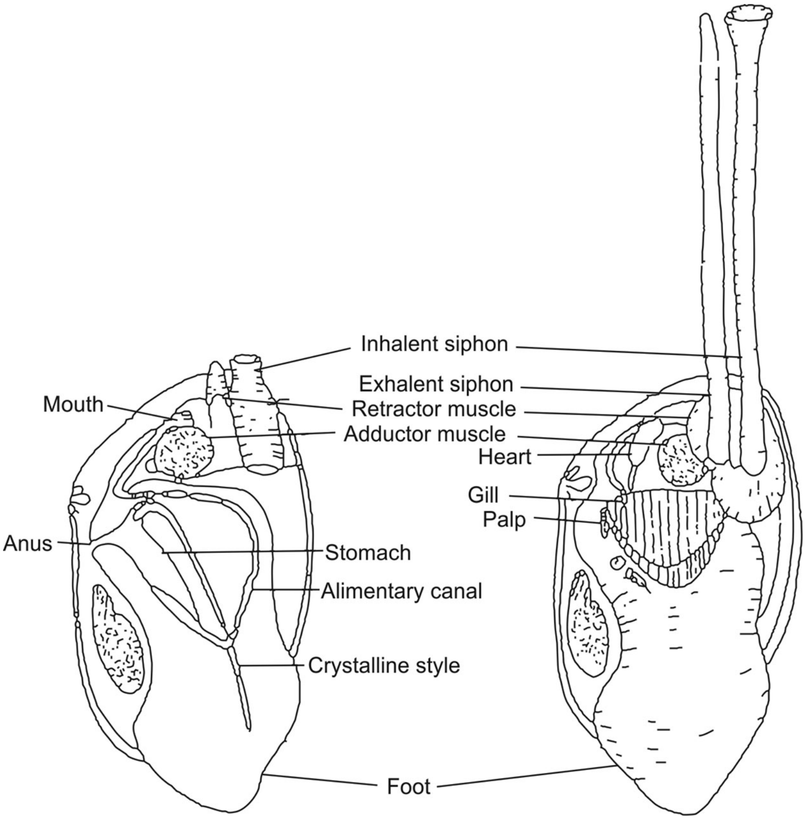

Figure 5. Internal anatomy of toheroa (*Paphies ventricosa*), with left valve and mantle removed. Figure reproduced from Rapson (1952).

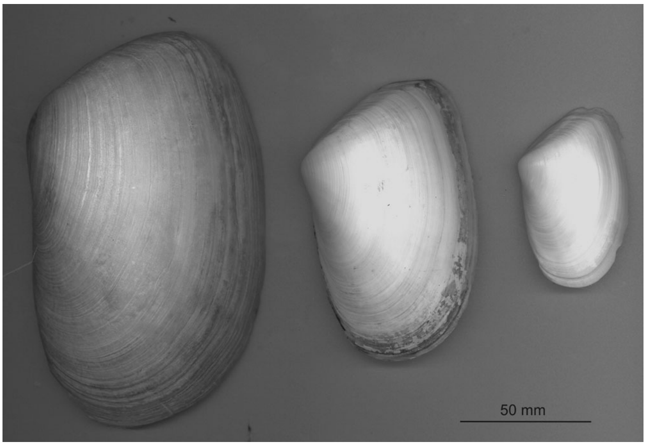

Figure 6. Left valves of toheroa (*Paphies ventricosa*) shells collected at Ripiro (153 mm), Oreti (108 mm) and Mt Maunganui (70 mm) beaches.

Reproduction and larval development

Toheroa are gonochoristic (separate sexes in different individuals and sex does not change over an individual's lifetime), although hermaphroditic individuals are very occasionally observed (Hoby 1933, Smith 2003). Smith (2003), using histology, recorded a 1:1 male to female sex ratio for toheroa at Ripiro. In contrast, the mātauranga in Taitokerau is that male toheroa are identifiable by their pink mantle colouration. These pink individuals are relatively rare and beds are assumed to be female dominated with a female to male sex ratio of approximately 80:1 (B. Searle and J. Te Tuhi, personal communication). The mātauranga is at odds to the observations of Smith (2003) who found no relationship between the sex of toheroa and their mantle colouration.

Estimations of the age and size at which toheroa reach sexual maturity vary by region. Redfearn (1974), studying northern toheroa, found that the majority of toheroa were reproductive at a length of 32 mm (<1 year) and all were mature by 47 mm. In Murihiku, Beentjes and Gilbert (2006b) found that toheroa reached sexual maturity by about 2 years (*c*. 76 mm). Toheroa reproduce by broadcast-spawning, releasing their gametes into the seawater for external fertilisation. In northern toheroa, primary gametogenesis occurs during autumn and winter, culminating in a major spawning event in early spring (Redfearn 1974; Smith 2003). Additional major spawning events may occur in summer (December–January) and autumn (March) (Redfearn 1974; Smith 2003). When conditions permit, northern toheroa appear able to spawn continuously over the entire year (B. Searle, personal communication). Like for many other temperate bivalves, food abundance and changes in water temperature are thought to primarily influence the onset and duration of spawning. Southern toheroa, which experience much cooler water and atmospheric temperatures, have two main spawning periods, the first in spring and a second in the late summer (Gadomski et al. 2015).

A high degree of synchrony in gametogenesis and spawning has been observed for both sexes. Although it appears that male and female gametes may mature at differing times, the shedding of gametes is well synchronised, a behaviour likely to increase fertilisation success in a turbulent surf zone (Smith 2003; Gadomski and Lamare 2015). The timing of spawning appears to follow environmental cues, with Smith (2003) recording major peaks in spawning activity (both *in situ* and *in vitro*) during new and full moon phases. Toheroa have been observed spawning *in situ* at Ripiro. In one instance, spawning was observed for a period of 10 minutes at night on an incoming tide when between 80 and 100 adult toheroa emerged from the sand with their siphons extended, releasing gametes in a stream from their exhalent siphon into the incoming waves (Akroyd 2002; Smith 2003). Adult females can release 15–20 million eggs during a single spawning event (Hoby 1933; Redfearn 1982). While the exact size-fecundity relationship is unknown, fecundity of female toheroa increases with size (Hoby 1933; Smith 2003).

The larvae of toheroa are planktonic. For northern toheroa, the pelagic larval duration is about 3 weeks (Redfearn 1982). For southern toheroa, the pelagic period may be closer to 6 or 7 weeks (Gadomski et al. 2015). Gadomski et al. (2015) found that the growth and development of larvae was temperature dependent with faster growth in warmer waters (20° vs. 12° or 16°C). Following a pelagic period, the larvae that are able to reach a suitable beach habitat and then settle out of the water column and into the surf zone, metamorphosing into juvenile toheroa (spat) with a length at settlement of 2 mm or less (Redfearn 1974). The morphology of embryonic and larval toheroa stages is typical of related bivalves (Booth 1977) and is described by Redfearn (1982) and Gadomski et al. (2015).

Settlement and distribution

At settlement, spat are collected in wave fronts and may be carried up the beach at any stage of the tide. During the interval of slack water just before each wave recedes from the beach, spat are able to dig themselves into the sand to a depth of 10–20 mm (Redfearn 1974). Initially, spat appear to be unable to retain good purchase in the substrate and are frequently resuspended out of the sediment. This cycle of passive transport through repeated settlement and resuspension over successive waves, tides and days gradually moves juveniles to the upper shore where they form a band just below the level of the high water mark (Redfearn 1974; Smith 2003; Beentjes 2010b; Williams, Sim-Smith, et al. 2013). Redfearn (1974) reported that juveniles are separated from the rest of the population, for the first 18 months after spatfall, either because they occupy different levels of the beach or because they form single cohort beds. However, these observations are in conflict with those made more recently at Ripiro (Williams, Ferguson, et al. 2013; P. Ross, personal communication) of mid-tide adult beds containing toheroa of all size classes.

Although it is not known whether toheroa use chemical, biological or physical cues, or a combination of these, to guide settlement, at Ripiro beach Smith (2003) found that densities of juvenile toheroa (less than 32 mm) on the upper shore were higher in areas directly above (upshore of) adult beds, compared to areas where no adult beds were present. This putative juvenile–adult association could be the result of: larval attraction to adult toheroa; hydrodynamic conditions that regularly deposit planktonic larvae, or post-settlement toheroa, at the same locations along the beach; or favourable environmental conditions that lead to higher recruitment or survival rates in certain areas. In contrast, at Oreti, toheroa of all sizes are spread along the entire length of the beach and there does not appear to be any clear relationship between juvenile and adult distribution (Beentjes and Gilbert 2006a; Beentjes 2010b). Adults, however, tend to be found at the highest densities at the southeast end of Oreti Beach where in 2009, 90% of adults were found in the first 3 km of the 17 km beach.

At both Ripiro and at Oreti beaches (but not Kāpiti-Horowhenua beaches; J. Tamihana, personal communication), larger toheroa tend to be found further down the shore, which may suggest that the degree of submergence experienced at this elevation provides the optimal feeding regime. While this distribution may expose them to greater wave forces, the growing toheroa, now with longer siphons, appear better able to maintain their position on the beach by burrowing to greater depths. It is possible that the involuntary dislodging of smaller and intermediate size toheroa by wave action may be responsible for the more variable positioning of these size classes across the intertidal zone. Where spat or juveniles become stranded above a receding tide due to cyclic changes in tidal height (lunar cycle), changes in atmospheric pressure (affecting sea level) or by waves of larger than normal amplitude, mortality due to desiccation or predation by birds (black-backed gulls, *Larus dominicanus*; red-billed gulls, *L. novaehollandiae scopulinus;* pied oyster catchers, *Haematopus finschi*) can be high (B. Searle, personal communication). Stranded toheroa are often unable to burrow into dry hard packed sand (P. Ross, personal communication), but may survive a tidal cycle (or more) unburied if atmospheric conditions are not too hot or dry (Cassie 1955; B. Searle, personal communication).

In Taitokerau, adult toheroa beds are most commonly found in areas subject to freshwater inputs, either near streams (possibly better described as ephemeral overland flows) and seeps, or where the water table lies close to the surface (Rapson 1954; Redfearn 1974; Akroyd 2002). Similarly, at Oreti, high density adult beds are most often found close to the Oreti River estuary (Beentjes 2010b). The mechanisms responsible for this freshwater association are unknown. Possible explanations include: that these areas remain moist and cool when the tide recedes (reducing the risk of desiccation); that freshwater inputs result in locally elevated concentrations of palatable phytoplankton; that the altered beach morphology associated with streams (embayments with reduced beach slope) aggregates phytoplankton and toheroa (both pre- and post-settlement); or that the freshwater inputs are modifying other physical or chemical properties of beach sediment making these areas more suitable for toheroa occupation. At present, stream associated beds at Ripiro tend to be small (5–50 m wide), dense (up to 1156 toheroa m^{-2}; Williams, Ferguson, et al. 2013), contain a range of size classes and are stable over time. During the 1970s, a period when the toheroa fishery was being closed due to declining populations, individual toheroa beds associated with streams were much larger than they are today and could occupy several hectares of beach and be hundreds of metres wide (Redfearn 1974). Away from streams and seeps, toheroa beds at Ripiro are more diffuse (>100 m across), contain toheroa at much lower densities and may be composed of a single size class (Rapson 1952; Redfearn 1974). These beds are often talked about as being transient and not persisting at a location over time, although this is not always the case (B. Searle, personal communication). Adult beds typically occur down to approximately mid-tide level (Redfearn 1974), although individual shellfish can be found all the way down to low-tide. It has been suggested that toheroa may occur subtidally, both adjacent to intertidal populations and also at locations where intertidal populations do not occur (Cassie 1951, 1955; Waugh and Greenway 1967; Greenway 1969). Despite several attempts to find these beds, using diver (Street 1971) and dredge surveys (Redfearn 1974), the existence of sub-littoral toheroa has not been recorded by scientists. However, former commercial tuatua harvesters at Ripiro have provided accounts of large toheroa occurring subtidally and have indicated that these subtidal toheroa have been used on multiple occasions to restock depleted intertidal beds. Tuatua, which typically occupy the lower intertidal and subtidal zones, can be abundant on North Island toheroa beaches. Although the distributions of these two species seldom overlap, recent surveys (2010 and 2011) found tuatua had largely replaced toheroa at Te Oneroa-a-Tōhē, and whilst toheroa densities were greater than tuatua at Ripiro, tuatua densities at this location were highest within toheroa beds (Williams, Ferguson, et al. 2013).

Growth

Growth rates of toheroa have been quantified by Rapson (1952), Cassie (1951, 1955), Redfearn (1974) and Beentjes and Gilbert (2006b) using a combination of length-frequency cohort analysis (with measurement of macroscopic shell rings) and mark and recapture data (Redfearn 1974; Beentjes and Gilbert 2006b). Kaitiaki in Taitokerau suggest that major shell rings are laid down at around September and March each year, with minor rings laid down on each full and new moon (B. Searle, personal communication). Further validation of these observations, and of earlier work, may be required before shell reading can be confidently used to assess growth and longevity (Naylor et al. 2010). In northern populations, new recruits grow initially at about 3.3 mm per month, and may reach 43 mm after 1 year, 71 mm after 2 years and 100 mm after 4–5 years (Redfearn 1974). In Murihiku, the analysis of mark-recapture data indicates that toheroa grow very fast initially, attaining a length of about 70 mm within the first year and 100 mm within 4–5 years (Beentjes and Gilbert 2006b). This contrasts with the estimates based on shell ring counts by Cassie (1955) who reported slower growth rates, with the minimum legal size (at that time; 76 mm) not attained until about 10 years. Neither dataset is capable of giving a categorical estimate of maximum age, but both are consistent with a maximum age of about 20 years as suggested by Cassie (1955).

Feeding

Toheroa are generalist filter feeders, consuming phytoplankton and organic debris which are separated in the alimentary canal (Cassie 1955). Surf diatoms of the genus *Chaetoceros* are some of the most predominant phytoplankton in exposed inshore coastal waters (Cassie-Cooper 1996; McLachlan and Brown 2006), with *Chaetoceros armatum* accounting for up to 96% of the phytoplankton in the water at Ripiro during winter months (Rapson 1954). The high-energy surf beach environment, where toheroa occur, can support a high biomass of diatoms (McLachlan and Brown 2006). Cassie (1955) observed dense phytoplankton blooms on the water surface at all beaches where toheroa were present. Heavy slicks of algae can be deposited onto the intertidal beach and at times are so thick and slippery that driving on the beach can be hazardous. Cassie (1955) hypothesised that toheroa rely on these algal blooms to obtain sufficient nutrition for growth and reproduction. Anecdotal reports suggest toheroa condition markedly improves after the autumn rains commence, coincident with the dense phytoplankton blooms, visible as a ‘greenish-brown scum on the beach and in the water’ (Hefford 1931; Cassie 1955).

Post-settlement movement

Although toheroa beds associated with streams or seeps may persist at a location over time (Rapson 1954; Redfearn 1974), bed position within a location can be quite variable. The along shore relocation of entire beds by 30 m or more has been observed over a single night (Redfearn 1974). Although the triggers of mass toheroa relocation are unknown, there is evidence that a variety of factors may influence bed movement and stability. For example, bed relocation has been recorded following storms (Akroyd 2002), and kaitiaki report that toheroa beds must move in response to the discarding of harvest-damaged (dead or dying) toheroa within a bed. Consequently, many Māori disapprove of harvesting (or survey) practises that damage unharvested animals or involve the processing of toheroa, or discarding of their waste, on the beach or near a toheroa bed.

Tagging experiments have shown that while the majority of toheroa are fairly sedentary, some individuals are highly mobile, moving between beds and over several kilometers (Greenway and Allen 1962). There is, however, some uncertainty around the relative importance of passive versus active movement in regulating post-settlement movement. While there is little doubt that toheroa may be involuntarily dislodged and moved by heavy swells, they have also been observed using the swash of waves to move up and down the beach in what has been assumed to be an active behaviour (Mestayer 1921; Redfearn 1974; Ellers 1995a, 1995b). Kaitiaki in Taitokerau have suggested that beds may move as often as every tidal cycle to track the cyclic pattern of changing tidal heights. It is this tidally driven movement, coupled with variability in atmospheric pressure and wave climate, which has been implicated in generating mass stranding and mortality events. Toheroa are often observed, particularly on the incoming tide, emerging out of the sand, with their siphons extended just ahead of a swash front for forward movement, or after a swash front for backward movement. As the swash wave passes over, toheroa release their foot from the substrate and are moved in the direction of the flow. As the wave recedes, the toheroa rapidly burrow back into the sediment (Redfearn 1974). Mestayer in 1921 wrote

> at one moment you will see the bare sand as the wave comes in, and immediately it starts to recede, simultaneously and in hundreds of thousands according to the size of the beds, the toheroa emerge from the sand end first, and go down with the receding water, and according to the set of the tide, either up or down the beach.

The mechanism facilitating the synchronicity of these movements is unknown. Active swash riding, in response to sound stimuli, has been observed in *Donax variabilis*, a North American surf clam (Ellers 1995a). These clams were observed riding only the largest 20% of waves (Ellers 1995b), a behaviour that maximises distance travelled and minimises the number of swash rides (and therefore exposure to predation) required per migration. An alternative hypothesis is that the ejection of toheroa from the sediment may be an involuntary consequence of increased pore water pressure ahead of an advancing swash front. This explanation may account for up-beach swash riding only. Swash riding has been observed to occur both day and night, with daytime swash riders vulnerable to predation by gulls (P. Ross, personal communication).

Sources of post-settlement mortality

Post-settlement mortality of toheroa is likely to be caused by numerous factors, both natural and anthropogenic (Table 1). Mass mortalities of toheroa populations appear to be relatively common and have usually occurred during summer months in northern populations (Williams, Sim-Smith, et al. 2013), and more frequently during winter months in the south (Eggleston and Hickman 1972). Although many mass mortalities have been observed (Cassie 1951; Redfearn 1974; Akroyd et al. 2002), few have been thoroughly investigated and there is in general only speculation as to the causes of individual events (Eggleston and Hickman 1972; Hine and Wesney 1997; Akroyd 2002; Ross et al. 2017). The most likely sources of post-settlement mortality were reviewed by Williams, Sim-Smith, et al. (2013) and include desiccation of individuals stranded above the upper intertidal during periods of hot weather; winter southerly storms in Murihiku that may dislodge toheroa, with the extreme cold then slowing or reducing their ability to rebury, making them vulnerable to exposure (freezing) and predation; sediment instability resulting in smothering or exposure to predation; toxic algal blooms (TAB) causing mortality via smothering and anoxia (as a result of the biological oxygen demand of senescent cells); predation by birds, crabs, fish and rays; mortality caused by beach vehicle traffic; human harvesting (formerly commercial and recreational, presently customary and illegal) and disease. Until recently, no specific diseases or parasites were known to afflict toheroa (Hine and Wesney 1997). However, a recent examination of toheroa at Ripiro recorded incidences of both gas-bubble disease and *Rickettsia*-like organisms (RLOs; Ross et al. 2017), a group of bacteria frequently associated with shellfish mass mortality events (Malouf et al. 1972; Wu et al. 2003; Zhu et al. 2012; Carvalho et al. 2013). Agrichemicals have also been implicated in toheroa mortality. In the 1970s, the pesticide Dieldrin, which is considered highly toxic to fish and aquatic invertebrates (Johnson and Finley 1980; Hoke et al. 1995), was used to control black beetle (*Heteronychus arator*) in pine forest plantations. It has been reported that toheroa have not grown near areas that were sprayed or where the pesticide was stockpiled on the beach prior to application by top dressing (Smith 2013; B. Searle, personal communication). Kaitiaki have also observed the disappearance of toheroa beds from areas adjacent to commercial forestry operations. These losses were attributed to the degradation of water quality in the streams flowing onto the beaches near toheroa beds (Smith 2013).

The biology of toheroa, like that of other intertidal surf clams, makes them highly vulnerable to overexploitation and collapse. Being intertidal they are readily accessible to fishers and their harvest incurs very low operating costs (McLachlan et al. 1996). For toheroa, human harvesting was undoubtedly an ecologically significant source of mortality before commercial and recreational harvesting ceased and a major contributor to the collapse of the fishery. However, in the present day, the significance of human harvesting (customary and illegal) as a source of mortality relative to other factors has not been quantified (Williams, Sim-Smith, et al. 2013). Based on our observations and communications with kaitiaki, honorary fisheries officers and residents at Ripiro, and to a lesser extent at other locations, it would appear that the levels of human harvesting are significant. Illegal harvesting is common with poaching events ranging in size from residents or visitors ‘just getting a feed every now and then’, which may be once a year or once a week, to large-scale illegal harvesting for the black market. Current harvest levels (illegal and authorised customary take) are largely unquantified and it is likely that the importance of harvest-related mortality varies between locations. This may explain regional differences in population dynamics and the sequence of events leading up to regional fisheries closures.

Current population structure

From the available time series data for the six main toheroa populations (Te Oneroa-a-Tōhē, Ripiro, Te Oneone Rangatira, Kāpiti-Horowhenua, Oreti and Bluecliffs), it is evident that there has been a general decline in the abundance of toheroa over time (Figure 4; Beentjes and Gilbert 2006a, 2006b; Williams, Sim-Smith, et al. 2013, Williams, Ferguson, et al. 2013). There is a great deal of variation in estimates of abundance, and not all populations have followed the same fluctuation trends. This again suggests that there may be different local drivers acting on populations rather than a major overriding influence at a national level. The overall downturn observed has not been as marked in some populations as others. Ripiro appears to hold greater densities of juveniles and young adult toheroa than other beaches, suggesting that recruitment is more consistent there than elsewhere (Figure 7). However, for unknown reasons very few large adult toheroa are found at Ripiro. During the 2010 survey, only 3% of the sampled population was larger than 75 mm (Figure 7; Williams, Ferguson, et al. 2013). At Te Oneroa-a-Tōhē and on the Kāpiti-Horowhenua coast toheroa are now scarce (Williams, Sim-Smith, et al. 2013; Newcombe et al. 2014; J. Tamihana, personal communication). Strong recruitment events are routinely recorded at Te Oneroa-a-Tōhē (L. Austen, personal communication), but recruits rarely persist into adulthood and beds containing animals of a harvestable size are either largely absent, or are a closely guarded secret (L. Austen, personal communication). Conversely, the population structures at Oreti and Bluecliffs are characteristically bimodal, with a strong adult mode of toheroa greater than 90 mm in length, very few intermediate size toheroa, and a juvenile mode of variable strength (Figure 7; Beentjes and Glibert 2006a, 2006b; Beentjes 2010a, 2010b). Beentjes (2010b) suggested that the likely explanation for this is that mortality of juveniles is high and relatively few survive through to the sub-adult size (40–75 mm). Those that do survive grow rapidly and the strong mode between 100 and 140 mm represents the accumulation of multiple cohorts. At Bluecliffs Beach, in Te Waewae Bay, significant beach erosion and loss of sand since the mid-1980s has exposed underlying gravel and cobble substrates, significantly reducing the availability of habitat suitable for toheroa (Beentjes and Glibert 2006a; Beentjes 2010a).

Factors preventing the recovery of toheroa

Despite 40+ years of protection, toheroa populations across New Zealand have, for unknown reasons, failed to recover. Similar patterns have been observed in other large, long-lived and good tasting intertidal bivalves worldwide (McLachlan et al. 1996). Surf clam fisheries, which tend to be more recreational or artisanal than commercial, are notoriously difficult to manage since numbers of harvesters cannot usually be controlled and exploitation must be limited solely by size, bag limit, season or area restrictions. In comparison to rocky reef environments where there are numerous examples of population recovery following the introduction of harvesting restrictions (Costello 2014), the

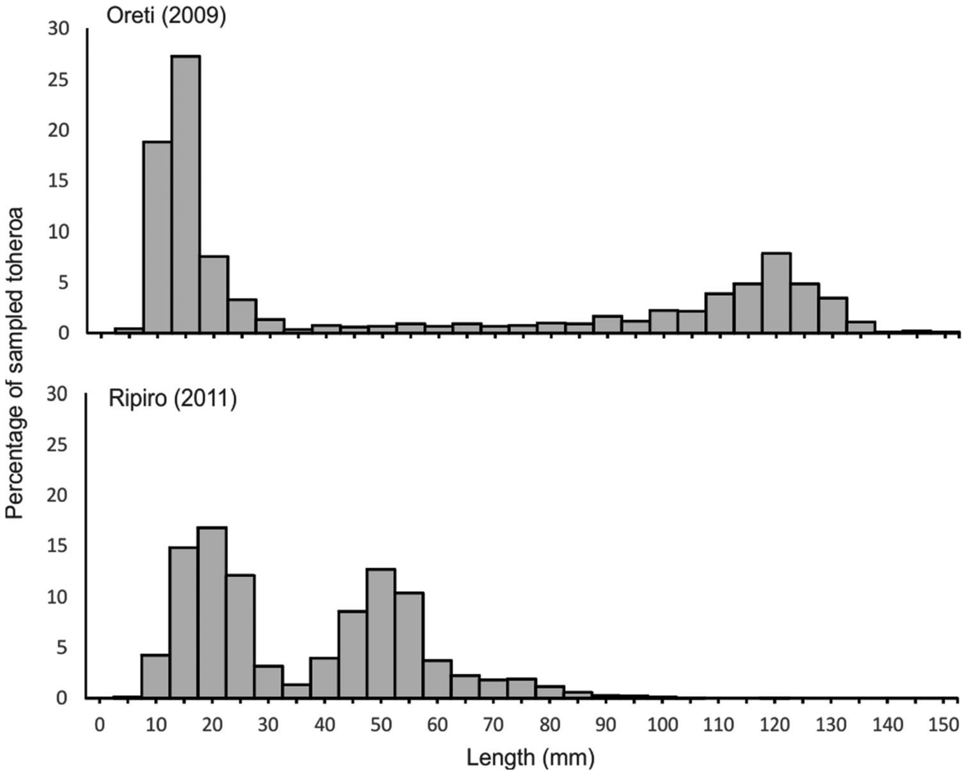

Figure 7. Length-frequency distribution of toheroa sampled during the 2009 at Oreti ($n = 1221$; Beentjes 2010b) and in 2011 survey at Ripiro ($n = 7578$, Williams, Ferguson, et al. 2013).

managed recovery of open coast beach species is rare (McLachlan et al. 1996; Ferguson et al. 2015). Where post-exploitation populations have failed to recover, continued overharvesting as well as a range of other threats including off-road vehicles, pollution, coastal engineering and coastal development have been implicated (McLachlan et al. 1996). Heasman et al. (2012) and Williams, Sim-Smith, et al. (2013) reviewed the factors considered most likely to be preventing the recovery of toheroa. Climate and weather, food availability, TABs, vehicle activity, water quality and changes in land use were identified as possible environmental factors (Table 1). Given the recent detection of gas-bubble disease and RLOs in toheroa (Ross et al. 2017), these ailments may be added to this list. A loss of stewardship ethic among Māori, the negative effects of preferential harvest of large toheroa and negative features of the customary harvest system were identified as possible human factors standing in the way of recovery (Smith 2013). Again, given our recent observations, it is likely that illegal harvesting may also be an important factor, particularly in Taitokerau where large toheroa are now uncommon. Of the factors mentioned above, the manner in which vehicles are driven on and have access to toheroa beaches, the way that lands adjacent to these beaches are used and levels of continued harvesting are seen as three areas where human impacts could be mitigated. Conversely, the effects of climate on food, larval supply or the occurrence of TABs are seemingly beyond immediate human control.

Vehicle effects

Studies in Australia, South Africa and the United States have documented the effects of vehicle activity on beach fauna. Impacts have included mortality in surf clams (*Donax serra* and *D. deltoids*) as a direct consequence of crushing (Van der Merwe and Van der Merwe 1991; Schlacher et al. 2008), reduced species richness and diversity of intertidal communities (MacLeod et al. 2009) and local extinctions and regional declines in vehicle sensitive species (Hubbard et al. 2014). Many of New Zealand's beaches, including Te Oneroa-a-Tōhē, Ripiro, the Kāpiti-Horowhenua beaches and Oreti, are designated state highways and are subject to high levels of vehicle traffic. By law, speeds are limited to 100 km per hour and erratic driving (loss of traction and 'doughnuts') is forbidden, although the extent to which this is monitored and managed varies between beaches. There is strong evidence that beach traffic can cause toheroa mortality (Redfearn 1974, Brunton 1978, Hooker and Redfearn 1998, Moller, Moller, et al. 2009), either directly through crushing, or indirectly through exposure, which increases the risk of desiccation or predation by birds. Moller, Moller, et al. (2009) found that low levels of vehicle activity do not cause significant mortality of adult toheroa, but even a single vehicle pass can cause significant mortality in juveniles, particularly those living high on the beach in soft sand. Consequently, beach events involving large numbers of vehicles, for example, beach fishing competitions or off-road vehicle races could result in high levels of juvenile mortality (Moller, Moller, et al. 2009).

Changes in land use

The effects of changing land use on coastal and nearshore ecosystems are well studied internationally and include disruption to the hydrologic cycle (Huber et al. 2008), accelerated soil erosion (Lohrer et al. 2004; Baptista Neto et al. 2013) and water quality deterioration (Leh et al. 2011; Ramos-Scharrón, et al. 2015; Seers and Shears 2015). Landscape modification has resulted in the degradation of ecosystems including coral reefs (Stender et al. 2014), estuaries (Pratt et al. 2014) and rocky reefs (Walker 2007; Pulfrich and Branch 2014). The effects of land use on surf beaches are less well studied (Schlacher et al. 2015).

In New Zealand, the land surrounding Te Oneroa-a-Tōhē, Ripiro and Te Oneone Rangatira was originally covered in native broadleaf forest (Smale et al. 1996). Much of this land was cleared by Māori 500–700 years ago (Coster 1989), with large areas of the remaining native vegetation removed by early European settlers (Cockayne 1911; Bacon 1976; McKelvey 1999). Large-scale planting of exotic marram grass (*Ammophila arenaria*) and tree lupin (*Lupinus arboreus*) was instigated in the early 1900s in an effort to stabilise sand dunes. Marram grass in particular altered the morphology of sand dunes and beach hydrology (Esler 1970; Hesp 1999; Müller 2011). In recent years, efforts have been made, across much of New Zealand, to restore natural dune plant vegetation. Numerous restoration programmes have focused on planting spinifex, pingao and sand tussock (*Poa billardierei*) for cultural, aesthetic and recreational values as well as conservation and biodiversity considerations (J. Te Tuhi & B. Young, personal communication; Bergin and Kimberley 1999).

From the 1950s to 1970s, much of the land adjacent to Te Oneroa-a-Tōhē (Aupouri State Forest), Ripiro (Poutu Forest) and Te Oneone Rangatira (Woodhill Forest) in Taitokerau and Waitarere (Waitarere Forest) and Tangimoana Beaches (Tangi Moana Forest) on the Horowhenua coast was converted to pine forest (*Pinus radiata*). Williams, Sim-Smith, et al. (2013) discuss in detail the consequences of afforestation, which include changes in groundwater chemistry (Staaf and Olsson 1994; Quinn et al. 1997), a reduction in soil moisture levels, water table height (Cromarty and Scott 1996; McKelvey 1999; Huber et al. 2008) and reduced freshwater seepage flowing onto Te Oneroa-a-Tōhē and Ripiro beaches. Ground water is also diverted away from coastal streams to support agriculture at some locations, further reducing freshwater inputs to the coast (P. Ross, personal communication). Many streams that formerly flowed onto the toheroa beaches of Taitokerau are no longer there (Williams, Sim-Smith, et al. 2013). Williams, Sim-Smith, et al. (2013) compared the number of water courses on historical versus modern day topographic maps and showed a reduction of 64% (53 of 83) at Te Oneroa-a-Tōhē and 40% (6 of 15) at Ripiro. Given the clear relationship that exists between toheroa beds and points of freshwater input onto beaches in northern New Zealand (Rapson 1954; Redfearn 1974; Williams, Sim-Smith, et al. 2013; Williams, Ferguson, et al. 2013), it is conceivable that reductions in freshwater flow may have contributed to the decline of toheroa. However, as the specific mechanism(s) behind the relationship are unknown, there can be no certainty, without further research.

Human harvesting

Worldwide, many populations of marine species, including surf clams, continue to decline despite legislation providing protection, mainly due to poaching and/or accidental mortality (McLachlan et al. 1996). Examples of ‘protected’ species where illegal harvesting is preventing recovery include bivalves and gastropods (Katsanevakis et al. 2011), sea turtles (Koch et al. 2006), Atlantic bluefin tuna, sharks and other fish species (Agnew et al. 2009; Techera and Klein 2011). For toheroa, much of the customary harvest is undocumented and the illegal harvest unquantified (Heasman et al. 2012; Williams, Sim-Smith, et al. 2013). Based on our recent observations in Taitokerau, illegal harvesting of ‘protected’ toheroa is widespread, frequent and has in some cases resulted in the reduction and disappearance of adult toheroa beds (P. Ross and J. Cope, personal communication). In Murihiku, a recent estimate suggests that the combined customary and illegal harvest of toheroa could easily account for as much as 13–50% of the toheroa population each year (Heasman et al. 2012).

Knowledge gaps and future research

The fauna of ocean coast beaches are cryptic and mobile and easily overlooked by ecologists, thus surf clams are generally understudied (McLachlan et al. 1996). Recruitment (including the role of nearshore hydrodynamics in settlement processes), density-dependent processes (that may lead to variation in growth, mortality and recruitment) and incidental mortality and disturbance associated with harvesting are topics that have previously been identified as deserving special consideration for future surf clam research (McLachlan et al. 1996). Since the collapse and closure of the toheroa fisheries, much of the research effort relating to this species has been invested in abundance surveys and stock assessments (reviewed by Beentjes and Gilbert 2006a, 2006b; Williams, Sim-Smith, et al. 2013). Studies furthering our understanding of toheroa life history and the factors preventing their recovery have been limited. Where researchers have conducted empirical studies, the knowledge gained has contributed to subsequent assessments of the possible obstacles to recovery (Heasman et al. 2012; Williams, Sim-Smith, et al. 2013). The authors of these empirical studies have in some cases suggested management actions to support restoration, for example, traffic management (Moller, Moller, et al. 2009) or temporal management of cultural harvest (Smith 2003). These suggestions have not been implemented. Population surveys will continue to be important in assessing the effectiveness of future management regimes, particularly where survey methodologies are comparable in time and space (Figure 4). However, on their own, surveys will not facilitate the recovery of toheroa or even necessarily provide the information needed to inform management and restoration efforts.

Survey data showing regional variation in population structure (Figure 7; Williams, Sim-Smith, et al. 2013) indicate that there are probably different local drivers acting on different populations. Some populations appear to be recruit limited (Murihiku and Kāpiti-Horowhenua) while in others the obstacles to recovery appear to be acting at later life stages. Understanding where and how life history bottlenecks are acting will be key to developing area specific management plans to support toheroa restoration. The geographical range of toheroa is subtropical to subantarctic (Figure 1) implying a degree of flexibility to large-scale oceanographic and atmospheric variation. Conversely, toheroa distribution within and among beaches can be highly variable indicating very specific habitat requirements. Together, these macro and mesoscale patterns suggest that the physical beach environment might be a more important determinant of beach habitability than climate, or that habitat variability is interacting with climate to determine distribution patterns.

It is still not clear what makes for optimal toheroa habitat, particularly, why toheroa occur where they do, or why their distribution patterns and population structures vary between northern and southern beaches. There is clearly an association between toheroa and freshwater inputs in northern New Zealand. There is currently no understanding of whether this is a response to the freshwater itself, the effects of freshwater on environmental parameters (such as grain size or beach temperature) or the beach morphology associated with streams retaining toheroa and delivering their food. Additionally, the fact that there is still uncertainty around the existence of sub-littoral toheroa, more than half a century after the possibility was first raised by Cassie (1951), is indicative of the paucity of our ecological knowledge of this species. The slow progress made in filling these gaps may result from the many difficulties associated with studying surf beach ecosystems (McLachan and Brown 2006). With a more complete understanding of what constitutes optimal toheroa habitat, and an appreciation of changing land use over time, it may be possible to determine if habitat components have been lost from areas where toheroa formerly thrived. With this knowledge, efforts could be made to adjust environmental management regimes to rehabilitate key habitat characteristics in support of restoration, for example, by altering the types of vegetation growing adjacent to key toheroa beds to restore the flow of groundwater to the coast.

The relative importance of self- versus external recruitment for the maintenance and recovery of toheroa populations is unknown. For species such as toheroa, which occur in fragmented populations (Figure 1), the exchange of individuals (connectivity) between populations is considered critical for population stability (Cowen et al. 2007). For toheroa, connectivity occurs solely via a dispersive larval phase (Ross et al. 2009). A possible consequence of the population decline and range contraction observed in toheroa is a decrease in among-population connectivity (Jones et al. 2007). Estimating connectivity is extremely challenging because the nature of marine ecosystems generally precludes the direct measurement of larval exchange among populations (Cowen et al. 2007). Dispersal of toheroa larvae is likely to be at the scale of 10s to 100s of km rather than 1000s of km (Sutton and Bowen 2011). Consequently, connectivity among all toheroa populations would not be expected (Figure 1). Having a better understanding of larval exchange among toheroa populations may help explain the observed population dynamics of toheroa, help with predicting their responses to environmental change and management regimes, and assist with designing conservation strategies to facilitate restoration through connectivity and larval recruitment.

The reseeding of toheroa populations with hatchery-reared spat (or juveniles) has been suggested as an alternative management approach for restoration (Newcombe et al. 2015). There is widespread interest in toheroa aquaculture, particularly from Māori groups interested in restoration of this taonga and in culturing toheroa as a commercial venture (various, personal communication). These two interests may ultimately be complimentary as the development of commercial toheroa aquaculture could facilitate the production of spat for the large-scale reseeding and enhancement of natural populations. Newcombe et al. (2015) discuss the challenges associated with adapting existing culture techniques to suit species living in high-energy environments. Redfearn (1982) and more recently Mandeno (1999), Smith (2003) and Gadomski et al. (2015) developed spawning and larval rearing techniques, and culture through to post-settlement size (*c.* 30 mm) was achieved at the Mahanga Bay shellfish hatchery in Wellington in the 1980s (P. Redfearn personal communication). At that time, toheroa were not considered to be of commercial interest and development of the species for aquaculture was not pursued.

While toheroa aquaculture does appear viable, a good understanding of the environmental factors and life history bottlenecks preventing the recovery of wild populations is essential before assessing the utility of aquaculture for enhancement and restoration. For example, reseeding for restoration is unlikely to be effective at beaches where beach habitat is no longer suitable (Beentjes et al. 2006) or where recruitment rates are high but survival past later life stages is low (i.e. Ripiro and Te Oneroa-a-Tōhē; Figure 7). Conversely, at beaches where populations are recruitment limited, reseeding may overcome natural obstacles to recovery. More information on natural recruitment patterns, population structure and ecology is required before embarking on reseeding projects.

The discovery of RLOs and gas-bubble disease in toheroa (Ross et al. 2017) is of concern and may to some extent help explain contemporary population dynamics and mass mortalities that have been recorded in toheroa and tuatua in Taitokerau (Williams, Sim-Smith, et al. 2013). More work is required to understand the interactions between these two conditions and to determine their distribution across species, space and time. The detection of RLOs will likely have implications for toheroa aquaculture and for the translocation of toheroa, and other shellfish, between beaches for reseeding or enhancement purposes. The spread of pathogens to unaffected populations should be avoided if possible.

Current management options

While there is a lot we do not know about the ecology of toheroa and the major sources of toheroa mortality, there are steps that could be taken immediately to help with restoration and management efforts (Table 1). For example, beach traffic can cause toheroa mortality, particularly in juveniles. In South Africa, motorised vehicles were banned from most beaches between 2001 and 2002 (DEAT 2004), primarily for the protection of endangered species (birds and turtles). The ban was not well received by off-road enthusiasts, and some other beach users, but did result in measurable ecological benefits for intertidal beach invertebrates (Lucrezi et al. 2014).

Removing vehicles from New Zealand beaches may not be a realistic, popular or desirable option. However, modifying driver behaviour at certain times and on certain sections of beach probably is. Schlacher et al. (2008) investigated the impacts of vehicle activity on the surf clam *Donax deltoides* in Australia and found that driving modes and patterns were key factors in determining clam mortality and physical habitat disturbance. Speed restrictions that alter driver behaviour could be introduced in key areas (adult beds and high recruitment areas) and beach users provided with recommendations for driving behaviour around important toheroa habitat (e.g. streams). Limiting the mass use of beaches by vehicles during the periods of high recruitment (late spring – early summer and early autumn; Redfearn 1974; Smith 2003; Gadomski et al. 2015), for example, in fishing contests, could reduce juvenile mortality and support recovery in recruit limited populations. Moller et al. (2009b) discuss seasonal or spatial closures and the insertion of physical barriers as a way of discouraging vehicles from transiting along the upper intertidal zone where juvenile toheroa are most abundant. Providing a rationale for any driving recommendations or regulations will undoubtedly be key to attaining buy-in and compliance from beach users.

Despite their status as New Zealand’s most protected shellfish, illegal harvesting of toheroa is widespread and frequent. As toheroa are no longer a commercially harvested species, the motivation, or commercial pressure, to enforce fisheries regulations is probably less than in other frequently poached kai moana, for example, scallops, paua or crayfish. Toheroa also occur on isolated stretches of coastline and there is a reliance on honorary (volunteer) fisheries officers and local communities to police fisheries regulations. It is clear that the resourcing of toheroa fisheries management has been insufficient to prevent widespread illegal harvesting. Alternative management approaches involving education and community involvement may be more successful. Information panels (interpretive signs) at major beach access ways explaining how to differentiate between toheroa and tuatua should be a minimum first step and might reduce rates of accidental harvesting. Similarly, providing the rationale around why toheroa harvesting (without a customary permit) is prohibited may raise some awareness around the significance and plight of toheroa and reduce intentional illegal harvesting. Involving local communities in toheroa research and management may result in an increased stewardship ethic, a greater willingness to comply with harvesting regulations and more efficient enforcement through community peer pressure and the reporting of illegal activity. The communities (both Māori and Pakeha) at the toheroa beaches are for the most part enthusiastic about toheroa restoration but in some cases feel abandoned by fisheries managers and unable to participate or contribute to the restoration process (various, personal communication; Memon et al. 2003; Gnanalingam and Hepburn 2015).

As kaitiaki of the whenua (land), the moana (sea) and kai (food), and as issuers of customary permits for the collection of protected species, Māori have an important role to play in ensuring the sustainability of toheroa for future generations. This is somewhat ironic, given that Māori were largely excluded from the management process for the duration of the commercial and recreational fisheries (Murton 2006). It was only after the fisheries had collapsed and interest from other user groups diminished, that responsibility for toheroa management was passed back to tangata whenua, the traditional managers of this resource. During this post-fishery period, toheroa populations have not recovered and there is a perception from within Māoridom that in its present form, the customary permit system does not promote sustainable customary harvest (Smith 2013).

In Taitokerau, one key area of concern is that resolutions issued at the iwi (tribe) level aiming to protect the toheroa resource, for example by placing rāhui (temporary closures) on harvesting, do not necessarily preclude individual hapu (subtribe) or marae from within that iwi, or from another iwi elsewhere, continuing to issue permits for customary harvest. Consequently, permit issuers may have limited or no connection to the beach, have little knowledge of the current status of the resource and little regard for its sustainability (Smith 2013). An alternative system may be required where customary permits can only be issued and executed by kaitiaki with a good understanding of the condition of local toheroa populations. Financial resourcing of kaitiaki positions, collaboration with fisheries managers and science providers and better co-operation among and within iwi will be required for such a system to work. Kaitiaki would then be in a position to monitor toheroa beds and would have the mana (status and authority) to allocate and enforce levels of customary harvest that would not compromise sustainability. Rāhui could be declared if toheroa populations were in decline or thought to be particularly vulnerable (Table 1). In Murihiku, Māori, Regional Council, the Department of Conservation and Police all play a part in toheroa management (R. Trainor, personal communication). In the far north (Te Hiku o Te Ika), the recent formation of the Te Oneroa-a-Tōhē Beach Board, with equal iwi and local authority membership, may represent an opportunity to develop this concept of a more collaborative, centralised and innovative management strategy (Te Hiku Claims Settlement Bill 2015).

Conclusions

In recent times, the contribution of environmental managers and marine scientists to toheroa management has largely been to conduct surveys that monitor the status of the discrete populations. Toheroa have not recovered and it is clear that the current management regime is not geared towards restoration. Unfortunately, the research community has not been able to provide any clear direction for alternative management approaches. There are too many possible explanations for the continued demise of toheroa and too little research has been conducted to address the uncertainties outlined above. More research is needed. But first, efforts must be made to overcome the distrust that can exist between Māori, resource managers and the research community. Researchers have a history of exploiting Matāuranga Māori (Māori knowledge), failing to report back to communities on the findings of their research, and tend to focus on research outputs rather than environmental outcomes for impacted communities (Waitangi Tribunal 2011; Broughton et al. 2015). Conversely, it can be difficult for researchers to work with Māori as the process of engagement and relationship building, which is crucial to collaborative research, can be intimidating and rarely fits within the short timeframes available for formulating research proposals or conducting research. As a consequence it can be challenging for non-Māori researchers to work on culturally important species and for Māori to access scientific knowledge to support restoration and management in their rohe.

If efforts to restore toheroa are to be successful, it will undoubtedly require collaboration and a willingness by all parties to step outside their traditional comfort zones. A better flow of information among interested groups is needed and may eventually build trust and allow for the development of more effective working relationships. Researchers working alongside local experts and kaitiaki will lead to better research outcomes. Engagement with local communities and resource users will lead to a better understanding of the human components of this ecological problem; community 'ownership' of toheroa restoration; and better uptake and enforcement of regulations or management plans. Importantly, collaboration and engagement will build capacity and knowledge within these coastal communities. As a consequence, communities will be empowered to take a leading role in the management of their rohe and to continue collecting ecological information beyond the limited timeframes usually associated with academic research projects.

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SHORT COMMUNICATION

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First detection of gas bubble disease and *Rickettsia*-like organisms in *Paphies ventricosa*, a New Zealand surf clam

P M Ross[1] | A Pande[2] | J.B Jones[2] | J Cope[1] | G Flowers[1]

[1]University of Waikato, Coastal Marine Field Station, Tauranga, New Zealand
[2]Animal Health Laboratory, Ministry for Primary Industries, Upper Hutt, New Zealand

Correspondence
Phil Ross, University of Waikato, Coastal Marine Field Station, Tauranga, New Zealand.
Email: phil.ross@waikato.ac.nz

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Gas bubble disease (GBD) is a non-infectious condition in aquatic organisms caused by supersaturated levels of total dissolved gas (TDG) in water (Bouck, 1980). GBD is analogous to "the bends" (decompression sickness) in human scuba divers (Barratt, Harch, & Van Meter, 2002). In fish, the disease can manifest externally as bubbles on the eyes, opercula, fins, body and mouth regions, and internally as bubbles in the blood and on gill arches (Espmark, Hjelde, & Baeverfjord, 2010). GBD has also been reported in invertebrates, including in shrimp, blue crab, oysters and clams (Johnson, 1976; Lightner, Salser, & Wheeler, 1985; Malouf, Keck, Maurer, & Epifanio, 1972). The effects of GBD can range from mild to lethal depending on the level of TDG supersaturation, the species affected, life history stage, animal health, depth distribution and water temperature (Beeman et al., 2003; Johnson, 1976; Smiley, Drawbridge, Okihiro, & Kaufmann, 2011).

Gas bubble disease is frequently observed in finfish aquaculture, where poor control of oxygenation can result in extreme saturation of TDG in water (Smiley et al., 2011). Gas bubble disease is less common in the wild, but has been recorded in fish living in the heated water discharges from power stations or below plunge pools from dams and spillways (Gulliver & Groeneveld, 2010; Mcinerny, 1990). Relative to finfish, there are very few accounts of GBD in invertebrates, particularly in the wild (Moiseev, Moiseeva, Ryazanova, & Lapteva, 2013). Malouf et al. (1972) described GBD in oysters and clams held in heated running sea water. In this instance, GBD caused blisters to form on the mantle and valves of oysters (*Crassostrea virginica* and *C. gigas*), and for gas bubbles to form on the gill filaments of both oysters and clams (*Mercenaria mercenaria*).

In November 2016, blisters were observed under the periostracum on the outer valve surfaces of *Paphies ventricosa* (toheroa; Figure 1) at Ripiro Beach on the west coast of northern New Zealand. Although prevalence rates of blisters were not quantified, they were observed on a high proportion of toheroa across approximately 40 km of coastline. Toheroa are a species of large intertidal surf clam endemic to New Zealand (Williams, Sim-Smith, & Paterson, 2013). At the start of the 20th century, extensive toheroa populations were present on exposed west-facing surf beaches of northern and central New Zealand and on the south coast of the South Island. Increased popularity and harvesting pressure from the early 1900s by both commercial and recreational fisheries depleted the resource (Murton, 2006; Williams, Sim-Smith, et al., 2013). By the mid-20th century, toheroa populations declined to levels where their commercial harvest was no longer viable. All commercial harvest ceased by 1969 and regional recreational fishery closures occurred from 1971 to 1980 (Williams, Sim-Smith, et al., 2013). Despite having been protected for between 35 and 45 years, toheroa populations nationwide have, for unknown reasons, failed to recover (Williams, Ferguson, & Tuck, 2013).

Following the detection of blistered toheroa shells at Ripiro Beach, ten live toheroa, ranging in length from 59 to 91 mm, were collected and sent to the Ministry for Primary Industries (MPI) Animal Health Laboratory (AHL) to be examined for the presence of exotic and endemic pathogens or other signs of ill health. After gross examination and dissection of shell blisters, tissue samples were fixed and embedded for histology; DNA extracted and screened; and the mantle and gills swabbed onto agar media for general bacterial culture. This examination revealed that blisters were located both under the periostracum and under the outer calcite layer above the foliate conchiolin, giving the blisters a thin translucent white cap of calcite. There was no evidence of gas bubbles in other tissues. It was concluded that GBD, as described by Malouf et al. (1972), was the cause of the observed blisters. The exact mechanisms by which toheroa may have been exposed to supersaturated levels of TDG in water or the reason that bubbles appear to have only formed on the outer surfaces of toheroa shells are unknown. Current hypotheses regarding exposure to TDG supersaturation include the rapid heating of sea or groundwater percolating through hot intertidal sand (up to

FIGURE 1 Blisters under the periostracum and outer calcite layer of the outer valve surfaces of a toheroa (*Paphies ventricosa*; shell length = 80 mm)

40°C; J. Cope, *unpublished data*) or the heating of sea water retained within the shell and tissues of the toheroa buried in sun-heated sand while the tide is out. For example, if sea water with an initial temperature of 18°C was heated to 30°C within a toheroa, oxygen solubility would drop from 7.48 to 6.09 mg/L, exposing the toheroa to oxygen supersaturation of 122%, a level sufficient to cause GBD-related symptoms in a range of fish species (Geist, Linley, Cullinan, & Deng, 2013; Smiley et al., 2011; Weiland, Mesa, & Maule, 1999).

In addition to the identification of GBD in toheroa, bacterial isolation identified several species of aquatic environmental bacteria. This included *Rhanella* sp., a bacterium associated with gut flora and sand that is not commonly seen in New Zealand shellfish (*pers.obs.*). *Rickettsia*-like organisms (RLOs) were also present in the gills of all ten toheroa examined, where they disrupted gill architecture. RLOs are obligate, intracellular parasites associated with a variety of vertebrate and invertebrate hosts (Gollas-Galván, Avila-Villa, Martínez-Porchas, & Hernandez-Lopez, 2014). Despite their importance as causative agents of severe mortality outbreaks in farmed aquatic species, little is known about their life cycle or host range (Ferrantini et al., 2009). RLOs were first detected in marine bivalves in the 1970s (Harshbarger, Chang, & Otto, 1977). They are typically transmitted directly between hosts via water-borne transmission and may be found free within host cell cytoplasm or within intercytoplasmic vacuoles (Friedman & Crosson, 2012; Travers Boettcher Miller, Roque, & Friedman, 2015). Although RLO infections in teleost fish have been extensively studied (Rozas & Enríquez, 2014; Stride, Polkinghorne, & Nowak, 2014), those affecting molluscs, other than the RLO causing withering syndrome in abalone, have not (Tavers et al., 2015). RLOs have been associated with diseases and mortality in scallops, abalone, clams and oysters (Carvahlo, Poersch, & Romano, 2013; Moore, Robbins, & Friedman, 2000; Sun & Wu, 2004). Although not all RLO infections result in mortality, information relating to the immune responses of molluscs to RLOs is scarce (Gollas-Galván et al., 2014). Since 2015, RLOs have been associated with at least six New Zealand shellfish mortalities events, investigated by the MPI AHL (A. Pande, *pers. obs*). The known New Zealand shellfish hosts of RLOs include scallops (*Pecten novaezelandiae*), pipis (*Paphies australis*), mussels (*Perna canaliculus*), cockles (*Austrovenus stutchburyi*) and now toheroa (Hine & Diggles, 2002; B. Jones, *pers. obs.*).

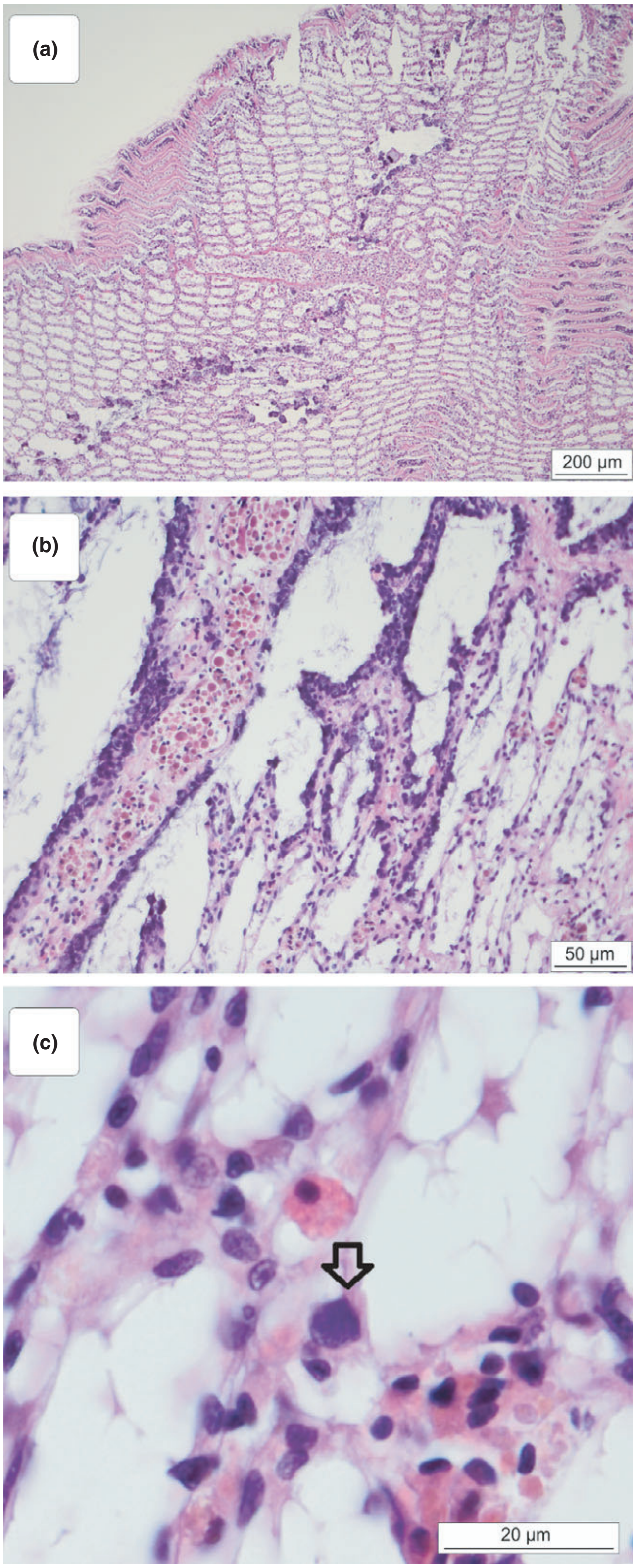

FIGURE 2 Haematoxylin- and eosin-stained toheroa (*Paphies ventricosa*) gill tissues at 10× (a), 40× (b) and 100× (in oil) (c) magnification. RLO-affected cells stain intensely basophilic (dark purple). RLOs are associated with areas where gill architecture is damaged (i.e., gill lattice is broken). Panel c shows an infected epithelial cell (indicated by arrow) immediately below an eosinophilic granulocyte. Two more granulocytes and several hyaline haemocytes are in the vessel to the right of the infected cell. ×100 oil

In toheroa, histology revealed colonies of RLOs within the branchial epithelia (gills) of all specimens and damage to host epithelial cells. The observed damage consisted of broken connections between the lateral ordinary filaments where epithelial cells are focally infected with RLOs leaving holes in the branchial lattice structure (Figure 2). Following the collection of GBD-affected toheroa at Ripiro Beach, there was some evidence of shellfish mortality including: areas of beach with greater than usual numbers of recently deceased (still hinged with intact periostracum) toheroa and tuatua (*Paphies subtriangulata;* J. Cope, *pers. obs.*); observations of recently deceased toheroa shells with blistered periostracum (Figure 1); and in some locations the smell of decaying shellfish emanating from the sand at known shellfish beds (B. Searle, *pers. comm.*).

Because the taxonomy of RLOs is poorly resolved, it is difficult to know at this stage whether RLOs observed in New Zealand molluscs are all the same species, are the causes of mortality events observed in toheroa (or other shellfish species), or whether the toheroa RLOs are native or introduced. Mass mortalities in toheroa have been reported in 1888, 1900, 1917, 1932, 1938, 1956–1959, 1970–1971, 2001 and 2013 (Williams, Sim-Smith, et al., 2013). Few of these events have been thoroughly investigated, and there is only speculation as to the causes of individual events (Akroyd, 2002; Carbines, 1997; Eggleston & Hickman, 1972; Hine & Wesney, 1997; Williams, Sim-Smith, et al., 2013). It is possible that RLOs have contributed to some of these mortality events, potentially in conjunction with GBD or other stressors. Mortalities in aquatic organisms are often multifactorial involving primary and secondary pathogens with effects that may be instigated or exacerbated by stressful environmental conditions. For example, Weiland et al. (1999) reported that chinook salmon with a bacterial infection were more vulnerable to gas bubble disease than healthy fish. In the case of toheroa, it is unknown whether RLOs are related to the detection of GBD, whether one condition is facilitating the other through increased vulnerability to TDG supersaturation or pathogens, or whether there are other factors at play. Targeted investigations will be required to ascertain causative mechanisms.

The discovery of RLOs and gas bubble disease in toheroa is of interest and may ultimately explain observed toheroa mass mortality events and the failure of toheroa to recover from unsustainable harvesting practices of the 20th century (Williams, Sim-Smith, et al., 2013). More work is required to understand the physiological consequences of these two conditions, any interactions between them, and to determine their distribution across species, space (locations) and time (seasonal patterns). The spread of pathogens to unaffected populations should be avoided. Consequently, the detection of RLOs will likely have implications for future toheroa aquaculture and for the translocation of toheroa, and other shellfish, between beaches for aquaculture, reseeding or enhancement purposes.

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