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Birds vs. Clams

Assessing the Impacts of South Island Pied Oystercatcher Predation on Toheroa at Ripiro Beach, New Zealand

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Abstract

Managing the recovery of interacting species, such as predator and prey, is one of the most challenging factors of an ecosystem-based conservation approach. The actions taken to protect one species may be in conflict with the actions necessary to protect another. For example, the recovery of a predator in an ecosystem can lead to a significant conservation conflict between the protected predator and its protected prey. In these instances, research is required to determine whether a perceived conflict is in fact happening in order to inform proper management decisions. In New Zealand, a conservation conflict exists between an endemic, recovering shorebird, the South Island pied oystercatcher (*Haematopus ostralegus finschi*), and an endemic surf clam, the toheroa (*Paphies ventricosa*) at Ripiro Beach, Northland. The toheroa was overharvested until the populations collapsed, with commercial and recreational harvesting bans put in place by the 1970s. The toheroa has continued to decline, and the cause is currently unknown. Oystercatcher predation has been implicated as the reason toheroa populations have not recovered. There have even been calls to cull the birds to protect the clams. Currently, there is no information that would facilitate conservation management in determining the appropriate action to take. My thesis aimed to investigate the claims surrounding this perceived interspecific conflict. It sought to examine the predator-prey interactions between the two species by answering the following three questions: 1) what are the spatio-temporal associations between oystercatchers and toheroa, 2) what is the composition of the oystercatcher's diet, and 3) what size toheroa are the birds taking?

Bird surveys were conducted to examine the distribution of oystercatchers monthly from March 2019 to February 2020. Oystercatcher foraging behaviour was observed to collect information on prey type and prey location. Feeding holes left by oystercatcher bills at predation sites were examined to determine oystercatcher predation success. A population survey was conducted on toheroa beds exposed to oystercatcher predation versus control beds to assess if there were differences in the density and size structure between toheroa populations.

Results did not support the hypothesis that the oystercatchers are the cause behind the limited recovery of the toheroa, but they did indicate that the birds may be having localised impacts. There was limited overlap with toheroa, as the birds were found predominantly at the southern half of Ripiro Beach and were only associated with two major toheroa beds. Observations found that bivalves are a significant food resource for oystercatchers and the birds have a high predation success rate. There was a significant difference in the density and size structure between toheroa populations in beds that were oystercatcher predation sites and those at no-predation sites. However, even in the areas with the most intense oystercatcher predation, toheroa have persisted over time. While there potentially is a small local impact, overall, the South Island pied oystercatcher is not responsible for the continuing decline of the toheroa across the whole of Ripiro Beach and are not causing devastation as claimed.

The perceived conservation conflict between the two endemic species is likely incorrect. This research demonstrates the importance of acquiring information on interacting species prior to management action to protect one of those species. We are now in the position to inform correct conservation management. Information presented in this thesis can be used to support conservation managers in making informed decisions to protect both the toheroa and the South Island pied oystercatcher.

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Chapter 1

Introduction

1.1 Conservation Conflict

One of the greatest conservation challenges of our time is managing the simultaneous recovery of interacting species and their environment (Lee *et al.*, 2016). Our understanding of the importance of ecosystems and ecological processes has grown significantly over the past 20 to 30 years and with that increase in awareness has come a shift from single-species conservation management to ecosystem-based management (Poiani *et al.*, 2000; Casazza *et al.*, 2016). In contrast to single-species management, an ecosystem-based approach aims to conserve interactions and to identify the needs and conflicting objectives of different species (Williams *et al.*, 2011).

Predator species worldwide have suffered huge depletions in their populations as a result of human activities such as overexploitation, culling and habitat destruction (Prugh *et al.*, 2009; Ritchie & Johnson, 2009). Predators play a crucial role in stabilising food webs and promoting prey diversity, so the outcome of predator loss has been wide-reaching and resulted in significant negative effects on ecosystems (Brechtel *et al.*, 2019; Pringle *et al.*, 2019). For example, removal of predator fish populations via overexploitation resulted in a trophic cascade that caused the collapse of an entire salt-marsh ecosystem in Massachusetts, U.S. (Altieri *et al.*, 2012). Similarly, in Australia, disease-induced loss of the predatory Tasmanian devil (*Sarcophilus harrisii*) triggered a mesopredator release of feral cats (*Felis catus*) which, in turn, led to a rapid decline of eastern quoll (*Dasyurus viverrinus*) (Hollings *et al.*, 2014). Consequently, the successful recovery of a particular predator species has been one of the major goals of a single-species conservation approach (Marshall *et al.*, 2016). However, the actions taken to protect one species may be in conflict with the actions necessary to protect another. Following just a single-species management approach, the recovery of a predator can lead to a significant conservation conflict. The three key conservation conflicts that arise from predator recovery are 1) increased competition with humans for the same prey, 2) several predator populations competing for the same prey, and 3) protected predators consuming protected prey

(Marshall *et al.*, 2016). These challenges are not mutually exclusive and may contribute to the increasing complexity of managing interacting species through an ecosystem-based approach. Predators are a vital part of any ecosystem but they are also perceived as the greatest cause of mortality for various threatened species (Stringham & Robinson, 2015). Predator populations can present difficulties for wildlife management if their prey are likewise endangered or have significant economic and cultural value to humans (Thirgood *et al.*, 2000).

There are numerous examples of conservation conflicts between protected predator and prey species. For example, Californian sea otters (*Enhydra lutris nereis*) and black abalone (*Haliotis cracherodii*); Cape fur seals (*Arctocephalus pusillus pusillus*) and threatened South African seabird prey such as the Cape cormorant (*Phalacrocorax capensis*); and orca (*Orcinus orca*) in the Northeast Pacific and its prey, Chinook salmon (*Oncorhynchus tshawytscha*) (David *et al.*, 2003; Raimondi *et al.*, 2015; Marshall *et al.*, 2016). Management responses to these types of conservation conflicts include exclosures (fencing), diversionary feeding, translocation and lethal removal (Clarke & Schedvin, 1997; Stringham & Robinson, 2015; Kubasiewicz *et al.*, 2016; Newsome *et al.*, 2017; Beggs *et al.*, 2019b). Of these ecological management actions, lethal control (or culling) is among the most widely practised but usually occurs without monitoring of efficacy and often results in unpredictable outcomes. For instance, if a particular prey species is endangered, conservation management decisions may involve the removal of a predator species, even if the predator was not responsible for the decline in the prey populations to begin with (Wiese *et al.*, 2008). Indeed, lethal control of a predator has been accepted as a conservation strategy in absence of proof of substantial effects on a prey population (Wiese *et al.*, 2008). Examples of lethal predator control to support prey recovery are selective culling of Cape fur seals to protect Cape gannets (*Morus capensis*) in South Africa; the removal of lesser black-backed gulls (*Larus fascus*) to increase oystercatcher (*Haematopus ostralegus*) breeding success in Scotland; and an experimental study of culling predators such as the striped skunk (*Mephitis mephitis*) and coyote (*Canis latrans*) to increase survival of mallard ducklings (*Anas platyrhynchos*) in North America (Harris & Wanless, 1997; Pearse & Ratti, 2004; Makhado *et al.*, 2009). In the example mentioned above, Harris and Wanless (1997) investigated the effects of lesser black-backed gulls' removal on oystercatcher populations on the Isle of

May in Scotland. A large-scale gull control programme was implemented in 1972 which continued (at a reduced level) until 1988. Before the control of the gulls, the area had a small but stable breeding population of oystercatchers, which in contrast to other British populations during that time, was not increasing in numbers. Interestingly, the number of oystercatcher breeding territories increased immediately after gull control was executed, however, breeding success did not. The authors attributed their findings to an increase in attractiveness of the area as a breeding site for the oystercatchers due to the reduced number of gulls, although with gull predation still causing the deaths of oystercatcher chicks. A study by Makhado *et al.* (2009) examined the efficacy of culling Cape fur seals to reduce mortality of Cape gannets (61 Cape fur seals that had been seen killing gannet fledglings were selectively culled in 2006 to 2007) and noted that the cull immediately reduced the mortality rate of the gannets. However, after only a week, other seals had commenced predation of the gannet fledglings. In this instance, culling was temporarily effective but suggests the management strategy is not beneficial in the long term. Predators are vital in regulating prey populations but there are often other factors (such as overexploitation, climate change and habitat alteration) contributing to the decline in prey abundances, directly or indirectly, which may negate the aims of lethal predator control (Wiese *et al.*, 2008; Laws, 2017; Perissi *et al.*, 2017). These cases show that it is highly important to recognise the complexity of a predator-prey relationship when attempting to manage the abundance of a predator for an effective ecosystem-based management approach (Wiese et al, 2008). To justify lethal control of a protected predator, culling must improve ecosystem function and the desired outcome must be measurable (Beggs *et al.*, 2019a).

The act of culling is based on the assumption that a reduction in predator abundance will increase prey numbers, however, predator-prey interactions are too complex for such a simplistic view. Thus, for protected predators and protected prey to be managed effectively, it is crucial to know if the predator does impact the prey population and to what degree (Bowen & Lidgard, 2013). Essentially, the effects that predators have on prey behaviour, abundance, density and size need to be understood before any management actions occur (Lee *et al.*, 2016).

1.2 Toheroa

In New Zealand (Aotearoa), a conservation conflict exists between an endemic, recovering shorebird, the South Island pied oystercatcher (*Haematopus ostralegus finschi*), and a protected surf clam, the toheroa (*Paphies ventricosa*) at Ripiro Beach (Ripiro Waka te Haua), Northland (Te Tai Tokerau). Limited information exists on the predator-prey dynamics of the two species. The South Island pied oystercatcher (tōrea) has been implicated as the reason why toheroa populations are continuing to decline at this beach and there have been calls for the birds to be culled in order to protect the shellfish.

Toheroa, a bivalve endemic to New Zealand, is an iconic and taonga (treasured) species. The shellfish are found on high energy surf beaches around the country (Beentjes *et al.*, 2006). Toheroa are the largest clams in New Zealand, reaching up to 180 mm in length and are closely related to the well-known shellfish pipi (*Paphies australis*) and tuatua (*Paphies subtriangulata*) (Cook, 2010).

Toheroa were and still are found mainly on west coast beaches in the North Island (Te Ika-a-Māui) including Ninety Mile (Te-Oneroa-a-Tōhē), Ripiro, Muriwai, on the Kāpiti-Horowhenua coast, and in the South Island at Oreti beach and Bluecliffs beach (in Te Waewae Bay) (Redfearn, 1974; Akroyd et al., 2002; Ross et al., 2018a) (Figure 1.1). Before the arrival of Europeans to New Zealand, these shellfish were an important food source for Māori living near the toheroa beaches. Some Māori view toheroa as part of their whakapapa (genealogy), and the shellfish used to be (and occasionally still are) given to visitors as a symbol of respect through maanakitanga (generosity and hospitality) (Akroyd *et al.*, 2002; Ross *et al.*, 2018a). By the end of the 1800s, Pākehā (New Zealanders of European descent) had learnt of toheroa as a valuable food commodity with the first toheroa cannery opening in 1904 at Ripiro Beach, Northland and the second in 1911 (Murton, 2006). Production peaked in 1940 and by the 1960s a ban on commercial harvesting was created as the toheroa populations had declined to levels where the fishery was no longer sustainable (Akroyd *et al.*, 2002; Murton, 2006). In the 1970s, recreational harvesting was also banned. Despite over four decades of protection, toheroa populations have not recovered thus far (Millar & Olsen, 1995; Ross *et al.*, 2018a). At present, harvesting toheroa is illegal except for controlled customary harvest when permits are issued by the local kaitiaki (guardians) to both Māori and Pākehā for special occasions such as tangihanga (funerals) and hui (meetings) (Akroyd *et al.*, 2002; Ross *et al.*, 2018a).

Toheroa can typically be found intertidally, with juveniles commonly settling at the high tide mark and the larger clams found between the low tide and mid-tide mark. They can be buried up to 30 cm under the substrate where they extend their siphons to the surface in order to filter feed and excrete waste (Redfearn, 1974; Beentjes *et al.*, 2006). Major toheroa beds are generally associated with freshwater streams and bays which possibly offer the bivalves the ability to withstand adverse environmental conditions, provide thermal refuge and aid in preventing desiccation that can result in mortality (Redfearn, 1974; Brunton, 1976; Cope, 2018). Many factors have been attributed to the continuing decline of toheroa populations including, but not limited to, beach erosion, disease, climate change, crushing by vehicles, illegal and customary harvest and predation by birds, specifically, the South Island pied oystercatcher (Redfearn, 1974; Brunton, 1976; Beentjes *et al.*, 2006; Ross *et al.*, 2018a; Ross *et al.*, 2018b).

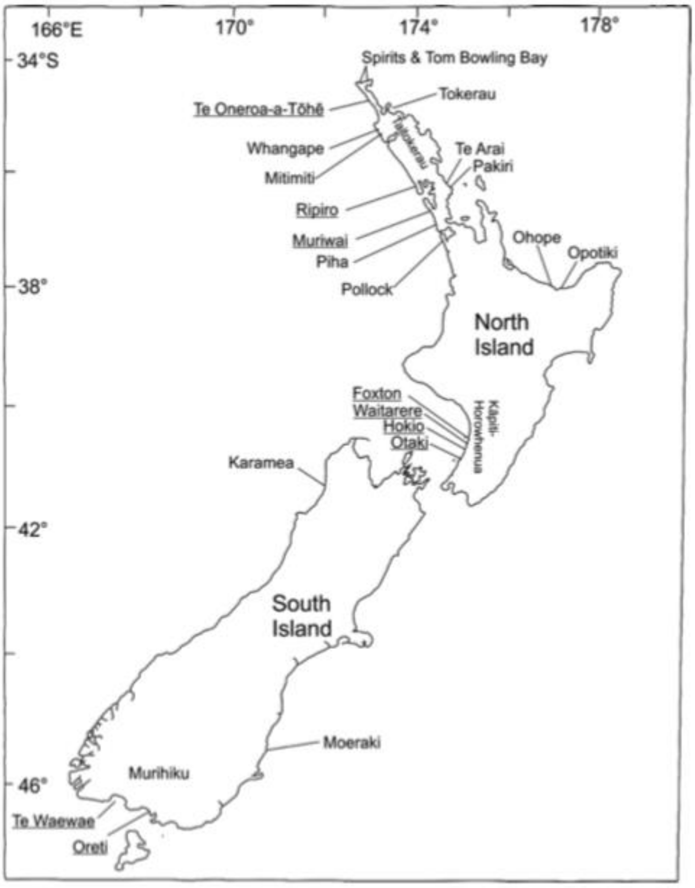

Figure 1.1 Distribution of New Zealand toheroa populations. Major populations are underlined (Ross *et al.*, 2018a).

1.3 South Island Pied Oystercatcher (Tōrea)

Oystercatchers are a group of shorebirds which form the Haematopodidae family and are found on every continent, excluding Antarctica. Their distribution is generally coastal with few species found inland and they are known for their long bills, large size and conspicuous plumage (Heppleston, 1973; Sagar, 2000). New Zealand is home to three oystercatcher species: the South Island pied oystercatcher (*Haematopus finschi*), the variable oystercatcher (*Haematopus unicolor*) and the Chatham Island oystercatcher (*Haematopus chathamensis*) (Baker, 1974a; Kinsky, 1980). Outside of their breeding season, the South Island pied and the variable oystercatchers can be found distributed throughout the two main islands of New Zealand whilst the Chatham Islands oystercatcher is only found on the Chatham Islands (Rēkohu) (Banks & Paterson, 2007). The South Island pied oystercatcher can be distinguished from the pied form of the variable oystercatcher by the sharp border between the lower white and upper black plumage on the chest, distinct white bar beneath its shoulder and its smaller size (Banks & Paterson, 2007; Heather & Robertson, 2015) (Figure 1.2). The South Island pied oystercatcher is New Zealand's most abundant oystercatcher and since becoming protected in 1940, their numbers have increased considerably (Figure 1.3). The most recent winter census conducted in June-July 2018 indicated a total population size of 69,105 South Island pied oystercatchers, down 4000 from 2017 (Baker, 1973; Riegan, 2018, 2019).

Figure 1.2 The South Island pied oystercatcher (photo by L. Vallyon).

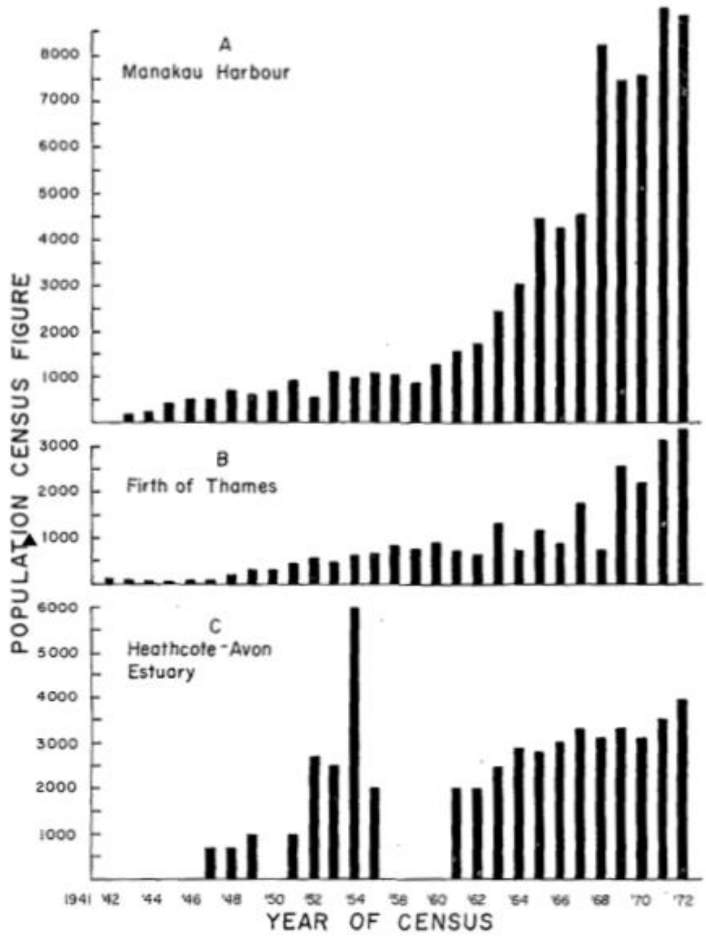

Figure 1.3 Winter census data for the South Island pied oystercatcher at three major wintering sites (Baker, 1973).

The South Island pied oystercatcher (hereafter referred to as oystercatcher) primarily breed inland in the Canterbury (Katapere) area of the South Island (Te Waipounamu) on braided riverbeds or farmland adjacent to riverbeds (Sagar, 2000; Banks & Paterson, 2007). Following the completion of the breeding season between late December and early February, the oystercatchers begin their migration to spend their non-breeding months in coastal areas around the country with the majority settling in the north of the North Island (Sagar & Geddes, 1999; Dowding & Murphy, 2001) (Figure 1.4). Here, they gather in large flocks in areas where the food supply is sufficient such as in bays, estuaries or harbours (Baker, 1973). The birds begin their return migration southwards in late June until the beginning of August (Dowding & Murphy, 2001).

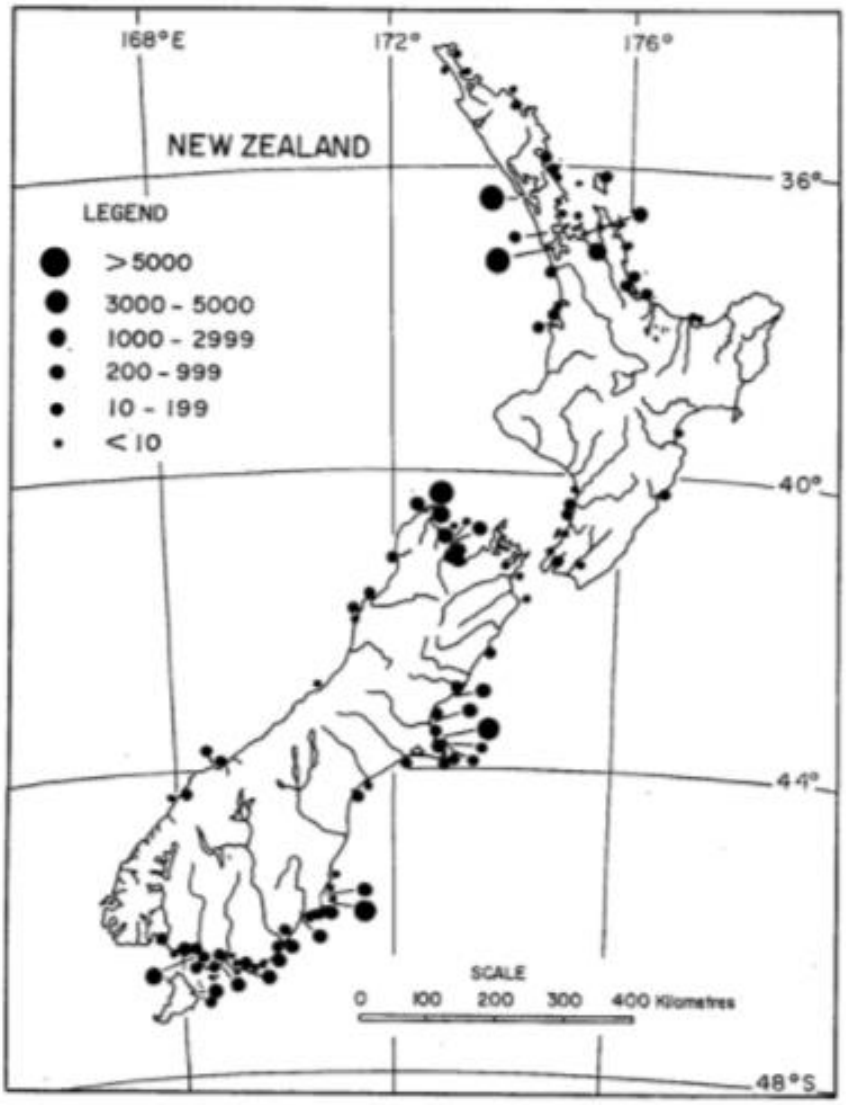

Figure 1.4 Winter distribution of South Island pied oystercatchers (Baker, 1973).

The oystercatchers are natural predators to animals living in the littoral zone such as crustaceans, bivalves, gastropods, limpets, polychaetes and chitons. They use prey-specific methods to exploit different types of prey and are behaviourally and morphologically adapted to feed on coastal and estuarine bivalves (Baker, 1974b).

1.4 Conflict at Ripiro Beach, New Zealand

Historically, Ripiro Beach has been the site of the highest numbers of toheroa in Northland, with aggregations of the clams forming distinct beds along the length of the beach (Akroyd *et al.*, 2002). As mentioned above, the toheroa has continued to decline since their protection in the 1970s and populations at Ripiro Beach are no exception. Nevertheless, Ripiro Beach still supports the largest remaining toheroa population in New Zealand. Researchers have recently begun pursuing knowledge on the continuing decline of the toheroa, but the cause is currently unknown. In the absence of an official explanation, locals living near the toheroa beaches have begun to speculate on reasons why the precious shellfish have not recovered. One of the suggestions for the lack of recovery, which has created a conservation conflict, is predation by the South Island pied oystercatcher. The birds have been seen with their bills in the sand predating on, what is assumed to be, toheroa. Consequently, in media stories related to toheroa, oystercatchers are often portrayed negatively, including in articles with headlines such as: "*Call to cull native birds taking toheroa*", "*Toheroa thieves caught on video?*", "*Shell shock: Toheroa beach wipe-out*" and "*Toheroa beds under threat*" (Barrington, 2014b; Barrington, 2014a; Dickey, 2014; RadioNZ, 2014). Oystercatchers are specialist bivalve predators, yet there is no information to support the claims that the predation pressure by oystercatchers on toheroa is significant enough to inhibit the recovery of the local toheroa populations. Unfortunately, even with the lack of evidence, there have been some reports that the protected birds have been illegally shot and there are now calls to cull the oystercatchers in order to protect the toheroa. This is a classic example of a conservation conflict with calls to kill one threatened endemic species in order to protect and facilitate recovery of another threatened endemic species. It remains unclear to what degree the oystercatchers at Ripiro Beach select toheroa as prey, where the majority of the oystercatcher predation on Ripiro Beach takes place and how the potential removal of the birds from Ripiro Beach could affect the ecosystem. Previous research has shown that removal of a predator seldom increases prey abundance as a direct result (Harris & Wanless, 1997; Makhado *et al.*, 2009). It is imperative to describe the relationship between predator and prey and the potential ecological effects of altering that relationship prior to implementing a particular management plan, especially if that management approach is lethal control of a protected species (Goodrich & Buskirk, 1995; Wootton, 1997; Wiese *et al.*, 2008; Lee *et al.*, 2016).

1.5 Research Significance

Little research has been conducted on the South Island pied oystercatcher and, to my knowledge, no research has been conducted on the predator-prey relationship between these native oystercatchers and the toheroa. Because both the oystercatchers and toheroa are protected and endemic to New Zealand, this makes research into the claims surrounding the perceived interspecific conflict especially important. Culling the oystercatchers without information on their relationship with toheroa could lead to unpredictable outcomes. Locals living near toheroa beaches are very passionate about this shellfish and there is an eagerness to aid their recovery. My research aims to fill some of the existing knowledge gaps surrounding the relationship between the toheroa and oystercatchers so as to facilitate decision-making on the correct conservation management action of the two species.

1.6 Thesis Aims and Structure

In my thesis I aim to investigate the following research questions to determine what influence the oystercatchers may be having on toheroa populations:

1) What are the spatial and temporal distribution patterns of South Island pied oystercatchers on Ripiro Beach and how are these associated with the locations of major toheroa beds?

2) What type of prey are the oystercatchers taking, how much prey are they taking and what percentage of their diet is comprised of toheroa?

3) What size toheroa are the oystercatchers predominantly predating on?

As part of a much larger research project on toheroa, my supervisor Dr Phil Ross has obtained a special permit (SP706-2) from the Ministry of Primary Industries to gather toheroa for research purposes. Dr Ross is also working in collaboration with and has support from the local iwi and kaitiaki (Te Roroa and Te Uri o Hau) for research surrounding toheroa on Ripiro Beach. An animal ethics application was submitted to the University of Waikato Animal Ethics Committee for this research, but no permission was needed for the collection of an invertebrate nor for the observation of oystercatchers.

1.6.1 Thesis Structure

In Chapter 1, I introduce the concept of conservation conflict and review literature on toheroa and the South Island pied oystercatcher. This chapter describes the perceived interspecific conflict between the oystercatchers and toheroa at Ripiro Beach and identifies the importance of pursuing knowledge on the relationship between the two native species before management decisions are made. The chapter finishes with this project's research questions and the thesis outline.

In Chapter 2, I focus on determining oystercatcher distribution patterns on Ripiro Beach. I present the results of 12 months of bird surveys which reveal the temporal and spatial distribution patterns of the oystercatchers relative to the distribution of major toheroa beds.

In Chapter 3, I examine oystercatcher foraging ecology with a section on behavioural observations made over the course of the research project, in addition to a more quantitative section detailing the amount and type of prey taken by oystercatchers and the percentage of their diet that includes toheroa.

In Chapter 4, I conduct two studies to investigate oystercatcher prey choice. First, I investigate oystercatcher predation success rate by excavating shellfish from oystercatcher predation holes. Second, I examine the local impact of oystercatcher predation at two major toheroa beds. Surveys of toheroa population size structure were conducted at beds where oystercatcher predation is relatively intense and at control sites where oystercatchers have not been observed to forage.

In Chapter 5, I discuss the findings and limitations of this research project. Future research ideas are proposed, and a summary is offered to inform conservation management action.

Chapter 2

Spatio-temporal Associations Between Oystercatchers and Toheroa

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2.1 Introduction

The availability of food is a crucial component of habitat selection by shorebirds that feed on invertebrate prey in coastal areas (Schlacher *et al.*, 2014). Though many factors influence the choice of foraging sites by shorebirds, for example, individual specialisation, substrate coarseness and competition (Colwell & Landrum, 1993; Nol *et al.*, 2014; Courbin *et al.*, 2018), high fidelity sites are generally sites with consistent levels of available food (Rutten *et al.*, 2010; Schlacher *et al.*, 2014). At large spatial scales (regional or between estuaries), many studies have recorded a relationship between prey density and the concentration of predator shorebirds (Colwell & Landrum, 1993; Colwell, 2010; Schlacher *et al.*, 2014). For example, Spruzen *et al.* (2008) demonstrated that there was a positive correlation between invertebrate biomass and shorebird foraging density in Robinns Passage wetlands, Australia; Ribeiro *et al.* (2004) found that shorebird predators select their habitat based on the density of their preferred prey with Ruddy turnstones (*Arenaria interpres*) foraging in areas with high densities of their preferred crab prey and white-rumped sandpipers (*Calidris fuscicollis*) searching in areas with greater concentrations of polychaetes, one of their favoured food items.

Optimal foraging theory assumes that the foraging distribution of a predator will be non-random (Krebs, 1994; Barbosa, 1996) with some models predicting that there is a direct association between prey density and foraging distribution (Macarthur & Pianka, 1966; Barbosa, 1996). Relative to optimal foraging theory, spatial distribution of predators can be anticipated through two behavioural responses; the numerical aggregative response and the ideal free distribution (Fretwell & Lucas, 1969; Charnov, 1976; Sutherland, 1983). The aggregative response describes the increase in predator density at sites of high prey biomass in order for the predators to individually maximise food intake per unit time (Sutherland, 1982, 1983; Johnstone & Norris, 2000). However, interference (any interaction which reduces foraging efficiency, for example, kleptoparasitism) becomes more common at sites with high prey density due to increased predator density and subsequent competition for food (Sutherland, 1983; Barbosa, 1996). Bijleveld *et al.* (2012) provide an example of interference in foraging shorebirds. In this study, the authors designed a comprehensive experiment that examined interference amongst captured redknots (*Calidris canutus*) predating on bivalves in an experimental arena (representative of a food patch). One of the main findings of their study was that food intake decreased with an increase in bird numbers in the food patch (Bijleveld *et al.*, 2012). In another study on redknots, Quaintenne *et al.* (2011) modelled different potential distribution patterns of the birds in Western Europe and found that their distribution was best explained by the ideal free distribution model. The authors suggested this was due to interference at foraging sites. Thus, the ideal free distribution predicts that predators will distribute themselves amongst different food patches, even to areas of poor prey density (in contrast to the aggregative response), so that each individual will have the same feeding rate (Sutherland, 1983).

Though prey density may be a defining feature in foraging site selection, studies have shown that abiotic factors of the habitat can also influence where predators choose to distribute themselves (Ntiamoa-Baidu *et al.*, 1998; Finn *et al.*, 2007; Lunardi *et al.*, 2012). Physical characteristics such as salinity and substrate strongly influence the dispersal of shorebirds via their impact on the distribution and accessibility of their invertebrate prey (Colwell & Landrum, 1993; Schlacher *et al.*, 2014). For example, the wetness of the substrate in coastal areas due to tidal inundation may affect the availability of benthic invertebrates to shorebirds. Substrate wetness increases the activity of benthic prey, making them more vulnerable to predation while also increasing penetrability of the substrate to shorebirds' beaks (Colwell & Landrum, 1993; Barbosa, 1996). Finn *et al.* (2007) found that eastern curlews (*Numenius madagascariensis*) in Australia preferred areas with less resistant substrates than sites with the most resistant substrates, as shown by bird densities being three times higher in areas of less resistant substrate. Consequently, prey density may affect habitat choice of nonbreeding shorebirds although at smaller spatial scales the physical characteristics of the habitat will also influence the choice of foraging sites of predators.

In summary, environmental factors as well as the behavioural responses of predatory shorebirds are likely to govern the pattern of respective prey mortality in a particular habitat (Sutherland, 1982). This concept is applicable to the present study, under the assumption that the distribution and density of toheroa along the length of Ripiro Beach may influence the spatial distribution of nonbreeding oystercatchers. At a smaller spatial scale, abiotic factors and competition/interference might additionally influence the oystercatchers' foraging site choice. The foraging patterns of the oystercatchers will, in turn, have an effect on prey mortality at particular foraging sites. As discussed in Chapter 1, oystercatchers have been implicated in the continuing decline of the toheroa populations on Ripiro Beach (Ross *et al.*, 2018a). At present, there is a lack of knowledge on the foraging patterns of these birds on this particular beach. However, this knowledge could be used to understand the level of conflict between these two protected species and inform conservation and management efforts. As a first step in determining the impact oystercatcher predation may be having on toheroa populations, it is crucial to establish if there is an overlap in the spatial and temporal distributions of the two species in question. If their distributions do not demonstrate an association, it can be assumed that there may be other factors limiting the recovery of toheroa. Therefore, the main aim of this chapter will be to determine how much of the Ripiro Beach toheroa population is exposed to oystercatcher predation.

2.2 Aims and Hypotheses

The aim of this study is to investigate the spatial and temporal foraging patterns of oystercatchers and determine their association with major toheroa beds on Ripiro Beach. It is hoped that this information could be used as a means to determine when and where oystercatchers are potentially predating on toheroa. Based on the literature discussed in Chapter 1 and Chapter 2, three hypotheses can be formulated:

1. The South Island pied oystercatcher will be mainly foraging on Ripiro Beach during its nonbreeding months, which range from January to July. Therefore, it is assumed that during the nonbreeding months higher numbers of oystercatchers will be present on the beach compared to the breeding months between July to December (Sagar & Geddes, 1999).

2. Optimal foraging theory and the aggregative response predict the birds will be found foraging in areas of high prey density. Consequently, it can be hypothesised that the oystercatchers will be found foraging near toheroa beds which are often associated with freshwater inputs onto the beach.
3. During times of high predator density, the ideal free distribution predicts that predators will avoid interference by distributing themselves in a way as to maximise food intake. Thus, it can be assumed that when there are high numbers of oystercatchers on the beach (for example, nonbreeding months) they will be dispersed further along the length of the beach.

2.3 Methods

2.3.1 Study Site: Ripiro Beach (Ripiro Waka te Haua)

Ripiro Beach is located on the west coast of Northland (Te Tai Tokerau) in the North Island (Te Ika-a-Māui) of New Zealand (Aotearoa). The beach stretches from Maunganui Bluff in the north to Pouto Peninsula in the south. Between Maunganui Bluff and the settlement of Glink’s Gully, the beach is backed by sandstone cliffs which begin to turn inland south of Glink’s Gully (Figure 2.1). South of this point, sand dunes become wider and are increasingly more common towards Pouto Point (Greenway, 1969; Redfearn, 1974). Along Ripiro Beach, there are numerous shallow streams that flow from inland onto the beach. Many of these streams have dried up in recent years (Williams et al., 2013 as cited in Cope, 2018). Toheroa are often associated with these areas, living in dense beds in and around these streams and freshwater seeps. Other intertidal fauna found on Ripiro Beach include tuatua, crustaceans and polychaete worms (Redfearn, 1974).

Figure 2.1 Sandstone cliffs and stream at Ripiro Beach (photo by L. Vallyon).

2.3.2 Oystercatcher Surveys

To determine the spatial and temporal distribution of oystercatchers, bird surveys were conducted monthly from March 2019 to January 2020 (a final bird survey will be conducted in February 2020 following the submission of this thesis). Each month, bird counts were conducted between 1-3 days within one week. Multiple bird counts on a single day or across consecutive days were conducted to determine variability in bird distribution and density, or the influence of environmental conditions such as wind. In March, April and September 2019 and January 2020, only one bird survey was conducted. In May, three were conducted and in the remaining months two bird surveys were conducted per month.

Ripiro Beach is officially recognised as a state highway and is the country's longest driveable beach at around 72 kilometres long, from Maunganui Bluff to Pouto Point (Redfearn, 1974). Rather than surveying the whole length of the beach, the survey area began from Omamari in the north to Pouto Point in the south (just north of Pouto Point) (Figure 2.2). The survey area was approximately 62 kilometres. The whole length of the beach was not surveyed as no oystercatchers were seen north of Omamari and the sand at the southernmost end was hazardous for driving. The beach was travelled by four-wheel drive vehicle with one person driving and a second (or sometimes third) person recording. On sighting of the oystercatchers, the vehicle would slow down and come to a complete stop in order to record GPS coordinates of birds using a Garmin GPSMAP 64s.

A group of South Island pied oystercatchers was defined as, “a distinct flock foraging together with or without the presence of another shorebird species”. A flock was defined as, “a group of birds where all the nearest neighbour distances were within 100 metres”. Two adjacent flocks were considered separate if the two nearest individuals of each flock were more than 100 metres away from the other (Yasué, 2005).

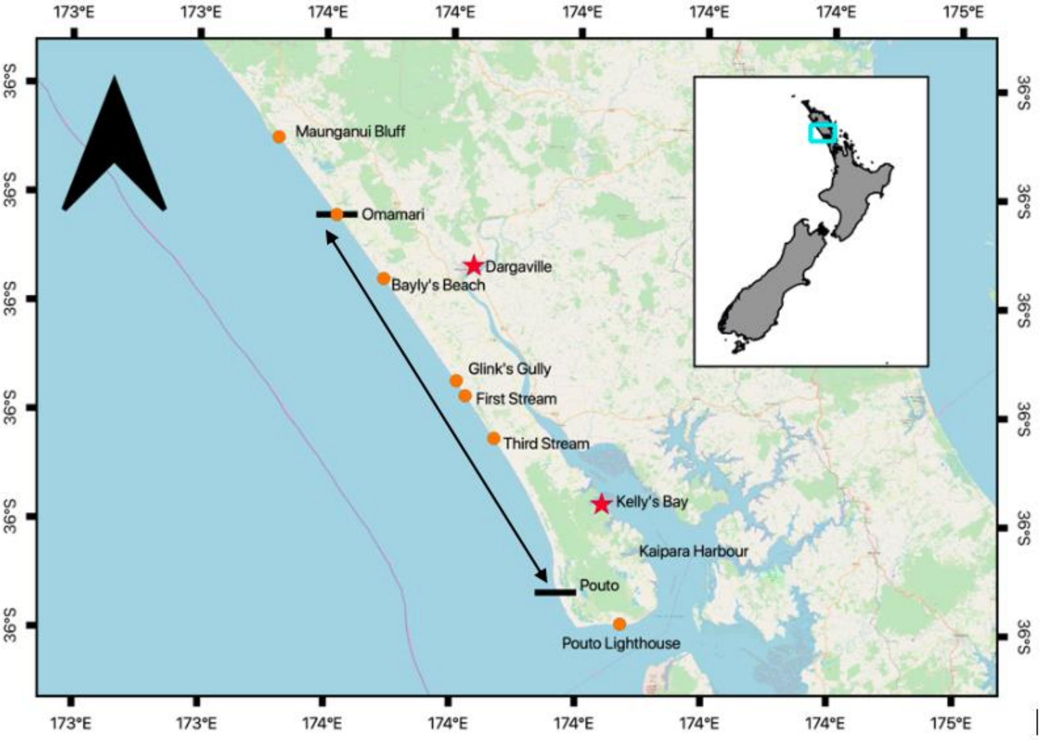


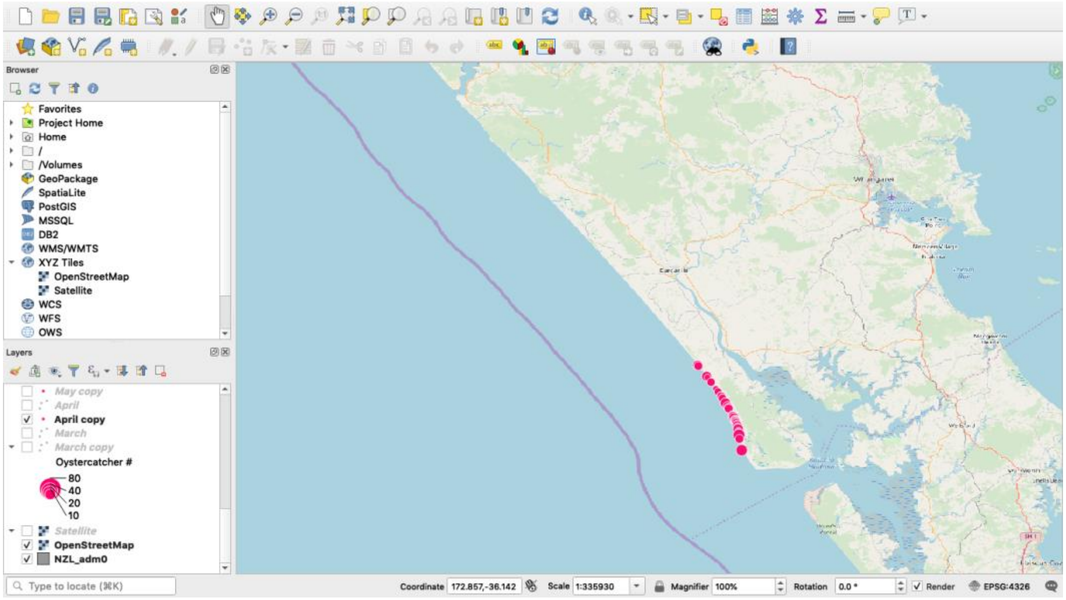
Figure 2.2 Map showing project survey area; black bars indicate northern and southern-most points of survey area. Orange dots specify key settlements and streams. Coordinate reference system: WGS 84 (EPSG: 4326). Spatial data obtained from DIVA-GIS and openlayers plugin (QGIS).

The vehicle would stop as near to the flock as possible without alarming or disturbing the birds. Counts were made from inside the vehicle with the aid of binoculars (Burnsco™) and were conducted from left to right. At least two observers performed counts at any given site simultaneously in order to obtain an accurate number. Counts were taken on groups of South Island pied oystercatchers, black-backed gulls (*Larus dominicanus*), red-billed gulls (*Larus novaehollandiae*) and any other species that were found to be within a 50 metre radius of the oystercatchers. Weather, tidal state, time of count and position of birds on the beach (upper vs. lower intertidal) were also recorded.

2.3.3 Map Construction

Bird distributions were visualised using the open source geographic information system program Quantum GIS (QGIS) (version 2.4.8-Madeira). Multiple maps were created including: the project survey area, oystercatcher predation and size structure study sites (see Chapter 4), overlapping oystercatcher and toheroa distributions, and oystercatcher spatial distribution by month. GPS coordinates were converted from degrees, decimal minutes to decimal degrees (DDlat and DDlong) using Excel. Comma separated value (CSV) output files were produced in order to be compatible with QGIS. A map was created by adding a “layer” of the decimal degree coordinates (CSV file) on a “NZ shape file” that had been downloaded from the internet (openlayers plugin in QGIS; Figure 2.3). Next, a print layout would be generated in order to be able to edit the map (for example, add grids or north arrows; Figure 2.4).

Monthly oystercatcher distribution maps were created using counts from the first bird survey of each month. A map displaying the associations between oystercatchers and toheroa was also created. This was prepared by selecting the GPS coordinates of areas on the beach that had the highest number of oystercatchers per month (from the first bird survey of each month). Coordinates were selected in this manner as they were the sites that had consistent numbers of oystercatchers throughout the year. September and October counts were not included as only 2 and 1 oystercatchers were recorded, respectively. The major toheroa beds were then added to the map by using the GPS coordinates of the six main toheroa beds (also streams) that are found along Ripiro Beach: Island, Baylys Beach, Kopawai, Mahuta Gap, First Stream and Third Stream.



☐ May copy
☐ April
☑ April copy
☐ March
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☐ Satellite
☑ OpenStreetMap
☑ NZL_adm0

Coordinate 172.857,-36.142
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Rotation 0.0 °
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EPSG:4326

Figure 2.3 Screenshot showing example of QGIS project layout. The main screen displays the current project. The bottom left box has all the layers that have been added to the project. In this example, the current active layers are a NZ shape layer, an open streetmap layer and the April oystercatcher bird survey GPS points.

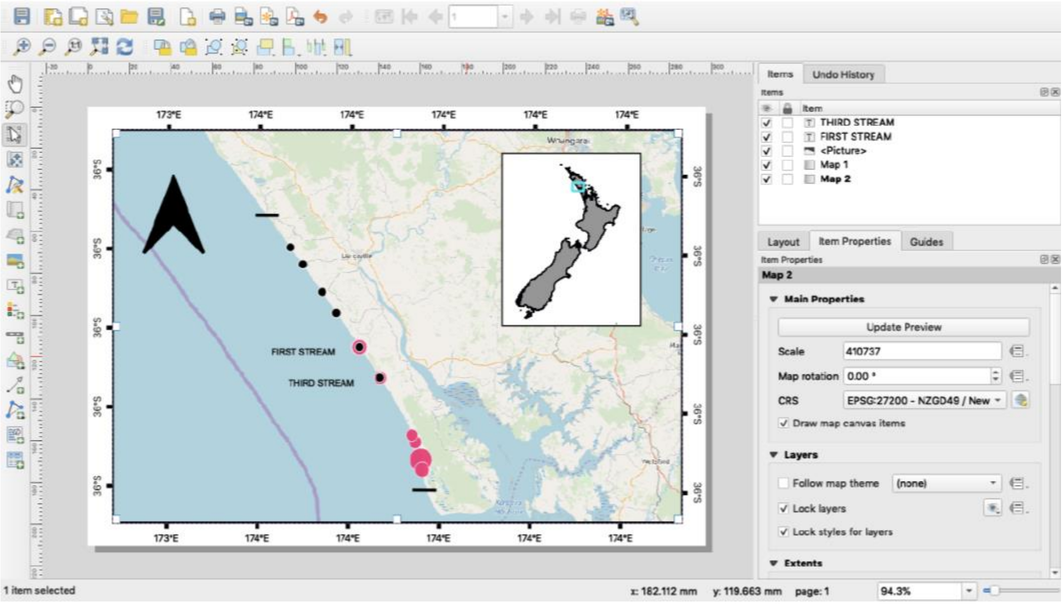

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Figure 2.4 Screenshot showing example of QGIS print layout. The main screen displays actively working maps. The right-hand side contains the main properties of the currently selected map which enables editing of the map e.g. scale and size.

2.3.4 Data Analysis

Data were collated and presented using descriptive statistics. Monthly oystercatcher counts were presented in a table with mean count and SD calculated. Monthly oystercatcher count data and oystercatcher count data at First and Third

Stream were presented in graphs. All calculations were performed, and tables and graphs created using Microsoft Excel. As mentioned above, bird surveys were conducted between 1 to 3 times each month within a one-week period (on single or consecutive days). Thus, when plotting oystercatcher numbers over time, the mean count was used for the months in which more than one bird survey was conducted.

2.4 Results

2.4.1 Temporal Distribution

The number of oystercatchers on Ripiro Beach varied over time. Abundance changed over the course of the year with numbers peaking in March 2019 at 322 birds and then steadily decreasing to 0 oystercatchers in December 2019. There was a sudden increase in oystercatcher numbers in January 2020 with a total count of 134 individuals. The total oystercatcher counts for each month are reported in Figure 2.5 and Table 2.1. Recorded counts were March n = 322, April n = 159, May n = 153 (± 19.55), June n = 96 (± 0.71), July n = 33 (± 9.9), August n = 23 (± 1.41), September n = 2, October n = 7 (± 3.52), November n = 2 (± 0.71), December n = 0, January n = 134. These numbers are consistent with the first hypothesis: that oystercatcher abundance is greatest during their nonbreeding months of January to July.

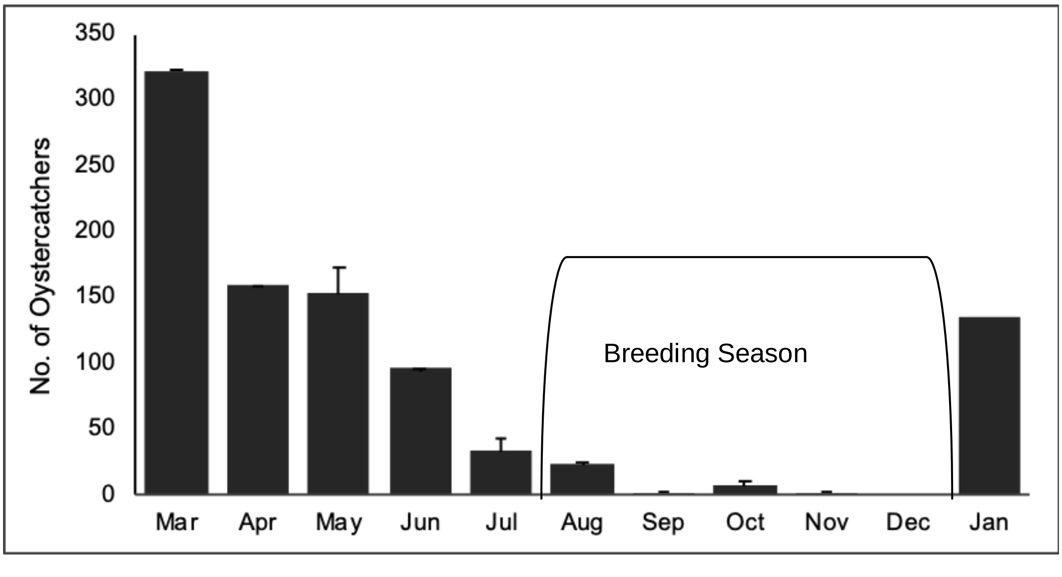


Figure 2.5 Total count of oystercatchers per month. Mean count was used for months May, June, July, August, October, November. Error bars are SD.

Table 2.1 Average count of oystercatchers each month bird surveys were conducted.

Month	Survey #	Mean #	SD (±)	Min	Max
March	1	322	"-"	"-"	"-"
April	1	159	"-"	"-"	"-"
May	3	153	19.55	134	173
June	2	96	0.71	95	96
July	2	33	9.9	26	40
August	2	23	1.41	22	24
September	1	2	"-"	"-"	"-"
October	2	7	3.54	4	9
November	2	2	0.71	1	2
December	2	0	"-"	"-"	"-"
January	1	134	"-"	"-"	"-"

2.4.2 Spatial Distribution

Oystercatchers were not evenly distributed across the beach and their spatial distribution varied over time (Figure 2.6). They were found predominantly at the southern half of Ripiro Beach (Glink's Gully and south) and were located frequently in relatively high numbers at First Stream, Third Stream and towards the southern end of the survey area. In March and October 2019 and January 2020, oystercatchers were present primarily at the southern end of the beach. April, May and June 2019 show the oystercatchers distributing themselves further north up to First Stream. In March, there were 83 birds in a single flock near Pouto Point. In April, the largest flock of 14 birds was also found relatively nearby. The largest flock counted in January (n = 38) was likewise in close proximity to Pouto Point. The few oystercatchers that were on the beach in August, September and November were found mainly at First Stream and Third Stream. May and October were the only months in which birds were seen at and north of Glink's Gully (approximate survey area halfway point), albeit in extremely small numbers (for example n = 1).

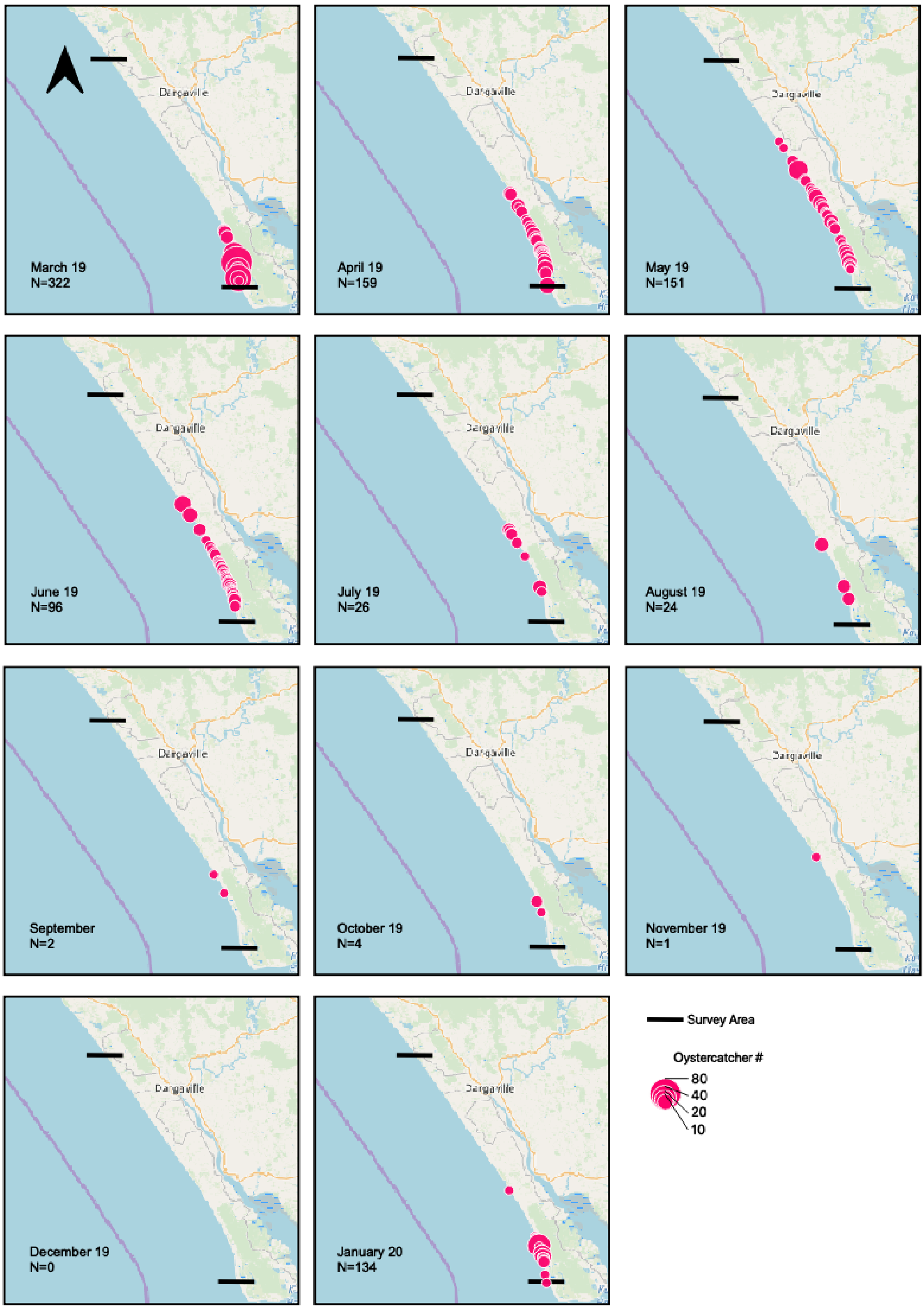


Figure 2.6 Oystercatcher distribution across all months that bird surveys were conducted. Larger circles represent higher numbers of oystercatchers. Each individual map displays the mean number of oystercatchers counted per month.

2.4.3 Oystercatcher and Toheroa Association

Oystercatchers showed high site fidelity to specific foraging areas on the beach throughout the year. The most preferred spots over the year were First Stream, Third Stream and just north of the southern end of the survey area (Pouto Point). First Stream and Third Stream are sites of major toheroa beds (Figure 2.7). In May, in all three surveys conducted, First Stream had at least 15 individuals in a flock. The largest flock (n = 15) counted in June from the first survey was also foraging at First Stream, while the second survey that month counted 17 birds at First Stream (Figure 2.8). Birds were frequently found foraging at Third Stream throughout the year with May having the largest flock sizes of 12 individuals in the first survey taken and 30 individuals in the third survey taken (Figure 2.9).

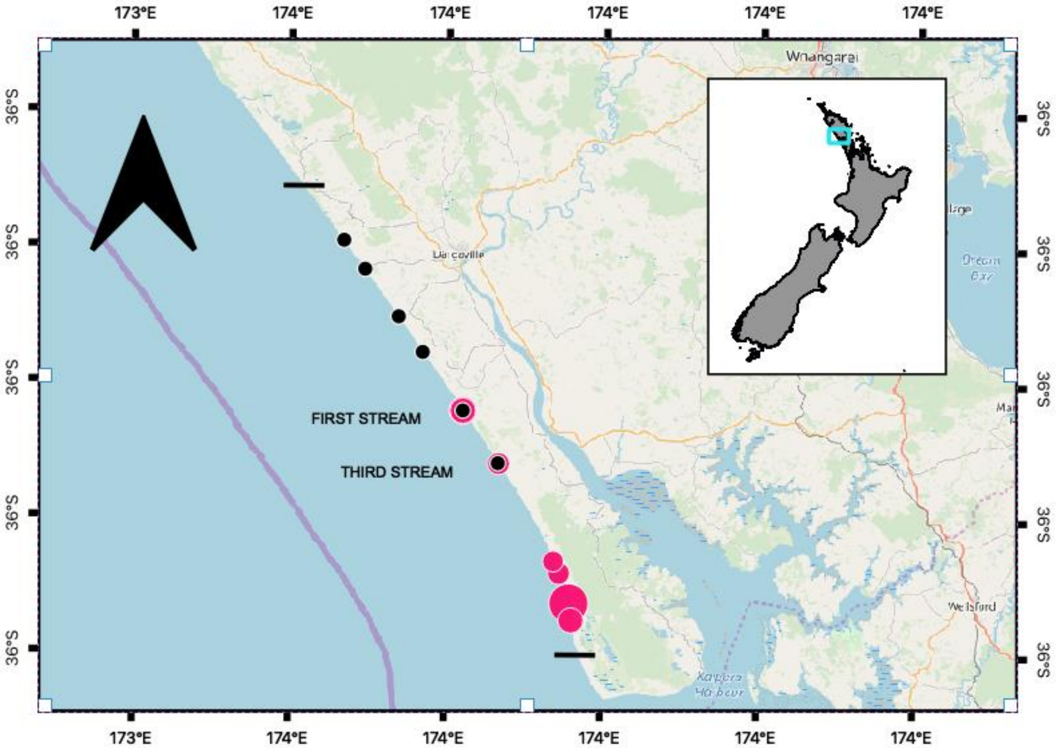


Figure 2.7 Map displays sites on beach where oystercatcher and toheroa distributions overlap: First Stream and Third Stream. Black circles represent major toheroa beds. Pink circles represent sites where high numbers of oystercatchers are found each month.

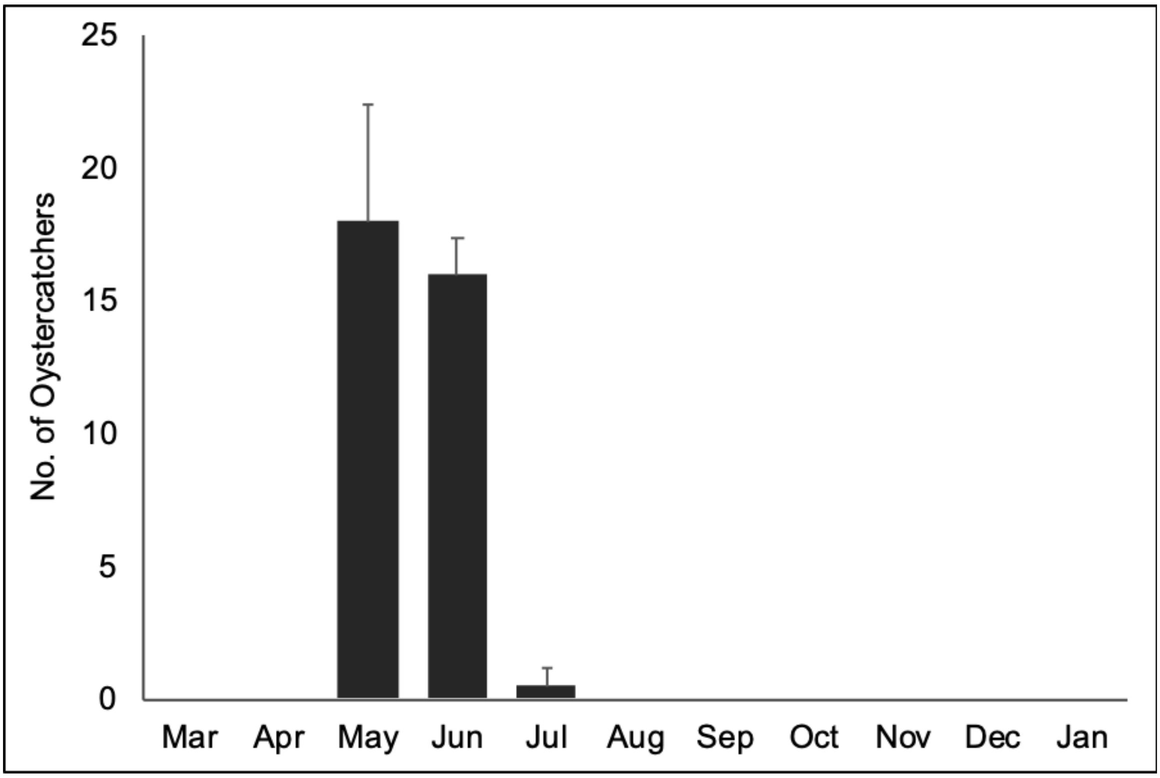


Figure 2.8 Number of oystercatchers at First Stream throughout the year. Error bars are SD.

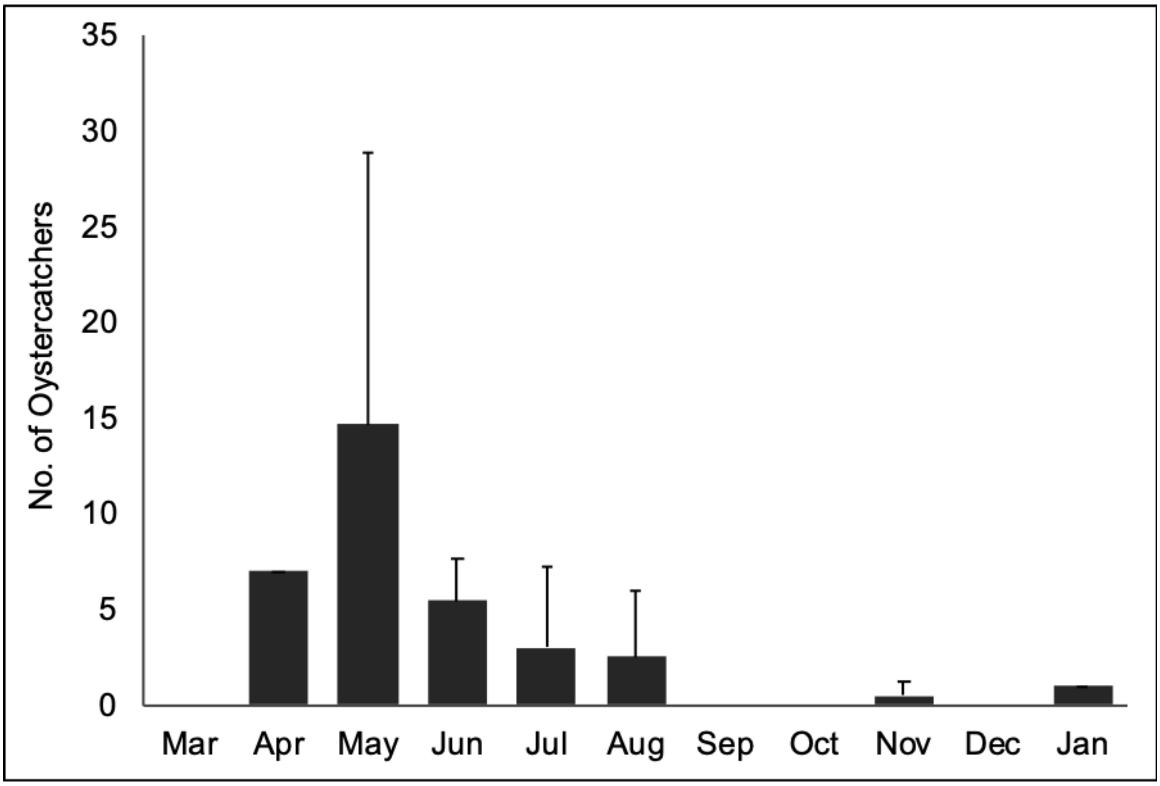


Figure 2.9 Number of oystercatchers at Third Stream throughout the year. Error bars are SD.

2.5 Discussion

South Island pied oystercatcher numbers and distribution varied over time. During the nonbreeding months (January to July) higher numbers of oystercatchers were found on the beach. The results have shown that oystercatcher presence on Ripiro Beach throughout a one-year period support the first hypothesis that numbers will be higher during the oystercatcher nonbreeding season. These findings clearly indicate that intense oystercatcher predation is only occurring in approximately six-month intervals every year. Though the oystercatchers did not aggregate at all major toheroa beds along Ripiro Beach, they did, in fact, show a preference for toheroa beds found at First Stream and Third Stream. The close spatial association between the oystercatchers and toheroa at these beds support the second hypothesis which proposes that oystercatchers will aggregate in areas of high prey density. Conversely, the finding that the oystercatchers were not found foraging on the toheroa beds/streams further north was unexpected.

The oystercatchers were distributed non-randomly along the beach, concentrated towards the southern half of the beach throughout the year. As shown by various studies investigating food availability and foraging site selection (Colwell & Landrum, 1993; Spruzen *et al.*, 2008; Schwemmer *et al.*, 2016), the aggregative response assumes that the distribution of a predator will be correlated with areas of high prey density. Thus, from the findings of the current study, it can be assumed that the areas frequented by oystercatchers (the southern part of the survey area, First Stream and Third Stream) have sufficient amounts of available food to support the numbers of oystercatchers when they are present at these sites. Alternatively, the distribution patterns of the oystercatchers on Ripiro Beach may simply be explained by optimal foraging theory. For example, it would take more time and energy to fly from their roost in the Kaipara Harbour to the northern section of the beach. Perhaps there is sufficient availability of prey all year at First Stream and Third Stream and southwards to not require the birds to forage in the north. In addition, they may be avoiding the more populated areas where they would be exposed to higher levels of human disturbance (Fitzpatrick & Bouchez, 1998; Verhulst *et al.*, 2001).

The third hypothesis of this study proposed that oystercatchers would follow the ideal free distribution to avoid interference at foraging sites, by spreading out at times when oystercatcher numbers were high. This was not the case. March 2019 and January 2020 saw some of the highest numbers of oystercatchers foraging on Ripiro Beach, but they demonstrated the smallest dispersal of oystercatchers of all months. During these months, the majority of birds foraged towards the southern end of the beach near the end of the survey area. Only in April and May did the birds begin dispersing further north along the beach. It appears as though interference may not be an important factor in the choice of foraging sites by oystercatchers. Perhaps there is adequate prey abundance in the areas they are foraging, limiting the occurrence of interspecific competition. As the year progressed, the birds were found further and further north. Therefore, it is hypothesised that the oystercatchers forage at the southern end of the beach closest to their roosting grounds at the beginning of the nonbreeding season. As they deplete the prey resources from this area of the beach, the oystercatchers are forced to forage further north to locate more prey.

Based on the findings from this chapter, there is evidence suggesting that the majority of toheroa populations on Ripiro Beach are not exposed to oystercatcher predation. However, the toheroa inhabiting the beds at First Stream and Third Stream may be facing a relatively high amount of predation by the oystercatchers for some of the year. It is important to note, however, that the numbers of oystercatchers foraging on these beds peaked in May at around 15 individuals at any one time (based on observations from bird surveys). Consequently, the total number of oystercatchers placing predation pressure on toheroa at these sites is still comparatively low. Yet, it should be mentioned that toheroa can be found isolated from major toheroa beds. For example, juvenile toheroa are often settled along the beach randomly, depending on the way in which they were carried ashore (Redfearn, 1974). It is possible then, that oystercatchers are predating on toheroa in areas other than major toheroa beds. Nevertheless, the majority of large toheroa beds are located at the northern half of the beach, where the oystercatchers are not observed. Therefore, it is anticipated that other factors (for example, adjacent land use change, crushing by vehicles and illegal human harvesting) are contributing to the beach-wide decline in toheroa numbers (Ross *et al.*, 2018a).

2.5.1 Limitations

Bird surveys were conducted on neap tides as these tides were the best for driving on the beach. Thus, it is possible that oystercatcher presence on the beach may have been different at other times of the tidal cycle, for example during spring tides. Consequently, the numbers and distribution of oystercatchers along Ripiro Beach shown in this study may not be representative of oystercatcher distribution patterns at all times of the month. Likewise, bird surveys were generally conducted relatively early in day (~08:00-09:00) as the low water period on neap tides tended to coincide with early mornings. It is possible that not all birds had arrived at the beach from their roost and that numbers were potentially underrepresented. However, in multiple bird surveys done in one day in July, counts were consistent across the whole day, but the number of individuals at foraging locations was different, indicating that the oystercatchers move around the beach throughout the day.

2.5.2 Conclusion

Oystercatcher distribution patterns were non-random, and the birds showed high site fidelity throughout the year. Bird numbers were relatively low (~ 25 on average) for most months of the year except March, April, May 2019 and January 2020. Their distribution patterns did not support the ideal free distribution but rather the oystercatchers were limited to the southern half of the beach. Therefore, it is concluded that only a small part of the Ripiro Beach toheroa population is exposed to oystercatcher predation throughout the year. Accordingly, the claims that the South Island pied oystercatcher are responsible for the continuing decline of toheroa populations cannot be supported by the data found in this study, as the oystercatchers are not found across the whole of Ripiro Beach and the distributions of the two species do not entirely overlap. However, there are associations between oystercatchers and toheroa at two streams (First Stream and Third Stream). It must be noted, though, that the beds at First Stream and Third Stream are still quite large and comparable in size to those beds in the northern half of the beach (P. Ross pers comm.; pers. obs.). Based on what has been observed in this study, impact from oystercatcher predation on toheroa is unlikely to be widespread but there may be local impacts on the two toheroa populations that are exposed to oystercatcher predation. Thus, the next step is to understand the behaviour and foraging ecology of oystercatchers present on the toheroa beds. Are the birds eating toheroa and if so, what size, and how many? The next chapter will address these questions.

Chapter 3

Oystercatcher Foraging Ecology and Diet Composition

3.1 Introduction

Oystercatchers are known to forage on a wide variety of invertebrates including bivalves, marine and terrestrial worms, crustaceans and insects in intertidal areas such as mudflats, exposed beaches and rocky shores (Heppleston, 1971; Dare & Mercer, 1973; Thibault, 2008). Nonetheless, bivalves are thought to be the predominant prey of most oystercatcher species worldwide (Hulscher, 1996). This is due to the fact that oystercatchers are both behaviourally and morphologically adapted to capturing and handling benthic molluscan prey, giving oystercatchers a selective advantage over many other shorebird species foraging in the intertidal zone (Hulscher, 1996). Oystercatchers are such adept predators that they are even known to alter their diet seasonally or according to environmental conditions, changing the form of their bill to suit the specific prey (Hulscher, 1996). These advanced predation skills can impact on local populations of the prey species that are preferred by the oystercatchers. In a study on foraging behaviour of American oystercatchers (*Haematopus palliates*), Tuckwell and Nol (1997) found that over just one season (from autumn to winter) the density of oysters declined considerably. The authors attribute this decrease to the predation by the oystercatchers. Likewise, Frank (1982) showed that black oystercatchers (*Haematopus bachmani*) in Oregon, USA exerted significant pressure on their limpet prey over one season, influencing their distributions and reducing their numbers. These studies show the proficiency of oystercatchers as predators and their ability to significantly impact a prey species over a short time frame.

Oystercatchers use two main methods of handling shellfish: stabbing and hammering (Norton-Griffiths, 1967; Dare & Mercer, 1973; Baker, 1974b; Hulscher, 1996; Bachmann & Martínez, 1999). Stabbing has been described as inserting the bill between the valves of the mollusc to severe the abductor muscle in order to be able to extract the contents of the shellfish (Norton-Griffiths, 1967; Bachmann & Martínez, 1999). Hammering involves striking through the ventral or dorsal shell of the bivalve repeatedly until it breaks (Norton-Griffiths, 1967; Zieritz *et al.*, 2012). These shorebirds are capable of opening molluscs by pulling them out of the substrate or handling them whilst they are still buried (Wanink & Zwarts, 1985; Bachmann & Martínez, 1999). Bachmann and Martínez (1999) found that American oystercatchers foraging in a lagoon in Argentina locate food by making pecks on the surface of the substrate to detect prey and then deep probes to capture the located individual(s). The authors suggested that oystercatchers foraging in this study use the siphon holes of the bivalves to pinpoint their prey visually (Bachmann & Martínez, 1999). Oystercatchers have also been found to locate their prey using a tactile method described as rapid pecking, stitching or sewing, in which the bird makes a series of short probes into the substrate with its bill partly open while slowly moving forward (Baker, 1974b; Lauro & Nol, 1995; Hulscher, 1996). Hulscher (1982) proposes that the type of foraging technique can be associated with the kind of prey that the bird is searching for. For example, slow pecking for worms and rapid pecking for buried bivalves. The birds generally forage in the lower intertidal zone, close to the water's edge while walking parallel to the water (Bachmann & Martínez, 1999; Aplin & Cockburn, 2012). Thus, the tides are an integral part of the foraging ecology of oystercatchers, principally because the stage of the tidal cycle determines the birds' access to their intertidal prey (Heppleston, 1971; Aplin & Cockburn, 2012). Aplin and Cockburn (2012) found that Sooty oystercatchers (*Haematopus fuliginosus*) in Australia forage only during the two hours either side of low tide. Similarly, another study in Northern Ireland showed that oystercatchers would arrive to the beach from their roost around three to four hours before low tide but would rest or preen rather than forage immediately. Only once the water had receded (around three hours either side of low tide) did the birds begin to forage (Fitzpatrick & Bouchez, 1998).

Although there have been numerous studies conducted on the feeding behaviour and prey type of oystercatchers overseas, little research has focused on oystercatchers here in New Zealand. Baker (1974b) conducted one of the few studies dedicated to feeding methods of the various oystercatcher species living in New Zealand. The author studied the feeding behaviour of South Island pied oystercatchers at the Heathcote-Avon estuary in Canterbury in the South Island (as well as the variable and Chatham Island oystercatchers in other locations). He discovered that the South Island pied oystercatcher is adapted to forage on benthic bivalves in estuaries and oceanic beaches (for example cockles, pipi, tuatua), in comparison to the variable oystercatcher which exploits chiton and limpets on rocky shores. Baker suggests that the oystercatchers locate their prey visually by searching for the siphon holes made by molluscs buried under the substrate. In soft substrates (where siphon holes are covered by water), it appears as if the oystercatchers use the rapid pecking or sewing technique aforementioned, in which they locate prey by touch. Baker (1974b) noted that bivalve flesh was extracted by the bird, by thrusting its bill in between the valves and forcing them apart by snapping off the abductor muscles. This study by Baker (1974b) provides considerable insight into the foraging ecology of the oystercatchers in New Zealand. However, it did not examine their predation on toheroa, a species of clam, which can bury itself much deeper than many other New Zealand intertidal molluscs (Kondo & Stace, 1995; Cook, 2010). To the best of my knowledge, no one has examined the feeding behaviour and diet composition of oystercatchers on toheroa on Ripiro Beach. Therefore, the overarching goal of this chapter is to gain a better understanding of South Island pied oystercatcher foraging behaviour at Ripiro Beach, Northland. The information gathered from this study may be used to assess the impact of oystercatchers on toheroa populations.

To achieve this goal, I conducted an observational study of oystercatcher foraging behaviour on Ripiro Beach including collecting information on prey type, searching techniques, handling techniques and prey location in order to answer three main questions:

1) What type of prey do oystercatchers consume?
2) How much prey do they consume and what proportion of their diet is comprised of toheroa?
3) Is there a difference between the prey types consumed by oystercatchers foraging at stream-associated toheroa beds compared to those foraging elsewhere?

3.2 Methods

Behavioural data were collected on randomly selected focal individuals (Altmann, 1974) from different flocks on any given sampling day. Every second flock was sampled using a random number generator either producing the number 1 or 2 in order to determine if the first flock sampled would be the first or second encountered of the survey area. Preliminary oystercatcher filming aimed to randomly select different flocks down the length of the beach using a random number generator. However, the decision was made to change to every second flock as it was found that much time was wasted driving between randomly selected flocks. Due to time constraints imposed by the tides and the necessity to collect other data on the same day (for example, conducting bird surveys discussed in Chapter 2), flock selection did not always begin at the same location but rather began either from the northern end of the survey area (driving south) or vice versa.

Oystercatchers were given three minutes to resume ‘normal’ behaviour after researcher vehicle arrival. Preferably, this acclimation period would have been longer (10 minutes) to reduce observer effects. However, trial and error during preliminary observations showed that after 10 minutes the oystercatchers had sometimes moved so far away that they could no longer be filmed. Consequently, the acclimation period was reduced to three minutes.

Observations occurred over nine days in the months of May (four days), June (two days) and July 2019 (three days) and were always made during neap tides. In July, filming took place solely at Third Stream over a two-day period where oystercatchers were observed and filmed for approximately eight hours each day. Sampling was conducted in this manner to gain information on oystercatcher behaviour at a highly popular foraging site that is associated with a large toheroa bed. The variation in filming methodology is not ideal but due to time constraints of the project in addition to the tides, I considered it to be the best use of limited time.

The first focal individual in a flock was selected by choosing the oystercatcher closest to the researcher. Successive birds were selected in the same manner. As the oystercatchers moved around rapidly and in all directions (when foraging), the closest individual to the researcher at the onset of filming was almost always a different individual from that just filmed. If the closest individual did happen to be the bird just previously filmed, the nearest bird to the right of the individual was selected (as the birds were not individually marked, it is possible that the same individual may have been filmed more than once on a sampling day). Focal individuals were filmed from no more than 50 metres away, but it is possible that during filming a bird may have moved over 50 metres away without the observer realising. Video recording began immediately after selection of an individual with a minimum recording time of 1 minute and a maximum recording time of 25 mins. A focal observation ceased if the individual walked or flew out of view or if the bird stopped foraging for over one minute.

Observations were conducted on both the ebb and flood tide, approximately three hours either side of low tide. The following was recorded for each sample: ebb or flood tide, low tide time, time of filming, weather, zone on the beach, GPS location of flock, predominant flock activity and flock size. All videos were taken using a Nikon COOLPIX P1000 camera on a customised, hand-made camera mount (Figure 3.1) that could be either attached to the door of the vehicle or used as a stand-alone unit on the beach (to minimise bird disturbance and to save time setting up and disassembling a tripod).

Figure 3.1 Image showing custom-fabricated, vehicle door camera mount attached to vehicle whilst filming oystercatchers on Ripiro Beach (photo by M. Bennion).

3.2.1 Video Analysis

Observations were conducted to determine the main type of prey oystercatchers were consuming, how much prey they were taking, and the techniques used in capturing and handling their prey. During video analysis, prey were categorised as either polychaete, bivalve or unidentifiable. It was not possible to identify prey with greater certainty from the distance at which I filmed. Foraging was defined as: the oystercatcher is actively searching for, handling or consuming prey (Aplin & Cockburn, 2012). The consumption of a prey item was defined as: the final swallow of that prey item before shifting to another behavioural event or state.

Analysis of video footage was carried out using an open source behavioural coding programme Solomon Coder (version: beta 17.03.22). Preliminary analyses were conducted on 20 videos to refine behavioural definitions, create an ethogram

(Table 3.1) and for training purposes. A configuration sheet was created to present all behavioural and non-behavioural variables as “buttons” within the program (Table 3.1, Table 3.2). When the focal individual performed a specific behaviour, the corresponding “button” was selected (Figure 3.2). After the analysis of a video was completed, the coding sheet was saved, and an output of the data was exported to Excel for later statistical analysis. The following behavioural and non-behavioural variables were calculated per individual:

1. Number of pecks per minute.
2. Number of sewing bouts per minute.
3. Number of probes per minute.
4. Prey intake rate (number of prey consumed per minute).

A total of 7.5 hours of footage from 71 focal animal videos were observed and coded during formal video analysis. Eighteen of the 71 videos (25%) were re-analysed for both intra- and inter-observer reliability testing. These were randomly selected using a random number generator app and re-analysed both by myself and another independent observer. The independent observer was given the ethogram detailing the behavioural definitions and was trained on Solomon Coder before formal analysis began.

Table 3.1 Ethogram of oystercatcher behaviour recorded during video analysis.

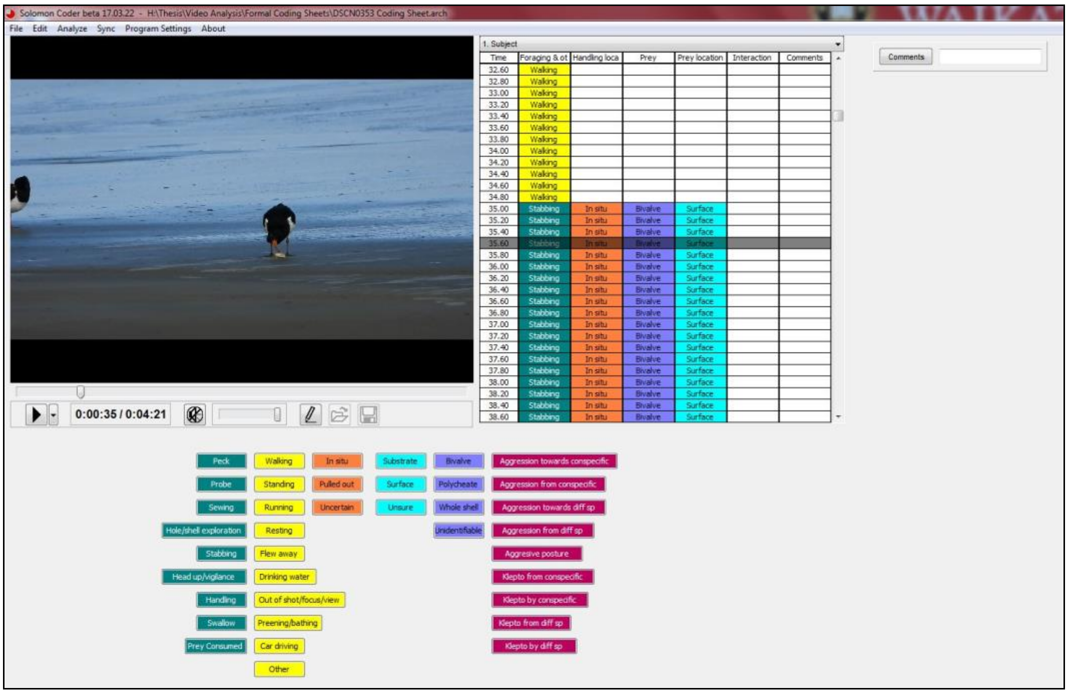
Behaviour	**Definition**	**Category**
Peck	A single movement of the head in which attention is directed at one spot and an almost fully closed bill penetrates the substrate, just below the surface. Pecks are directed in front of or slightly to either side of the bird. A number of touches can be made at this one spot but it is considered one peck (Hulscher, 1996).	Detecting/localising prey
Probe	Bird penetrates the substrate on the same spot by making a side to side movement with its head or a series of rapidly executed up and down movements of the slightly opened bill. Bill enters the substrate deeper than a peck or a sew and can gradually penetrate the substrate up to the base of the bill (García *et al.*, 2010).	Detecting/localising prey
Sewing	Composed of distinct bouts of vertical probes made while the bird moves slowly forwards. The bill is opened 1-2 mm & moves straight up and down at a rate of 3-7 times per second. Between sewing bouts, the bill is wholly retracted from the substrate and reinserted after the bird has moved forward a few centimetres or further (Hulscher, 1996).	Detecting/localising prey
Hole/shell exploration	Investigating a hole that has been created by another bird or shell that has previously been handled by another bird.	Detecting/localising prey
Stabbing	The bird makes downward jab movements with its bill between the valves of the clam, the flesh is loosened from the shell by scissoring the mantle attachments before it is swallowed. Bird may rotate its body around the bivalve.	Bivalve handling
Handling*	Bird handles prey after capture and before swallowing.	Other handling
Swallow	Prey item is grasped in the oystercatcher's beak. Head is then lifted upwards and prey is cast backward and down towards the throat to be consumed.	Consumption
Aggression from conspecific	Bird is confronted by a conspecific and may defend food or run away from the other oystercatcher.	Interaction
Aggression towards conspecific	Bird assumes a hunched posture towards conspecific, may spread its wings and run or jump towards another oystercatcher.	Interaction
Aggression from different species	Bird is confronted by a member of a different bird species and may defend food or run away from other bird.	Interaction

Behaviour	Definition	Category
Aggression towards different species	Bird assumes a hunched posture towards member of another bird species, may spread its wings and walk/run after another bird.	Interaction
Aggressive posture	Bird assumes hunched posture and may spread its wings.	Interaction
Kleptoparasitism by conspecific	Bird is confronted by another oystercatcher and has its prey stolen.	Interaction
Kleptoparasitism from conspecific	Bird interacts aggressively with another oystercatcher and steals its prey.	Interaction
Kleptoparasitism by different species	Bird is confronted by a member of a different species and has its prey stolen.	Interaction
Kleptoparasitism from different species	Bird interacts aggressively with member of a different species and steals prey.	Interaction
Head up/vigilance	Raises head and may look around at its environment. Sometimes done during sewing bouts and during handling a prey item.	Non-foraging behaviour
Walking	Moving in one direction, one foot after another, with head up. Including between sewing bouts.	Non-foraging behaviour
Standing	Stationary in one spot.	Non-foraging behaviour
Running	Moving in one direction, one foot after another, with head up. At a faster pace than walking.	Non-foraging behaviour
Drinking water	Bird dips or probes bill into water, raises head facing upwards and swallows.	Non-foraging behaviour
Resting	Bird is standing or lying down in one place. Head can be resting in feathers.	Non-foraging behaviour
Bathing/preening	Bird cleans its neck, wings, feather etc with its own beak. May use freshwater to bathe.	Non-foraging behaviour
Flew away	The bird flew away out of shot, filming ended.	Non-foraging behaviour
Other	For all other non-defined behaviours.	Non-foraging behaviour

*There was no definition or "button" created for the infrequent occasions in which oystercatchers did not handle their prey but rather swallowed immediately after capture. In this instance, the cell was left blank and "not handled" was recorded in comments and added to data after video analysis was complete. The same process occurred for instances in which the prey was handled *in situ* first and then pulled out of the substrate and was recorded in comments as "both".

Table 3.2 Non-behavioural variables recorded during video analysis.

Variable	**Definition**	**Category**
Prey consumed	A prey item was successfully consumed.	Feeding Event
Out of shot/focus/view	Bird moves out of shot momentarily, camera is out of focus, view of individual is blocked by another bird or bill cannot be seen.	Other
Car driving	Car drove past and momentarily blocked bird from view.	Other
In situ	Bird handles prey where it was found.	Handling location
Pulled out	Prey is removed from substrate by inserting the bill into the substrate and pulling strongly upward.	Handling location
Uncertain	Uncertain where prey was handled.	Handling location
Substrate	Prey was found underneath the substrate.	Prey location
Surface	Prey was found on the surface of the substrate.	Prey location
Unsure	Not clear if prey was found on surface or in substrate.	Prey location
Bivalve	Can usually tell if prey is a bivalve by the way bird handles. Will most likely use a stabbing technique to capture prey.	Prey type
Polychaete	Can usually tell if prey is a worm as the bird appears to follow the prey along in the substrate with its bill.	Prey type
Whole shell	Bird consumes whole shell.	Prey type
Unidentifiable	Prey cannot be identified.	Prey type



Time	Foraging & ot	Handling loca	Prey	Prey location	Interaction	Comments
32.60	Walking					
32.80	Walking					
33.00	Walking					
33.20	Walking					
33.40	Walking					
33.60	Walking					
33.80	Walking					
34.00	Walking					
34.20	Walking					
34.40	Walking					
34.60	Walking					
34.80	Walking					
35.00	Stabbing	In situ	Bivalve	Surface		
35.20	Stabbing	In situ	Bivalve	Surface		
35.40	Stabbing	In situ	Bivalve	Surface		
35.60	Stabbing	In situ	Bivalve	Surface		
35.80	Stabbing	In situ	Bivalve	Surface		
36.00	Stabbing	In situ	Bivalve	Surface		
36.20	Stabbing	In situ	Bivalve	Surface		
36.40	Stabbing	In situ	Bivalve	Surface		
36.60	Stabbing	In situ	Bivalve	Surface		
36.80	Stabbing	In situ	Bivalve	Surface		
37.00	Stabbing	In situ	Bivalve	Surface		
37.20	Stabbing	In situ	Bivalve	Surface		
37.40	Stabbing	In situ	Bivalve	Surface		
37.60	Stabbing	In situ	Bivalve	Surface		
37.80	Stabbing	In situ	Bivalve	Surface		
38.00	Stabbing	In situ	Bivalve	Surface		
38.20	Stabbing	In situ	Bivalve	Surface		
38.40	Stabbing	In situ	Bivalve	Surface		
38.60	Stabbing	In situ	Bivalve	Surface		

Figure 3.2 A screenshot of the Solomon Coder configuration sheet during analysis of a video. The video being watched is on the left-hand side of the image and the table where behaviour is coded is on the right of the video. The lower half of the image shows the different "buttons" that get activated when a particular behaviour or variable is being coded.

3.2.2 Statistical Analyses

All statistical analyses were performed in Statistica (V. 13) and figures were made using Statistica or Microsoft Excel. The accepted level of significance for all statistical tests was ≤ 0.05. To examine the diet composition of the oystercatchers, where prey was found, handling location and prey type versus handling method, descriptive statistics, graphs and tables were formulated.

To determine if there was any statistical difference in prey intake rate (prey per minute) in oystercatchers that foraged at different site types (i.e. stream-associated toheroa beds or elsewhere), a Mann-Whitney U test was applied as the data did not meet the assumption of normality (Shapiro-Wilk for both stream ($W = 0.52$, $p < 0.01$) and non-stream data ($W = 0.81$, $p < 0.01$)).

Prey type data were categorical and did not meet the assumption of normality (Shapiro-Wilk for bivalve $W = 0.58$, $p < 0.01$, for polychaete $W = 0.37$, $p < 0.01$, for unidentifiable $W = 0.49$, $p < 0.01$). Separate Mann-Whitney U tests for all prey types, for example, bivalve, polychaete and unidentifiable were conducted to identify differences in prey types between foraging sites (i.e. streams versus not streams). As non-parametric statistics were used, box plots were formulated to present the difference in medians between prey intake rate and prey type at different foraging site types.

The reliability of video analysis was examined by intra-observer and inter-observer reliability testing and analysed using Pearson's correlations.

3.3 Results

3.3.1 Ad lib Observations

3.3.1.1 Searching

Oystercatchers used two different techniques when searching for and detecting prey: pecking and sewing. Pecking was generally used when the oystercatchers were foraging in the mid to high intertidal zone on substrate that was relatively dry and compact. It appeared as if they were locating their prey visually; walking at a relatively fast pace and increasing the pace just before they would peck on the surface of the substrate, as if they had seen an indication of a potential prey item on the substrate. Occasionally, the birds would probe into the hard substrate, either successfully or unsuccessfully (Figure 3.3). Whilst pecking in the higher intertidal zone, the birds only ever captured bivalves (usually relatively small) and unidentifiable prey, but never polychaetes. When foraging in the lower intertidal zone (wet substrate), the oystercatchers mainly used the sewing technique described in the introduction. This appeared as if it were both a visual and tactile foraging strategy as they would walk in between sewing bouts to a particular spot in the substrate which appeared to give an indication of prey presence.

3.3.1.2 Handling

The exact moment a particular prey item was located could be recognised fairly certainly depending on the type of prey. For polychaete prey, during a sewing bout, the oystercatchers would suddenly and rapidly probe into the substrate and perform a series of probes in a manner that appeared to follow the worm attempting to escape. If the prey were a bivalve, the bird would either be walking and pecking or sewing, until the moment of location when it would stop suddenly, close its bill and more often than not, rotates its body to begin stabbing of the clam. Sometimes the bird would decide to pull the bivalve out rather than open *in situ*. In this instance, the bird would open its bill wider, probe into the substrate and perform an upward pulling motion by bracing its legs and raising its head. It would generally take a few tugs before the clam was successfully pulled out. Oystercatchers were frequently forced to run a far distance with the clams in their bills to avoid having their prey item stolen by conspecifics or, more often, gulls. Once finding a suitable location, the birds would begin to stab into the bivalves and perform a scissoring like motion with their bill, as if cutting the flesh from the valves of the clam. Hammering of clams was not observed at all.

Figure 3.3 An oystercatcher probing into the substrate at Kellys Bay (photo by L. Vallyon).

3.3.1.3 Kellys Bay and Feeding Rhythms

Though not measured directly, it appears that the Ripiro Beach oystercatchers display similar feeding rhythms to their overseas conspecifics (Heppleston, 1971; Levings *et al.*, 1986; Fitzpatrick & Bouchez, 1998; Aplin & Cockburn, 2012). A visit to Kellys Bay (a known roosting site of the oystercatchers; Figure 2.2) in May 2019 gave an indication into the birds' feeding rhythms. At the time of low tide (08:30), only a few (~20) oystercatchers were foraging in the bay. After talking with local residents, it was discovered that the oystercatchers leave their roost just before low tide (roughly one hour prior) and do not return until high tide. Around an hour and a half before high tide (14:30), there were roughly 200 oystercatchers in the bay, mostly walking and bathing. By high tide, at least 1,000 oystercatchers (and other shorebirds) could be seen at the bay, most of which had arrived in large flocks coming from the south (Figure 3.4). From observations made on Ripiro Beach at Third Stream over two days in July 2019, the oystercatchers arrived at the stream (potentially from Kellys Bay or from the south of the survey area) around one hour after sunrise, presumably following a diurnal feeding rhythm. Most would rest or preen on arrival before beginning to forage around one hour later. During the day, the oystercatchers switched between resting, preening and foraging and flocks of oystercatchers would come and go throughout the day.

Figure 3.4 South Island pied oystercatchers preparing to roost at Kellys Bay (photo by L. Vallyon).

3.3.1.4 Interactions and Interference

Foraging oystercatchers often interacted aggressively towards one another by performing displays of aggressive postures, running or flying at each other, piping, fighting and stealing each other's prey. Kleptoparasitism, however, occurred mainly by gulls (black-backed or red-billed) from oystercatchers. In most instances, a gull would notice an oystercatcher handling a prey item and wait until the moment the oystercatcher had the prey in its bill. The gull would then attack the oystercatcher, forcing it to either swallow quickly, drop the prey item or fly away. Oystercatchers were never seen stealing food from other species. Interactions appear to have occurred more frequently at streams.

3.3.2 Quantitative Results

3.3.2.1 Feeding Rate and Prey Composition

On average an oystercatcher made 3.3 pecks (± 4.2), 6.9 sewing bouts (± 5.2) and 2.2 probes (± 1.9) per minute. The oystercatchers consumed an average of 0.5 (± 0.7) prey per minute. Across all 71 oystercatchers a total of 239 prey items were consumed; 135 bivalves (56%), 59 polychaetes (25%) and 45 unidentifiable items (19%) (Figure 3.5). Of all prey items consumed, 196 (80%) were found in the substrate, 21 (10%) on the surface and 22 (10%) were categorised as "unsure" (Figure 3.6). When handling prey, 116 (49%) of prey items were handled *in situ* (where they were found), 77 (32%) were pulled out from the substrate, 29 (12%) were categorised as "uncertain", 14 (6%) were not handled and 3 (1%) were handled both *in situ* and pulled out (Figure 3.7). Most of the prey handled *in situ* were bivalves while most of the prey pulled out of the substrate were polychaetes (Figure 3.8). Only 2.3 minutes of total video footage recorded did not show oystercatchers "in shot".

Pearson's correlations show that all recorded variables used in subsequent statistical analyses had a strong positive correlation (intra-observer and inter-observer $p > 0.90$). The exceptions to this were "surface" (prey location) (inter-observer $p = 0.28$), "unidentifiable" (prey) (intra-observer $p = 0.75$, inter-observer $p = 0.60$), "unsure" (prey location) (intra-observer $p = 0.37$, inter-observer $p = 0.32$) and "uncertain" (where handled) (intra-observer $p = 0.42$, inter-observer $p = 0.69$).

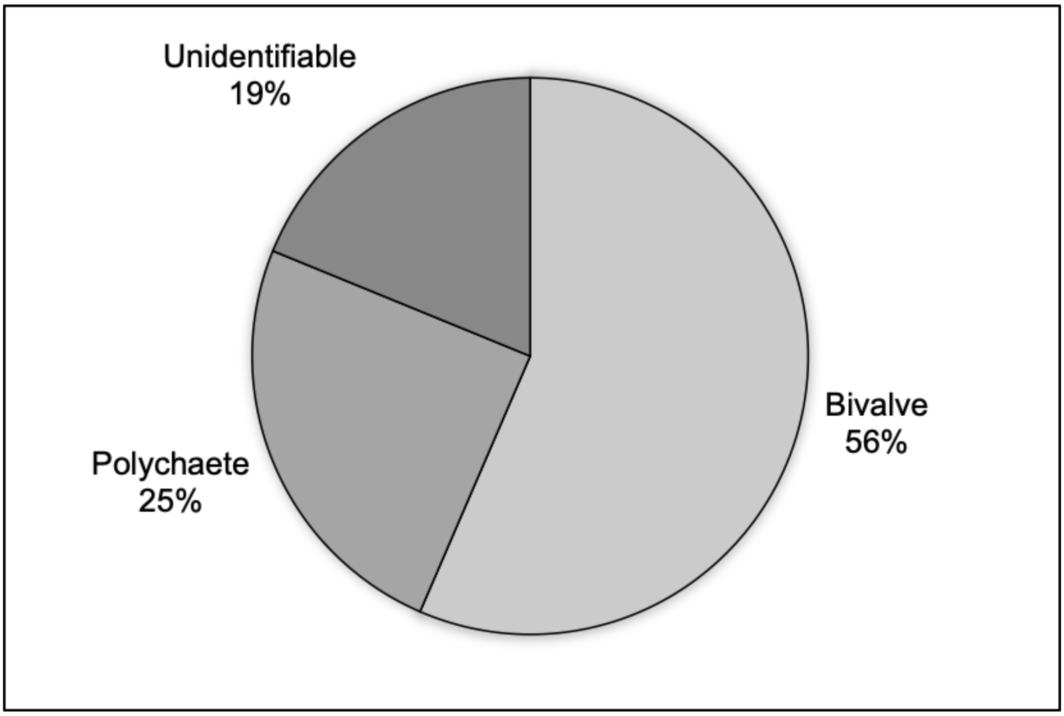


Figure 3.5 Proportion of different prey types consumed across all 71 oystercatchers. Bivalves represent more than half of the oystercatcher diet.

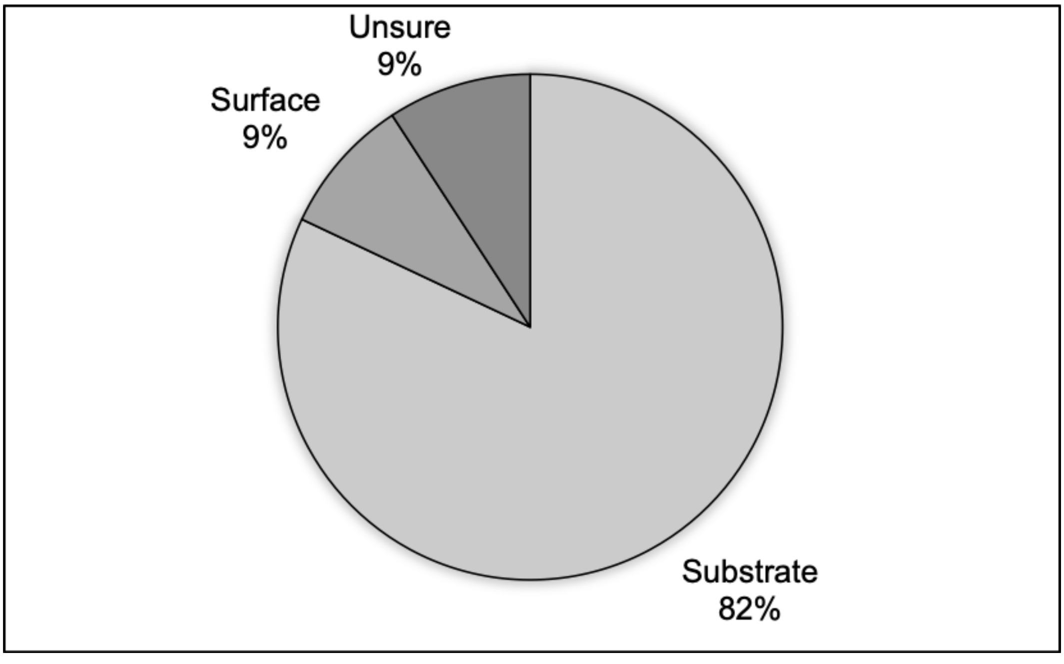


Figure 3.6 The location where oystercatchers most commonly found their prey.

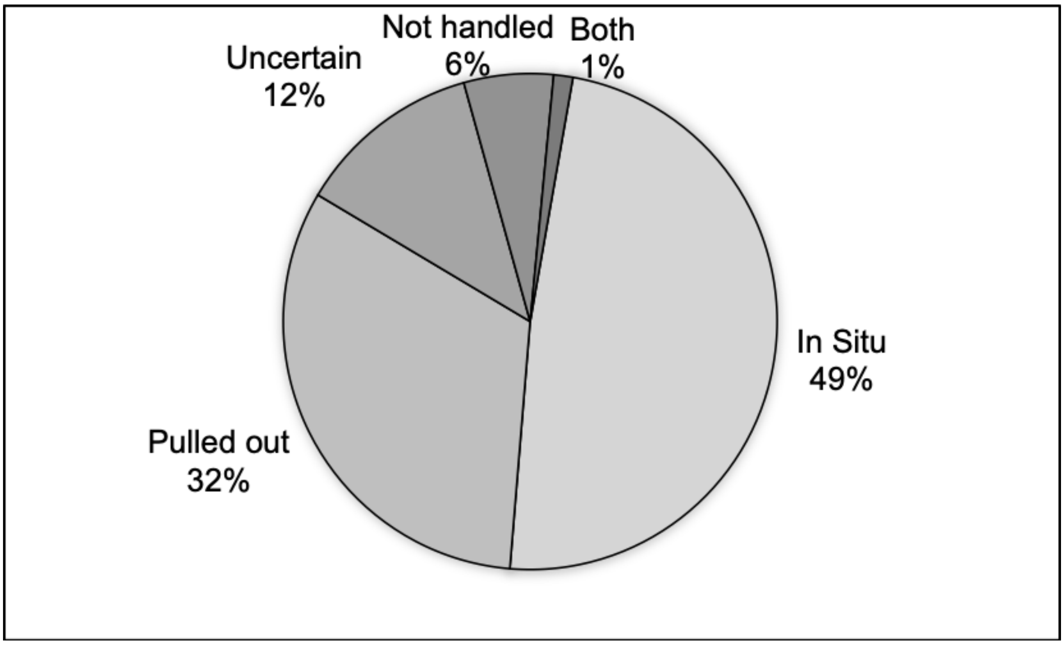


Figure 3.7 The handling locations of prey oystercatchers were observed consuming.

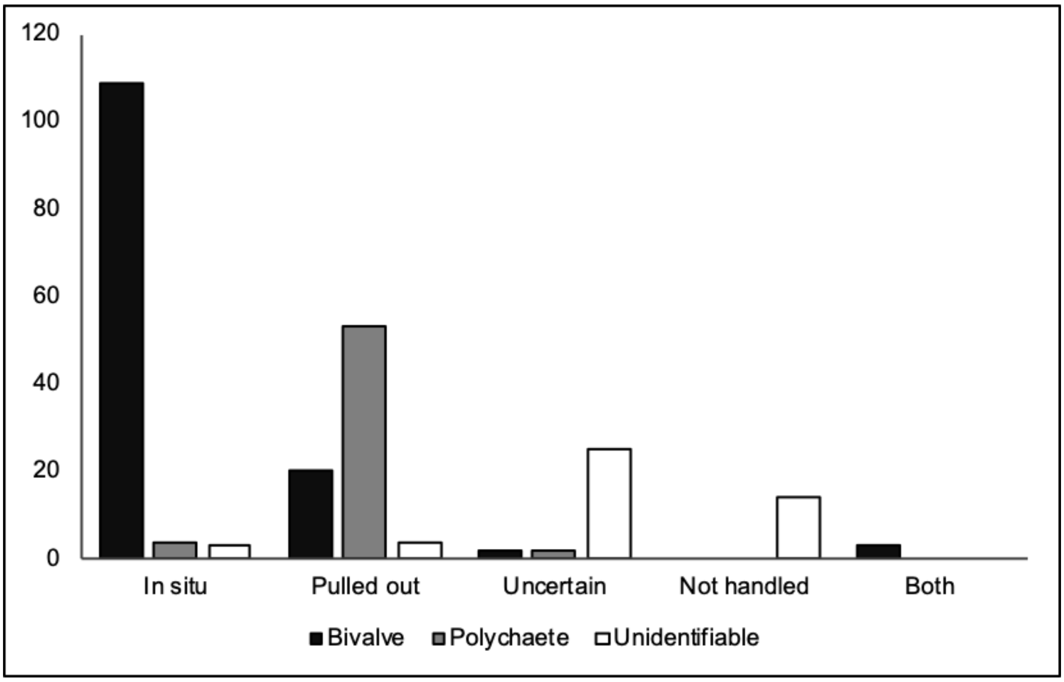


Figure 3.8 Locations in which particular prey types were handled.

3.3.2.2 Differences between Site Types

On average, oystercatchers predating in areas that were not associated with toheroa beds (streams) had a higher prey intake rate (Table 3.3). There was a significant difference in the medians of prey intake rate (prey per minute) of oystercatchers at different foraging sites (stream-associated toheroa beds versus sites elsewhere) (Z-adj = -2.89, p < 0.01) (Figure 3.9).

Table 3.3 Difference between mean prey intake rate (per minute) in sites not associated with toheroa beds versus stream-associated toheroa beds.

Site Type	Mean	SD (±)	Min	Max
No stream	0.77	0.86	0	3.07
Stream	0.26	0.48	0	2.73

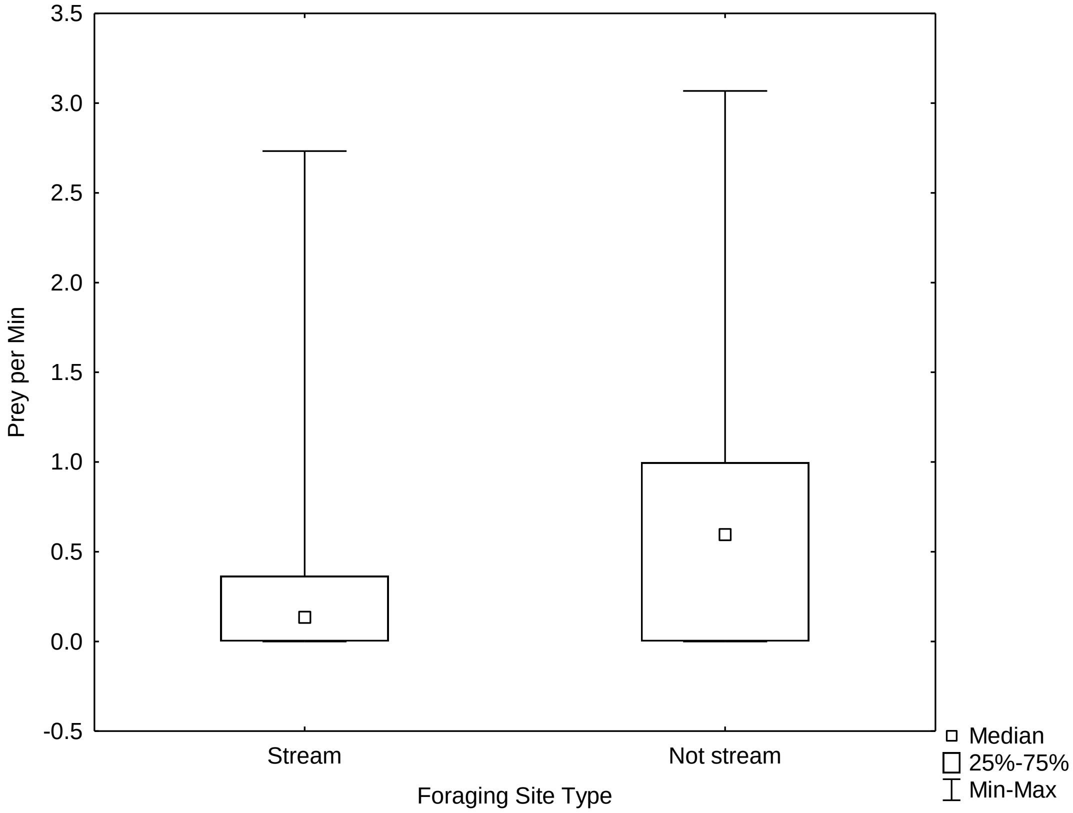


Figure 3.9 Box plots showing significant differences in medians of oystercatcher prey intake rate between two different foraging site types. Oystercatchers foraging in areas not associated with stream-associated toheroa beds had higher prey intake per minute.

There was no statistically significant difference between site type (i.e. stream-associated toheroa beds versus sites not associated with toheroa beds) in the amount of bivalve (Z-adj = -0.64, p = 0.51) (Figure 3.10) and unidentifiable (Z-adj = -1.58, p = 0.11) prey items that were consumed by oystercatchers. However, there was a significant difference (Z-adj = -4.05, p < 0.01) between site types in the amount of polychaete worms that oystercatchers consumed. Polychaete worms were never consumed at foraging sites that featured streams.

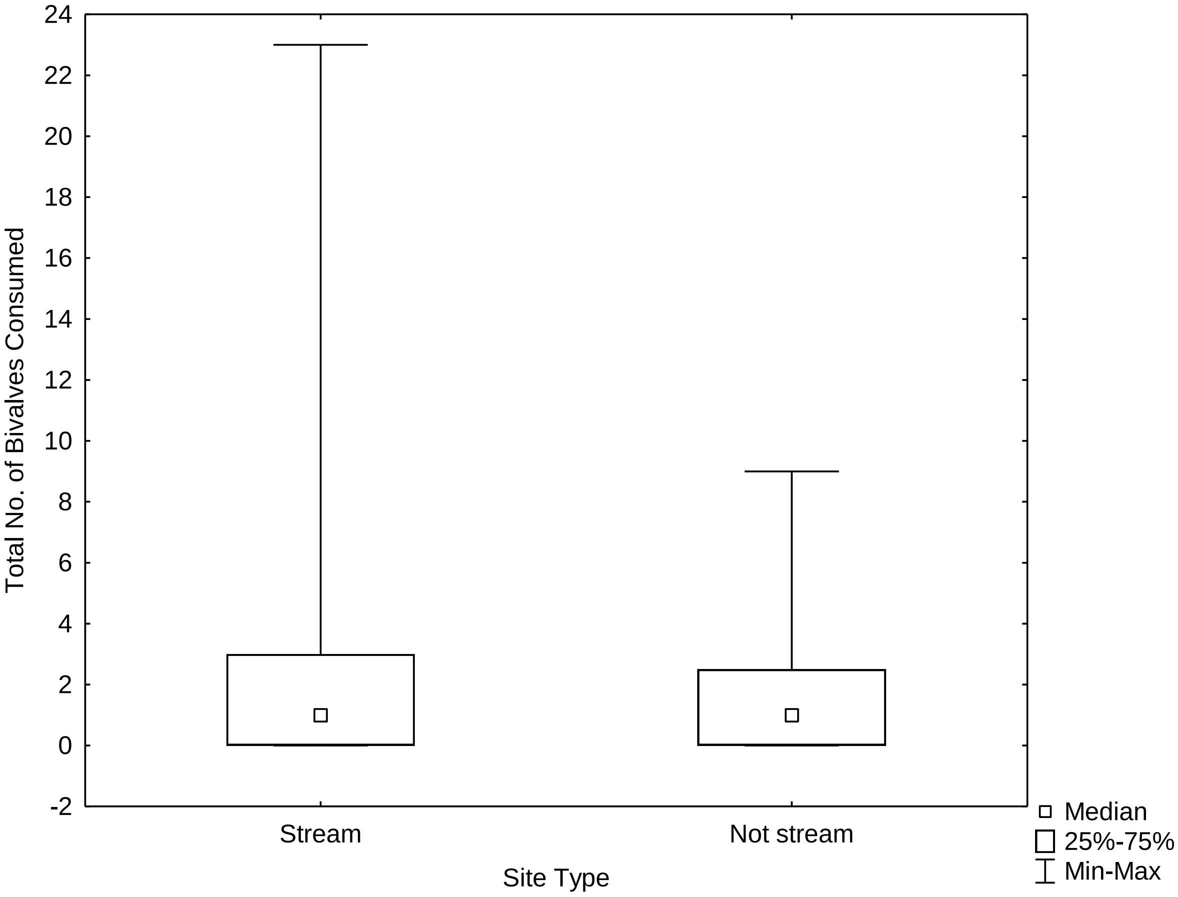


Figure 3.10 Box plot shows there is no significant difference in the median amount of bivalves consumed by oystercatchers foraging at stream-associated toheroa beds in comparison to those foraging in different areas.

3.4 Discussion

The aim of this chapter was to observe the foraging behaviour of the oystercatchers in order to identify what type and quantity of prey the birds consume and determine if there is a difference in prey types consumed between freshwater inputs (toheroa beds) and those oystercatchers foraging elsewhere. Newspapers articles have reported on calls for the culling of the South Island pied oystercatcher. Articles can be quoted stating: “learned how to dig for young toheroa, and were destroying entire beds”, “toheroa thieves” and “oystercatchers get their long beaks into the tube which toheroa extend to the surface of low-water sand and suck the mollusc from its shell” (Barrington, 2014b; Barrington, 2014a;

RadioNZ, 2014). Behavioural observations of these oystercatchers show that only some aspects of their foraging are consistent with the claims made in these articles. For example, oystercatchers are definitely capable of eating toheroa (of a specific size) and are extremely adept at removing the animals from their shells while still in the substrate. However, the oystercatchers are definitely not "destroying entire beds". Oystercatchers were observed to spend much of their day preening and resting with a minimum amount of time actively foraging.

The results from this study revealed that the main type of prey that oystercatchers are consuming on Ripiro Beach are bivalves (potentially both toheroa and tuatua) and polychaete worms. It is possible that they are also foraging on crustaceans that were not identified or misidentified during video analyses. Bivalves represented over half of the oystercatchers' diet, signifying that the oystercatchers may rely heavily on sustenance from this type of prey. Unexpectedly, when prey type was compared at different foraging site types (streams with toheroa beds versus sites elsewhere), there was no significant difference in the number of bivalves consumed by the oystercatchers. These findings suggest that the oystercatchers may have the capacity to put significant predation pressure on toheroa at Ripiro Beach. However, it is important to consider two factors when interpreting these results: 1) the oystercatchers have mainly been found foraging south of Glink's Gully (the southern half of the survey area) (see Chapter 2) and 2) it is impossible to tell how much of the bivalve population being consumed consists of toheroa. Therefore, if the oystercatchers are, in fact, having an impact on bivalve populations, it is not along the entire beach (72 km) but rather very locally (for example at First and Third Stream) and it is equally possible that the oystercatchers are consuming toheroa and tuatua.

Prey information was also examined in this study by quantifying factors such as prey location, handling technique and handling location. Oystercatchers found 80% of their prey underneath the substrate and just under half of all prey items were handled *in situ*. The Ripiro Beach oystercatchers only ever used the stabbing (and never hammering) technique to open their clam prey. Baker (1974b) also noted this, stating that bivalves on oceanic beachers are never opened by hammering as oceanic bivalve shells are distinctively thicker than their estuarine counterparts. Oystercatchers at a coastal lagoon off the Atlantic Ocean in Argentina were never observed to hammer their stout razor clam (*Tagelus* *plebeius*) prey, known to live intertidally on sandy beaches, possibly their shells are also too thick (Bachmann & Martínez, 1999).

Across all oystercatchers observed in this study, the average prey intake rate was half a prey item per one-minute foraging. The results demonstrated that there was a significant difference between the amount of prey consumed per minute at different foraging site types (those associated with streams/toheroa beds versus those foraging elsewhere). Interestingly, oystercatchers not foraging at freshwater seeps consumed more prey per minute than those foraging at streams. It is conceivable that levels of interference were higher at stream foraging sites as flock size was generally greater in those foraging site types. Another possibility is that the oystercatchers were consuming larger bivalves at stream-associated toheroa beds, which require longer handling times than smaller bivalve or polychaete prey that the birds are finding elsewhere.

3.4.1 Limitations

In general, this was a difficult study and a large amount of time was spent developing methodology. The study site is remote and there was a limited amount of time to conduct research (a few days a month). One of the main limitations to this was that individual focal sampling only ever occurred during neap tides. The tidal cycle has shown to have a significant influence on the foraging behaviour of oystercatcher species as the tides govern the birds' access to intertidal food supplies (Aplin & Cockburn, 2012). For example, a study by Aplin and Cockburn (2012) found that oystercatchers consumed different types of prey depending on the time of the tidal cycle. On neap tides, the oystercatchers were observed eating mainly limpets, bivalves and other small molluscs whereas on spring times, the birds were mainly eating polychaetes and crustaceans. It is possible that the Ripiro Beach oystercatchers may consume different proportions of the prey available at different tidal cycles.

The inability to identify bivalves to a species level through observation and video analysis is an obvious limitation. Oystercatchers have been observed consuming both toheroa and tuatua in this study, so it is difficult to say whether oystercatchers have a preference for either one. To make matters more difficult, tuatua are often found mixed in amongst toheroa in beds, in addition to toheroa being found outside of ‘main’ beds.

Results from intra-observer and inter-observer reliability testing mainly proved to have high Pearsons’s correlations ($p > 0.90$), however, there were some categorical variables in which the reliability was low. These variables were used in instances in which the other observer or myself were not certain of which variable corresponded with the event that occurred during video analysis. The variables were “unidentifiable” prey, “uncertain” where handled and “unsure” where found. It is important to note that the handling categories “not handled” and “both” (handled *in situ* and pulled out) did not undergo reliability testing, as they were not added as “buttons” during video analysis. This was due to the fact that they did not occur during preliminary video analysis and thus were not included in variable definition creation. Only during formal analyses were they observed and thus noted in “comments” and added to prey data later. Nevertheless, important categories (such as “bivalve”, “polychaete”, “*in situ*”) had high correlations ($p > 0.90$) for both intra-observer and inter-observer reliability testing and thus were measured confidently.

3.4.2 Conclusion

Bivalves are a significant food resource for oystercatchers foraging on Ripiro Beach. In general, the prey intake rate of oystercatchers appears to be relatively low with the birds consuming an average of one prey item per two minutes. It is important to note that they only spend a minimum amount of time foraging per day (observations showed around 3-4 hours maximum of active foraging). Chapter 2 demonstrated that the oystercatchers are not evenly distributed across the beach but forage predominantly in areas south of Glink’s Gully. They are regularly found at First Stream and Third Stream: two major toheroa beds. Interestingly, the number of bivalves consumed between streams (toheroa beds) and other foraging sites does not differ, suggesting that the birds are consuming equal quantities of bivalves down the southern end of the beach as at streams/toheroa beds. In addition, consumption of worms only occurs in areas not associated with freshwater. These results potentially help to explain the distribution patterns found from the study in Chapter 2. If the oystercatchers have higher prey intake rates and a greater variety of prey in areas not associated with streams, then foraging at the southern end of the beach would prove optimal. Therefore, oystercatchers may be having a local impact on toheroa populations on Ripiro Beach. The next chapter aims to investigate this further by examining oystercatcher predation success rate and toheroa density and size structure at First Stream and Third Stream.

Chapter 4
Oystercatcher Prey Size Selection

4.1 Introduction

Optimal diet theory assumes that predators strive to maximise their rate of energy intake by foraging in a manner that yields the greatest amount of profitability for the minimum amount of time taken to search for and handle prey (Macarthur & Pianka, 1966; Hughes, 1993; Giraldeau, 2008; Zieritz *et al.*, 2012). Hence, prey selection by predators is commonly understood within this optimality approach by following two main assumptions: 1) predators should only accept prey items that will provide optimal energetic profitability in the long term (Charnov, 1976; Rutten *et al.*, 2006), and 2) predators should take progressively less profitable prey as their preferred prey reserves become depleted (Hughes, 1993). A study by Ward (1991) provides an example of prey selection by examining the choice of size classes of bivalves by two different shorebird species. The author measured the availability of different sized clams, observed the diet of kelp gulls (*Larus dominicanus*) and African black oystercatchers (*Haematopus moquini*) and determined the searching and handling times for various clam size classes. The study found that the oystercatchers selected both small and large clams, regardless of the abundance of large clams. In contrast, gulls selected only large clams (> 40 mm) though other size classes were also available. The author attributes this disparity in size preference to differences of energy expenditure of the two species by their individual clam handling techniques (for example, gulls dropping clams is energetically more expensive). Whilst foraging, oystercatchers can be presented with a range of different prey sizes that offer diverse energetic outcomes and handling efforts within just one prey species (Leopold *et al.*, 1989). In order to make the most profitable choice, the oystercatcher should choose a specific size of prey that returns the most energy for the least amount of time handling. Consequently, it can be assumed that each oystercatcher has an upper and lower size limit in which the prey item is no longer profitable, with handling time increasing with larger prey and flesh content decreasing with smaller prey (Leopold *et al.*, 1989).

Oystercatchers have been described as being extremely prey selective; Sutherland and Ens (1987, p. 187) state: “the food supply of the oystercatchers appears exceedingly abundant. There may be as many as a thousand mussels per square metre, yet oystercatchers will walk many metres before selecting one”. A study by Hilgerloh and Pfeifer (2002) investigated the preferred size of mussels on tidal flats used by foraging oystercatchers (in addition to other shorebirds) in Germany. They found that the preferred size class (~50 mm) of mussel for the oystercatchers was the most abundant class. The study also showed that when the preferred size class was not available, the oystercatchers would select mussels smaller than their preferred size, but they would choose the largest of those (Hilgerloh & Pfeifer, 2002). Similarly, a study by Nagarajan *et al.* (2002) demonstrates that European oystercatchers were highly selective when foraging on mussels in England, selecting those only between 35 and 50 mm in length.

In contrast, it has also been proposed that prey selection for oystercatchers might be more of a passive process (known as ‘passive selection’) than what is described above (Hulscher, 1982). Optimal diet theory assumes that the predator is capable of distinguishing between food items of varying profitability when searching for and handling prey (Giraldeau, 2008). However, in a study on prey size and feeding site selection by Leopold *et al.* (1989), oystercatchers were experimentally examined for their preference between feeding patches and prey items of varying quality. The authors found that size of cockle and mussel prey was relatively unimportant in terms of selection criteria. Instead, the results demonstrated that food patch quality (patches where prey items had larger flesh contents) preceded and rather, determined the size selection of prey. Dominant birds were found in patches of higher quality and thus, consumed larger prey items (Leopold *et al.*, 1989). Within an oystercatcher’s foraging habitat, the bird must first select an optimal feeding patch, select a preferred prey species and only then can it choose from different size classes (Leopold *et al.*, 1989). Hulscher (1982) takes this argument even further, noting that oystercatchers select benthic prey based on what is accessible to them at a specific foraging site. Different sized prey are capable of burying themselves at different depths, therefore intermediate sized clams are often selected by oystercatchers as the larger ones are generally out of reach (Leopold *et al.*, 1989; Zwarts & Wanink, 1993).

Research into oystercatcher prey choice is important, as prey selection can have significant consequences for both prey and predator populations. For example, prey selection can influence predator distribution patterns, impact prey growth and affect predator-prey population dynamics (Rutten *et al.*, 2006). Likewise, preference for a particular prey size class by a predator may have significant outcomes when that predator is removing a specific subset from the prey population. For instance, Levings *et al.* (1986) examined prey selection and feeding rate of American oystercatchers foraging on the coast of Panama. The authors hypothesised that the shorebirds may have a substantial impact on the abundance, distribution and size structure of their prey population. The study compared the density of specific prey sizes shown to be consumed by the oystercatchers (at different foraging sites), with the average number of prey consumed in a feeding bout. Results showed that predation rate significantly altered the size structure and abundance of local populations of the oystercatchers' preferred prey species, at least in the short term (Levings *et al.*, 1986). In another example, a study by Goss-Custard *et al.* (2001) revealed that oystercatchers depleted their preferred prey size (30-60 mm) in density by 25% and by 12% overall.

The results presented in Chapter 1 and Chapter 2 demonstrate that the oystercatchers foraging on Ripiro Beach display high site fidelity for the toheroa beds at First Stream and Third Stream and at sites towards the southern end of the survey area. It has also been demonstrated that they display a preference for bivalve prey. Thus, the next logical step is to determine if oystercatchers have a preferred species of bivalve and a preferred prey size. If so, predation may be having a local impact on the size structure and density of toheroa populations at oystercatcher foraging sites on Ripiro Beach. These unknowns are addressed in this chapter in two separate studies that were undertaken to investigate oystercatcher prey choice on Ripiro Beach. In the first study, I aim to investigate predation success, prey type and size choice at oystercatcher foraging sites. This study will provide the information required to interpret the observations made in Chapter 2 and 3. In the second study, I investigate the population size structure of toheroa beds that were and were not subjected to oystercatcher predation to determine the impacts of oystercatcher foraging on toheroa size structure. If the oystercatchers foraging at First Stream and Third Stream are selecting one specific toheroa size class, the cumulative effect of this selection could potentially lead to a decrease in abundance of that size class at the two toheroa beds.

4.1.1 Aims and Hypotheses

Oystercatcher Predation Success Study:

The objective of this study is to investigate oystercatcher predation success and prey choice at various predation sites on Ripiro Beach. This study will attempt to answer three main questions:

1) What is the success rate of oystercatcher predation attempts?
2) What species of bivalves (toheroa or tuatua) are oystercatcher predating on?
3) What is the preferred prey size of the oystercatchers?

These questions will be tested by examining the feeding holes made by oystercatcher bills to determine if feeding was successful and by measuring the size of clams consumed in those probe holes.

Toheroa Size Structure Study:

The objective of this study is to investigate the density and size structure of toheroa populations living in four different streams along Ripiro Beach. This research will be conducted in an attempt to gain a better understanding into the potential predation pressure oystercatchers may be placing on a particular toheroa size class at known foraging sites. This study will have two null hypotheses: 1) there will be no difference in the density of toheroa populations living in beds that are subjected to oystercatcher predation compared to beds that are not 2) there will be no difference in the size structure of toheroa beds that are subjected to oystercatcher predation compared to beds that are not. These hypotheses will be tested by conducting a population survey from toheroa living in four major beds along Ripiro Beach.

4.2 Oystercatcher Predation Success

4.2.1 Methods

Sampling took place over one day in March (preliminary sampling), two days in June and two days in August. The length of the beach was travelled by vehicle either from the northern end of the survey area (Omamari) or the southern end of the survey area (near Pouto Point). The beach was scanned for evidence of oystercatcher predation sites. Predation sites were found by looking for areas on the beach that had distinct holes in the substrate which had been made by the probe of an oystercatcher's bill (Figure 4.2). Holes made by oystercatcher bills could be distinguished quite easily from holes made by other shorebird species as the holes were very narrow (like the bill). In contrast, a gull leaves a mark behind in the sand that the represents an "x" when extracting clam prey. The first predation site located on any given sampling day was chosen to make the best use of limited time imposed by the tidal cycle. Once a predation site was found, the GPS coordinates of the site were recorded. The zone of beach and other environmental factors were noted, for example, if the site was near to a freshwater seep or stream. Five sites were sampled in total. The first site was First Stream, the second site was Third Stream, the third site was located just south of Third Stream, the fourth and fifth sites, hereafter referred to as South 1 and South 2, were towards the southern end of the survey area (Figure 4.1).

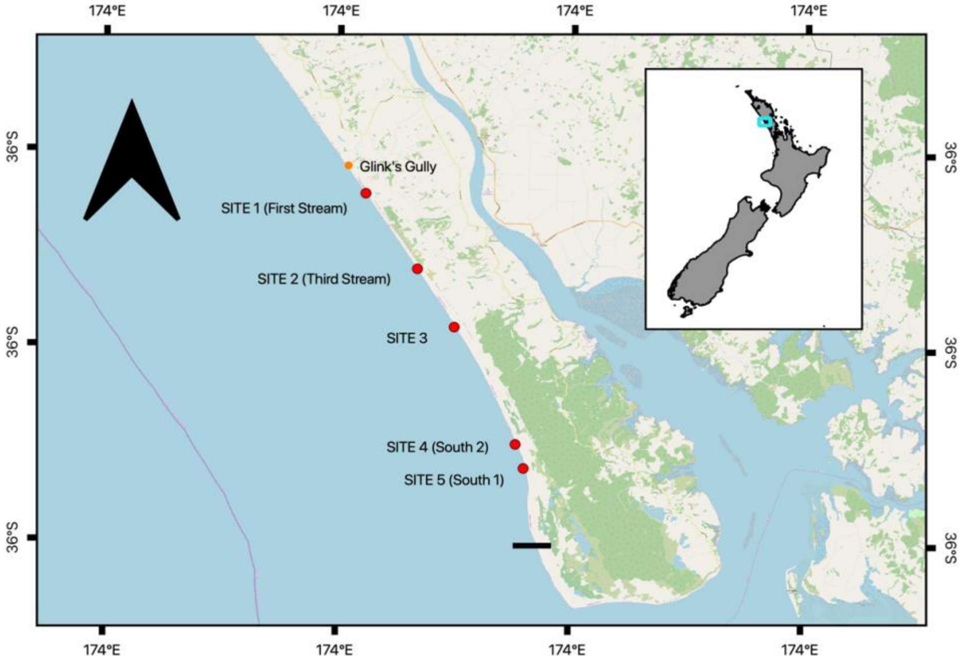


Figure 4.1 Map displays oystercatcher predation sites.

Figure 4.2 Probe holes at an oystercatcher predation site on Ripiro Beach (photo by M. Bennion).

The centre of the predation site was approximated (from the distribution of peck holes) and a circle with a diameter of 30 m was drawn in the sand around this point (Akroyd *et al.*, 2002). The intention was to excavate every feeding hole within the circle, but in practice this was not possible at predation sites where there was an extremely high number of holes. Hole investigations proceeded as follows: the hole was identified as either a regular or a frenzy hole (defined below), the hole depth was measured, the clam was excavated, the species was determined, the length of clam was measured and finally, the condition of clam was recorded (Figure 4.3).

Figure 4.3 Collecting data and excavating shells from an oystercatcher predation site (photo by L. Rynkowski).

Probe holes were recorded as either ‘regular hole’ or a ‘frenzy hole’ depending on the oystercatcher footprints associated with the hole. A ‘regular’ hole was a relatively clean probe into the sand with footprints indicating the oystercatcher had probed and then continued walking along the beach. A ‘frenzy hole’ was described as a probe in which the oystercatcher had rotated its bill and body and left footprints encircling the hole (Figure 4.4). In addition, the sand surrounding the hole may have be disturbed. Baker (1974b) has observed oystercatchers rotating their bodies 90° with their bill in the substrate in order to force the valves of the shellfish apart and weaken the abductor muscles of the valves. Another study found empty American razor clam (*Ensis leei*) shells surrounded by footprints and bill marks (Swennen *et al.*, 1985). It was therefore assumed that a 'frenzy hole' was potentially associated with an attempt to extract a clam.

Figure 4.4 Frenzy hole left by an oystercatcher whilst handling a bivalve in relatively wet substrate (photo by L. Vallyon).

Burying depth of clams was defined as the distance between the mud surface and the upper edge of the shell (Zwarts & Wanink, 1993). To measure burying depth of a bivalve, a chopstick (approximately the same diameter as an oystercatcher's bill and 22.5 cm long) was gently placed into the sand until it came in contact with a shell. The chopstick was then taken out of the sand (marking the point at which the chopstick reached the top of the substrate) and using a calliper on the chopstick, the depth (mm) of the hole was recorded. Subsequently, the clam was then dug up by hand and identified by species: toheroa or tuatua. A hole in which no bivalve was excavated was likewise noted. The length (mm) of the clam was recorded, using a calliper. Finally, the state or condition that the bivalve was in was recorded. This included whether the animal 1) was healthy and intact 2) had a damaged shell, 3) had its siphons snipped off, 4) was partly gone (there was still some flesh content remaining in the shell but this predation still would have resulted in mortality), or 5) was gone entirely. In order to determine the state of a toheroa's siphons, the animal was placed inside a bucket of water for 3 minutes to encourage it to extend its siphons. If it did not, it was assumed that the siphons had been damaged or snipped off by an oystercatcher.

4.2.1.1 Statistical Analyses

All statistical analyses were performed in Statistica (V. 13) and figures were made using Statistica or Microsoft Excel. The accepted level of significance for all statistical tests was ≤ 0.05. Descriptive statistics, maps, graphs and tables were formulated to demonstrate the location of oystercatcher predation sites versus oystercatcher high fidelity sites (see Chapter 2), the proportion of predation sites which had bivalve shells remaining, the ratio of bivalve species that were consumed and the proportion of predation success.

A comparison of prey size structure across predation sites was conducted as follows. The toheroa length data of each site were tested for normality using a Shapiro-Wilk test. Site 3 was excluded from analysis due to the high number of probe holes that did not contain shells. Length data did not comply with the assumptions of normality (First Stream $W = 0.93$, $p < 0.01$; Third Stream $W = 0.78$, $p < 0.01$; South 1 $W = 0.95$, $p < 0.05$) except for at the South 2 site ($W = 0.96$, $p > 0.05$). Levene ($F = 20.87$, ($p < 0.01$) and Brown-Forsythe ($F = 7.16$, ($p < 0.01$) tests indicated that variances were not homogenous. Therefore, a Kruskal-Wallis ANOVA test was used to compare the median length (mm) of prey at each of the oystercatcher predation sites. A Kruskal-Wallis post-hoc multiple comparisons test was applied to determine which sites significantly differed in their median prey length (mm).

As non-parametric statistics were used, box plots were formulated to present the difference in medians between prey size at different foraging site types.

4.2.2 Results

Four of the five oystercatcher predation sites were high fidelity sites identified in Chapter 2. These were First Stream, Third Stream, South 1 and South 2 (Figure 4.5). All sites were distinctly different from one another in terms of prey species, size and condition. At Site 3 (just south of Third Stream) 90% of probe holes did not have a shell in or nearby them. Possibly, these holes did not contain any clams, they were buried too deep for the oystercatchers or the shells had been swallowed whole. South 1 and South 2 had predation holes that contained exclusively newly recruited clams smaller than 30 mm. Sites 1 and 2 were toheroa beds at Third Stream and First Stream, respectively. The prey featured at First Stream consisted of 87% tuatua. Prey composition at Third Stream was 37% tuatua, 29% toheroa and the remaining 34% were probe holes that had no shell in or around them. Of 216 probe holes sampled, only 45 (21%) were labelled as a "frenzy hole". From every predation hole (n = 216) sampled, 161 (75%) of shells were present within the holes/substrate, 49 (22%) of the predation holes had no shell in or near them and 6 (3%) of holes had a shell just next to them (Figure 4.6). Of the predation holes (n = 167) containing shells, 91 (54%) were unidentifiable shellfish (too small to distinguish), 62 (37%) were tuatua and 14 (8%) were toheroa (Figure 4.7). Of the 167 clams that were present within the excavated predation holes, 42 (25%) appeared healthy and unaffected by predation (Figure 4.10), 9 (5%) had damaged shells but otherwise appeared unharmed, 9 (5%) had lost some flesh, 107 (64%) had all of the flesh contents removed from the shell (Figure 4.8; Figure 4.9). No clams were recorded with just their siphons snipped off.

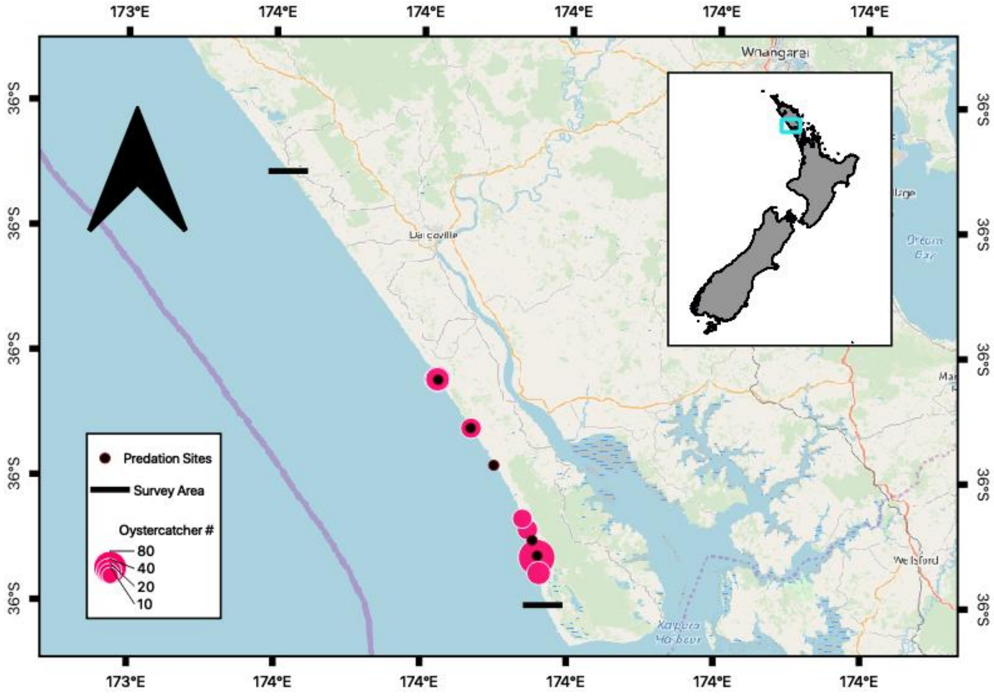


Figure 4.5 Map displays the oystercatcher predation sites located in the study (black dots) and the oystercatcher high fidelity sites (pink circles) taken from Chapter 2.

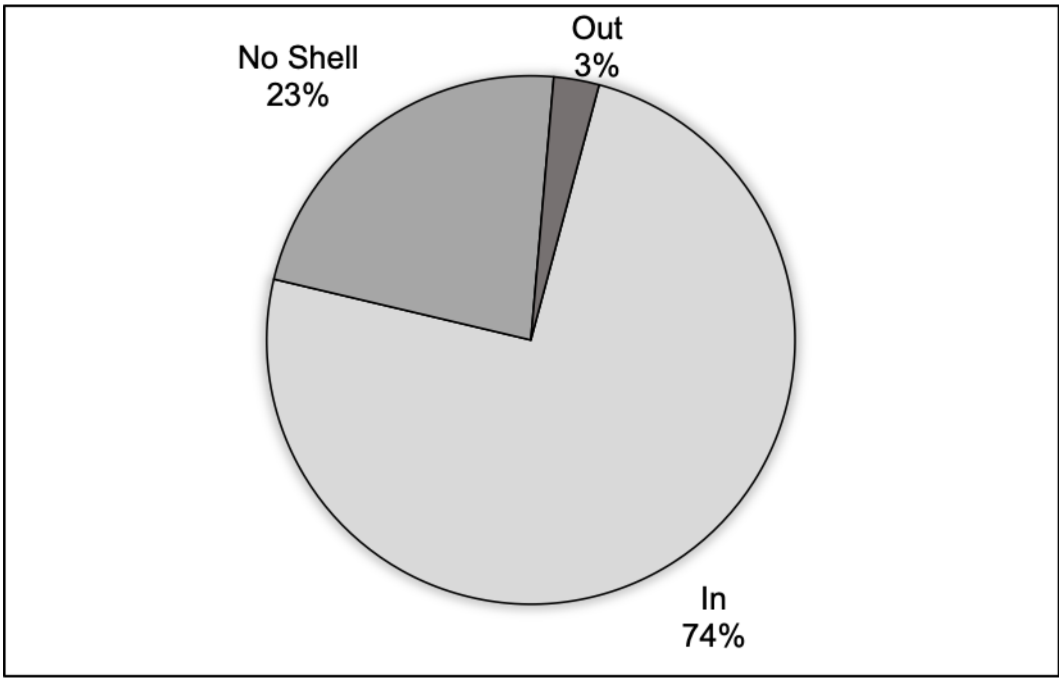


Figure 4.6 Proportion of oystercatcher predation holes which had shells remaining in the hole, no shells and shells found just outside the hole.

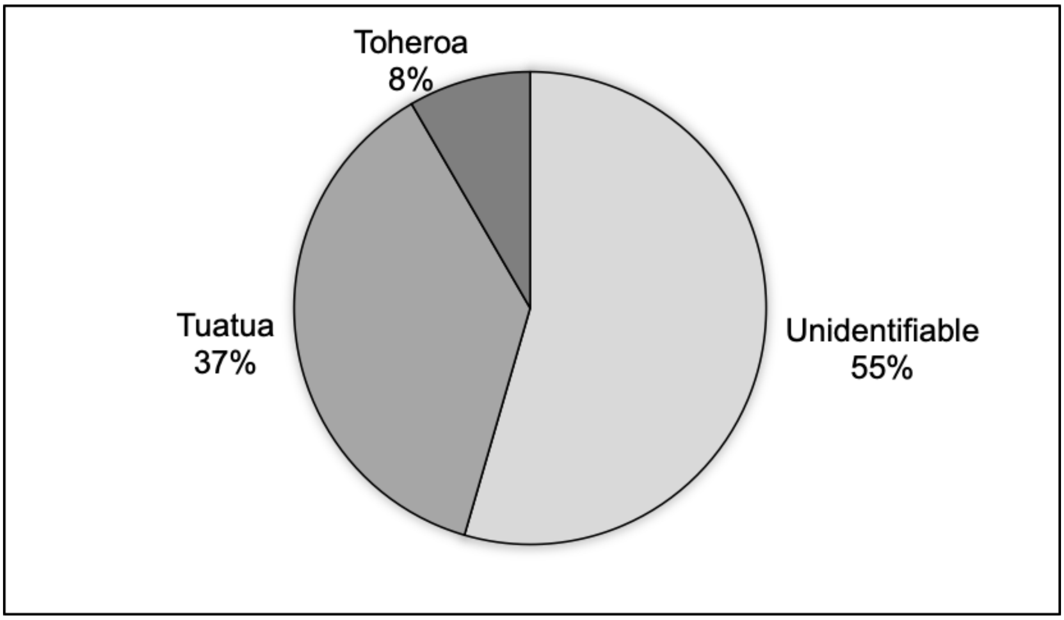


Figure 4.7 Proportion of bivalve species sampled in oystercatcher predation study.

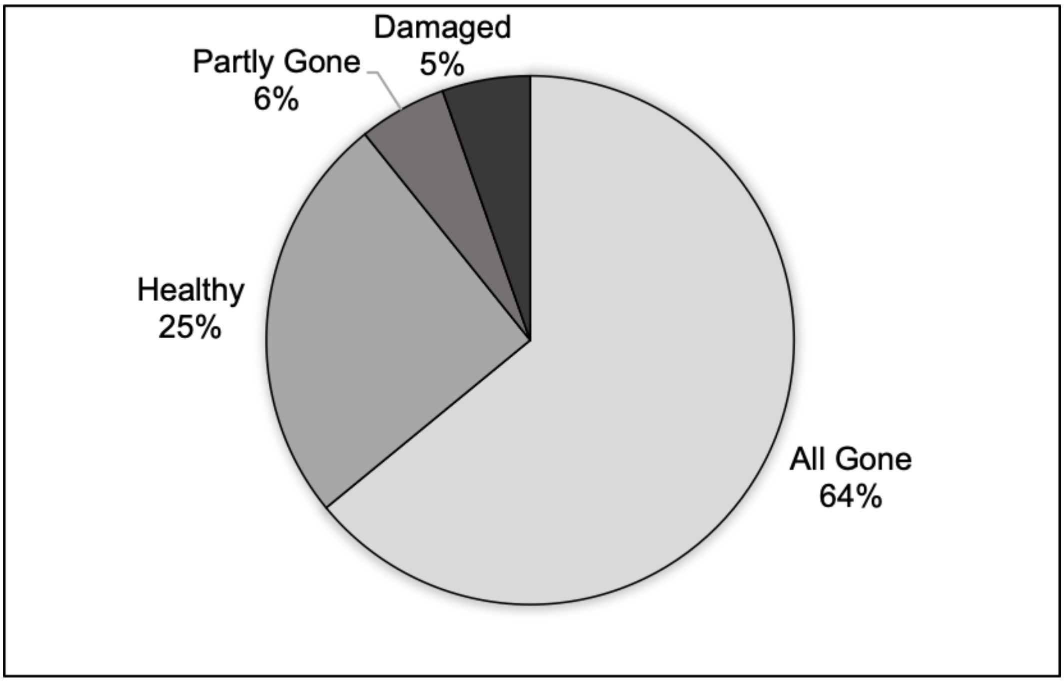


Figure 4.8 Proportion of predation holes that contained shells that had all the contents removed, were healthy, had part of their contents gone or were damaged.

Figure 4.9 A probe hole left by an oystercatcher in which a clam has been handled *in situ*. The whole contents of the mollusc have been extracted (photo by L. Vallyon).

Figure 4.10 A healthy toheroa excavated from an oystercatcher predation site (photo by L. Rynkowski).

Median prey size differed significantly between sites ($H = 107.22$, $p < 0.01$) (Figure 4.11). The mean length (mm) at First Stream was 42 mm (± 3.99) and the mean length (mm) at Third Stream was 35 mm (± 11.64). Bivalves consumed at the southern sites were smaller: the mean length (mm) at South 1 was 18 mm (± 3.62) and the mean length (mm) at South 2 was 17 mm (± 3.24). This is consistent with the fact that First and Third Stream are adult toheroa beds while the southern sites are not (Table 4.1).

Table 4.1 The mean length (mm) of prey sampled at four oystercatcher predation sites.

Predation Site	Mean	SD (±)	Min	Max
First Stream	42.28	3.99	31	54
Third Stream	35.26	11.64	9	53
South 1	18.62	3.62	11	29
South 2	17.5	3.24	11	25

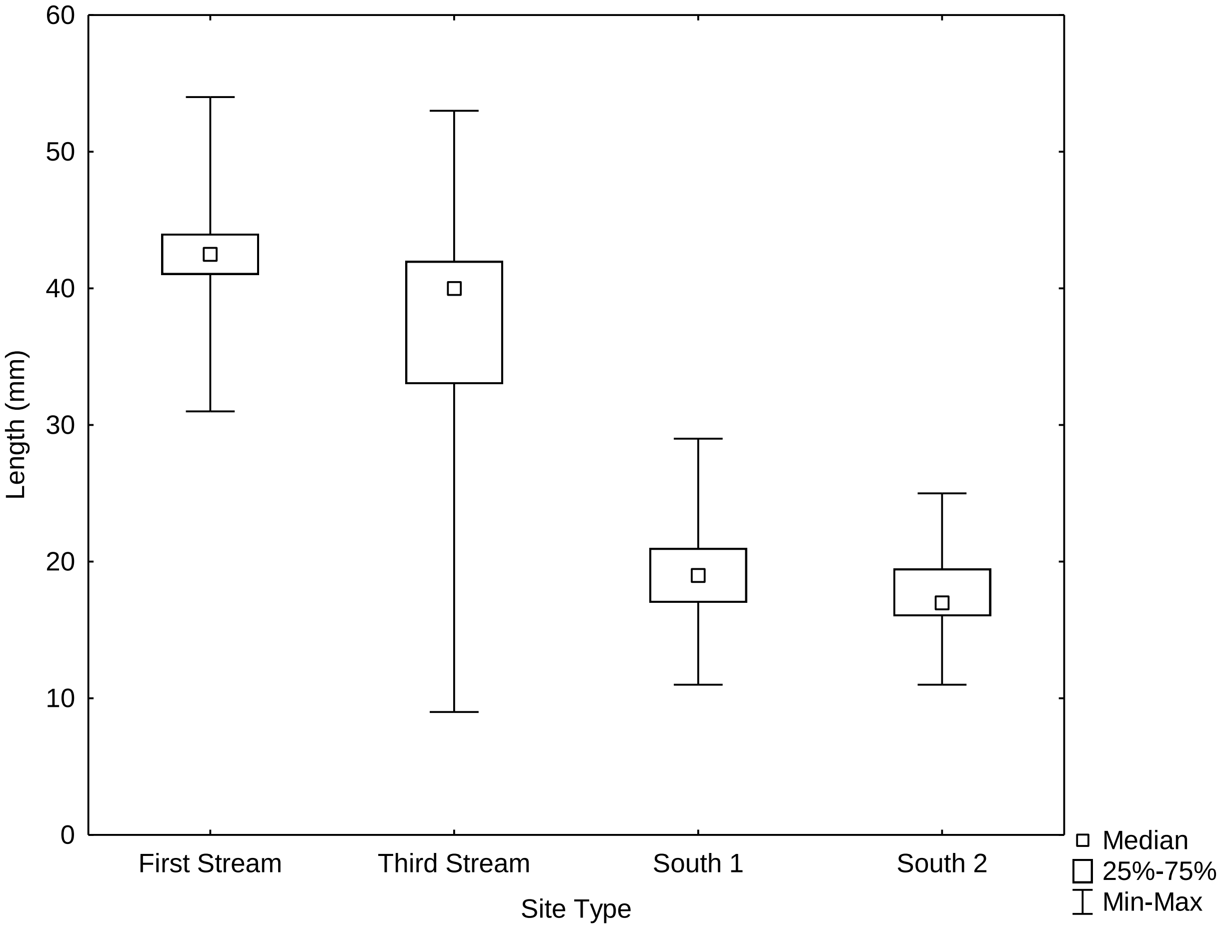


Figure 4.11 Box plot showing significant difference in median length (mm) of prey oystercatchers are choosing to predate on at four different oystercatcher predation success study sites. The sites at the southern end of the survey area did not differ in their median length (mm).

4.3 Toheroa Size Structure

4.3.1 Methods

Two toheroa beds (First Stream and Third Stream) consistently visited by a high number of oystercatchers throughout the year and two beds (Kopawai and Mahuta Gap) where oystercatchers were not (or rarely) observed throughout the year were chosen as sampling sites (Figure 4.12). Ten 0.25 m_2 quadrats were haphazardly positioned on each bed and all clams within each quadrat were excavated and measured (Figure 4.13). Rather than excavating quadrats by spade, which results in high toheroa mortality, seawater was bucketed into quadrats to liquefy the sand to make it easier to excavate toheroa by hand from the substrate. Once excavated, toheroa were placed in a sieve and rinsed in seawater (Figure 4.14). The maximum length of each clam was measured using a calliper and then returned to the substrate. Weather, low tide and approximate time of sampling were also recorded.

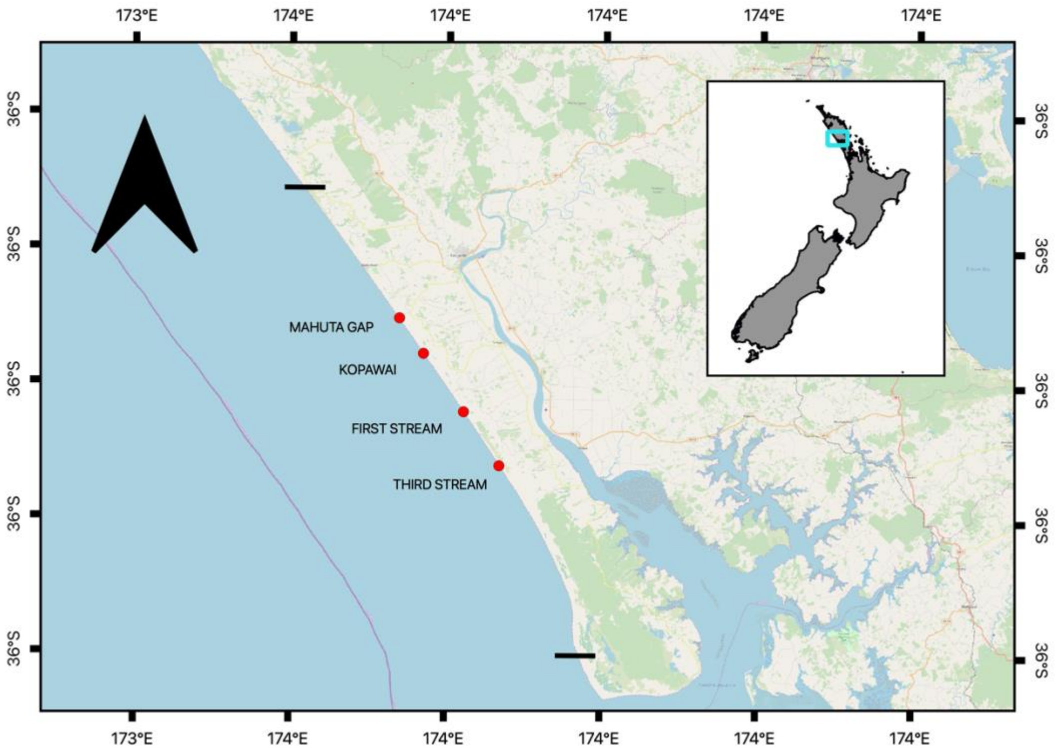


Figure 4.12 Map displays the four sampling sites used in the toheroa size structure and population density study.

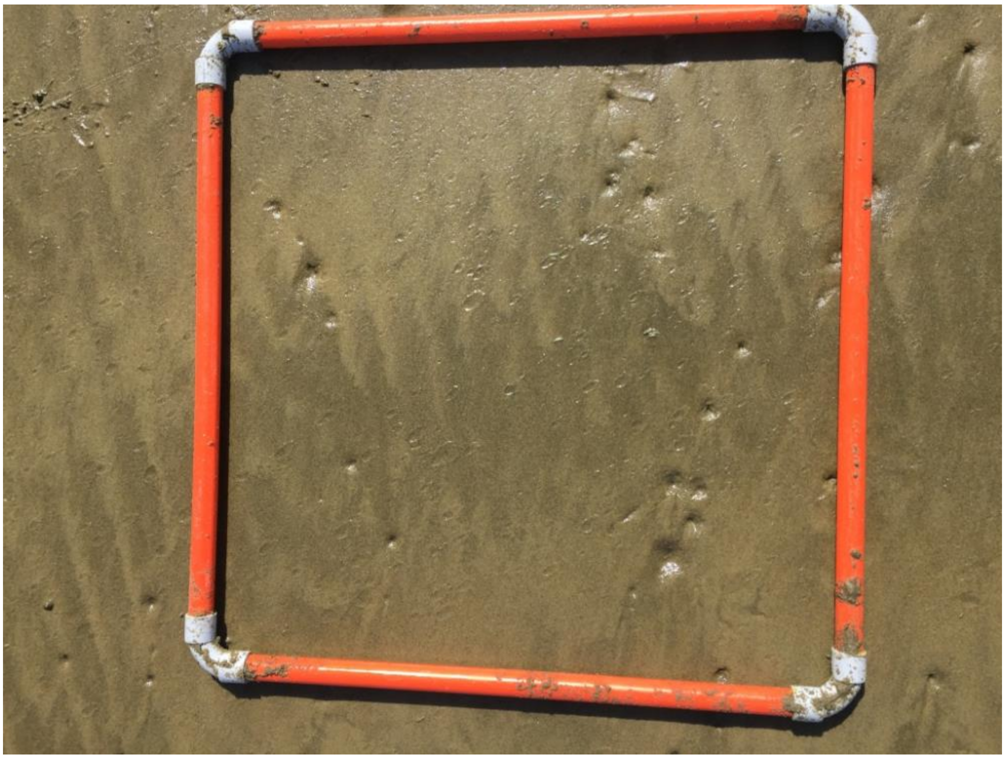


Figure 4.13 Toheroa siphon holes within a quadrat that was excavated for the toheroa population survey (photo by L. Vallyon).

Figure 4.14 Toheroa ready to be measured for the toheroa population survey (photo by L. Vallyon).

Sampling occurred over three days in September 2019. First Stream was successfully surveyed on 23/09/19, Third Stream and Mahuta Gap were successfully surveyed on 25/09/19. The survey of the Kopawai bed started on the 24/09/19 but torrential rain and gale force winds made it difficult to determine the location of the bed and sampling was abandoned after three quadrats. The remaining seven quadrats were sampled the following day.

4.3.1.1 Statistical Analyses

All statistical analyses were performed in Statistica (V. 13) and figures were made using Statistica or Microsoft Excel. The accepted level of significance for all statistical tests was ≤ 0.05. Descriptive statistics, graphs and tables were formulated to demonstrate the difference between frequencies of toheroa size structure and densities between streams that are subject to predation by oystercatchers versus streams that are not.

4.3.1.1.1 Toheroa Density between Sites

To test the null hypothesis that there would be no difference in density of toheroa populations at different site types (oystercatcher predation sites versus no-predation sites), First Stream and Third Stream (predation sites) density per m_2 data were pooled and Mahuta Gap and Kopawai (no predation) density per m_2 data were pooled. A Shapiro-Wilk test was applied to test the assumptions of normality. Pooled predation density data were not normally distributed ($W = 0.83$, $p < 0.01$) but no-predation density data was ($W = 0.91$, $p > 0.05$). As the data was in frequencies (count data), a Mann-Whitney U test was used to test for a significant difference in the median density of toheroa between oystercatcher predation and no-predation streams.

To compare the densities per m_2 of toheroa at each stream against all other streams, the density data of each bed were tested for normality using a Shapiro-Wilk test. The density data for all sites were normally distributed (Mahuta Gap $W = 0.95$, $p > 0.05$; Kopawai $W = 0.85$, $p > 0.05$; First Stream $W = 0.85$, $p > 0.05$; Third Stream $W= 0.89$, $p > 0.05$). Levene ($F = 6.25$, $p < 0.01$) and Brown-Forsythe ($F = 4.93$, $p < 0.01$) tests showed variances were not homogenous. Therefore, a Kruskal-Wallis ANOVA test was used to compare the median densities per m_2 of toheroa at each of the four sites. A Kruskal-Wallis post-hoc multiple comparisons test was applied to determine which streams significantly differed in their median toheroa density.

As non-parametric statistics were used, box plots were formulated to present the difference in median density of toheroa populations at different foraging site types.

4.3.1.1.2 Toheroa Size between Sites

To test the null hypothesis that there would be no difference in size structure of the toheroa populations experiencing different levels of oystercatcher predation, First Stream and Third Stream (predation sites) toheroa length data were pooled and Mahuta Gap and Kopawai (no-predation sites) toheroa length data were pooled. A Shapiro-Wilk test was applied to test the assumptions of normality.

Length frequency data were not normally distributed (predation sites W = 0.98, p < 0.01; no-predation sites W = 0.92, p < 0.01). Levene (F = 8.26, p < 0.01) and a Brown-Forsythe (F = 12.93, p < 0.01) tests showed variances were not homogenous. Therefore, a Mann-Whitney U test was used to test for differences in the median length (mm) of toheroa between oystercatcher predation and no-predation streams.

To compare the length of toheroa at each bed against all other beds, the length (mm) data of each stream was tested for normality using a Shapiro-Wilk test. Length data were not normally distributed (Third Stream W = 0.95, p < 0.01; Mahuta Gap W = 0.91, p < 0.01; Kopawai W = 0.93) except for First Stream data (W = 0.99, p > 0.05). A Levene (F = 68.56, p < 0.01) and Brown-Forsythe (F = 40.93, p < 0.01) tests showed variances were not homogenous. Therefore, a Kruskal-Wallis ANOVA test was used to compare the median length (mm) of toheroa at each of the four sites. A Kruskal-Wallis post-hoc multiple comparisons test was applied to determine which streams significantly differed in their median toheroa length (mm).

As non-parametric statistics were used, box plots were formulated to present the difference in median size structure of toheroa populations at different foraging site types.

4.3.2 Results

4.3.2.1 Toheroa Density

There was a significant difference (Z-adj = -3.71, p < 0.01) in the median density per m_2 of toheroa in streams that are subjected to oystercatcher predation pressure compared to streams without oystercatcher predation (Figure 4.15). Sites with no oystercatcher predation have a significantly higher median density per m_2. The mean density per m_2 of toheroa living in streams that are oystercatcher predation sites (First Stream and Third Stream) is 122.4 (± 70.18) toheroa per m_2. The mean density of toheroa living in streams where oystercatchers are not exerting predation pressure is 257.8 (± 130.8) toheroa per m_2 (Table 4.2).

Table 4.2 Mean density of toheroa per m^2 in oystercatcher predation sites in comparison to sites without oystercatcher predation pressure.

Site Type	Mean	SD (±)	Min	Max
Predation	122.4	70.18	52	324
No Predation	257.8	130.8	60	500

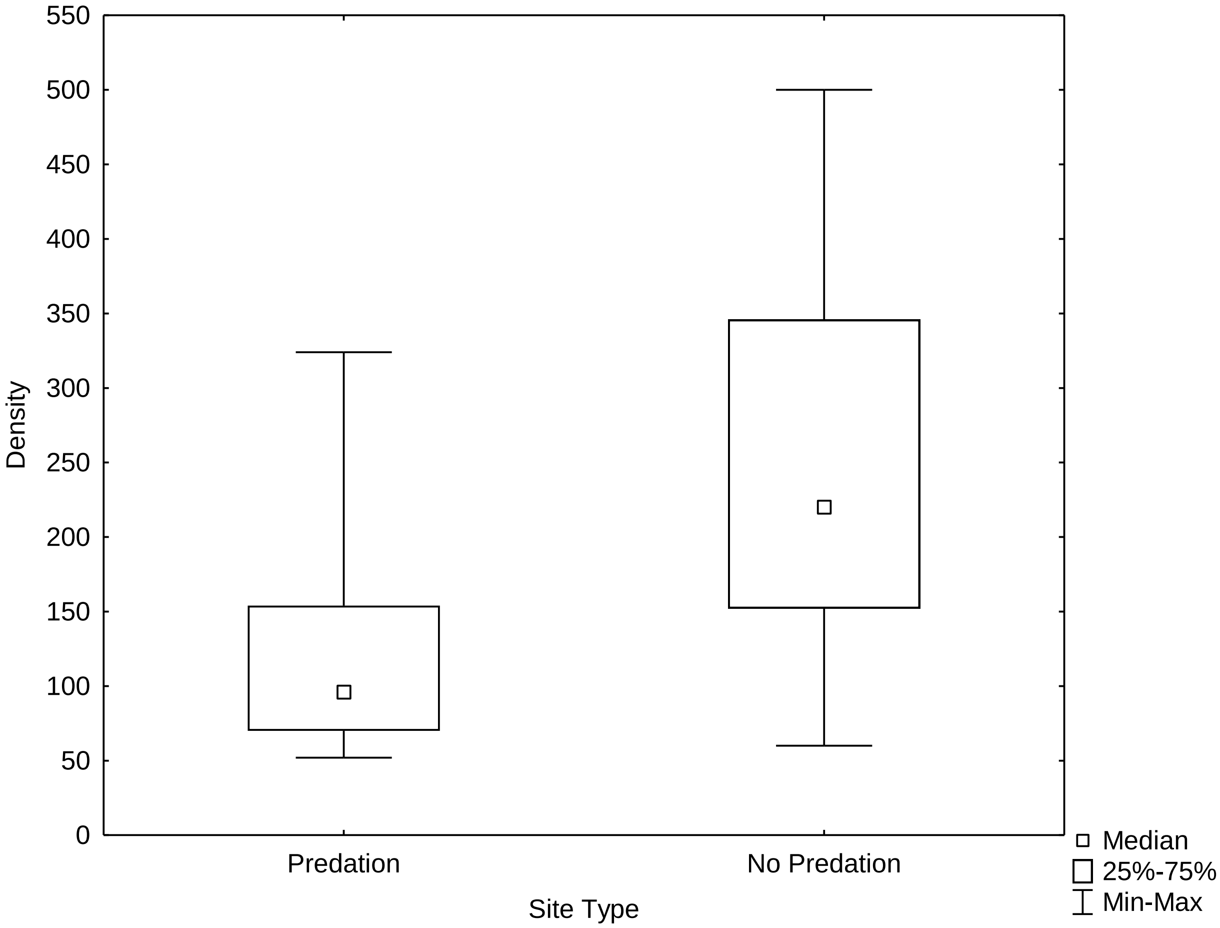


Figure 4.15 Box plots showing significant difference in the median density per m^2 of toheroa populations living in streams subjected to oystercatcher predation compared to those that are no-predation sites. The density of toheroa is higher at no-predation sites.

There was a significant difference ($H = 12.64$, $p < 0.01$) between the medians in toheroa density per m^2 at all four toheroa study sites; First Stream, Third Stream, Mahuta Gap and Kopawai (Figure 4.16). The post-hoc multiple comparisons test showed First Stream and Third Stream as not significantly different from each other, Mahuta Gap density as not significantly different from other streams except for First Stream, and Kopawai toheroa density as significantly different from First

Stream and Third Stream. The mean density per m2 of toheroa living in the four streams is as follows: First Stream = 97.2 (± 37.48), Third Stream = 147.6 (± 87.07), Mahuta Gap = 206.8 (± 93.49) and Kopawai = 308.8 (± 146.97) (Table 4.3).

Table 4.3 Mean toheroa density per m2 for all sites.

Site Type	Mean	SD (±)	Min	Max
First Stream*	97.2	37.48	64	172
Third Stream*	147.6	87.07	52	324
Mahuta Gap	206.8	93.49	60	400
Kopawai	308.8	146.97	148	500

*Indicates predation sites.

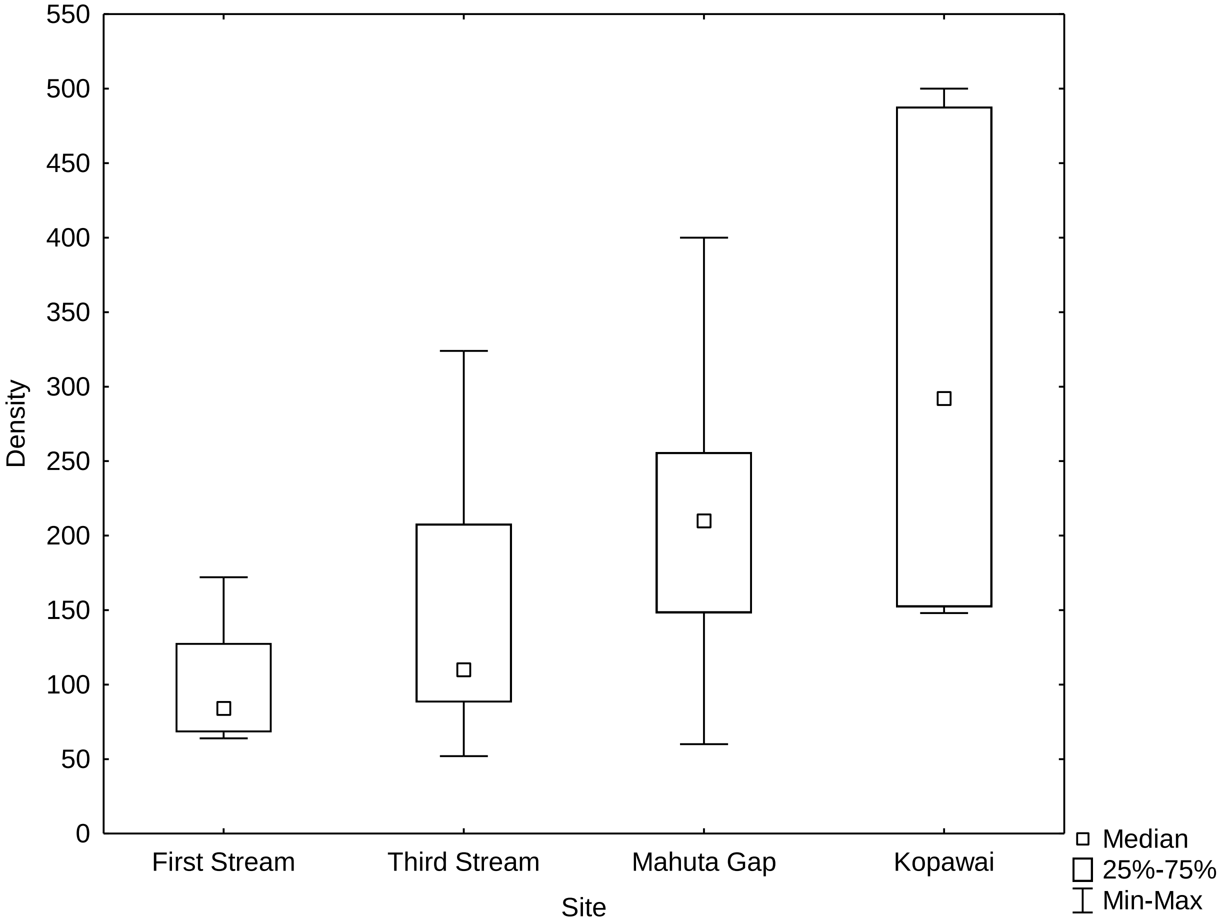


Figure 4.16 Box plot showing differences in the median density per m2 of toheroa at all site types. Kopawai is significantly different from First Stream and Third Stream.

4.3.2.2 Toheroa Size between Sites

The median size of toheroa varied significantly between beds subjected to predation and beds that were not subjected to predation (Z-adj = 12.43, $p < 0.01$) (Figure 4.17). The mean length (mm) at predation sites (First Stream and Third Stream) was 59.76 (± 17.61) mm compared to 49.55 (± 16.82) mm at Mahuta Gap and Kopawai where oystercatchers were not observed (Table 4.4).

Table 4.4 The mean length (mm) of toheroa living in stream-associated beds subjected to oystercatcher predation compared to streams that are not.

Site Type	Mean	SD (±)	Min	Max
Predation	59.76	17.61	16	101.5
No Predation	49.55	16.82	18	103

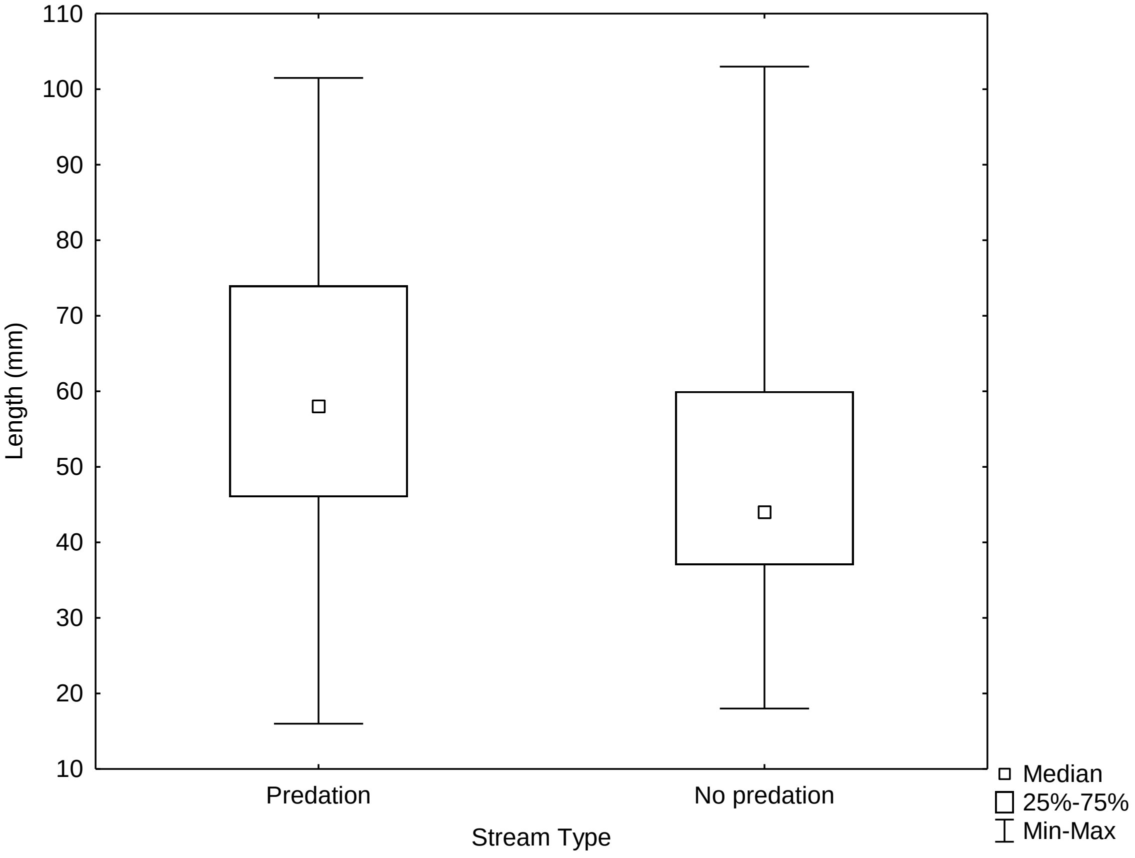


Figure 4.17 Difference in median length (mm) of toheroa between streams that are subjected to oystercatcher predation and those that are not.

When analysed individually (rather than being pooled by predation level) there were significant differences between sites ($p < 0.01$) (Figure 4.18). The post-hoc multiple comparisons test ($p < 0.01$) showed there was a significant difference in the toheroa size (mm) with all site-by-site comparisons significant except for First Stream and Third Stream (predation sites). The mean length of toheroa living in the four streams is as follows: First Stream = 58 mm (± 16.96), Third Stream = 61 mm (± 17.98), Mahuta Gap = 53 mm (± 20.12) and Kopawai = 47 mm (± 13.71) (Table 4.5). On average toheroa are larger at predation sites.

Table 4.5 The mean length (mm) of toheroa living in all four study sites.

Site Type	Mean	SD (±)	Min	Max
First Stream*	58.29	16.96	16	102
Third Stream*	60.73	17.98	25	99
Mahuta Gap	53.3	20.12	18	98
Kopawai	47.09	13.71	19	103

*Indicates predation sites.

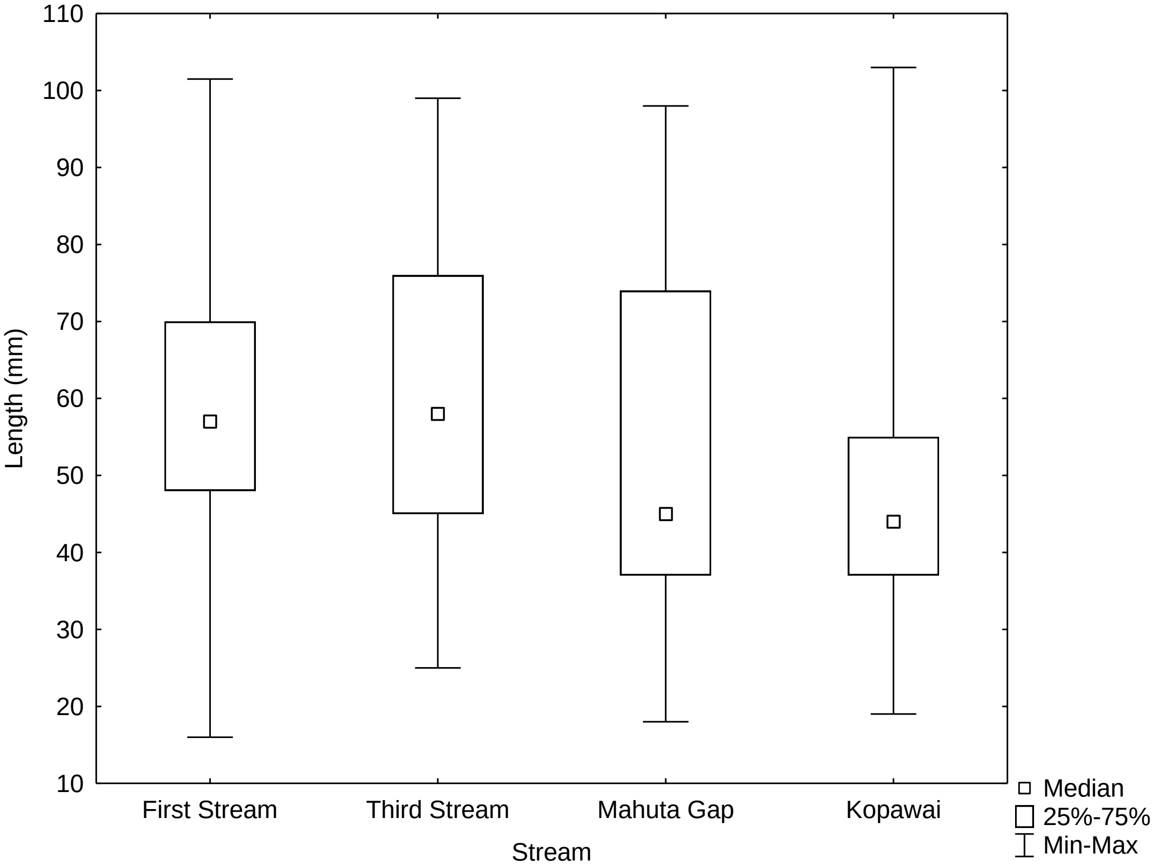


Figure 4.18 Box plot showing significant differences in median length (mm) of toheroa at four different sites (streams) except for those found at First Stream and Third Stream (oystercatcher predation sites).

4.3.2.3 Size Frequency Distributions

Third Stream and Mahuta Gap appear bimodal and have two different cohorts of toheroa (with higher frequencies of toheroa sized 75 to 90 mm) whereas First Stream and Kopawai appear to have only one (Figure 4.19). Kopawai has a relatively large amount of toheroa sized 60 to 70 mm in comparison to all the other sites. Toheroa sized between 30 to 45 mm are the most abundant size class of no-predation sites (49% of the population) in comparison to predation sites in which those size classes consist of only 21% of the population.

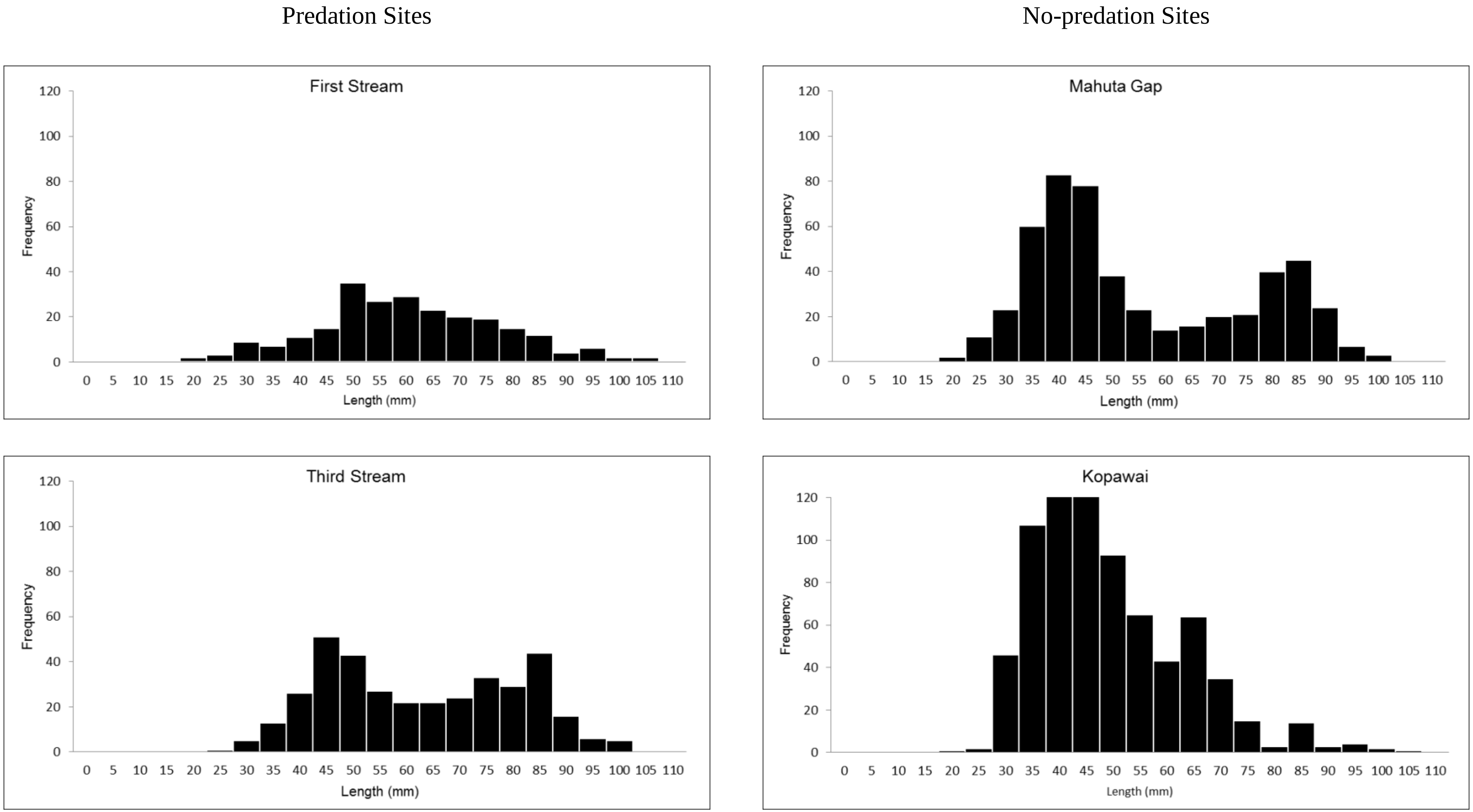


Figure 4.19 Length frequency distribution of toheroa beds. Left side displays predation sites; right side display no-predation sites.

4.4 Discussion

Oystercatcher Predation Success Study

Oystercatchers are extremely skilled at foraging on bivalves. Results from the oystercatcher predation study demonstrate that the birds have a high predation success rate, with 64% of the prey items sampled at the predation sites having been completely removed from their shells. This success rate does not appear to be impacted by the size of prey, as the clams consumed ranged in size from 9 mm to 54 mm. Site 3 (south of Third Stream) contained a high percentage of probe holes that did not include shells nor were any found near to the holes. This could be due to a variety of factors: perhaps there were no bivalves present in the substrate or the clams at that site may have been so small they were swallowed whole. Alternatively, the prey may have been relatively large bivalves that were buried out of reach of the oystercatcher's bill as the depth of bivalves has been recognised as a function of size (Zwarts & Wanink, 1993). An oystercatcher has a maximum bill length of 90 mm whereas large toheroa can be buried up to a depth of 30 cm (Hulscher, 1982; Cook, 2010). Zwarts and Wanink (1991) state that only a small fraction of prey in any given area is harvestable (defined as profitable and available) to a shorebird. Many profitable prey are inaccessible, while those that are accessible are often ignored due to their low profitability. For example, in a study investigating harvestable food supply for shorebirds near the Wadden Sea, Zwarts and Wanink (1993) found that 89% of all potential prey for the knot shorebird consisted of prey items that were buried too deeply or were unprofitable (too small or too large). These studies indicate that although oystercatchers are extremely adept predators, only a small portion of their prey biomass are harvestable and, therefore, most will not be impacted by their predation.

South 1 and South 2 sites consisted only of juvenile bivalves that were too small to identify to a species level. Most of the prey at these predation sites had been extracted from the shell *in situ*, with the shell remaining behind in the hole. These sites also had the highest numbers of predation holes that resulted in success, for example, South 2 had an 83% success rate, compared to First Stream which had a success rate of only 49%. It is necessary to state, however, that a lower "success rate" at some sites may not be an accurate indication of success but rather a factor of prey choice. These "unsuccessful" predation holes may have contained bivalves which were purposefully deemed unprofitable by the oystercatcher. For example, in March 2019 during preliminary data collection, the toheroa found in predation holes at that particular site had a mean length of 61.7 mm (relatively large bivalves). However, of all the probe holes that were sampled, 68% were healthy toheroa. Thus, at sites with larger prey items and a wider variety of sizes (for example, First Stream and Third Stream), the oystercatchers are potentially choosing to handle particular prey items over others, resulting in a perceived lower success rate.

Consumption of specific prey size classes appeared to be (to some extent) determined by feeding patch location. In the south, the oystercatchers were predating on small recruits whilst further north they were foraging on toheroa beds which contain a wide size range of individuals. In the beds, the oystercatchers were mainly choosing intermediate size prey (30 to 50 mm). These beds also contain larger toheroa (up to ~ 100 mm) which have greater flesh content, but these larger clams were not chosen by the oystercatchers as prey. As mentioned above, the oystercatchers may have been foraging optimally, avoiding prey with longer handling times. It should be highlighted that optimal prey size might vary between sites, depending on what size classes are available at each site (Hilgerloh & Pfeifer, 2002). Therefore, the selection process for the Ripiro Beach oystercatchers may be a more passive one.

Toheroa Size Structure Study

With the time and resources available for this project, it was not possible to conduct a full survey of each bed to estimate total population size. To assess potential oystercatcher predation impact, the density measures collected in the size structure study were used as a proxy. Toheroa densities at oystercatcher predation sites (First Stream and Third Stream) were significantly lower than those at no-predation sites (Mahuta Gap and Kopawai). Based on the results from this study, it can be anticipated that oystercatchers may be having a significant impact on these two beds by reducing toheroa density at these predation sites. However, lower toheroa density at these sites could be due to a range of interrelated reasons such as disease, land use change or abiotic factors (Cope, 2018; Ross *et al.*, 2018a). The environmental conditions of these beds may be different to those in the north. For example, First Stream and Third Stream are at the very southern limits of toheroa beds on Ripiro Beach. In the past, toheroa beds could be found south of First Stream and Third Stream but have now gone as the streams in the south have dried up. In this case, it might be that First Stream and Third Stream are marginal habitat that, today, naturally do not support high densities (P.Ross pers comm.).

There were also significant differences in the size structure of the toheroa populations living in the beds subjected to oystercatcher predation in comparison to the no-predation beds. There was a reduced amount of toheroa sized between 30 and 50 mm and a larger average toheroa size in beds that were oystercatcher predation sites. This size difference could potentially be attributed to oystercatcher prey choice. As mentioned above, oystercatchers appear to have a preference for small and intermediate sized bivalves and tend to ignore larger prey size classes. Interestingly, oystercatchers have been found to take smaller prey than predicted from an optimal diet model. For example, Sutherland and Ens (1987) determined that both wild and captive oystercatchers consumed smaller mussels than expected, no matter what handling technique they were using. Similarly, a study by Rutten *et al.* (2006) investigating optimal prey choice in oystercatchers found that the oystercatchers were choosing smaller prey sizes that would not maximise their energy intake rate as predicted by optimal foraging. The authors suggest this is to minimise the risk of bill damage that could occur by targeting large prey items (Rutten *et al.*, 2006). Perhaps, the oystercatchers on Ripiro Beach have an upper size limit of toheroa of around 50 mm to reduce handling times and minimise the risk of bill damage.

4.4.1 Limitations

A main limitation to the oystercatcher predation success study was the inability to distinguish between juvenile toheroa and tuatua. As a result, unidentifiable prey were overrepresented in the results when, in fact, it is highly likely that the oystercatchers were predating on juvenile toheroa. Nevertheless, a large amount of small toheroa are undoubtedly predated on by oystercatchers, gulls, bar-tailed godwits (*Limosa lapponica*) and the many other shorebird species present on Ripiro Beach (Redfearn, 1974; pers. obs.) The predation sites (South 1 and South

2) where these small clams were found do not support adult toheroa, suggesting the environmental conditions at those sites are less than optimal. Without moving to a better environment, it can be assumed living there would result in toheroa mortality (for example, from desiccation), with or without shorebird predation.

Predation sites were only situated in the mid-high intertidal zone as they were the locations in which probe holes remained visible in the substrate without being covered by the tide. In general, from observations made in Chapter 3, oystercatchers primarily foraged in the lower intertidal zone. Consequently, the results from the predation success study are not necessarily a full representation of the oystercatchers' general success rate or prey type and size selection.

In the toheroa size structure study, only the bivalves that could be felt by hand were excavated from the substrate and put into the sieve. Therefore, very small juvenile toheroa (< 10 mm) were not measured and are underrepresented in the size frequency of the toheroa populations. Nonetheless, the size structure results ought to be fairly accurate in terms of oystercatcher prey size choice, as it can be assumed that oystercatchers are not foraging on prey containing such minimum flesh content.

4.4.2 Conclusion

Oystercatchers are very successful predators; they handle most of their prey *in situ* and are capable of consuming the entire contents of their molluscan prey. They prefer to consume juvenile to intermediate sized toheroa and tuatua. The results from the predation success study show that oystercatchers are mainly consuming bivalves between 40 to 50 mm from the toheroa beds at First Stream and Third Stream. These findings are reinforced by the results from the toheroa size structure study where the predation sites (First Stream and Third Stream) have significantly less toheroa sized 30 to 50 mm. The oystercatchers were also found to be consuming a large number of juvenile clams between 9 and 20 mm in length. The South Island pied oystercatchers are potentially placing predation pressure on toheroa ranging in size between 10 and 50 mm (potential lower and upper size limit) at the southern half of Ripiro Beach. However, the toheroa beds that are exposed to the most intense oystercatcher predation (First Stream and Third Stream) still have a relatively wide range of sizes and abundance of toheroa. For example, it has been reported that these beds have contained consistent levels of toheroa throughout each year for the past six years (P.Ross pers comm.). To conclude, oystercatchers are potentially having a very localised impact on toheroa populations. It is possible they are altering the size structure of the two toheroa beds by removing small to intermediate size classes, thereby reducing density and abundance.

Chapter 5
General Discussion

5.1 Summary

Anthropological activities such as habitat destruction and overexploitation have led to a huge reduction in the abundance of predator species worldwide (Prugh *et al.*, 2009). Predators are known for stabilising trophic food webs, promoting prey diversity and playing a role in ecosystem nutrient recycling (Schmitz *et al.*, 2010; Brechtel *et al.*, 2019; Pringle *et al.*, 2019). Thus, the ecological function of predators in any ecosystem is invaluable. This awareness has guided predator recovery into becoming one of the major global conservation goals (Marshall *et al.*, 2016). Single-species management has been the most utilised approach of predator conservation efforts and without considering other species in the ecosystem, has often resulted in recovery efforts being hindered by emerging conservation conflicts (Van Beveren *et al.*, 2017). A rise in predator abundance has increased competition between predator species competing for the same prey, increased competition with humans for the same prey and increased the likelihood of recovered predators consuming protected prey (Marshall *et al.*, 2016). Ironically, following efforts of predator protection and recovery, ecological management actions are now being considered to reduce apparent conservation conflicts between recovered predators and valued prey species. Lethal control (culling) is a common practice implemented when an increase in prey abundance is desired and when predators are assumed to be inhibiting prey numbers (Wiese *et al.*, 2008). A multitude of cases have shown that culling often does not produce the desired results and can lead to unpredictable ecological outcomes (Harris & Wanless, 1997; Wiese *et al.*, 2008; Makhado *et al.*, 2009). This emphasises the importance of managing endangered species through an ecosystem-based approach (rather than single-species management) in order to meet the needs of different species and understand predator-prey interactions prior to making decisions such as lethal control (Williams *et al.*, 2011; Van Beveren *et al.*, 2017).

The focus of this thesis was the conservation conflict between the endemic surf clam, the toheroa and the endemic shorebird, the South Island pied oystercatcher. Despite there being limited information on the predator-prey dynamics of these two species, speculation about oystercatchers causing the continued decline of toheroa at Ripiro Beach (Northland) has led to calls for oystercatchers to be culled, thereby, protecting one endemic species from the “devasting” predation effects of another. The overarching research objectives of this thesis were to (a) obtain information on the perceived conflict between these two endemic species and (b) establish what influence oystercatchers may be having on toheroa populations. Research was directed towards three main areas: 1) spatial and temporal associations of oystercatchers and toheroa 2) oystercatcher foraging behaviour and diet composition and 3) oystercatcher prey size preference.

5.2 Key Findings

5.2.1 Spatio-temporal Associations

Bird surveys (Chapter 2) revealed that both the distribution and abundance of oystercatchers at Ripiro Beach varied over time. As expected, the number of oystercatchers foraging on the beach was highest during their nonbreeding season, from January to July. The abundance of oystercatchers peaked in March 2019 at just over 300, while none were sighted in December 2019 (breeding season). The birds were distributed non-randomly along the length of the beach. They were almost exclusively observed on the southern half of the beach south of Glink’s Gully (the approximate midway point of the survey area).

While the distribution of the oystercatchers does overlap with some of the current distribution of toheroa beds (First Stream and Third Stream), the majority of major toheroa beds were seen north of the observed oystercatcher distribution (pers. obs.). A 2002 toheroa survey also found that the majority of toheroa beds occurred in the area between Baylys Beach and Glink’s Gully, as did a later survey in 2008 which reported that half of all toheroa were found in the most northern quarter (20 km) of the beach (Akroyd *et al.*, 2002; Akroyd *et al.*, 2008). These studies are consistent with my observations that the majority of toheroa beds were north of Glink’s Gully, areas in which I never observed oystercatchers foraging (although locals have reported that this does occur). While two of the major toheroa beds (First Stream and Third Stream) are consistently used as oystercatcher foraging sites, my observations suggest that the majority of toheroa populations on Ripiro Beach are not subjected to significant oystercatcher predation.

5.2.2 Oystercatcher Foraging Ecology

Observations of oystercatcher foraging behaviour (Chapter 3) showed that the oystercatchers are behaviourally and morphologically adapted to eating bivalves and are capable of entirely removing toheroa (and tuatua) from their shells (either within or removed from the substrate). When foraging, oystercatchers consumed predominantly bivalves with an average of one prey item every two minutes of foraging. However, a large proportion of their day was spent in activities other than foraging, for example, resting and preening. I estimate that oystercatchers spend three to four hours of each day actively foraging. Prey intake rate varied with habitat. Rates were significantly higher for oystercatchers foraging away from stream-associated toheroa beds. Surprisingly, there was no significant difference in the number of bivalves consumed between oystercatchers which were foraging at streams or those that were foraging elsewhere. However, there may have been a difference in the size class or species of bivalve they were consuming. These findings indicate that the availability and abundance of food resources away from major toheroa beds is adequate to sustain the foraging oystercatchers. This could include prey items such as juvenile toheroa, tuatua or other intertidal invertebrates such as polychaetes. If they are consuming sufficient quantities of prey in the southern part of the beach (closest to their roost in the Kaipara Harbour), optimal foraging theory predicts there would be no need for the birds to distribute themselves any further north. It is possible that when those food resources are depleted, the oystercatchers are driven further north to forage on the major toheroa beds. This hypothesis could potentially clarify the distribution patterns of the oystercatchers found in Chapter 2 and explains sightings of oystercatchers by locals claiming to have seen the birds foraging further north, predating on adult toheroa beds.

5.2.3 Oystercatcher Prey Choice

Oystercatchers foraging on Ripiro Beach had a high predation success rate (Chapter 4). They are experts at foraging on bivalves, with 64% of predation attempts resulting in the extraction of entire clams from their shells. Foraging site location determined prey size selection. Oystercatchers foraging at the very southern end of Ripiro Beach consumed juvenile/spat bivalves (either toheroa or tuatua) between 10 and 20 mm in length, while larger clams were consumed at major toheroa beds (intermediate sized prey between 30 and 50 mm). These major toheroa beds contain a wide variety of different sized prey items yet the larger bivalves (> 50 mm) were generally ignored. The toheroa beds at First Stream and Third Stream (predation sites) contained toheroa at significantly lower densities than beds further north at Mahuta Gap and Kopawai (non-predation sites; Chapter 4). At toheroa beds subjected to oystercatcher predation, the average toheroa size was larger (60 mm) in comparison to the no-predation toheroa beds (50 mm). The frequency of toheroa sized between 30-50 mm at predation sites was considerably less (33% of the population) than at no-predation sites where toheroa of that size range made up 59% percent of the population.

In general, the size structure of the toheroa populations differed significantly in beds that were subjected to oystercatcher predation to those that were not exposed. These data suggest that oystercatcher predation can alter abundance and population structure in the areas they forage, by consuming small and intermediate sized toheroa. In this case, the effect appears restricted to the southernmost toheroa beds (First Stream and Third Stream) and southern end of the beach only. Thus, oystercatcher predation may be restricting the size structure composition of toheroa at the southern half of Ripiro Beach to predominantly larger size classes.

This project was undertaken as a response to public perception surrounding the oystercatchers and an eagerness to aid the recovery of the toheroa by Ripiro Beach locals. In the absence of knowledge and a desire for a solution, people are wanting to see actions taken (in the form of oystercatcher culling) towards the recovery of the precious shellfish. Accordingly, it could be assumed that culling of the oystercatchers is one such action that could, in theory, work. Taking all of the findings from this thesis into consideration, they reveal that the oystercatchers have the capacity to exert significant predation pressure on toheroa by altering size structure and density of toheroa populations. However, the oystercatchers' distribution patterns only overlap with the shellfish at two main toheroa beds and are not impacting toheroa across the whole length of the beach. Consequently, the reason behind the continuing decline of the toheroa is still unknown. In this case, I consider that there is no conservation conflict occurring on Ripiro Beach. Culling the oystercatchers would lead to unpredictable outcomes and is unlikely to result in a direct increase of toheroa abundance. I believe the oystercatchers and toheroa should be managed through an ecosystem-based approach to preserve the predator-prey interactions of the two species. As the locals living near Ripiro Beach are so passionate about the shellfish, it is important that information gathered in this research is communicated back to the public in an attempt to end speculation on the impact of oystercatcher predation on the toheroa.

5.3 Future Recommendations

All data collection for this thesis was conducted on the neap tide as that was the most practical phase of the tidal cycle for driving on the beach. As most shorebird foraging rhythms are strictly governed by the tidal cycle (Heppleston, 1971; Aplin & Cockburn, 2012; Kimbro, 2012), the distribution patterns, diet composition, prey intake rate and predation success rate of the oystercatchers may be considerably different at other stages of the cycle, such as during spring tides. For example, oystercatcher densities on a mussel bed in England were lowest on spring tides and highest on neap tides (Goss-Custard, 1987). Similarly, oystercatchers have been found to consume vastly different prey items on spring and neap tides (for example limpets and bivalves on neap and polychaetes and crustaceans on spring) (Aplin & Cockburn, 2012). Relatedly, bird surveys for Chapter 2 were conducted around two hours either side of low tide. Dias *et al.* (2006) suggest that performing bird counts only during the low tide period can provide inaccurate estimates of foraging habitat use of shorebirds. Future studies could look into conducting similar research on oystercatcher foraging ecology and distribution but at different stages of the tidal cycle (for example, spring and neap, high and low tide). Such observations would provide an indication of the periodic differences between oystercatcher and toheroa associations and further identify the impact oystercatchers may be having on toheroa populations.

I set out to find the diet composition of the oystercatchers, more specifically, the percentage of their diet that was comprised of toheroa. In general, it proved difficult to identify oystercatcher prey items to a species level throughout this research project. This was a major limitation as many of the prey items were categorised as unidentifiable prey when not being able to distinguish between toheroa and tuatua. Thus, I believe that amount of toheroa consumed by oystercatchers was underrepresented in the results of this project. With more time invested into developing identification methods and skills between the two bivalve species, future research could attempt to improve accuracy of oystercatcher prey identification at Ripiro Beach.

Observations on oystercatchers were made through focal individual sampling in an attempt to gain the maximum amount of information on foraging behaviour with the limited time available for this research project. To further explore the ecology of oystercatcher predation on Ripiro Beach, scan sampling on flocks of oystercatchers could be conducted to collect information on the birds' activities throughout the day (Altmann, 1974). For example, activity budgets could be recorded, measuring the amount of time oystercatchers spend actively foraging, preening, resting and performing other behaviours. Thus, oystercatcher prey intake rate could be quantified in terms of daily consumption or total hours spent foraging per day. This would give a more precise indication into how much toheroa the oystercatchers are consuming per day.

One of the most direct methods of testing oystercatcher predation impact would be to conduct toheroa population surveys along the whole length of Ripiro Beach in order to determine toheroa population size. These data could then be compared to prey intake rate of oystercatchers at their specific foraging sites. If sampling were to occur every month at the same toheroa beds, for example, over a one-year period, it could be possible to assess the impact of oystercatcher predation on toheroa over time.

Limitations aside, the observations from these chapters have provided a preliminary framework into methods that can be used for investigating the predator-prey relationship between oystercatchers and toheroa. Future research could use data obtained in this thesis to model toheroa mortality patterns by oystercatcher predation. For example, Wanink and Zwarts (2001) utilised optimal prey choice models and field data collected on oystercatcher densities to estimate the biomass of prey taken by the oystercatchers on a monthly basis on tidal flats at the Dutch Wadden Sea. In another study aimed at reducing shellfish-shorebird-commercial fisheries conflict, behaviour-based modelling was used to predict the mortality of mussels from oystercatcher predation over one winter season (Caldow *et al.*, 2004). Perhaps models could be generated using the oystercatcher spatial and temporal distribution patterns, foraging behaviour and prey choice data to estimate impacts on toheroa mortality at Ripiro Beach.

5.4 Conclusion

Oystercatchers have been implicated in the continued demise of toheroa at Ripiro Beach. However, the results of this research do not support this hypothesis. It has been shown that there is limited overlap between the species. Where overlap does occur, the oystercatchers are feeding predominantly on small to intermediate sized bivalves. It is possible that the oystercatchers may be having local effects on the toheroa population structure in the areas used as foraging sites by the oystercatchers. Overall, the results from the study suggest that the South Island pied oystercatcher is not responsible for the continuing decline of the toheroa and is not causing devasting effects to the populations as claimed. This research is significant when put in the broader context of conservation conflict worldwide as it provides another example of the difficulties that can be present when trying to understand the dynamics of predator-prey relationships. Unsuccessful examples of lethal control, discussed in this thesis, highlighted the importance of recognising the complexity of predator-prey relationships for an ecosystem-based management approach and before undertaking such severe actions as predator control. In this instance, I consider the calls to cull the oystercatcher are unfounded and may lead to unpredictable and unwanted outcomes for the ecosystem at Ripiro Beach. Instead, I believe the oystercatchers and the toheroa should be managed through an ecosystem-based approach, preserving the interaction of the two endemic New Zealand species.

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Appendices

Appendix A: Bird Survey Record Sheet

	Bird Survey									
Date:		Observer:			Low tide:		Start time:		End time:	
Temp:	Rain:	Wind:			Species:					
Site #	Lat:	Long:	Beach zone:	Count time:	SIPO	Variable	Red-billed	Blackbacked	Other	Comments:

Appendix B: Behaviour Filming Record Sheet

Behavioural Filming			Weather:										
Observer:			Rain:	Temp:	Wind:								
Date:		Low tide:											
Flock #	Activity	Size	Lat	Long	Sample #	Zone	Ebb/Flow	Start Time 1	End time:	Comments:			

Appendix C: Predation Success Record Sheet

			Predation Success										
Date:			Recorder:		Location:			Site #		Zone:		Freshwater seep: Y / N	
Depth(mm)	**In or Out**	**Species:**	**Condition:**	**Length(mm)**	**Frenzy Hole: Y/N**		**Comments:**						

Appendix D: Size Structure Record Sheet

Toheroa Size Structure			Weather:			Stream:		Low tide:												
Date:	Observer:		Rain:	Temp:	Wind:	Lat:		Long:	Sampling time:											
Quadrat #	Length (mm):	Species	Quadrat #	Length (mm)	Species	Quadrat #	Length (mm)	Species	Quadrat #	Length (mm)	Species	Quadrat #	Length (mm)	Species	Quadrat #	Length (mm)	Species	Quadrat #	Length (mm)	Species

Appendix E: Scales and Codes

Temperature in °C:

1	freezing	<0
2	cold	0-5
3	cool	5-11
4	mild	11-16
5	warm	16-22
6	hot	>22

Wind:

0 none
1 light breeze
2 windy
3 strong winds/gusts

Rain:

0 none
1 drizzle
2 light
3 moderate
4 heavy

Tidal Zone Code

LIZ: Low intertidal zone-only exposed to air at the lowest of low tides and is primarily marine habitat.

MIZ: Mid intertidal zone-regularly exposed and submerged by waves.

HIZ: Only covered by the highest of high tides and much of the time is spent as terrestrial habitat.

Animal Condition Code

H: Healthy
D: Damaged shell
S: Siphons gone
P: Partly gone
W: Whole clam gone

V: Toheroa
S: Tuatua

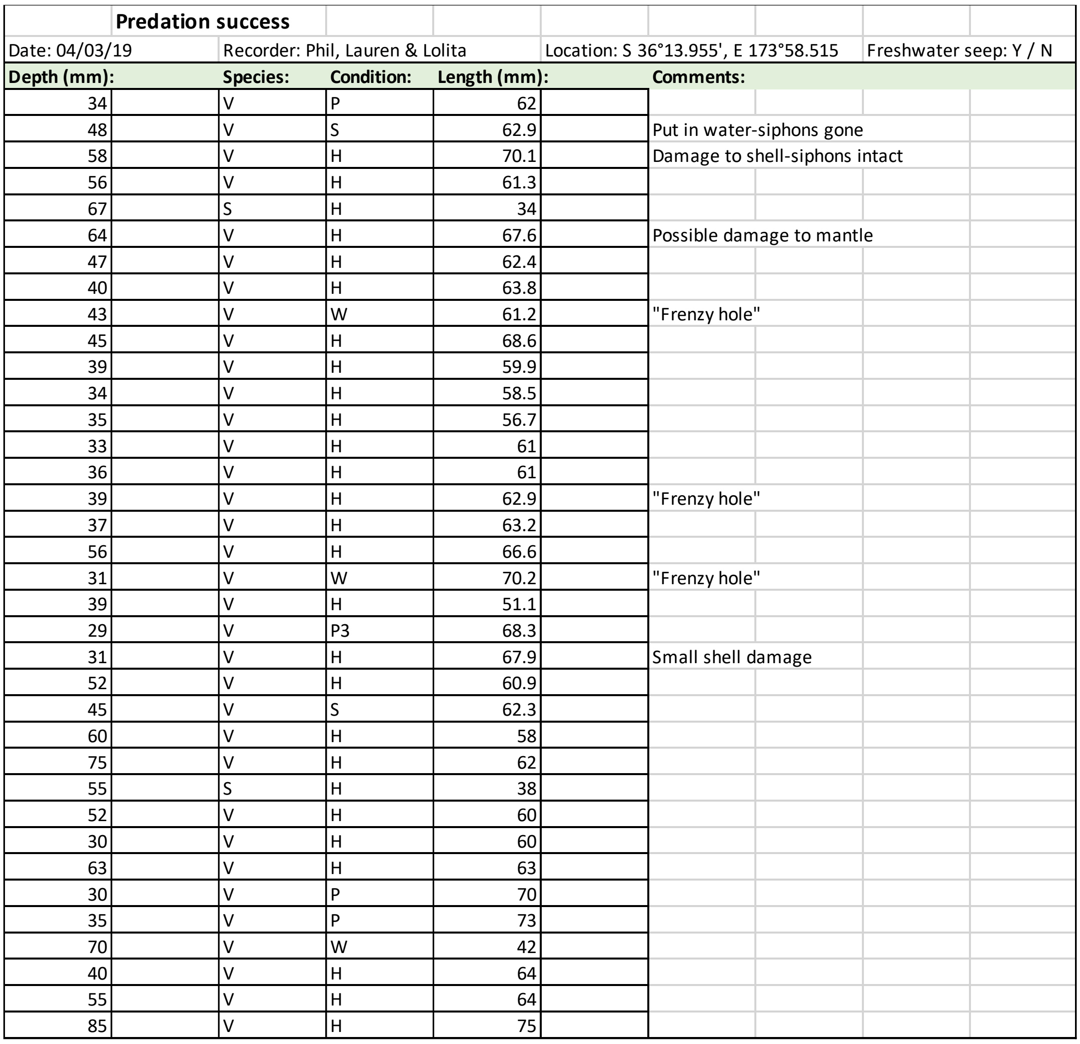
Appendix F: Predation Success Pilot Study

Introduction

The purpose of this study was to determine the methods required to undertake the predation success study presented in Chapter 4 of this thesis. The aim was to investigate the oystercatcher's predation success rate on toheroa at an oystercatcher predation sites.

Methods

The methods used in this study were similar to that of the official predation success study, except that there was no specified sampling area and holes were chosen at random to excavate. Therefore, the data from this study was not included in statistical analyses. No results will be presented here, rather, just the raw data collected from this study.



	Predation success								
Date: 04/03/19		Recorder: Phil, Lauren & Lolita			Location: S 36°13.955', E 173°58.515			Freshwater seep: Y / N	
Depth (mm):		**Species:**	**Condition:**	**Length (mm):**		**Comments:**			
34		V	P	62					
48		V	S	62.9		Put in water-siphons gone			
58		V	H	70.1		Damage to shell-siphons intact			
56		V	H	61.3					
67		S	H	34					
64		V	H	67.6		Possible damage to mantle			
47		V	H	62.4					
40		V	H	63.8					
43		V	W	61.2		"Frenzy hole"			
45		V	H	68.6					
39		V	H	59.9					
34		V	H	58.5					
35		V	H	56.7					
33		V	H	61					
36		V	H	61					
39		V	H	62.9		"Frenzy hole"			
37		V	H	63.2					
56		V	H	66.6					
31		V	W	70.2		"Frenzy hole"			
39		V	H	51.1					
29		V	P3	68.3					
31		V	H	67.9		Small shell damage			
52		V	H	60.9					
45		V	S	62.3					
60		V	H	58					
75		V	H	62					
55		S	H	38					
52		V	H	60					
30		V	H	60					
63		V	H	63					
30		V	P	70					
35		V	P	73					
70		V	W	42					
40		V	H	64					
55		V	H	64					
85		V	H	75					