

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

The Foraging Ecology of Non-breeding Wrybills (*Anarhynchus frontalis*) in the Firth of Thames

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science
in
Ecology

At Massey University, Palmerston North, New Zealand



**Rachel Jayne Withington
2015**

Abstract

The Firth of Thames in the North Island of New Zealand is one of the most important wintering sites for Wrybills (*Anarhynchus frontalis*), second only to the Manukau Harbour. Together these two estuarine areas support approximately 85% of the entire Wrybill population between late summer and early spring each year. While the breeding biology and ecology on their braided river breeding grounds in the South Island have been well documented, the foraging ecology of Wrybills in their non-breeding habitats has not been deeply studied. Wrybills possess a uniquely shaped bill considered to be an adaptation to their life on the South Island braided rivers during their breeding months. However, despite this they use their bill very effectively on the tidal flats of their winter habitats. In this thesis I studied the foraging ecology of Wrybills in the western Firth of Thames, with a focus on the factors affecting their low-tide feeding distribution, and how diet and intake rates varied with foraging mode.

The distribution of foraging Wrybills was correlated with a number of environmental variables (sediment type, sediment softness, water content, and polychaete abundance and biomass). Foraging Wrybills showed a preference for areas of tidal flat close to shore with soft sediment and high polychaete biomass.

Wrybills exhibited different foraging modes that were used in areas with different environmental conditions. Birds fed (1) visually, walking slowly and obtaining most of their biomass intakes from large polychaete worms, (2) by tactile means, capturing mainly small worms or (3) a combination of the visual and tactile methods. Visual feeding tended to occur in drier, sandier sediments and tactile in wetter, muddier areas close to shore. Despite proportionately different intakes of large and small polychaete worms across the different foraging modes, the total biomass intake rates were similar. In addition to polychaete captures, tactile foragers in particular frequently took mouthfuls of sediment, an action which raised the possibility that they may be feeding on surficial biofilm. Stable isotope analysis of Wrybill faeces, blood and feathers revealed some evidence of biofilm feeding in Wrybills at the Firth of Thames.

Acknowledgments

Firstly, thank you to my supervisors Phil Battley and Alistair Robertson. Thank you for your wisdom, enthusiasm, encouragement, and your proof reading skills. Phil, your passion and interest for shorebirds is what got me interested in them, in fact it was through your summer project at Foxton Estuary that I saw a Wrybill for the first time and realised that they were what I wanted to study.

A massive thank you has to go to everyone who was at the Pukorokoro Miranda Shorebird Centre during my stay there, the volunteers and the staff, particularly Keith Woodley, who gave me a place to stay, made me feel welcome and shared their knowledge with me throughout my fieldwork in the Firth of Thames. To the Pukorokoro Miranda Shorebird Centre Trust thank you for awarding me with the Sibson Award for this study, this was so very much appreciated. Thank you to Adrian Riegen and everyone who helped out during the cannon netting. Thank you Phil Battley, Gillian Vaughan, Ian Southey, and Kristelle Wi for helping with the collection of the blood, feather and faecal samples from the Wrybills caught.

Thank you to Karyne Rogers, Andy Phillips and the team at GNS science National Isotope Centre in Wellington who gave their time, knowledge and use of equipment to carry out the stable isotope analysis. William and Judy Wright, thank you for providing me with a place to stay and delicious meals in Wellington whilst I got the sample preparation done.

Thank you to Cleland Wallace for the penetrometer creation, Anja Moebis for sharing her time and knowledge to help me learn and carry out analysis of my sediment samples, and Niki Murray for the microscopy of the Wrybill tongue. Thank you to Massey University and the Ecology department for providing me with funding for this project and to help me get through the year.

To James Bowden, thank you for the use of your video camera, and for trusting me to look after it on some very muddy tidal flats! It achieved some great footage of foraging Wrybills. To my flatmates, thank you for your support in this endeavour, your endless entertainment and welcome distractions.

Finally, a huge thank you has to go to my parents who have been so supportive through the years of my study; I couldn't have done this without your love and support (both emotionally and financially!) I appreciate it so much. Thank you to my sister who has always been there to talk to and hang out

with when I needed a break and who can always make me laugh. To Nando, thank you for believing in me and supporting me through this and a very big thank you for spending a week with me during my fieldwork, I know that you didn't enjoy wading in and sorting through all of that mud but it helped me immensely and I am very grateful.

Table of Contents

Abstract.....	i
Acknowledgments.....	ii
1 General Introduction.....	1
1.1 Introduction.....	1
1.2 Wrybills.....	2
1.2.1 Bill Morphology and Use.....	3
1.2.2 Wrybill Feeding in the Firth of Thames.....	6
1.3 Shorebird Feeding Ecology.....	9
1.3.1 Biofilm Feeding.....	9
1.4 Stable Isotope Analysis in Ecology.....	11
1.5 Thesis Outline and Structure.....	12
2 The Feeding Distribution and Activity of Wrybills (<i>Anarhynchus frontalis</i>) in the Firth of Thames in Relation to Environmental Factors.....	14
2.1 Abstract.....	14
2.2 Introduction.....	14
2.3 Methods.....	16
2.3.1 Study Site.....	16
2.3.2 Wrybill Counts.....	18
2.3.3 Sample Collection.....	18
2.3.3.1 Sediment Samples.....	18
2.3.3.2 Polychaete Worm Samples.....	18
2.3.3.3 Penetrometer Readings.....	19
2.3.4 Sample Analysis.....	19
2.3.4.1 Sediment.....	19
2.3.4.2 Polychaete Worms.....	20
2.3.5 Distribution Maps and Balloon Plots.....	21
2.3.6 Correlation Test.....	21
2.3.7 Data Modelling.....	21
2.4 Results.....	22
2.4.1 Wrybill Foraging Distribution.....	22
2.4.2 Environmental Factors Distribution.....	22
2.4.3 Polychaete Worm Size and Frequency.....	25

2.4.4	Model Selection	28
2.5	Discussion.....	30
3	Different foraging modes and evidence of biofilm feeding in Wrybills (<i>Anarhynchus frontalis</i>) at the Firth of Thames.....	35
3.1	Abstract.....	35
3.2	Introduction	35
3.3	Methods.....	38
3.3.1	Study Site	38
3.3.2	Videoring of Wrybills	39
3.3.2.1	Video Recording	39
3.3.2.2	Video Analysis	39
3.3.2.3	Graphics and Statistical Analysis.....	40
3.3.3	Stable Isotope Sample Collection	40
3.3.3.1	Water Samples	41
3.3.3.2	Polychaete Samples	41
3.3.3.3	Sediment Samples.....	41
3.3.3.4	Biofilm Samples.....	41
3.3.3.5	Blood, Feather, and Faeces Samples.....	42
3.3.4	Stable Isotope Preparation	43
3.3.4.1	Water	43
3.3.4.2	Polychaetes	44
3.3.4.3	Sediment and Biofilm.....	44
3.3.4.4	Blood	44
3.3.4.5	Feathers	44
3.3.4.6	Faeces.....	45
3.3.5	Stable Isotope Analysis	45
3.4	Results.....	46
3.4.1	Video Results.....	46
3.4.1.1	Distribution of Different Foraging Modes.....	46
3.4.1.2	Differences between Foraging Modes.....	46
3.4.2	Handling Times of Polychaete Worms.....	51
3.4.3	Stable Isotope Results.....	51
3.5	Discussion.....	54
3.5.1	Foraging Modes	54

3.5.2	Diet Composition	56
4	General Discussion	60
5	References.....	67

1 General Introduction

1.1 Introduction

Wrybills (*Anarhynchus frontalis*) are a small shorebird endemic to New Zealand. They belong to the family containing plovers and dotterels (The Charadiidae), a group in which the Wrybills stand out because of their unique sideways-bent bill (Davies 1997, Riegen and Dowding 2003) (Figure 1). Over the winter period Wrybills migrate from their breeding grounds on the South Island braided rivers up to estuarine areas of the North Island, in particular The Firth of Thames and Manukau Harbour. While in the Firth of Thames Wrybills feed out on the intertidal mudflats as they are exposed by the receding tide (Pukorokoro Miranda Shorebird Centre 2015, Riegen and Dowding 2003). Although their bent bill is thought to be an adaptation for feeding among rocks on their braided river breeding grounds, they also use it very effectively on their winter mudflat habitats (Turbott 1970).

Shorebirds have traditionally been considered opportunistic feeders that feed mainly on soft bodied macro-invertebrates such as polychaete worms when they are feeding on mud flat habitats. However, in recent years this view has been challenged somewhat after a combination of foraging analysis, tongue and bill morphology, video recordings, stable isotope analysis and energy budgets that have provided convincing evidence that Western Sandpipers (*Calidris mauri*), a small shorebird, feed on surface biofilm on their intertidal estuarine habitat (Colwell 2010, Kuwae et al. 2008, Mathot et al. 2010). At their winter habitat Wrybills fit into the conventional view of shorebird feeding, as they are often seen pulling worms out of the mud on tidal flats. However, they also spend a large amount of time feeding in very soft, wet sediment where they move their curved bill rapidly through the mud in a sweeping or 'sluicing' motion. This mode of feeding differs from what is typically seen in other plovers and as a result the possibility of biofilm feeding by Wrybills has been raised (Auckland Regional Council 2007, Riegen and Dowding 2003, Woodley 2012).

This thesis provides additional understanding of the foraging ecology of Wrybills, a unique bird that has not been deeply studied, particularly in their non-breeding habitats. This introductory chapter provides an overview of what is known about Wrybills relevant to this study, their bill morphology and their wintering habitat in the Firth of Thames. It also covers the use of stable isotope analysis in the field of avian ecology and relevant information on shorebird feeding ecology, in particular biofilm feeding.

1.2 Wrybills

The Wrybill or Ngutuparore is a small, (c. 50 g), shorebird endemic to New Zealand. It is the sole member of the genus *Anarhynchus* (Davies 1997, Dowding 2013). Although a number of its characteristics, notably its colouration and behaviour bear a resemblance to members the Charadriidae family, their curved bill distinguishes them.

Wrybills have a north-south migration within New Zealand; they breed on braided river beds of the South Island from late winter through until mid-summer. On these riverbeds they feed on freshwater invertebrates such as mayfly and caddisfly larvae (Turbott 1970). After breeding the majority of the Wrybill population migrates up to tidal flats in the Auckland region, in particular the Firth of Thames and the Manukau Harbour. Combined, both of these areas are thought to support about 85% of the total population of Wrybill (Riegen and Dowding 2003). Miranda in The Firth of Thames as a result it is considered one of the most important wintering grounds for Wrybills (Pukorokoro Miranda Shorebird Centre 2015, Riegen and Dowding 2003).

The total population of Wrybills is thought to be between 4500 and 5000 but there is concern that the population is declining (Dowding and Moore 2006, Riegen and Dowding 2003). The population size is estimated by counting the wintering flocks in the North Island, because the highly cryptic conditions on the braided rivers make an accurate census down there practically impossible (BirdLife International 2012, Riegen and Dowding 2003). In recent years the winter counts have suggested that there has been a shift in Wrybill numbers between the two main wintering sites, The Firth of Thames and Manukau Harbour. The number of Wrybills in The Firth of Thames has been falling but numbers in the Manukau Harbour have been rising. However, the reason for this apparent shift is not known (Riegen and Dowding 2003). The preferred feeding habitat of Wrybills (soft wet mud) still appears to be abundant in The Firth of Thames. Some possibilities include; habitat degradation (including the spread of mangroves over traditional shorebird habitat) or predation (Riegen and Dowding 2003). Alternatively, habitat could be improving in the Manukau Harbour, rather than any deterioration in the Firth of Thames (Auckland Regional Council 2007). Wrybills are classified as vulnerable by the International Union for the Conservation of Nature (IUCN) and nationally vulnerable by the Department of Conservation (BirdLife International 2012, Robertson et al. 2013). This classification comes about because of the small population with a declining population trend considered to be threatened by habitat degradation and introduced predators (BirdLife International 2012, Robertson et al. 2013).

1.2.1 Bill Morphology and Use

The bill of a Wrybill is 2.8–3.0 cm long and the lowermost third curves to the right 12–26° and ends in a sharp tip (Burton 1972, Riegen and Dowding 2003) (Figure 1 upper). Although there is asymmetry in the bill of Wrybills, investigations into the head and neck anatomy in a Wrybill specimen showed very little asymmetry in other features of the head and neck (Burton 1972). The bill itself however is more complex structurally than just being curved sideways. Where the bill curves the mandibles are not merely bent horizontally, they are twisted inwards on the convex side of the bill as the upper mandible overlaps the lower (Figure 1 lower). On the concave side of the bill a slight opening remains as the bill is closed. Towards the tip of the bill the mandibles meet normally (Figure 1 middle). The resulting structure is described by Potts (as cited in Woodley, 2012) as resembling ‘a curved pipe, with a very slight twist’. The consequence of this elaborate bill structure is that if the left side of the bill is laid lowest then the bill can function as a gathering mechanism-like a spoon (Woodley 2012).

The purpose of this intricate bill structure has been debated for many years. In 1870 Potts concluded that the Wrybill’s bill was specially adapted for the stony riverbed environment on which they breed (Potts 1870). He suggested that the bill structure would allow a Wrybill to search for its food beneath the stones of the river beds as the curve of the bill would allow it to fit close to the stones and follow insects retreating underneath. Then as the mandibles closed, water and insects would be able to be drawn up through the tube that is formed (Buller 1873, Potts 1870, Woodley 2012). Consequently, the Wrybill would be able to gather food from places otherwise inaccessible hence gaining an advantage. While Walter Buller (1873) supported this explanation for the unique bill structure by Potts, a number of others were sceptical of it including Hutton (1873) and Stead (1932). Their scepticism arose from the fact that Wrybills spend only a few months a year on the river beds of the south island; for the rest of the year they reside on mud flats in the North Island which do not consist of stones beneath which prey is hidden. Therefore the abnormality would be of no advantage for the majority of the year (Hutton 1873, Stead 1932). Hutton was also of the opinion that because he had never witnessed a Wrybill move around a stone on the river bed more often than any other birds the curved bill could not be for this purpose. The debate continued into the 1970s when Turbott (1970) observed the feeding actions of Wrybills on the mud flats of the North Island. He observed that as the Wrybills fed in the soft mud they would characteristically



Figure 1. External structure of a Wrybill beak. Upper: from above showing the curvature of the bill. Middle: right-hand side showing the inside curve of the bill and the slight opening that remains when closed. Lower: left-hand side showing the outer curve of the bill. Note the rear-facing denticles on the upper mandible used to help secure polychaetes, and the slight overlap of the upper mandible over the lower towards the tip. Photos: P.Battley, Massey University.

tilt their head to the right and then move their bill from right to left, against the curve of the bill, within the mud, resulting in a grasping action as the bill is utilised from angle to tip. Such a feeding method appeared to be highly efficient (Turbott 1970). In addition to Wrybills feeding in this manner, Turbott also observed them feeding on the mudflats in a more normal, dotterel-like manner in which they would pick up food items with the tip of their bill, however, when doing so they would still sweep down and to the left (Turbott 1970). Turbott was also of the opinion that during the breeding season on the braided rivers Wrybills fed in the soft mud drifts on the river beds rather than beneath the stones, consequently making Potts explanation for the purpose of the bent bill seem unlikely.

In 1979 Ray Pierce, an ecologist, published the results and conclusions of his study of Wrybills which had been carried out on the Rakaia and Cass Rivers in the South Island. He felt that the above debate centred on the authors forming their own impressions rather than making quantitative measurements (Pierce 1979, Woodley 2012). His study found that the main food item for Wrybills on these braided river beds were mayfly and caddisfly larvae and that mayfly larval abundance seemed to be the determinant of where Wrybills would favour feeding. Mayfly larvae were most commonly found on stones partially covered with algae and free of silt, conditions suited to riffles in the river and not soft muddy drifts. Mayfly larvae were also found to be negatively phototactic and were mostly found beneath stones during the day (Pierce 1979, Woodley 2012). Pierce concluded that the unusual bill possessed by Wrybills seems to be adapted to retrieve mayfly and caddisfly larvae from beneath submerged stones where Wrybills are unable to see them. The shape of their bill allows the Wrybills to open their mandibles while their bill is beneath a stone, giving them sufficient movement to capture their larval prey (Pierce 1979, Woodley 2012). Once the larvae become active later in the day and in warmer temperatures a bent bill may also allow the larvae to be retrieved from the curved surface of the stones with more ease (Pierce 1979).

During late winter and early spring the low water temperatures in the braided rivers keep the larvae on which Wrybills feed inactive for longer periods, therefore, sight alone cannot be relied on to feed within the rivers (Pierce 1979). As a consequence, any modification, behavioural or morphological, that increases the ability to capture larval prey will have a survival value. Such a trait is likely to be of even greater value to Wrybills due to their short legs which inhibit their ability to forage in deeper water where the density of the larval prey is higher (Pierce 1979, Woodley 2012). Pierce (1979) speculated that during the Pleistocene the survival value of a bent bill would have been even higher for Wrybills and evolutionary forces even stronger as cool periods prevailed. The efficient intake of

food that resulted from the bent bill in cooler water temperatures would have allowed Wrybills to persist while other bird species became extinct (Pierce 1979, Woodley 2012).

1.2.2 Wrybill Feeding in the Firth of Thames

The Firth of Thames is located about 52 kilometres southeast of Auckland in the North Island of New Zealand. Over 80 species of coastal birds have been recorded in The Firth of Thames (Brownell 2004, Cromarty and Scott 1995). In 1990 the southern and western shores of The Firth of Thames were designated a Ramsar site, encompassing about 8,500 ha of intertidal area (Brownell 2004, Cromarty and Scott 1995). The most important tidal stretch for shorebirds is between Taramaire to the north and Pukorokoro Miranda Stream further south, the intertidal mud flats contain abundant shorebird food including shellfish and worms while the shell banks and fields surrounding them provide vital roosting sites for the shorebirds (Brownell 2004).

When Wrybills are feeding on the expansive tidal flats in the Firth of Thames they appear to exhibit different modes of feeding depending on the nature of mud that they are feeding on (Anderson 2003, Brownell 2004, Riegen and Dowding 2003). They are often seen feeding in soft mud close to shore, exposed as the tide recedes; in these areas of mud the feet and a large proportion of the legs of the Wrybills sink into the soft mud as they stand on it (Figure 2 left). However, there are also firmer, sandier areas amongst the softer patches and also further out on which they feed, and when Wrybills stand on the mud in these areas they tend to remain standing on the surface (Brownell 2004) (Figure 2 right). Feeding Wrybills can be seen pulling polychaete worms out of the mud and swallowing them (Figure 3), and have been known to eat what seem to be insects from the surface of the mud and small fish from time to time (Anderson 2003, Burton 1972, Dowding 2013, Turbott 1970). Although the sideways-bent bill is considered to be an adaptation to feeding on the riverbeds,



Figure 2. Wrybills feeding on different sediments. Left: Wrybill feeding on soft muddy sediment. Right: Wrybill feeding on harder sediment. Images are extracted from video used in Chapter3.

the Wrybills use the bill very effectively on the tidal mudflats of their wintering grounds (Auckland Regional Council 2007, Pierce 1979, Riegen and Dowding 2003, Turbott 1970). Wrybills can be seen 'biting' mouthfuls of soft wet sediment on the mudflats (Figure 4); they also use their bill in a gathering manner by sweeping it from side to side, a method often described as 'scything' or 'sluicing'. Sluicing or scything is a non-visual feeding method often used by birds in soft, muddy substrates; it has been seen in Avocets (*Recurvirostra avosetta*), Greenshanks (*Tringa nebularia*), Redshanks (*T. totanus*), and Pied Stilts (*Himantopus himantopus*) (Battley et al. 2003, Pierce 1985). In these birds the head, neck and bill are held at a low angle and the bill is swept from one side to the other. These birds will lift their head after each sweep, take a step and then sweep again in the opposite direction, the result being up to hundreds of sweeps per minute. In Wrybills this action is considered to provide an efficient means of feeding in the mud with a curved bill. With a straight bill this action requires a lot more effort and can even result in the bird's face touching the mud (Anderson 2003, Auckland Regional Council 2007, Riegen and Dowding 2003, Turbott 1970).



Figure 3. A Wrybill capturing and extracting a large polychaete worm from the mud. Images are extracted from video used in Chapter 3.



Figure 4. A Wrybill feeding in soft mud 'biting' the sediment. Images are extracted from video used in Chapter 3.

Wrybills, as expected for a plover, are also visual feeders and can be seen pecking at the mud to remove organisms from the sediment. Their bent bill means that in order to use this pecking method they must rotate their head so the end of the bill is pointing at the mud surface (Anderson 2003, Pierce 1979, Turbott 1970). In addition to feeding on polychaete worms Wrybills also forage in soft and wet sediment where they commonly use a sweeping 'sluicing' action yet may not visibly capture prey (Anderson 2003, Auckland Regional Council 2007). Hay (1984) found that this characteristic feeding method was used 31 percent of the time on the northern mud flats (as cited in Woodley 2012). This distinctive method of feeding has raised the possibility that Wrybills are feeding on biofilm from the surface of the mud. Biofilm feeding has previously been recognised in Western Sandpipers, a small shorebird and biofilm is known to exist on the surface of the mud in The Firth of Thames (Auckland Regional Council 2007, Brownell 2004, Kuwae et al. 2008).

1.3 Shorebird Feeding Ecology

Non-breeding shorebirds often use tidal flats within harbours and estuaries worldwide. These estuarine areas often contain intertidal mudflats that are rich in benthic invertebrates, the draw card for the large numbers of shorebirds that inhabit intertidal areas (Dias et al. 2009, Woodley 2012). The importance of tidal habitat for shorebirds is illustrated by the huge proportion of shorebirds that incorporate coastal sites into their existence – eighty percent (Woodley 2012). Shorebirds typically possess relatively long legs and long bills in comparison to their body size and also commonly have a streamlined body with powerful wings, traits that assist with foraging on mud flats and migration (Woodley 2012).

Shorebirds are traditionally considered to be opportunistic feeders, and their diet is thought to be dependent on the relative abundances of their often macroinvertebrate prey. Shorebirds tend to concentrate in areas where their prey are most abundant and available and this distribution is seen at a number of spatial scales (Colwell 2010, Finn et al. 2008, Mathot et al. 2010). Recent studies have shown that while the diets at the species level may seem opportunistic, individual variation and specialisation in both feeding behaviour and diet may occur (Mathot et al. 2010). Plant material is typically uncommon in the diet of most shorebird species, although there are exceptions such as some arctic migrants (e.g. Black-tailed Godwit *Limosa limosa*, Marbled Godwit *L. fedoa* and Hudsonian Godwit *L. haemastica*) that are known to feed on seasonal fruits, tubers, seeds, sago pondweed, and other plant material (Colwell 2010, Gratto-Trevor 2000, Robin et al. 2013). Generally the daily energy requirement of shorebirds is met predominantly by the consumption of soft-bodied macroinvertebrates, such as polychaete worms, bivalves, crustaceans and insects. Some large shorebirds are known to consume lizards and fish as part of their diet (Battley et al. 2003, Colwell 2010). However, in recent years there has been insight into the importance of biofilm grazing through a number of studies, a finding which has opened the door to a fresh perspective of shorebird feeding ecology (Colwell 2010, Kuwae et al. 2008, Mathot et al. 2010, Reyes 2013).

1.3.1 Biofilm Feeding

Over the last few years there has been evidence that small sandpipers Western Sandpipers, Red-necked Stint (*C. ruficollis*) and Dunlin (*C. alpina*) feed on a layer of surface biofilm in their inter-tidal habitat using a brush-like tongue (Kuwae et al. 2008, Kuwae et al. 2012). Biofilm is a food source

previously only considered to be consumed by rasping invertebrates and some species of fish (Elner et al. 2005, Kuwae et al. 2008). Biofilm is a dense layer about 0.01–2.0mm thick that is found on the surface of intertidal mud flats. It is a mucilaginous matrix containing microbes, organic detritus and sediment held together by secretions from benthic bacteria and microphytobenthos (Kuwae et al. 2008, Mathot et al. 2010, Reyes 2013).

Elner et al. (2005) examined the bill and tongue structure of Western Sandpipers and Dunlin and discovered that both species had distinctive microstructural details, with each species having unique tongue papillae as well as copious mucus. In addition to morphological analysis the foraging behaviour of both species was also looked at, they were seen to characteristically 'dab' rapidly at the mud surface as opposed to pecking. Furthermore the Western Sandpipers tended to follow the receding tide, feeding in wet sediment where biofilm was more likely to be than on a dry mud surface. The unique morphology and foraging observations of the species led to the suggestion of biofilm feeding, particularly in Western Sandpipers. Kuwae et al. (2008) built upon these previous findings and used videos of feeding behaviour, stomach content analysis, stable isotope analysis and energy budget models to provide evidence that Western Sandpipers were incorporating biofilm into their diets. Their video indicated that the Western Sandpipers were grazing on biofilm; they showed a feeding behaviour distinct from the pecking and probing for invertebrate prey seen in many shorebirds (Kuwae et al. 2008). The videos also revealed a low average prey capture rate of visible surface prey. Stable isotope analysis of the stomach contents found that the stomach content signature was closest to and overlapped the signatures of biofilm and microphytobenthos. This result indicated that biofilm and microphytobenthos make up the majority of material ingested, while invertebrates are a relatively small source. In contrast, the signature of the droppings was relatively invertebrate dominated, suggesting that the invertebrates are digested by Western Sandpipers to a lesser extent than the biofilm and microphytobenthos (Kuwae et al. 2008). This finding has raised the question of whether a similar diet may be found in other shorebirds, particularly small species. The distinctive foraging mode exhibited by Wrybills in soft, wet sediment appears to be a good candidate for investigation.

Possible reasons for biofilm grazing from shorebirds include; a way of protecting long-distance migrants from nutritional uncertainty, a means of reducing both inter and intra species competition for food on the mud flats, and a way of providing a source of rich and immediately consumable energy (Kuwae et al. 2008). Biofilm has been shown to vary over short (days) and long term scales as well as over spatial scales in relation to light, sediment, temperature, salinity, nutrient availability, tides and exposure time, and rain (Reyes 2013). Consequently although biofilm can be considered a

predictable resource within intertidal ecosystems, it will display a natural variability, as with any living community (Reyes 2013). Biofilm and its occurrence in particular areas are at risk both directly and indirectly, from threats including; coastal development, changes in hydrodynamic processes, and grazing by invasive gastropods (Kuwaie et al. 2008, Reyes 2013). It is important therefore to understand the relevance of biofilm as a food source for shorebirds, as if it is a main component of the diet for some shorebird species then declines in biofilm availability could have adverse effects on shorebird populations (Kuwaie et al. 2008).

1.4 Stable Isotope Analysis in Ecology

Stable isotope analysis has become increasingly common in ecology over the last 20 years as its ability to provide information about dietary patterns within ecosystems has been recognised (Hobson and Clark 1992, Inger and Bearhop 2008). Stable isotope analysis takes advantage of the fact that the number of neutrons within the nucleus of an element will naturally differ – these different forms are referred to as isotopes. In the most biologically important elements such as Carbon (C), Nitrogen (N), Oxygen (O), and Hydrogen (H) the lightest stable isotope is a lot more common than its heavier form. The minute differences in mass between the stable isotopes of an element cause subtle changes in how they behave in chemical reactions which in turn subtly alters the ratio of heavy to light isotopes (Fry 2008, Inger and Bearhop 2008). This process is known as isotopic fractionation and it is this that leads to the variation in isotopic signatures that occur between different organisms and across different habitats (Fry 2008, Inger and Bearhop 2008).

Stable isotopes can be a very useful tool in ecology, especially in foraging studies because isotopic signatures will differ between different dietary items and this variability is reflected in the tissues of consumers (Inger and Bearhop 2008). The isotope composition of animal tissue reflects the diet of the animal at the time of tissue synthesis. The result being that different tissues will reflect an animal's diet over different time scales. Blood, for example, turns over reasonably rapidly in birds and will provide information on the diet or habitat of an animal a few days to weeks before the sample collection (Inger and Bearhop 2008). In contrast, a tissue such as feathers will provide information on the diet or habitat over the time they took to grow, often spanning several weeks (Fry 2008, Inger and Bearhop 2008). A mass spectrometer is used to measure the relative abundances of the stable isotopes and expresses the measurement as a ratio of the heavy to light forms of the element of interest. This ratio can then be standardised against reference samples and it is presented as parts per thousand (‰) using the symbol (δ) (Inger and Bearhop 2008).

As consumers ingest, digest and assimilate their food there is a shift in the isotopic ratios resulting in a predictable difference between the isotopic values of the diet and the consumer; the size of this shift is referred to as the trophic enrichment factor. Tissues of consumers will be enriched with respect to their diet after assimilation because heavier isotopes are discriminated against in biological reactions (Bocher et al. 2014, Inger and Bearhop 2008). Dietary studies using stable isotope analysis tend to use the stable isotopes of Carbon (ratio of ^{13}C to ^{12}C) and Nitrogen (ratio of ^{15}N to ^{14}N). The ratios of carbon isotopes ordinarily have a narrow 'enrichment' between trophic levels (commonly 0–1‰). However, the ratios of nitrogen isotopes generally vary a bit more. Consumer tissues tend to become enriched with ^{15}N compared to the diet as lighter ^{14}N is lost to nitrogenous waste products. There is often a trophic enrichment factor of 2–5‰ for nitrogen for each trophic level (Bocher et al. 2014, Inger and Bearhop 2008, Tavares et al. 2009)

Stable isotope ecology is beginning to play an important role in the understanding of the diets of birds over time and space. When combined with conventional methods, stable isotope analysis becomes a powerful tool and provides dietary information which may not be possible to achieve using conventional methods alone (Bocher et al. 2014, Inger and Bearhop 2008). Conventional methods of diet studies such as stomach contents and faecal analysis often glean information from a single 'snapshot' in time of an animal's diet without providing longer-term diet information, unless they are collected over a long period of time. Such analyses also reflect only what is ingested and do not reveal what is important in terms of assimilation (Bocher et al. 2014, Hobson and Clark 1992, Inger and Bearhop 2008). In comparison, stable isotope analysis of tissues can provide information on the proportion of the diet made up by particular prey items. Additionally, all of this information can be gathered through tissues such as blood, feathers, and claws without having to kill the animal of interest (Bocher et al. 2014, Hobson and Clark 1992, Inger and Bearhop 2008).

1.5 Thesis Outline and Structure

The overall aim of this thesis is to understand how Wrybill use the tidal flats on the western side of their main wintering site at the Firth of Thames when foraging, by exploring factors affecting their distribution and determining their diet composition by direct and indirect methods.

The thesis contains two research chapters (Chapters Two and Three), an introductory chapter (Chapter One) and a general discussion chapter (Chapter Four). This format has resulted in some

unavoidable repetition, but this has been limited wherever possible. The chapter outlines are as follows:

Chapter One provides an overview of the relevant information known about Wrybills, outlines the morphology of their curved bill and the debate surrounding its evolution, and outlines the feeding of Wrybills at their wintering site in The Firth of Thames. Additionally there is also an overview of shorebird feeding, in particular the recent discovery of biofilm feeding in shorebird species and the use of stable isotope ecology in avian dietary studies.

Chapter Two examines the distribution of environmental factors on the mudflats in the Firth of Thames (such as polychaete worm abundance and biomass and sediment characteristics), how they influence the distribution of foraging Wrybills and what the best predictors of Wrybill distribution are.

Chapter Three examines the different foraging modes exhibited by Wrybills on the mudflats in the Firth of Thames. It looks at the differences between them in terms of actions performed while feeding and the intakes achieved in each feeding mode and uses stable isotope analysis to investigate the possibility that Wrybills are feeding on biofilm.

Chapter Four summarises the results from chapters two and three, looks at the historical wintering knowledge of Wrybills, historical conditions in the Firth of Thames, and the contemporary changes that have occurred in the two main wintering sites for Wrybills, the Firth of Thames and Manukau Harbour. It discusses the future course of study of Wrybills on their wintering grounds and the limitations of this study.

The work in this study was carried out with approval from the Massey University Animal Ethics Committee (protocol 13/72) and the Department of Conservation (Wildlife Act Authority 38111-FAU), and with approval from the Iwi Ngati Paoa of the Firth of Thames.

2 The Feeding Distribution and Activity of Wrybills (*Anarhynchus frontalis*) in the Firth of Thames in Relation to Environmental Factors

2.1 Abstract

The distribution of shorebirds across tidal flats can be influenced by numerous factors including the biomass of their benthic invertebrate prey, sediment properties, distance to their roost site and the level of human disturbance. Sediment properties such as water content, particle size and resistance are important to consider in terms of shorebird distribution because not only do they have direct and indirect effects on benthic invertebrates and in turn the shorebirds feeding on them but sediment properties also influence how accessible the benthic invertebrates are to shorebirds. To investigate factors influencing the distribution of feeding Wrybills in the Firth of Thames (a main wintering site) the distribution of feeding Wrybills was surveyed, sediments and benthic invertebrate samples were collected, and sediment resistance was measured over a large sampling grid. Wrybill distribution, polychaete abundance and biomass, sediment water content and particle sizes were all spatially heterogeneous across the tidal flat. The distribution of feeding Wrybills could be best predicted by distance to shore, polychaete biomass and sediment softness (penetrometer depth) with numbers of foraging Wrybills expected to increase with penetrometer depth and polychaete biomass but decrease with distance from shore. These results indicate that prey accessibility is just as important, if not more important, than prey biomass itself in the distribution of foraging Wrybills.

2.2 Introduction

Many shorebirds spend their non-breeding seasons on intertidal mudflats where they feed almost exclusively on benthic invertebrates, and often the distribution of these shorebirds is predicted by the biomass of benthic invertebrate prey (Bolduc and Afton 2004, Finn et al. 2008). However, there are other variables that can influence shorebird distribution, including: properties of the substrate, distance to roost site, and the level of human disturbance (Finn et al. 2007, Lunardi et al. 2012). The properties of the substrate upon which shorebirds feed may be particularly important factors to consider in the understanding of shorebird distribution because not only does it influence the benthic invertebrates present, but it also influences how accessible they are to shorebirds.

Substrate properties such as particle size, water content, oxygen penetration, organic matter, salinity, and penetrability can affect benthic invertebrates both directly and indirectly which, in turn, will have an impact on the shorebirds present (Bolduc and Afton 2004). Sediment particle size determines the penetration depth of oxygen and water as well as the amount of interstitial space available to invertebrates. Sediments with high resistance, therefore low penetrability, often have lower invertebrate densities in comparison to sediments with low resistance and high penetrability, thought to result from less habitat availability and growth limitations. (Finn et al. 2008, VanDusen et al. 2012). Primary producers such as algae and bacteria upon which benthic invertebrates feed are also influenced by substrate properties, in particular, the amount of organic matter, particle size, salinity, and water transparency (Bolduc and Afton 2004, Rose and Nol 2010).

The density of shorebird prey may not be the only important factor influencing shorebird distribution, accessibility to prey is likely to be just as important. Sediment composition variables including, grain size, water content, and sediment resistance or penetrability can also affect shorebird distribution (Yates et al. 1993). Although these factors influence the type and abundance of invertebrate prey present, they also influence how accessible this prey is to shorebirds, that is, they influence the ability of a shorebird to search for and capture its prey particularly when using tactile foraging methods (Finn et al. 2008, Granadeiro et al. 2007, Lunardi et al. 2012).

Shorebird bills are able to penetrate deeper and with greater ease in search of prey in sediments with low resistance (Finn et al. 2008). Such sediments also tend to be less porous and retain more water, keeping invertebrates closer to the surface of the sediment and therefore more accessible to shorebirds (Finn et al. 2008, VanDusen et al. 2012). In contrast, sediments with high resistance and a high percentage of coarse particles tend to impede the penetrative ability of foraging shorebirds and therefore their ability to detect and capture prey. Coarse particles not only act as obstacles, they also cause water to drain faster, making benthic invertebrates retreat deep into their burrows and out of reach of shorebirds (Finn et al. 2008). Shorebirds feeding by tactile means will have less foraging success under such conditions. Visual foragers however, may be better suited as benthic invertebrates tend to use coarse material as refuges (VanDusen et al. 2012). Several shorebird species are known to switch between visual and tactile feeding modes depending on the sediment resistance (Finn et al. 2008).

When Wrybills feed on the mudflats in the Firth of Thames they appear to have a preference for soft, wet mud close to shore, in which they use their bill in a tactile 'scything' motion (Riegen and Dowding 2003). Wrybills can also be seen feeding on more solid mud, however on this sediment they appear to exhibit a much more visual based feeding method. There have been very few dietary

studies undertaken on Wrybills in their non-breeding ground; much of the focus has been on their braided river breeding grounds. Observations indicate that on their non-breeding grounds Wrybills tend to feed predominantly on polychaete worms but also on items from the surface of the mud (Anderson 2003, Burton 1972, Dowding 2013, Turbott 1970). In recent years there appears to have been a shift in Wrybill numbers between the Firth of Thames and Manukau Harbour, numbers have decreased in the Firth but increased in Manukau Harbour (Auckland Regional Council 2007, Riegen and Dowding 2003). The reason for this shift is not clear, especially as the soft, wet mud areas that Wrybills seem to favour still appears to be abundant in the Firth of Thames (Riegen and Dowding 2003). It is therefore important to understand which factors play key roles in the distribution of foraging Wrybills.

This study was designed to obtain information on the environmental factors influencing the distribution of foraging Wrybills on the western side of the Firth of Thames. It aimed to find out about how sediment variables and polychaete density changed over the mud flat, how these variables related to numbers of foraging Wrybills and which variables were the most important in predicting foraging Wrybill numbers.

2.3 Methods

2.3.1 Study Site

The Firth of Thames is located in the North Island of New Zealand about 52 kilometres southeast of Auckland. The study site was on the western side of the Firth of Thames at Pukorokoro Miranda where there are expansive tidal flats with plentiful food and roosting areas for shorebirds (Figure 6). Wrybills are frequently observed feeding on the southern mudflats which are about 3 km wide and on the narrower (about 1 km wide) northern mudflats.

A sampling grid with points 250 m apart was created using GIS software (using the New Zealand Transverse Mercator (NZTM) grid), these points spanning 5000 m north-south and 3000 m east-west. Points on the grid between the two main feeding areas were sampled every 500 m instead of 250 m (Figure 5). There were 78 sample points in total, including 12 additional samples taken in areas between grid points (Figure 5).



Figure 6. Location of the study site in the Firth of Thames in relation to Auckland in New Zealand.

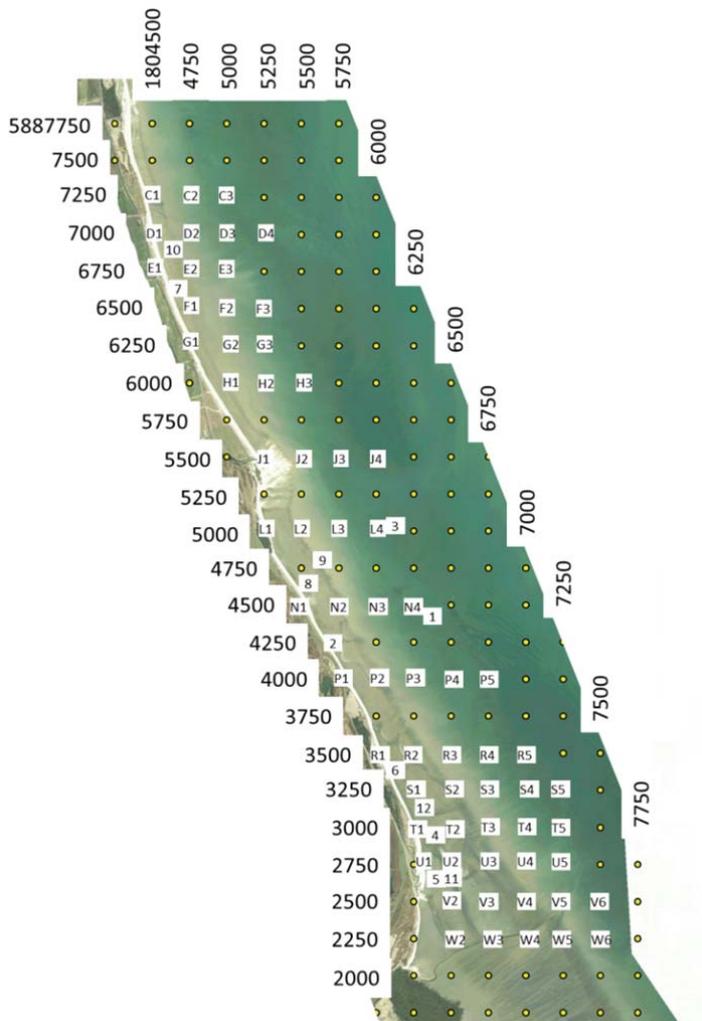


Figure 5. Sample points along the study site in the Firth of Thames. The labelled points are the points that were sampled.

2.3.2 Wrybill Counts

Counts of foraging Wrybills were made daily while out on the tidal flats. This involved scanning the surrounding area for foraging Wrybills using a spotting scope and counting groups of Wrybills foraging. I recorded the number of Wrybills foraging and their location and estimated distance from my GPS position. In total 300 counts were made.

2.3.3 Sample Collection

Sediment and invertebrate samples were taken at each grid point and additional points throughout late March to early May 2014. General observations of foraging Wrybills were also made over the study site including the number of foraging and resting Wrybills in an area, location (GPS coordinate), distance to the Wrybills, time, and what the closest grid point was.

2.3.3.1 Sediment Samples

Sediment samples were collected at each sample point in labelled 35 ml containers by scooping the container through the top surface of the mud and freezing it as soon as possible.

2.3.3.2 Polychaete Worm Samples

Invertebrate samples were taken using a core sampler made from a 1 m long PVC pipe (diameter 10.5 cm) covered by a plastic cap with a small air hole at the top and with a handle to provide leverage. The corer was pushed to a depth of 20 cm and the mud core was removed and placed upright in a bucket. The top 3 cm of the mud core was separated and sorted through first by softly breaking the mud apart and removing invertebrates with fine forceps. These were placed in a labelled 75 ml container with half a centimetre of sea water in the bottom. This was repeated for the remaining 17 cm of core sample.

An equal amount of 10% formalin was added to the sea water and invertebrates (if present) as soon as possible (preserving the invertebrates in 5% formalin). In the lab each sample was rinsed with water to remove the formalin and preserved with 70% ethanol until further analysis.

2.3.3.3 Penetrometer Readings

Sediment softness was measured at each sample point using a penetrometer. The penetrometer was made specifically for this study. It consists of a 30 cm long, 7 mm diameter, hollow metal tube attached to a circular base and a pointed metal rod (57 cm long, 5 mm diameter) which fits down the metal tube (Figure 7).

Penetrometer depth was measured at each sample site by placing the tube and base with the rod inside on top of the mud. The rod was lifted up 3 cm and dropped and the depth the rod went into the mud was measured. This was repeated three times at each sample site.

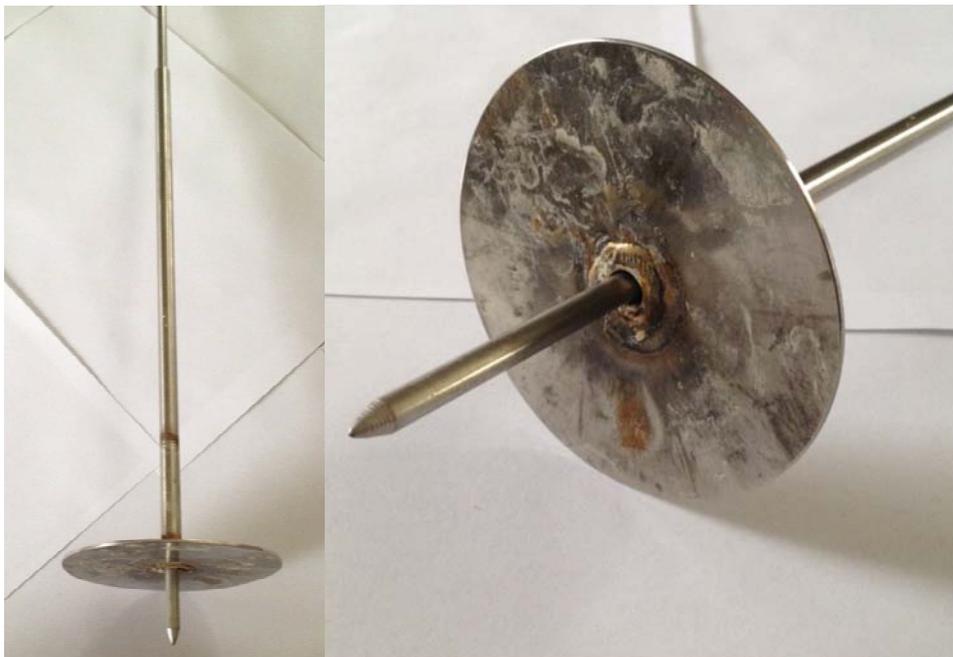


Figure 7. Penetrometer made specifically for this study to measure the sediment softness.

2.3.4 Sample Analysis

2.3.4.1 Sediment

Each sediment sample was put in a labelled aluminium dish, weighed oven dried at 50°C for 48 h, then reweighed to determine water content. Once all sediment samples were dry they were grouped for particle size analysis.

Sediment samples free of clay lumps and with very few or no particles larger than 3 mm were mixed and put through a splitter to evenly reduce the sample until about 7 g remained; this was placed into a small labelled container for analysis. Any particles larger than 3 mm were removed and weighed. Particle size was analysed using a HORIBA laser scattering particle size distribution analyser LA-950V2. The dry sediment samples were manually put into the water drawn by the analyser and analysed using a refraction index of 1.56 based on knowledge of the material within the sediments from the Firth of Thames area (Andesitic ash) (Anja Moebis, Soil and Earth Sciences Group, Massey University, personal communication, May 2015).

Sediment samples free of clay lumps but with many components larger than 3 mm in size were sieved through the following mesh sizes: 8.0 mm, 5.6 mm, 4.0 mm, 2.8 mm, 2.0 mm, 1.4 mm, 1.0 mm, 710 μm , and 500 μm . The sediment in each size class was weighed and about 7 g of sediment less than 500 μm was placed into a small labelled container to be analysed in the same way as above.

Sediment samples with a high clay component that had become very hard when dried were rewet and left to soak for a few days. Each sample was then placed in a small ultrasonic bath and stirred until the lumps of clay were broken up. The wet sediment samples were then placed in appropriate cylinders for particle size analysis using the same equipment and refraction index as above.

The particle size analyser provided the percentage of the sample in different size classes allowing the clay (≤ 0.002 mm), silt (0.063–0.0063 mm), and sand (0.063–2.0 mm) components to be calculated. For analysis the clay and silt components were combined to represent mud (0.002–0.063 mm). The gravel component (manually removed or sieved as above) was the weight of the particles larger than 3 mm (g) (Blott and Pye 2001).

2.3.4.2 Polychaete Worms

The length of each whole polychaete worm was measured and they were placed into crucibles by length in 1 cm size classes (0.1–1.0 cm, 1.1–2.0 cm etc.). Any especially fat polychaetes were put into their own crucible. Partial worms were identified as head, body or rear end if possible and put in their own crucible.

Worms were dried at 50°C for 24h, cooled in a silica gel desiccator and weighed, after which they were incinerated at 600°C in a furnace for 8 h, after which they were cooled and reweighed.

The ash-free dry mass (AFDM) was calculated for each crucible and from this the average biomass for each size class and the estimated biomass at each sample point. Based on the known area of the core sample both polychaete abundance per m² and polychaete biomass per m² were estimated.

2.3.5 Distribution Maps and Balloon Plots

The package 'ggplot2' was used in the statistical programme 'R' to construct bar graphs and balloon plots and contour maps showing the distribution of foraging Wrybills and environmental factors (Chang 2013).

2.3.6 Correlation Test

A correlation test was carried out on the environmental factor variables; this used the function 'cor.test' in 'R' but rewritten as 'cor.sig' (Si et al. 2014) to run with more than two vectors.

2.3.7 Data Modelling

Model selection was carried out in 'R' using the packages 'glmulti' and 'MuMIn' together to find the best predictors in the distribution of foraging Wrybills (Hartman 2013). The response variable was the number of foraging Wrybill and the predictor variables were: log of penetrometer depth (cm), water content (%), polychaete density (n m⁻²), log of polychaete biomass (g m⁻²), distance to roost (m), distance to shore (m), sediment mud content (%) and sediment gravel content (g) at each of the 78 sample points. Sand content and the biomass of an average polychaete worm were excluded from the model due to their close relationships with mud content and polychaete abundance and biomass respectively. A model was also run with water content removed due to its close relationship with mud content. Model averaging used the top seven models (within $\Delta 2$ AICc).

2.4 Results

2.4.1 Wrybill Foraging Distribution

Foraging Wrybills tended to favour particular areas of the tidal flat (Figure 8). Wrybills were found in the highest numbers foraging close to shore, the largest group consisting of 360 foraging Wrybills (Figure 8a). Two areas of the tidal flat stood out for foraging Wrybills, the southernmost area of the study site close to shore and the northernmost area of the study site, also close to shore (Figure 8b).

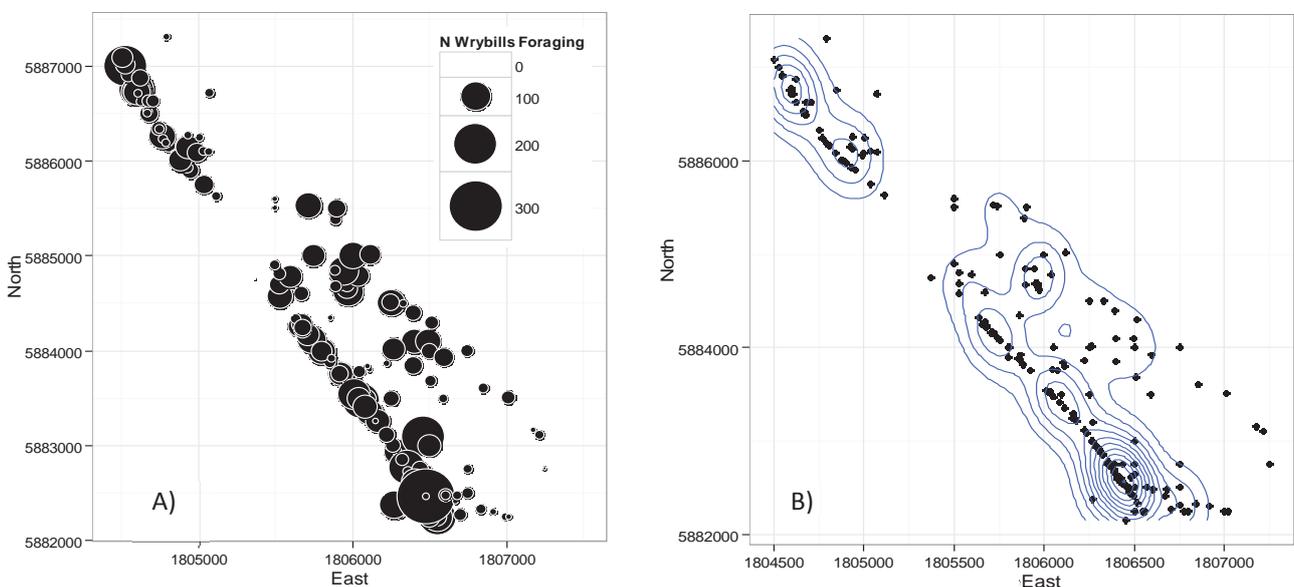


Figure 8. Distribution of foraging Wrybills across the western Firth of Thames. A) Flock sizes of foraging Wrybills (n=300 observations). B) Contour map of the foraging distribution. The shoreline follows the leftmost edge of the foraging distribution in A (see figure 6).

2.4.2 Environmental Factors Distribution

Polychaete abundances ranged from 0–3349 m^{-2} (average 705 m^{-2}) and were highest over the northern area of the tidal flat and close to the shore in the southern area (Figure 9a). Polychaete biomass ranged from 0–7.9 g m^{-2} (average 1.05 g m^{-2}) and the areas close to shore at the northern and southern ends stood out as having the highest polychaete biomass (Figure 9b). The biomass of the average worm (average 0.2 g m^{-2} , range 0–1.47 g m^{-2}) was high along the shore in the northern area of the study site but further south it was higher towards the low tide mark. There were also areas of high average worm biomass towards the middle of the study site (Figure 9c).

The mud was softest (higher penetrometer depth) in the middle of the mud flat towards the low tide mark, and close to shore at the southern end of the study site (Figure 9d). Penetrometer depths ranged from 1.23–10.38 cm with an average depth of 4.2 cm.

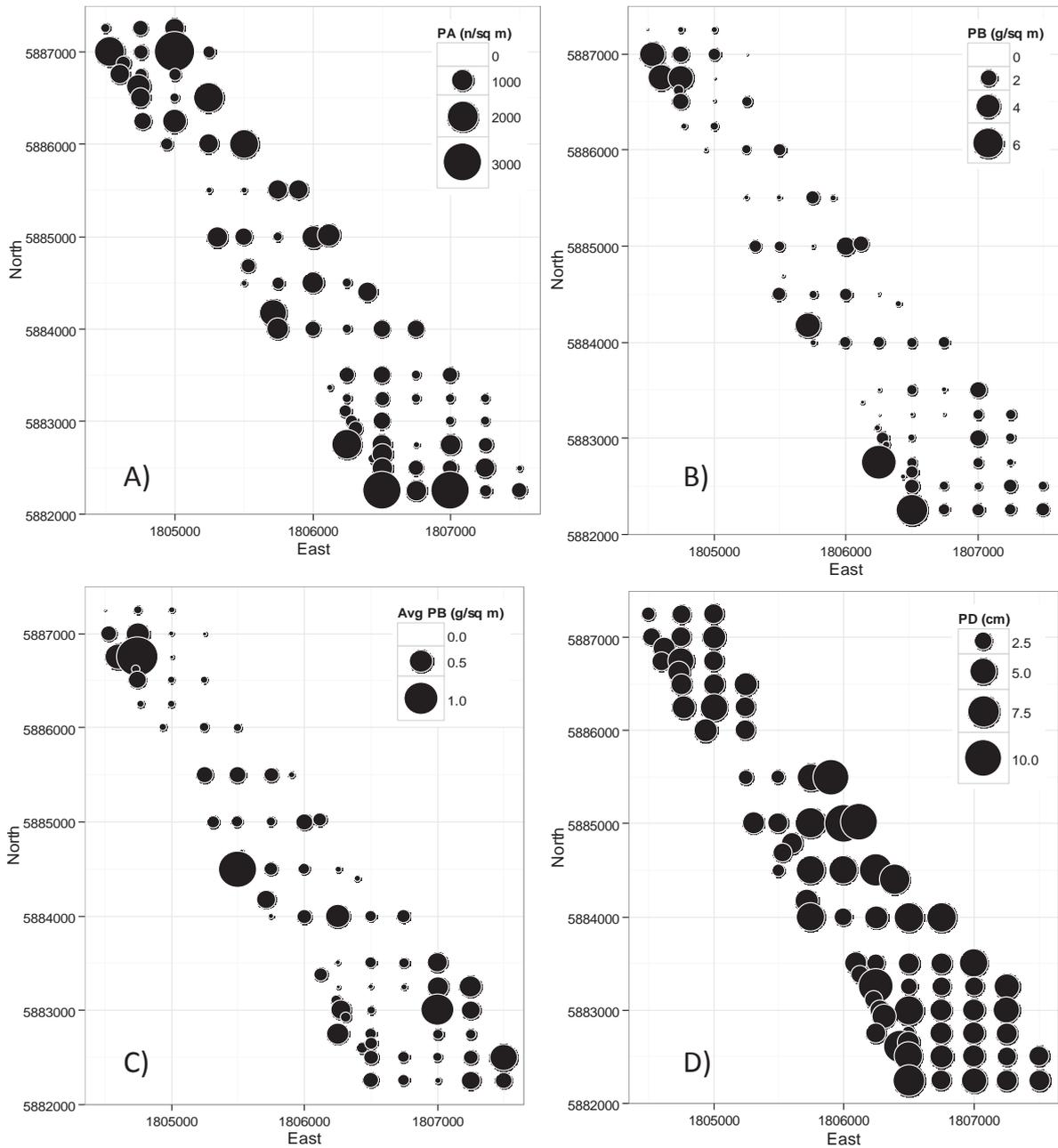


Figure 9. The distribution of A) PA polychaete abundance ($n\ m^{-2}$), B) PB polychaete biomass ($g\ m^{-2}$), C) biomass of the average polychaete worm ($g\ m^{-2}$), and D) PD penetrometer depth (cm) across the study site at the Firth of Thames.

Sediment water content ranged from 23–81% (averaging 44%). It was highest near the shoreline and directly out from Taramaire Stream (N5885000) (Figure 10a). The mud content (min 0.09%, max 87%, average 29%) was highest close to shore in the northern and southern areas and across the tidal flats in middle of the study site (Figure 10b). Sand content ranged from 13–99%, averaging 71%; it was the highest out from the shore, towards the low tide mark, inverse to mud content. At the northing 5884000 there was consistent sand content from the shore out to sea (Figure 10c). Gravel content (range 0–7.4 g, mean 0.5 g) was highest in the northern and middle areas of the tidal flat with very few large particles found at the southern end (Figure 10d).

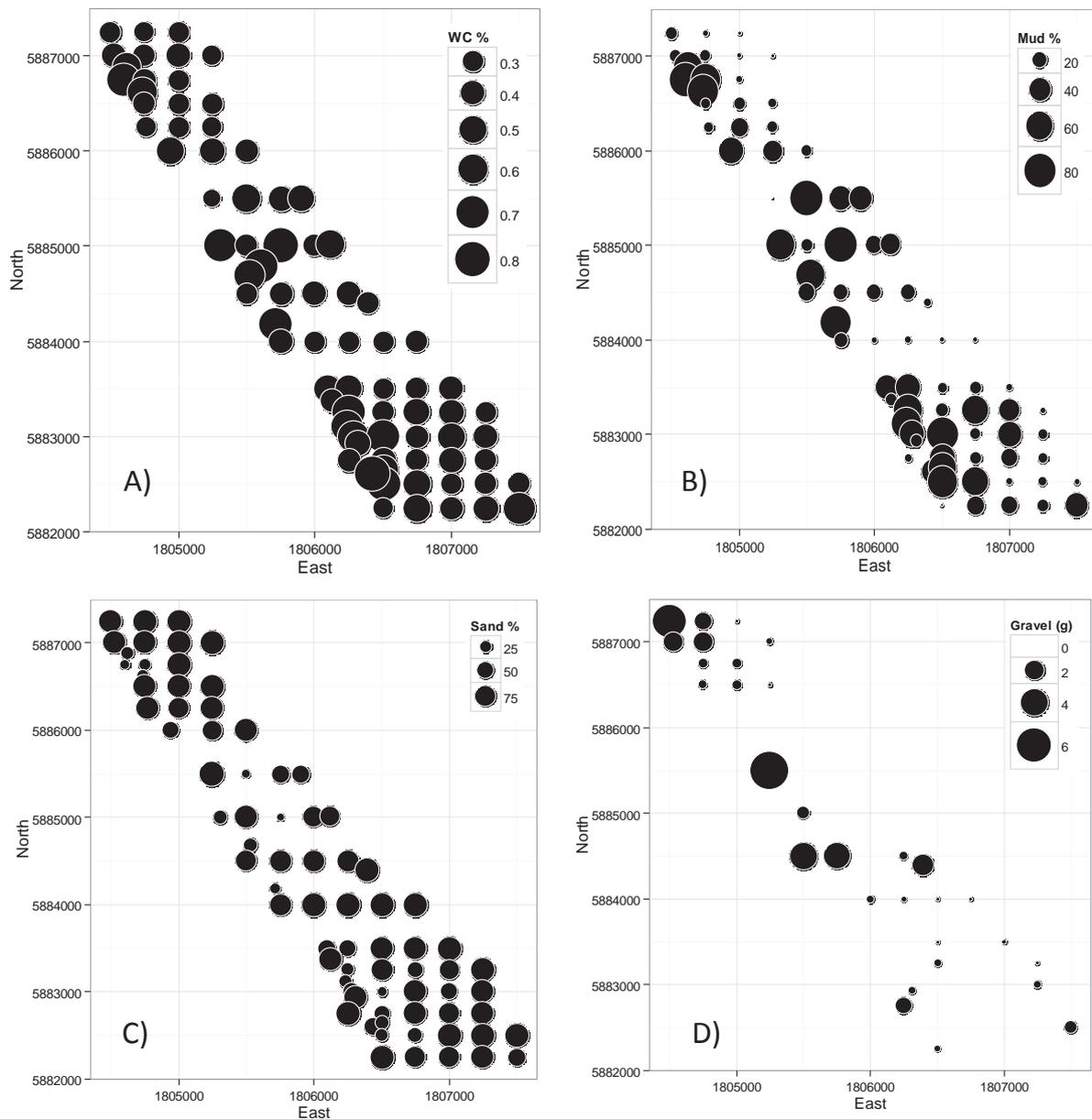


Figure 10. The distribution of sediment characteristics across the study site in the Firth of Thames. A) sediment water content (%) B) percentage of mud (0.002 – 0.063 mm), C) percentage sand (0.063mm – 2 mm), and D) the amount of ‘gravel’ (particles larger than 3 mm) weighed in grams.

Several environmental variables were significantly correlated with each other (Table 1). Penetrometer depth was positively related to distance to shore and negatively to gravel content. Water content was related positively to mud content and negatively to sand and gravel content, and distance to shore. Polychaete abundance was positively related to polychaete biomass. Distance to shore was negatively related to mud content and positively related to sand content and sand and mud content had a directly negative relationship with one another (Table 1).

2.4.3 Polychaete Worm Size and Frequency

The vast majority of polychaete worms collected were small (82% were smaller than 2 cm and 93% were smaller than 3 cm) (Figure 11a). The biomass of individual worms increased greatly with length (Figure 11b). However, the biomass over all was still dominated by small worms (Figure 11c), with worms smaller than 3 cm making up 56% of the total biomass.

The abundance and biomass of polychaete worms did not differ between the upper 3 cm and lower 17 cm of the sediment core samples (t-test, $p=0.2471$).

Table 1. Correlations between environmental factors. LogPD, log of the penetrometer depth (cm); WC, water content (%); PA, polychaete worm abundance ($n\ m^{-2}$); averagePB, average polychaete abundance ($g\ m^{-2}$); logPB, log of polychaete biomass ($g\ m^{-2}$); DR, distance to roost (m); DS, distance to shore (m); Sand (0.063 – 2 mm, percent); Mud (0.002 – 0.063 mm, percent); Gravel, weight of particles larger than 3 mm (g). Significance codes: < 0.001 = ***, < 0.001 – 0.01 = **, 0.01 – 0.05 = *.

	LogPD	WC	PA	AvgPB	LogPB	DR	DS	Sand	Gravel	Mud
LogPD										
WC	0.165									
PA	0.21	-0.077								
AveragePB	-0.15	-0.048	-0.121							
logPB	0.128	-0.002	0.53***	0.512***						
DR	-0.144	-0.185	0.082	-0.008	-0.06					
DS	0.305**	-0.289*	-0.082	0.04	0.061	-0.183				
Sand	-0.045	-0.874***	0.116	-0.1	-0.031	0.056	0.385***			
Gravel	-0.343**	-0.333**	-0.127	0.193	-0.54	0.264*	0.212	0.273*		
Mud	0.045	0.874***	-0.116	0.1	0.031	-0.056	-0.385***	-1***	-0.273*	

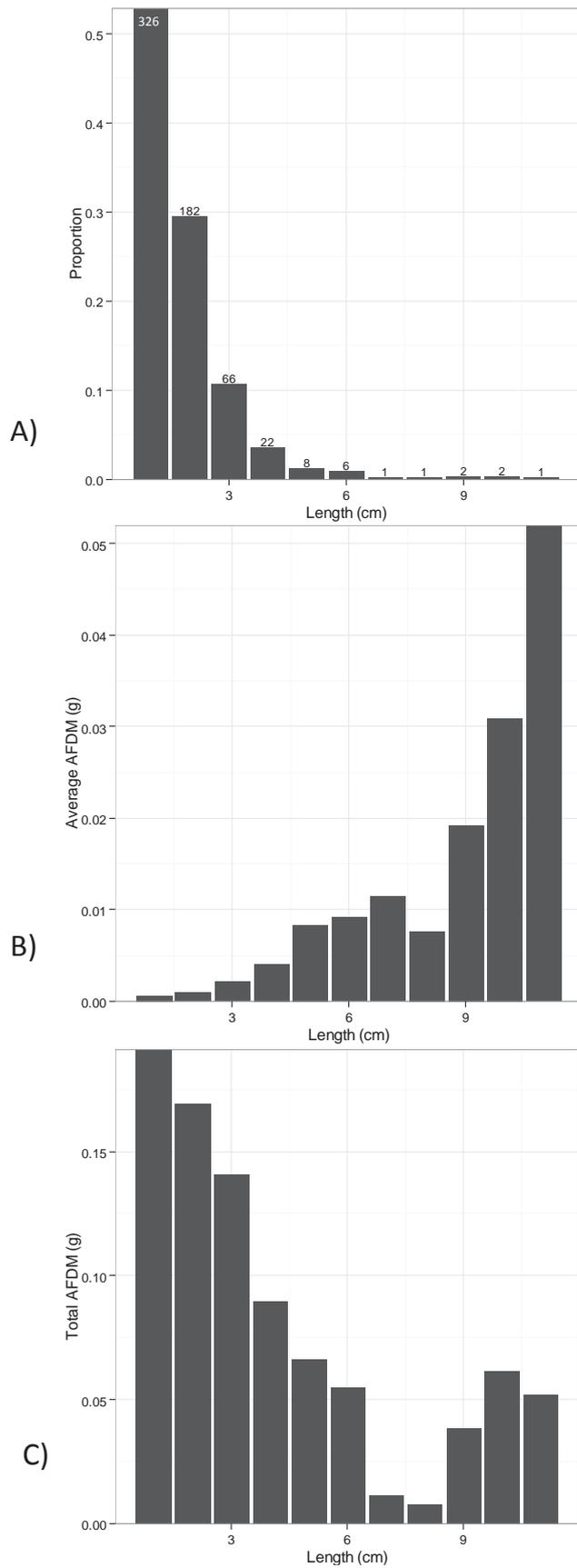


Figure 11. The size distribution (A), mean biomass per length class (B), and total biomass per length class (C) of polychaete worms collected in the Firth of Thames (n=651).

2.4.4 Model Selection

Model averaging of the top seven models (within ΔAIC of 2) (Table 2) revealed that the environmental variables, penetrometer depth, polychaete biomass and distance to shore were the best predictors of the number of foraging Wrybills (Table 3). Penetrometer depth and polychaete biomass showed a positive relationship with foraging Wrybills and distance to shore was negatively related to numbers of foraging Wrybills (Table 3).

Table 2. The top seven of 250 candidate models ($<2 \Delta AIC$) explaining numbers of foraging Wrybills with their components, AICc values and weights. LogPD, log of penetrometer depth (cm); LogPB, log of polychaete biomass ($g\ m^{-2}$); DS, distance to shore (m); Gravel, amount of gravel in sediment (g); Mud, sediment mud content (%); DR, distance to roost (m); WC, sediment water content (%).

Rank	Model	AICc	Weights
1	WrybillNumber $\sim 1 + \text{LogPD} + \text{logPB} + \text{DS} + \text{Gravel}$	941.4866	9.029401e-02
2	WrybillNumber $\sim 1 + \text{LogPD} + \text{WC} + \text{logPB} + \text{DS} + \text{Mud}$	941.6368	8.376052e-02
3	WrybillNumber $\sim 1 + \text{LogPD} + \text{logPB} + \text{DS} + \text{Mud}$	942.2304	6.224950e-02
4	WrybillNumber $\sim 1 + \text{LogPD} + \text{logPB} + \text{DR} + \text{DS} + \text{Gravel}$	942.7808	4.727492e-02
5	WrybillNumber $\sim 1 + \text{LogPD} + \text{WC} + \text{logPB} + \text{DS} + \text{Gravel}$	942.8983	4.457729e-02
6	WrybillNumber $\sim 1 + \text{LogPD} + \text{logPB} + \text{DR} + \text{DS} + \text{Mud}$	943.1786	3.874661e-02
7	WrybillNumber $\sim 1 + \text{LogPD} + \text{WC} + \text{DS} + \text{Mud}$	943.3604	3.537990e-02

Table 3. Model-average coefficients from the top seven models ($<2 \Delta AIC$). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. LogPD, log of penetrometer depth (cm); LogPB, log of polychaete biomass ($g\ m^{-2}$); DS, distance to shore (m); Gravel, amount of gravel in sediment (g); WC, water content in sediment (%); Mud, sediment mud content (%); DR= distance to roost (m).

	Estimate	Std. Error	Adjusted SE	z-value	Pr(> z)
(Intercept)	15.735761	83.831633	84.624657	0.186	0.85249
LogPD	218.368793	80.471377	81.870836	2.667	0.00765 **
LogPB	46.381561	22.509728	22.907988	2.025	0.04290 *
DS	-0.198022	0.047649	0.048470	4.085	4.4e-05 ***
Gravel	-9.510272	12.255701	12.467621	0.763	0.44558
WC	303.369356	226.855870	229.843667	1.320	0.18687
Mud	-0.660049	1.263733	1.276251	0.517	0.60503
DR	-0.009807	0.008978	0.009138	1.073	0.28318

Penetrometer depth and distance to shore were present in each of the top seven models (Table 2) and both had the highest relative importance (Figure 12). Polychaete biomass was present in six of the seven models and the other variables mud, gravel, water content and distance to roost were present in four or less of the top seven models (Table 2).

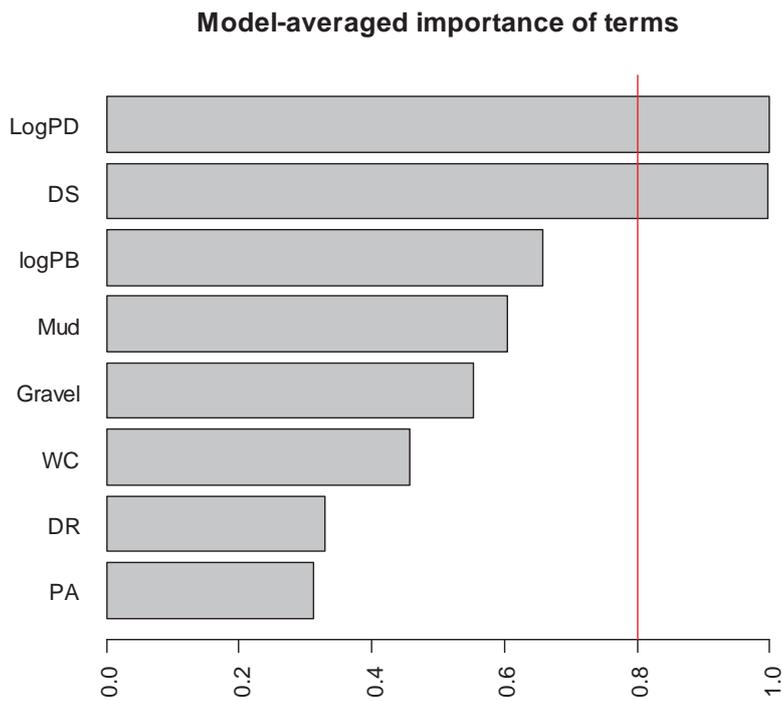


Figure 12. The relative importance of the environmental factors in predicting the number of foraging Wrybills. LogPD, log of penetrometer depth (cm); DS, distance to shore (m); LogPB, log of polychaete biomass (g m^{-2}); Mud, sediment mud content (%); Gravel, amount of gravel in sediment (g); WC, water content in sediment (%); DR, distance to roost (m); PA, polychaete abundance (n m^{-2}). These are averaged across all 250 models and includes one factor not in the seven models in Table 3.

When water content was removed from the model due to its close relationship with mud (Table 1) the relationship between mud and the number of Wrybills changed from being slightly negative (Table 3) to being moderately positive (Table 4).

Table 4. Model averaged coefficients of the top seven models with water content removed. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. LogPD, log of penetrometer depth (cm); LogPB, log of polychaete biomass (g m^{-2}); DS, distance to shore (m); Gravel, amount of gravel in sediment (g); Mud, sediment mud content (%); DR, distance to roost (m); PA, polychaete abundance (n m^{-2}).

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	55.734144	55.479868	56.373767	0.989	0.32283
LogPD	225.487835	80.301468	81.706684	2.76	0.00579 **
logPB	46.897573	22.930621	23.33642	2.01	0.04447 *
DS	-0.202451	0.046897	0.04771	4.243	2.2e-05 ***
Gravel	-10.677898	12.098126	12.31003	0.867	0.38571
Mud	0.21806	0.60543	0.615997	0.354	0.72334
DR	-0.009809	0.008979	0.009138	1.073	0.28308
PA	0.005259	0.025819	0.02628	0.2	0.8414

2.5 Discussion

The observations of foraging Wrybills along the tidal flats in the Firth of Thames revealed that the highest numbers of foraging Wrybills were found on the mud close to shore, with numbers particularly high in the southern and northern ends of the study site. The abundance and biomass of polychaete worms as well as sediment characteristics also showed spatial heterogeneity across the mudflat. The variables polychaete biomass, penetrometer depth, water content and mud content showed distribution patterns most similar visually to the distribution of foraging Wrybills. The sediment close to shore tended to have high water content, high mud content (low sand content) and high penetrability along the length of the mudflat. In the middle of the study site, at the mouth of the Taramaire Stream, water content, mud content, gravel content and penetrometer depth were also high.

A number of important relationships emerged between the environmental variables measured across the tidal flat. As distance from shore increased the sediment tended to have a higher sand content. The opposite relationship was seen with water content and mud content, which tended to be higher closer to shore. As expected from the results of other studies, mud content and water content had a strong, positive correlation while sand and gravel content both had a negative correlation with water content. Sediments with high mud content (a high clay and silt component) inherently tend to hold water due to their low porosity and consequent poor water drainage (Finn et al. 2008, VanDusen et al. 2012). In contrast, coarser sediments with high sand or gravel content tend to drain water faster (Finn et al. 2008). The consequence of this is that muddy areas of a mudflat

tend to remain covered in a thin layer of water as the tide recedes, and this is exactly what is seen on the tidal flats in the Firth of Thames.

The relationship revealed between penetrometer depth and sediment gravel content is also important. The penetrability of the sediment tended to decrease as the gravel content increased. This result clearly indicates how coarse material (such as shell fragments or stones) within the sediment can reduce sediment penetrability. This coarse material impeded the penetrometer in much the same way as it would a probing shorebird's bill, reducing their ability to detect and capture prey, as well as increasing risk of injury to the bill (Finn et al. 2008, Kuwae et al. 2010). As a consequence it is expected that foraging shorebirds, particularly those feeding using tactile probing actions, would avoid areas of the mudflat with coarse material and this was seen to some extent in the distribution of foraging Wrybills. Penetrometer depth emerged as a very important, positively correlated, predictor of foraging Wrybill numbers, and although gravel content was not an important predictor of Wrybill numbers, a negative relationship with foraging Wrybills did emerge.

The abundance, density or biomass of shorebird prey is known to strongly influence shorebird distribution and there are a number of studies that have demonstrated positive correlations between shorebird abundance and the density, biomass or abundance of their invertebrate prey (e.g. Colwell and Landrum 1993, Finn et al. 2008, Goss-Custard et al. 1977, Rose and Nol 2010, VanDusen et al. 2012). Goss-Custard et al. (1977) revealed a tendency for Redshank (*Tringa totanus*) and Eurasian Curlews (*Numenius arquata*) to feed in the highest densities in areas where the density of their invertebrate prey was greatest. Curlew density and Redshank density were strongly correlated with the density of their main prey ($r= 0.942$ and 0.732 respectively). More recently the density of Semi-palmated Plovers (*Charadrius semipalmatus*) on mudflats in the south-eastern USA was found to be predicted by the biomass of their invertebrate prey (Rose and Nol 2010), while shorebird and benthic invertebrate surveys in North Carolina revealed that shorebird distribution was strongly correlated with variation in the benthic invertebrate community ($\rho_s= 0.56$) (VanDusen et al. 2012), and the density of Eastern Curlews (*N. madagascariensis*) was found to have a strong positive correlation with both density and biomass of prey across 12 tidal flats ($r= 0.70$) (Finn et al. 2008). Although invertebrate prey is a predominant factor in shorebird distribution over tidal flats there are other important environmental factors to consider due to their influence on the type and number of benthic invertebrates present and how accessible they are to shorebirds (Finn et al. 2007, Finn et al. 2008, Goss-Custard and Yates 1992, Spruzen et al. 2008, VanDusen et al. 2012).

The abundance and biomass of polychaete worms in the Firth of Thames does not appear to be influenced by the sediment composition variables measured despite the results of other studies

indicating that relationships between the two are common; although there was spatial heterogeneity in polychaete abundance and biomass across the mudflat there was no clear relationship with any of the measured sediment variables indicating something else must be influencing their distribution. Particle size and sediment resistance influence benthic invertebrates indirectly. Sediment particle size can influence the penetration depth of oxygen and water and the interstitial space available within the sediment (Finn et al. 2008, VanDusen et al. 2012). Highly resistant sediments often have lower invertebrate densities in comparison to sediments with lower resistance because they tend to have less habitat available and also limit the size to which invertebrates can grow (Finn et al. 2008, VanDusen et al. 2012). The polychaete worms in the Firth of Thames don't appear to be influenced by these factors and may instead be influenced indirectly by factors that affect the algae and bacteria that they feed on such as organic content, salinity, and water transparency (which weren't measured in this study) (Alves et al. 2011, Bolduc and Afton 2004, Rose and Nol 2010). The higher the primary production, the higher the biomass of benthic invertebrates expected to be supported (Rose and Nol 2010). It is also possible that the polychaete worms in the Firth of Thames are under top-down control with their numbers and biomass being regulated by their shorebird predators on the tidal flat (Posey et al. 1995).

The vast majority of polychaete worms sampled across the tidal flat were small (< 3 cm in length) and despite the biomass of an individual worm greatly increasing with length, the total biomass of worms over the mudflat was dominated by small worms due to their vast numbers. The abundance and biomass of polychaete worms did not differ between the top 3 cm layer (the layer in which Wrybills can feasibly feed due to their bill length) and bottom layer of sediment. Small, medium and large sized worms were also found in both the top and bottom layers of sediment. This means that small, medium and large sized worms are all available to Wrybills as they feed, however Wrybills are much more likely to come across small worms by chance than larger worms. To capture a large polychaete worm is likely to require active searching.

Sediment variables such as grain size, water content, and penetrability or resistance can influence the ability of a shorebird to search for and capture its invertebrate prey, especially when foraging using tactile methods (Finn et al. 2008, Granadeiro et al. 2007, Lunardi et al. 2012). Sediment grain size has been shown to explain the distribution of shorebirds above and beyond its predictive ability in the composition of benthic invertebrate communities ($\rho_s = 0.69$). While variation in the benthic invertebrate community already had a strong correlation with shorebird distribution ($\rho_s = 0.56$), the incorporation of sediment grain size improved this correlation even further ($\rho_s = 0.71$) (VanDusen et al. 2012). This apparent direct effect of sediment composition on shorebird distribution was believed

to be caused by different sediment types altering the ability of shorebirds to access their invertebrate prey (VanDusen et al. 2012). Substrate resistance has also been found to be a good predictor of density and foraging success in Eastern Curlew and several sandpiper species, with substrates of low resistance resulting in higher densities of curlews and higher foraging success in sandpipers (Finn et al. 2008).

In order for a shorebird to be able to exploit the benthic invertebrate prey present on a mudflat they must be able to access it, that is be able to detect and capture it. If sediment has low resistance a feeding shorebird is able to penetrate the sediment deeper in search of its invertebrate prey (Finn et al. 2008). In addition to this, low resistance sediments tend to have high mud content and poor water drainage due to low porosity, as a result such areas remain covered in a thin layer of water as the tide recedes. (Finn et al. 2008). This high surface water content can cause prolonged surface activity by some invertebrates and as a result increased prey availability for shorebirds (Finn et al. 2008, VanDusen et al. 2012). In contrast, sediments with a high resistance and a high percentage of coarse particles such as shell fragments and stones can impede the ability of probing shorebirds to penetrate the sediment and detect and capture prey (Finn et al. 2008). Not only do these coarse sediments act as obstacles, they also cause water to drain faster and as a result invertebrates tend to retreat down into their burrows and out of reach of the shorebirds (Finn et al. 2008). Shorebirds that feed using visual methods appear to be better suited to these conditions as benthic invertebrates are known to use the coarse material as refuges, therefore remaining vulnerable to visual foragers (VanDusen et al. 2012).

Model averaging revealed that penetrometer depth, polychaete biomass and distance to shore were significant predictors of foraging Wrybill numbers. The numbers of foraging Wrybills are predicted to increase as penetrometer depth and polychaete biomass increase, and as distance to shore decreases, meaning the highest numbers of foraging Wrybills are expected to be in areas of the tidal flat close to shore with soft sediment and high polychaete biomass. This result indicates that while the biomass of invertebrate prey is an important factor in the distribution of Wrybills across the mudflat sampled however, it is not the only important factor; this is consistent with other shorebird studies which have revealed the importance of sediment composition variables such as grain size, water content, and sediment penetrability or resistance in the distribution of shorebirds (Finn et al. 2008, Granadeiro et al. 2007, Yates et al. 1993). These sediment characteristics can often influence the type, number, and biomass of invertebrates present, however, just as importantly, they also influence how accessible this prey is to shorebirds. In the case of Wrybills it appears that sediment

penetrability must play an important role in prey accessibility as it doesn't appear to greatly influence polychaete worms at the scale sampled.

3 Different foraging modes and evidence of biofilm feeding in Wrybills (*Anarhynchus frontalis*) at the Firth of Thames

3.1 Abstract

When shorebirds feed on tidal flats they are traditionally thought to feed primarily on benthic invertebrates using visual or tactile feeding methods which use predominantly pecking and probing bill actions. However, there are a number of shorebirds that exhibit feeding actions distinct from pecking and probing as well as shorebirds that switch foraging methods in response to the type of sediment they are feeding upon. In recent years the notion that shorebirds feed almost solely on benthic invertebrates has been challenged by the discovery that Western Sandpipers (*Calidris mauri*), Dunlins (*C. alpina*) and Red-necked Stints (*C. ruficollis*) incorporate biofilm into their diet using distinctive tongue spines and foraging actions. To investigate the diet and foraging modes of Wrybills in the Firth of Thames faecal, blood and feather samples along with source diet samples were collected and foraging Wrybills were videoed across the tidal flat. The results revealed that Wrybills exhibit a flexible foraging strategy on the tidal flats, feeding using visual or tactile cues or a mixture of both with the mode used seemingly influenced by sediment properties. The involvement of sediment biting and sluicing in the tactile feeding method followed by sediment being swallowed with no obvious prey capture raised the possibility of biofilm feeding in Wrybills. The stable isotope results reveal that this may be the case with some evidence of biofilm ingestion within the faecal signature and some dietary contribution of biofilm revealed by mixing models. This is the first evidence of biofilm feeding in a non-scolopacid shorebird.

3.2 Introduction

The non-breeding grounds of many shorebirds are estuarine or mudflat habitats upon which shorebirds are traditionally thought to feed almost exclusively on benthic invertebrates. When shorebirds feed on these habitats they often feed using one of two feeding methods: visual or tactile. Tactile feeding methods are considered best suited to fine sediments with low resistance in which a bird's bill is able to penetrate deeply in search of benthic prey (Finn et al. 2008, VanDusen et al. 2012). Fine sediment also tends to remain covered in a layer of water due to poor drainage; this

keeps invertebrates closer to the surface and more active, therefore easier for a tactile forager to reach (Finn et al. 2008, VanDusen et al. 2012). In contrast, visual foraging is thought to be better suited to areas of coarser sediment because invertebrates take refuge around coarse particles and remain vulnerable (VanDusen et al. 2012).

Most shorebirds use pecking and probing actions in visual and tactile feeding methods respectively to detect and capture invertebrate prey. However, there are a number of shorebirds that use surface tension transport or that dab, skim or graze the sediment, movements distinct from the characteristic pecking and probing of foraging shorebirds (Elner et al. 2005, Kuwae et al. 2008, Quinn and Hamilton 2012). There are also several small shorebird species that switch foraging methods depending on the type of sediment they are feeding upon (Kuwae et al. 2010). These shorebirds tend to feed using tactile methods on fine, low resistance sediments and will switch to feeding visually on coarse sediments with higher resistance (Finn et al. 2008, Kuwae et al. 2010). These shifts in response to environmental change may reflect the ability for shorebirds to make foraging decisions based on rewards and costs and ultimately the highest intake (Kuwae et al. 2010).

Biofilm is a film of densely packed microbes, organic detritus and sediment combined in a mucilaginous matrix secreted by bacteria and microphytobenthos, the film is about 0.01 mm to 2 mm thick (Elner et al. 2005, Kuwae et al. 2008, Mathot et al. 2010). Until recently rasping invertebrates and some specialised fish were considered to be the only consumers of biofilm (Kuwae et al. 2008, Mathot et al. 2010). Biofilm is a predictable resource on intertidal mudflats and consequently biofilm feeding is thought provide a solution to the environmental uncertainty of other food sources (Elner et al. 2005). A large amount of biofilm needs to be collected and ingested to get any energetic gain however; biofilm can be abundant across mudflats. It is richest in muddy areas of estuarine tidal flats with little sediment re-suspension by hydrodynamic forces (Kuwae et al. 2008). Until recently benthic invertebrates have been considered effectively the sole food source of shorebirds feeding on mudflats (Kuwae et al. 2008, Kuwae et al. 2012). That was until the discovery that Dunlin and to an even greater extent, Western Sandpipers, possessed tongue spines which raised the possibility of biofilm feeding (Elner et al. 2005). Following this was the finding that their stomachs contained a high proportion of sediment (Mathot et al. 2010) and that invertebrate prey consumed by Western Sandpipers could not account for their entire diet, leading to the finding that they were consuming surficial biofilm (Kuwae et al. 2008). The stomachs of Western Sandpipers and Dunlin were also found to contain a high proportion of sediment and more recently biofilm feeding has also been found in Red-necked Stints (Kuwae et al. 2012, Mathot et al. 2010). Western Sandpipers in particular possess behavioural and morphological traits that support their ability to

feed on biofilm with tongues covered in papillae, spines, and abundant mucus (Bocher et al. 2014, Elner et al. 2005, Mathot et al. 2010). Western Sandpipers also appear to 'dab' or 'graze' the surface of the mud during feeding, as opposed to the pecking or probing seen in other shorebirds. Additionally they follow the receding tide, feeding on the wet sediment left behind, areas where biofilm is likely to be present (Elner et al. 2005, Kuwae et al. 2008, Mathot et al. 2010). It is unlikely that these are the only shorebirds capable of feeding on biofilm considering the morphological, behavioural and ecological similarities between them and other small shorebirds (Mathot et al. 2010).

The traditional view of shorebird food webs on mudflat habitats is a simple chain which has biofilm as the basal trophic level, consumed by invertebrates which are, in turn, consumed by shorebirds. However, the recent studies revealing biofilm feeding in small shorebirds show that a direct trophic link, between small shorebirds and biofilm, has been missing in shorebird food webs and have resulted in the revision of the trophic position for small shorebirds. This link between biofilm and small shorebirds challenges the traditional view of shorebird food chains and indicates that shorebird population dynamics may respond to some environmental factors (those that influence biofilm density) more rapidly than thought in the past (Kuwae et al. 2012).

The shorebirds known to feed on biofilm (Red-necked Stints, Western Sandpipers and Dunlin) possess morphological and behavioural adaptations for biofilm feeding. The Western Sandpiper, Red-necked Stint and to a lesser extent Dunlin all have distinctive papillae and spines on their tongues as well as copious amounts of mucus. The tongue spines of the Western Sandpiper are particularly long and fine, appearing 'bristle-like' under a microscope (Elner et al. 2005, Mathot et al. 2010). These spines are thought to brush up or absorb a large amount of biofilm, with the biofilm adhering to the spines or mucus coating on the tongue (Elner et al. 2005). The transport mechanism following this is unknown but is likely to involve continuous movement of the biofilm into the oesophagus somehow. The backwards facing maxillary denticles may prevent the bolus of biofilm and sediment slipping out of the bill (Elner et al. 2005). Biofilm grazing is more likely to be present in small shorebirds with short bills. Body mass has a strong negative correlation with tongue spine length and area, and birds with a small body mass are expected to rely on biofilm more than larger birds based on energy budget calculations. Shorter bills are expected to be much more efficient for biofilm feeding given the presumed mechanics of biofilm transport up the bill (Elner et al. 2005, Kuwae et al. 2012). The development of tongue spines is phylogenetically dependent, suggesting that biofilm feeding may also be present only in certain groups. There are three groups of shorebirds that possess tongue spines: the sandpipers, shanks and plovers (Kuwae et al. 2012). Small

sandpipers are known to feed on biofilm and feed using predominantly tactile cues. Plovers however are traditionally considered a visual pecking species, therefore less likely to be biofilm feeders (Dias et al. 2009, Kuwae et al. 2012). The Wrybill is an exception here because it often feeds by tactile means.

A large proportion of Wrybill foraging tends to be on soft, wet sediment (Auckland Regional Council 2007, Brownell 2004, Riegen and Dowding 2003, Woodley 2012). In this sediment Wrybills move quickly and rapidly sweep their bills through or bite the wet sediment and there are very few obvious worm captures (a 'tactile' method). In the 1970s this particular feeding method was observed to be used 31 percent of the time on the mudflats (Woodley 2012). In contrast to this, when Wrybills are observed feeding on solid, sandier sediment they move slowly and carefully and every so often they quickly plunge their bill into the sediment, often emerging with a polychaete worm (a 'visual' method). The tendency for Wrybills to feed in soft, wet sediment with few obvious worm captures has raised the question of what the Wrybills are feeding on under such conditions. One possible answer is that they are feeding on biofilm (Auckland Regional Council 2007).

This study was designed to obtain information on the feeding modes used by foraging Wrybills on the western side of the Firth of Thames. It aimed to find out about how the different foraging modes exhibited by Wrybills differed from one another in terms of actions used, worms captured and estimated polychaete biomass consumed, how environmental factors influenced the foraging modes used, and whether the distinctive biting and sluicing action used by Wrybills incorporates biofilm into the diet.

3.3 Methods

3.3.1 Study Site

The study was conducted at Pukorokoro Miranda on the western side of the Firth of Thames in the North Island of New Zealand, about 52 kilometres southeast of Auckland (Figure 6). This site consisted of expansive mudflats with plentiful shorebird food and roosting areas.

The study site was 5 km long and ranged from 1–3 km wide. There were two main feeding sites for Wrybills within the study area: the northernmost area with mudflats about 1 km wide and the southernmost area with mudflats about 3 km wide. Wrybills were not seen feeding between these two sites as frequently (Figure 13).

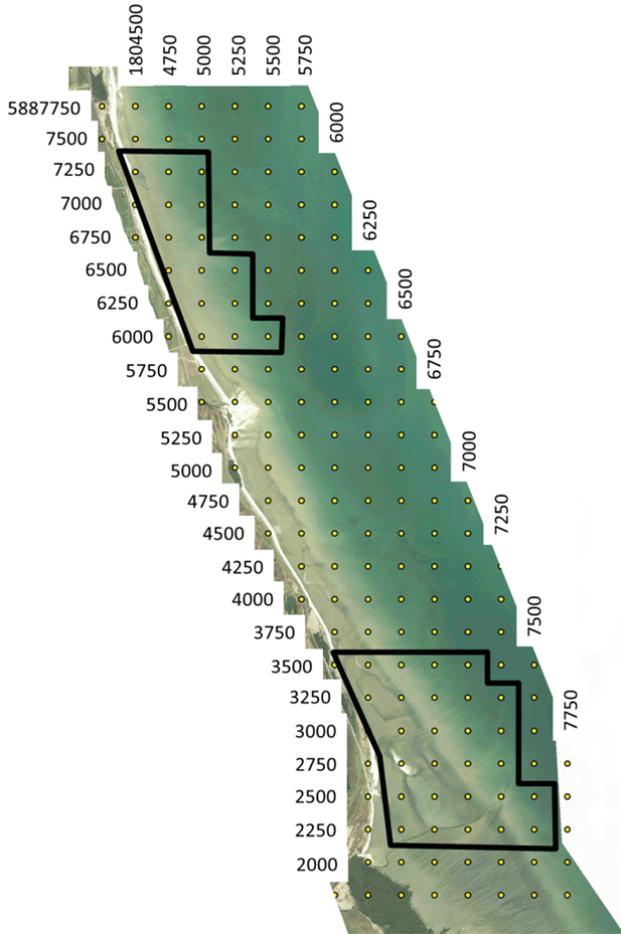


Figure 13. The study site in the Firth of Thames with the two main feeding areas for Wrybills outlined. Grid points are 250 m apart.

3.3.2 Videoing of Wrybills

3.3.2.1 Video Recording

Between late March and early May 2014, 219 foraging Wrybills were videoed across the study site using a *Sony HDR-XR160E* and tripod. Wrybills feeding within 5–20 m were randomly chosen and videoed for three minutes (where possible). The date, time, GPS position (NZTM) and estimated distance to the Wrybills were noted during the recording.

3.3.2.2 Video Analysis

The open-source computer programme Behavioural Observation Research Interactive Software (BORIS) was used to analyse the videos. The following behaviours were assigned a keystroke key: the point events: pace, peck, probe, bite/sluice (because these behaviours could be indistinguishable), bill in water, eat large worm, eat medium worm, eat small worm and swallow, and the state events: actively foraging, preening, bathing and running.

Each video was watched at 0.3x real speed and when one of the above behaviours was performed the corresponding key was pressed. Worm size was based on the size of the worm in comparison to the Wrybill bill (3.0 cm). Worms smaller than the bill were classed as small, those a similar size and up to twice as big were classed as medium and worms more than twice the size were classed as large. The feeding mode exhibited by each bird was noted (visual, tactile or a combination of both).

The *BORIS* programme recorded the keystrokes throughout each video including when the behaviour occurred, how long for, and the number of times. From the output the following could be calculated: total foraging time, the number of paces, pecks, probes, bites/sluices, swallows and foraging actions per minute, and the number of small, medium and large worms captured per minute and their biomasses (from the average biomasses calculated for small (0.00065 g), medium (0.0063 g) and large (0.024 g) worms from the sampling done in Chapter Two. The pacing rates before and after worm captures could also be calculated; these were calculated by averaging the pacing rate for four paces before and after a worm capture for each bird videoed ($n=214$, 2–10 captures per bird). Pacing rates were only calculated if there were four paces uninterrupted by another foraging action.

3.3.2.3 Graphics and Statistical Analysis

Scatterplots and distribution graphs were plotted using the package 'ggplot2' in R (Chang 2013). Boxplots and ANOVAs were created and calculated in R using the internal commands 'boxplot', 'aov' and 'TukeyHSD'. The effect sizes (Hedges g) of movement characteristics were calculated using an online calculator (Lenhard and Lenhard 2015).

3.3.3 Stable Isotope Sample Collection

The consumer tissues (blood, feathers and faeces) and potential food sources as well as sediment and water samples were collected for stable isotope analysis from 18–22 June 2014.

3.3.3.1 Water Samples

Two litres of sea water were collected at high tide from the Firth of Thames and frozen as soon as possible.

3.3.3.2 Polychaete Samples

Polychaete worms were collected with the same core sampler and method used in chapter two for the invertebrate core samples. They were collected from point U1 (Figure 5) where large numbers of Wrybills were seen feeding. The polychaetes were gently pulled from the mud cores using fine forceps. Each worm was rinsed with distilled water to remove as much sediment as possible, put in a container and frozen as soon as possible.

3.3.3.3 Sediment Samples

Sediment was collected in a one litre container from four sites over the study area: The northern, middle, and southern areas and from a pond behind the shell spit. The container was scooped through the sediment until full and frozen as soon as possible.

3.3.3.4 Biofilm Samples

Biofilm was collected from the mud surface by using a plastic spoon to scrape the thin film off the surface of the sediment and into a zip-lock bag (Figure 14). In very muddy areas the bottom of the spoon was pressed lightly onto the mud, picking up a thin layer which was rinsed into a zip-lock bag using distilled water. As little sediment as possible was collected in this process.



Figure 14. Biofilm on the surface of the mud in the Firth of Thames.

3.3.3.5 Blood, Feather, and Faeces Samples

Wrybills were caught using a cannon net on the shell bank as they came up to roost at high tide on the 21 June 2014. Of the Wrybills caught, forty previously banded birds were extracted from the nets and put into separate holding boxes for faecal sample collection.

The holding boxes were modified ice-cream containers with tinfoil lining the bottom to collect faeces and a large hole cut in the lid and a cut black stocking stretched over top. Wrybills were put in and taken out through the leg hole of the stocking (Figure 15). The tin foil at the bottom of the holding containers was folded up to contain the faeces and placed on ice until they could be frozen. Each bird was given an identifying number to link faeces, blood and feather samples.

About three capillary tubes (total ~ 200 μ l) of blood were collected from the wing vein of 38 Wrybills and put into 1.5 ml capillary tubes which were immediately put on ice until they could be frozen. Two axillary feathers were plucked from each bird and put in a labelled zip lock bag.



Figure 15. Wrybill holding containers to collect faecal samples, made from modified ice cream containers.

3.3.4 Stable Isotope Preparation

3.3.4.1 Water

The water was thawed and filtered through pre-combusted (at 400°C) *Whatman glass fibre filter papers* (25 mm, F). 300ml of water was filtered using a vacuum. There were four replicates; two were left untreated and two were treated with 1M HCl to remove any carbonates present. Treatment involved removing the vacuum, adding a few drops of HCl, leaving for two minutes and then reapplying the vacuum and a small amount of distilled water to rinse the acid off. The filter papers were left to dry overnight.

Excess filter paper was cut from the outside and 1/8th of each filter paper was cut out, folded as small as possible and placed into a 5 x 9 mm tin capsules. The tin capsules were folded into spheres for stable isotope analysis.

3.3.4.2 Polychaetes

The polychaete worms (small, medium and large) were freeze dried and crushed and 0.710–0.715 mg of each size were weighed into 4 x 6 mm tin capsules. The tin capsules were folded into spheres for stable isotope analysis.

3.3.4.3 Sediment and Biofilm

Sediment and biofilm preparation followed similar steps. The sediment and biofilm samples were freeze dried and ground into a fine powder (icing sugar consistency) using a mortar and pestle. To remove any carbonates subsamples of the sediment and biofilm were treated with 1M HCl. The remaining ground samples were placed into 15 ml tubes and left untreated.

24.850–25.086 mg of each sediment sample (both treated and untreated) were put into 5 x 9 mm tin capsules and 4.95–5.15 mg of each biofilm sample (both treated and untreated) were put into 4 x 6 mm tin capsules. Each capsule was folded into a sphere for stable isotope analysis.

3.3.4.4 Blood

Wrybill blood samples were freeze dried and ground into a powder. 0.50–0.52 mg of each blood sample was weighed into separate 4 x 6 mm tin capsules which were folded into spheres for stable isotope analysis.

3.3.4.5 Feathers

The feathers from each Wrybill were covered in a 2:1 chloroform methanol solution and left to soak overnight to remove any lipids. They were then rinsed using a clean solution, folded inside a labelled filter paper and left to dry.

Once dry 0.50–0.51 mg of feather barbs (avoiding the rachis) from each Wrybill were weighed into separate 4 x 6 mm tin capsules. Each tin capsule was folded into a sphere for stable isotope analysis, taking care to keep the contents inside the sphere.

3.3.4.6 *Faeces*

The Wrybill faeces were freeze dried and the faecal contents were carefully scraped from each sheet of tin foil to form a powder. 0.995–1.015 mg of faecal contents was weighed into separate 4 x 6 mm tin capsules which were folded into spheres for stable isotope analysis.

3.3.5 Stable Isotope Analysis

For each sample test runs were made to determine the weight required for a correct reading. The samples were analysed by combustion in a *Eurovector elemental analyser* coupled to an *Isoprime mass spectrometer* at the GNS Science Stable Isotope Laboratory in Gracefield, Wellington, New Zealand.

The results were reported with respect to VPDB and N-air and normalised to the internal standard Leucine (-23.0‰ for $\delta^{13}\text{C}$, 2.0‰ for $\delta^{15}\text{N}$) to assess reproducibility and precision. The analytical measurement for these measurements is 0.3‰ for $\delta^{15}\text{N}$ and 0.2‰ for $\delta^{13}\text{C}$.

The results were analysed using the package 'SIAR' in R (Inger et al. 2010). This analysis required consumer, sources and TEF (Trophic Enrichment Factors) files for analysis. Trophic enrichment factors of $1\text{‰} \pm 0.5$ for Carbon and $3.3\text{‰} \pm 0.5$ for Nitrogen these values are added to the sources, rather than subtracted from the consumer in this analysis programme (Bocher et al. 2014, Inger et al. 2010, Kuwae et al. 2008, Quinn and Hamilton 2012). For analysis the Carbon values of treated sources (carbonates removed) were used and the Nitrogen values of untreated sources were used. There were two feather outliers removed for this analysis; one of these outliers was likely to be a feather grown on the breeding ground with the signature closely resembling that of mayfly and caddisfly larvae (Gurau 2014) however the other one couldn't be explained and may have just been an error.

3.4 Results

3.4.1 Video Results

3.4.1.1 *Distribution of Different Foraging Modes*

From 214 Wrybills videoed foraging, 67 (31.3%) were classed as tactile feeding, 89 (41.6%) as visual feeding, and 58 (27.1%) as mixed feeding. Visual feeding tended to occur out from the shore towards the low tide line (Figure 16). In contrast, the tactile feeding was found almost solely along the shoreline, particularly in the northern and southern areas (Figure 16). Mixed feeding was also observed predominantly along the shore but sometimes further out on the mud flat (Figure 16).

3.4.1.2 *Differences between Foraging Modes*

Movement characteristics varied between the different foraging modes (all ANOVAs were significant at $P < 0.0001$, all effect sizes were large (> 0.8), $F_{2,211}$ ranging from 23.57–265.2; Table 5). Visual foragers tended to walk ‘slowly’ ($\bar{x}=95.4$ paces per minute), and make few foraging actions ($\bar{x}=7.6$ per minute) including few bites and sluices ($\bar{x}=1.86$ per minute). They captured low numbers of worms ($\bar{x}=1.56$ worms per minute) and swallowed unidentified food infrequently ($\bar{x}=1.9$ swallows per minute). On average, 43% of intakes by visual foragers did not result in a visible worm capture (Figure 17).

In contrast, tactile foragers tended to walk much faster ($\bar{x}=140$ paces per minute) and made many foraging actions ($\bar{x}=46.9$ per minute) including a high number of bites and sluices ($\bar{x}=35.0$ per minute). They captured a higher number of worms (7.4 worms per minute) and swallowed unidentified food sources often (28.0 swallows per minute). On average, 76% of intakes by tactile foragers did not result in a visible worm capture (Figure 17).

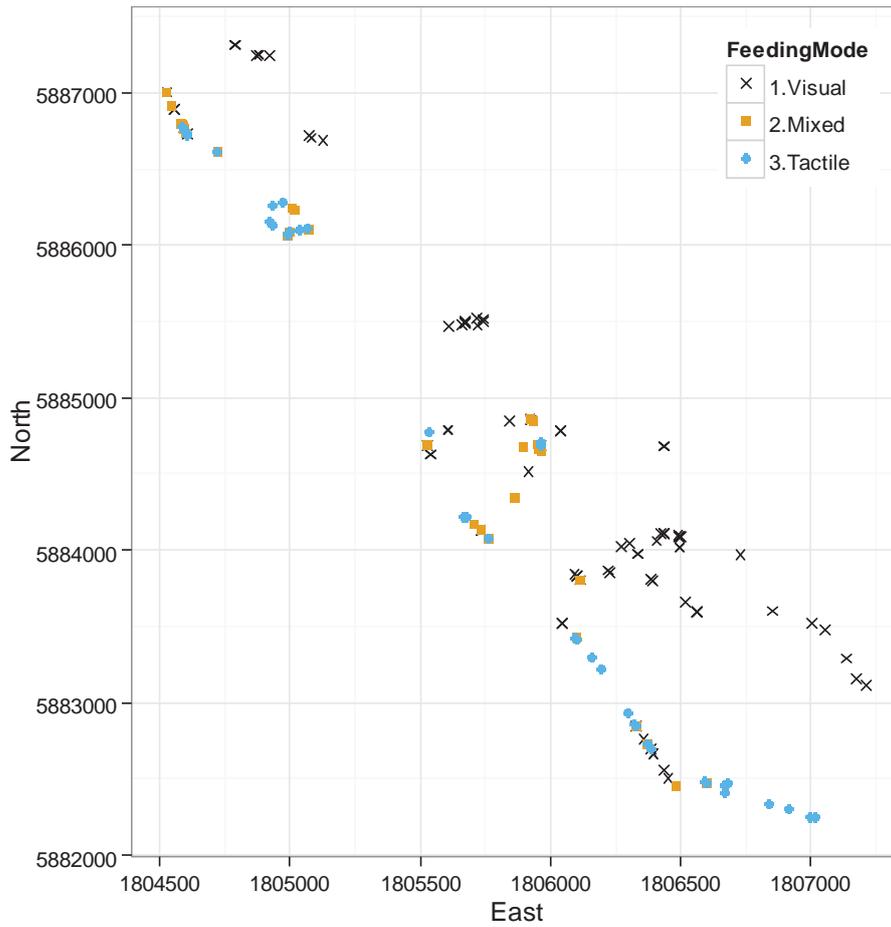


Figure 16. The distribution of Wrybill foraging modes: visual (n=89), mixed (n=58), and tactile (n=67) in the Firth of Thames from video analysis. The shoreline is not shown but it follows the south-western line of Wrybill foraging.

Table 5. The average values per minute for Paces, bites/slurps (Bite/Slu), foraging actions (ForagA), swallows (Swallows), worms captured (Worms), and proportion intake non-worm (Non-worm) by foraging mode. The F-values and P-values from ANOVA between foraging modes, and the Hedges g value between Visual and Tactile feeding modes.

	Paces	Bite/Slu	ForagA	Swallows	Worms	Non-worm
Visual	95.43	1.85	7.62	1.90	1.56	0.432
Mixed	122.21	14.27	29.39	12.6	4.31	0.705
Tactile	140	35.02	46.89	28.1	7.42	0.762
F_{2,211}	23.57	155.20	265.2	177.90	131.6	50.98
P	5.78e ⁻¹⁰	2.00e ⁻¹⁶				
Hedges g	1.4170	2.792	3.802	3.031	2.645	1.431

Mixed foragers tended to display intermediate characteristics, averaging 123.2 paces per minute, 14.2 bites and sluces per minute, 29.4 foraging actions per minute, 4.3 worm captures per minute and 12.6 swallows per minute. On average, 70% of intakes by mixed foragers did not result in a visible worm capture (Figure 17).

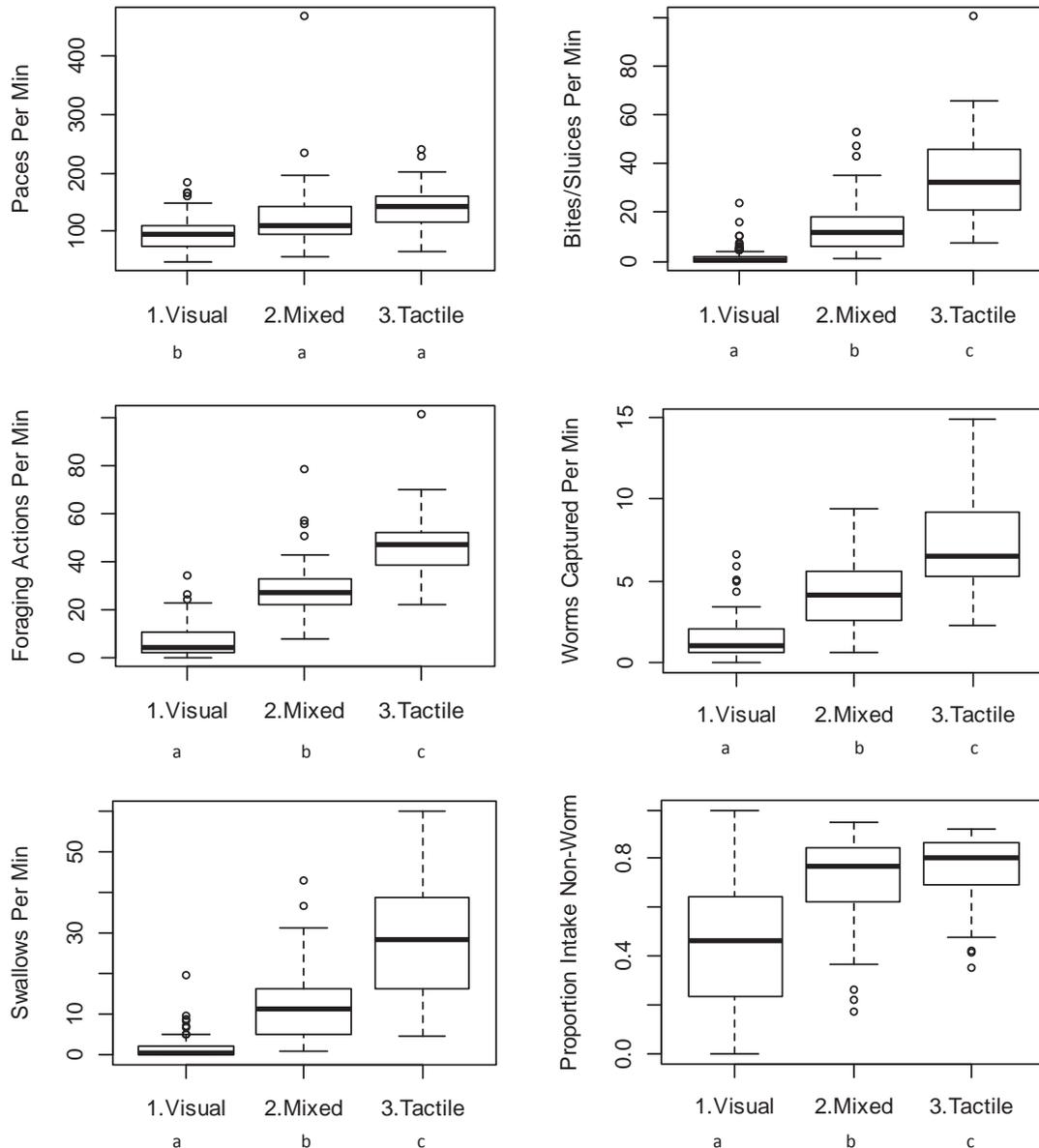


Figure 17. The characteristics and outcomes of the different foraging modes (visual, tactile and mixed) seen in Wrybills foraging at the Firth of Thames. Different letters (a, b or c) represent a significant difference between characteristics (Tukey post-hoc test; all significant differences were $P < 0.001$).

Visual foragers were estimated to obtain much greater biomass from large worms ($\bar{x}=0.0069 \text{ g min}^{-1}$) than medium or small worms ($\bar{x}=0.0034 \text{ g min}^{-1}$ and $0.0005 \text{ g min}^{-1}$ respectively; $F_{2,264}=30.02$, $P<0.001$), while the reverse was true for tactile feeders ($\bar{x}=0.0044$, $\bar{x}=0.004$, and $\bar{x}=0.011 \text{ g min}^{-1}$ of small, medium and large worms respectively; $F_{2,198}=22.67$, $P<0.001$). Mixed foragers were intermediate in all categories ($\bar{x}=0.0023 \text{ g min}^{-1}$ small worms, $0.0039 \text{ g min}^{-1}$ medium, and $0.0022 \text{ g min}^{-1}$ large worms; $F_{2,171}=4.654$, $P>0.01$). These differences were also significant between foraging modes: visual foragers were estimated to consume more biomass from large worms than did tactile or mixed feeders ($F_{2,211}=18.14$, $P<0.0001$), and tactile foragers consumed a greater biomass of small worms than the visual or mixed foragers ($F_{2,211}=164.6$, $P<0.0001$) (Figure 18). The estimated biomass of medium worms consumed was similar across the feeding modes ($F_{2,211}=0.592$, $P=0.554$) (Figure 18). In terms of total biomass consumed, however, the contrasting intakes of large and small worms balanced out all foraging methods had similar total intake rates ($F_{2,211}=1.537$, $P=0.217$) (Figure 18).

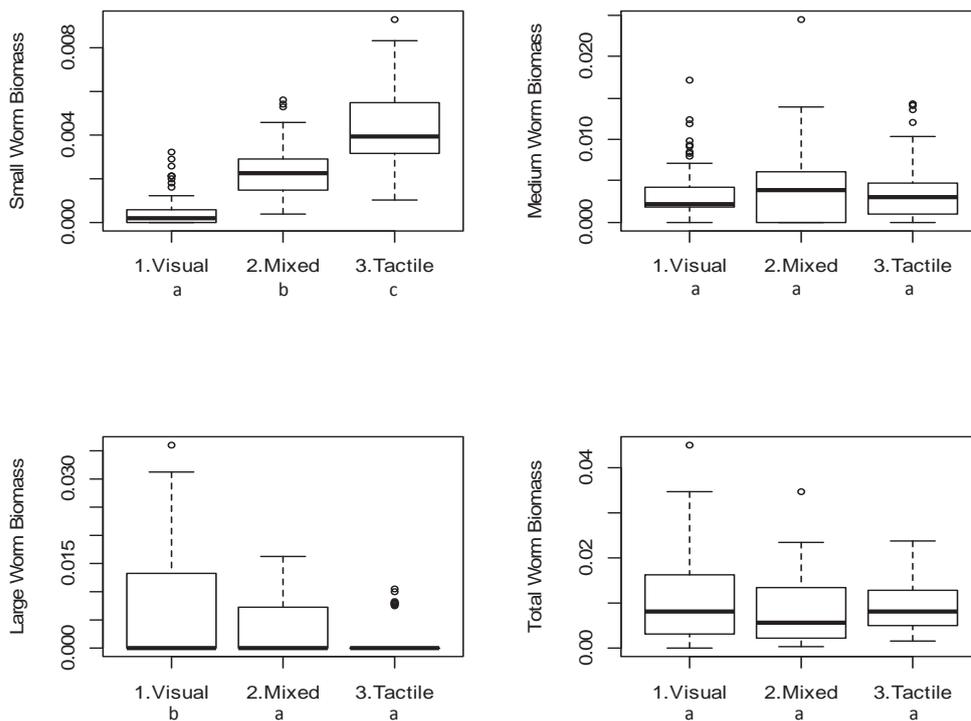


Figure 18. Biomass intake rates (g AFDM min^{-1}) of Wrybills exhibiting different foraging modes (visual, tactile and mixed) in the Firth of Thames. Small worms are estimated to be $<2 \text{ cm}$, medium $2\text{--}6 \text{ cm}$, and large $>6 \text{ cm}$. Different letters (a, b or c) represent a significant difference between characteristics. The same letter means that there was not a significant difference in that characteristic between those foraging modes.

Visual foragers showed a striking difference in pacing rate before and after a worm capture ($F_{1,176}=174$, $P<2e^{-16}$). Prior to capturing a worm, visual foragers paced at an average rate of 1.66 paces per second. After capturing a worm this increased dramatically to an average of 5.1 paces per second (Figure 19). In contrast, tactile and mixed foragers showed no difference in pace rate before (3.7 and 2.98 paces per second) and after (3.52 and 3.08 paces per second) worm capture ($F_{1,132}=1.183$, $P=0.279$ and $F_{1,114}=0.081$, $P=0.777$ respectively) (Figure 19).

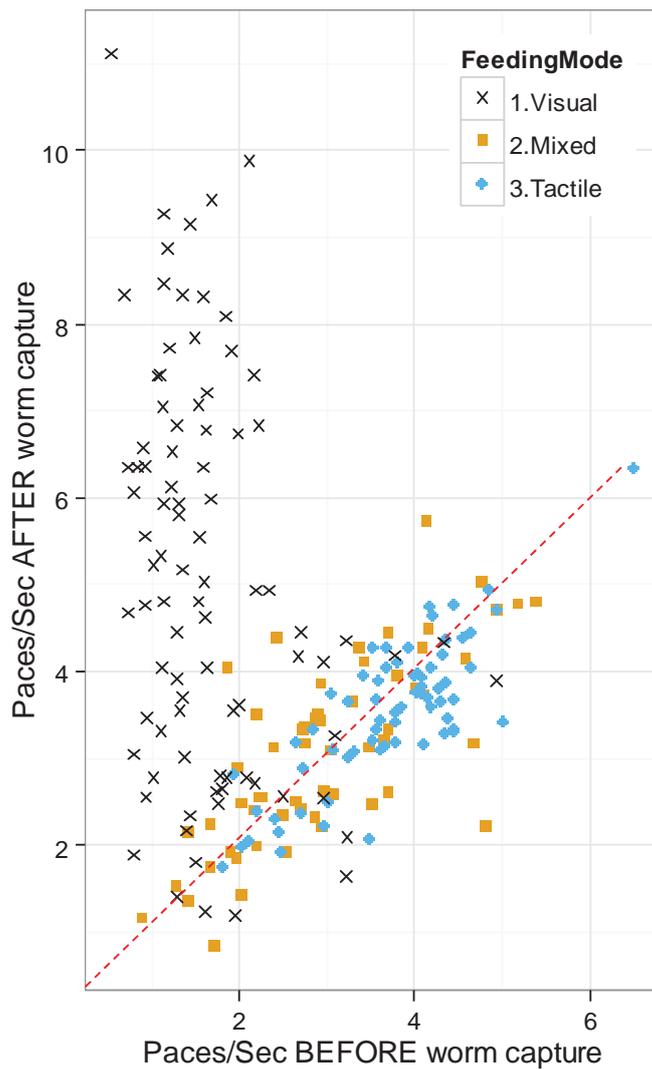


Figure 19. Pacing rates of Wrybills before and after a prey capture, by Wrybill feeding mode. Each point represents the average rate for four paces either side of a worm capture for each bird (n=214, with 2–10 captures per bird). Trend line showing the expected relationship if pacing rate was the same before and after worm capture.

Visual feeders, compared to mixed and tactile feeders, tended to feed in areas further from shore with lower water content, lower polychaete abundance, and higher sand content (therefore lower mud content) (Table 6). Additionally, tactile feeders tended to feed in areas with a lower gravel component (Table 6).

Table 6. The average environmental characteristics found in the areas frequented by visual-, mixed- and tactile-feeding Wrybills in the Firth of Thames. Different letters indicate a significant difference ($p < 0.05$). PD, penetrometer depth (cm); WC, sediment water content (%); PA, polychaete abundance ($n\ m^{-2}$); PB, polychaete biomass ($g\ AFDM\ m^{-2}$); DR, distance to roost (m); DS, distance to shore (m); Sand, sediment sand content (%), Gravel, sediment gravel content (g); Mud, sediment mud content (%). The F and P-values from ANOVA.

Feeding									
Mode	PD	WC	PA	PB	DR	DS	Sand	Gravel	Mud
Visual	4.66 (a)	0.41 (b)	715.0 (b)	1.30 (a)	2513 (ab)	470 (b)	76.3 (b)	0.30 (a)	23.7 (b)
Mixed	4.45 (a)	0.52 (a)	999.6 (a)	2.63 (b)	3124 (a)	174 (a)	55.5 (a)	0.35 (a)	44.5 (a)
Tactile	4.14 (a)	0.51 (a)	971.1 (a)	1.55 (a)	2154 (b)	153 (a)	55.7 (a)	0.07 (b)	44.3 (a)
$F_{2,210}$	1.393	11.38	5.856	9.731	6.109	38.94	14.82	4.146	14.82
P-value	0.251	$2.04e^{-5}$	0.00335	$9.08e^{-5}$	0.00264	$4.12e^{-15}$	$9.67e^{-7}$	0.0172	$9.67e^{-7}$

3.4.2 Handling Times of Polychaete Worms

The average handling times for the different sized polychaete worms were significantly different ($F_{2,393}=82.16$, $P<0.0001$). The average handling time for small worms ($\bar{x}=0.80$ sec, range 0.3–2.3 sec) was much less than that for large worms ($\bar{x}=5.43$ sec, range 1.0–38.3 sec) and medium worm handling time was intermediate ($\bar{x}=1.86$ sec, range 0.5–10.4 sec).

3.4.3 Stable Isotope Results

The signatures of Wrybill faeces ($\bar{x}=-13.8\ ‰C^{13}$, $13.4\ ‰N^{15}$) and blood ($\bar{x}=-13.6\ ‰C^{13}$, $14.7\ ‰N^{15}$) were similar to those of polychaetes in $‰C^{13}$ ($\bar{x}=-14.3\ ‰C^{13}$) but were higher in $‰N^{15}$ ($\bar{x}=15.6\ ‰N^{15}$). Signatures of faeces varied more than blood (faeces, -11.2 to $-15.5\ ‰C^{13}$ and 11.7 to $14.9\ ‰N^{15}$; blood, -13.0 to $-14.2\ ‰C^{13}$ and 13.7 to $15.2\ ‰N^{15}$) while feathers varied little and were higher on average in both Carbon and Nitrogen than polychaetes ($\bar{x}=-11.7\ ‰C^{13}$ and $16.6\ ‰N^{15}$, ranges -11.0 to $-12.2\ ‰C^{13}$ and 16.1 to $17.5\ ‰N^{15}$). The Nitrogen signatures of biofilm ($\bar{x}=10.5\ ‰N^{15}$, range

6.7 to 12.8 ‰ N^{15}) overlapped with those of faeces while the carbon signatures didn't quite overlap ($\bar{x} = -16.4$ ‰ C^{13} , range -15.9 to -17.1 ‰ C^{13}) but came close. The signatures of water and sediment had no overlap with any Wrybill tissues.

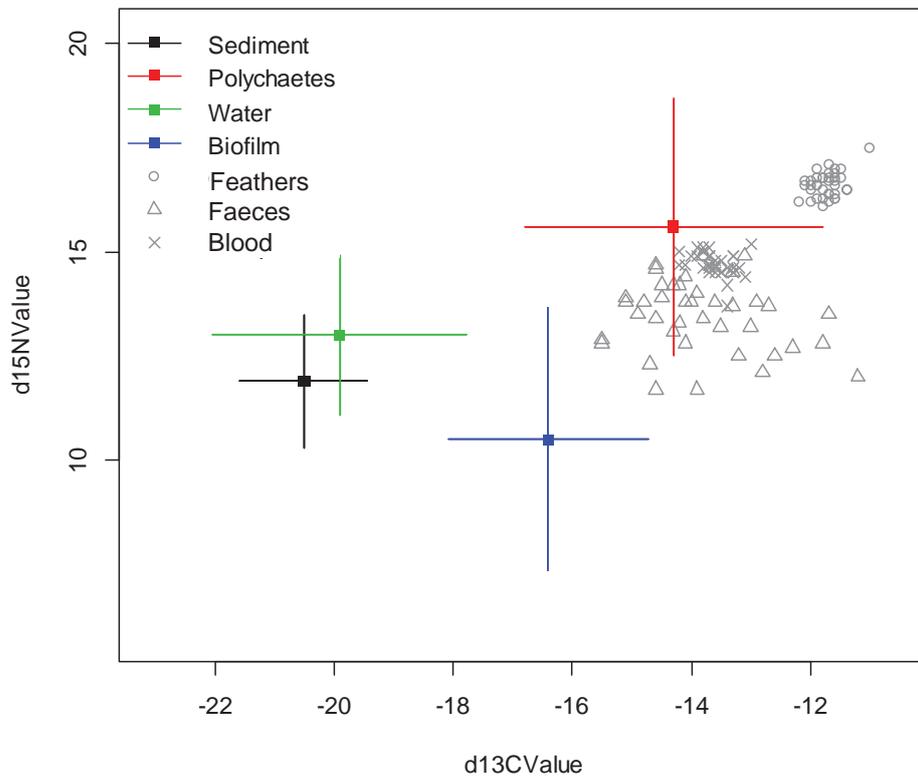


Figure 20. Stable isotope ratios of carbon and nitrogen in Wrybill feathers ($n = 38$), faeces ($n = 40$), and blood ($n = 38$) and sediment ($n = 4$), water ($n = 2$), biofilm ($n = 4$) and polychaetes ($n = 4$) in the Firth of Thames. A trophic enrichment factor of $1\text{‰} \pm 0.5$ for Carbon and $3.3\text{‰} \pm 0.5$ for Nitrogen was used.

Bayesian mixing models for faeces revealed a high dietary contribution of polychaetes of $\sim 60\%$ and a moderate dietary contribution of biofilm of $\sim 35\%$ (Figure 21 Middle). The calculated contribution of polychaete worms to blood and feathers was higher, approximately 85% and 95% respectively, with dietary biofilm contributing very little to feathers and approximately 10% to blood (Figure 21 upper and lower).

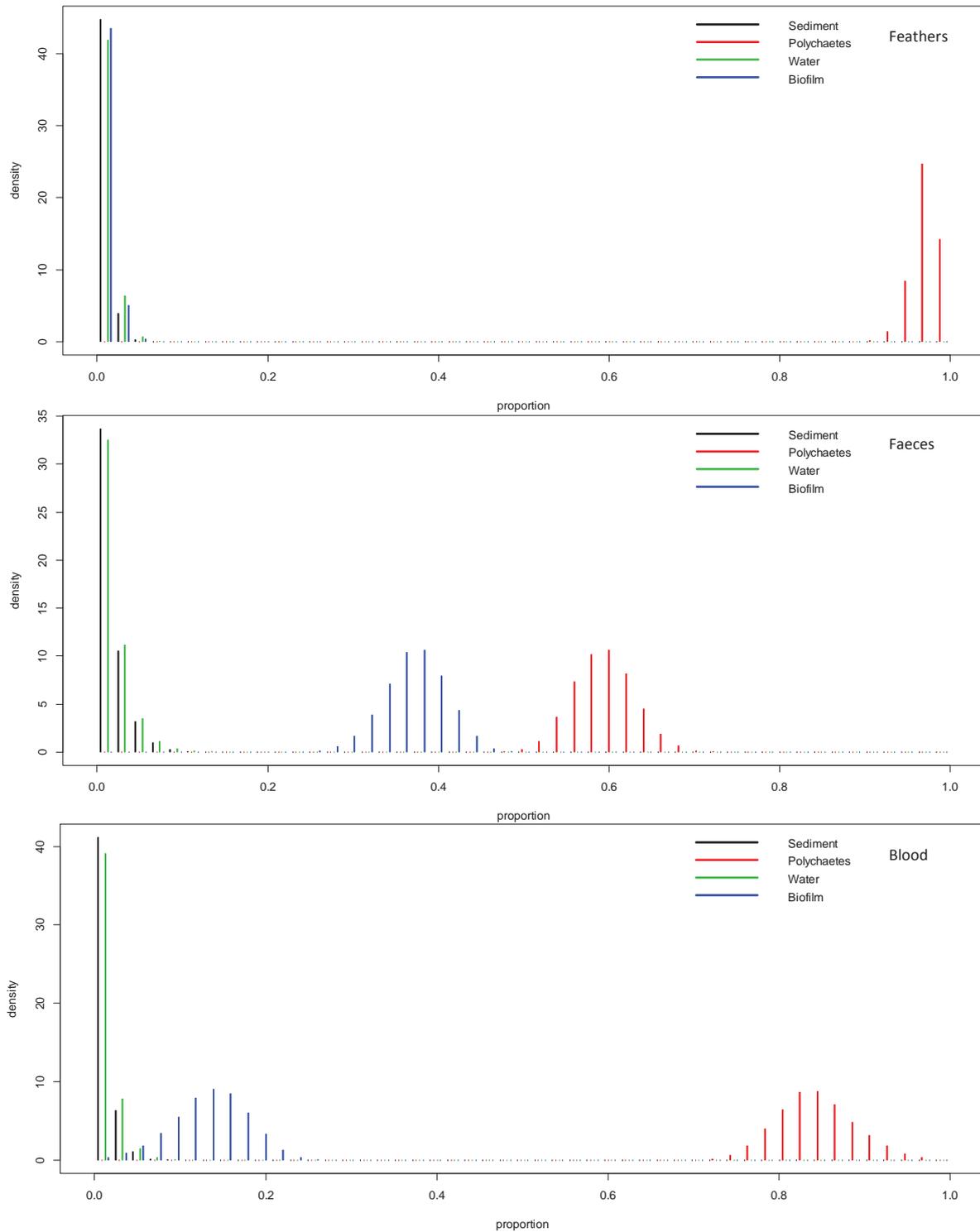


Figure 21. Bayesian stable isotope mixing model (in SIAR) of dietary contributions in Wrybill feathers, faeces and blood.

3.5 Discussion

3.5.1 Foraging Modes

Wrybills foraging on the western mudflats in the Firth of Thames exhibit different foraging modes: visual foraging, tactile foraging, and a mixture of these two (mixed foraging). While tactile and mixed foraging was seen predominantly in the mud close to shore, visual foraging tended to occur in areas further from the shore with a higher sand content (lower mud content), lower water content and lower polychaete abundance than was seen in the areas frequented by tactile and mixed foragers. Tactile foragers also tended to favour areas of the mudflat with low gravel content. This is in keeping with the notion that tactile feeding methods are considered to be better suited to fine sediments with low resistance and little coarse material. In such sediments the bird's bill is able to penetrate the sediment with ease and a low risk of bill damage (Finn et al. 2008, Kuwae et al. 2010). In addition to this, the inherently high water content of fine sediments tends to keep benthic invertebrates closer to the surface and more active keeping them easily accessible to tactile foragers (VanDusen et al. 2012). Visual foragers may be better suited to coarser sediments as found for foraging Wrybills (VanDusen et al. 2012).

The two foraging modes exhibited by Wrybills have distinct characteristics. Visually feeding Wrybills pace slowly as they search for their prey and will suddenly plunge their bill in the sediment and emerge with a captured worm; following this they quickly run away from this area and start the search again. In contrast the tactile foragers pace quickly and continuously bite or sweep their bill through the soft sediment. These differences were illustrated by summarising the actions seen in each mode. Visual foragers had a low number of paces, foraging actions, bites/sluices, worm captures, and unidentified swallows per minute, but over 50% of the intakes (swallowing actions) in a visual forager were a visible worm capture. Tactile foragers differed from visual foragers in all of these aspects; they had much higher paces, foraging actions, bites/sluices, worm captures and unidentified swallows per minute. In addition to this, less than 30% of the intakes by tactile foragers resulted in a visible worm capture. The mixed foragers demonstrated characteristics intermediate of visual and tactile foragers, which is expected by a feeding method which is combination of the two.

When searching for polychaetes visual foragers would pace slowly but once they had captured their prey their pacing rate would increase dramatically as they quickly moved from the area. Tactile and mixed foragers do not show the same characteristic; they show no difference in pacing rate before and after a worm capture. When prey has a continuous patchy distribution (as is often seen in

benthic invertebrates) the species feeding upon it tend to have an 'area restricted' searching pattern (ARS) (Dias et al. 2009, Santos et al. 2009, Weimerskirch et al. 2007). This is because there is a high probability of finding another prey in the near vicinity so by reducing searching speed and increasing turning the time spent within the same area is increased and so too is the likelihood of finding another prey item (Dias et al. 2009, Weimerskirch et al. 2007). However, this was not seen in the visual or the tactile feeding modes of Wrybills. There are two possible reasons for the striking difference in the pacing rates of visual foragers. (1) When a shorebird is feeding visually its ability to detect its prey is highly reliant on the activity of the prey (Dias et al. 2009). When a large worm is captured this takes time (as seen by the high average handling time) and it is likely that the vibrations from the capture will be detected from other worms nearby, causing them either to retreat into their burrows and out of reach or to cease their activity and become undetectable therefore a visually feeding bird will benefit from changing the search area (Dias et al. 2009). (2) Visually feeding Wrybills take predominantly large polychaete worms, however on the tidal flats large worms are uncommon compared to smaller worms. This means that the chances of a Wrybill finding another large worm in the same vicinity as the first one is lower than the chance of finding one in an unharvested patch, therefore upon capturing one large worm it may be beneficial to relocate.

Visual foragers were estimated to consume a very low biomass of small polychaete worms and a high biomass of large worms, while the opposite was true for tactile foragers; these were estimated to consume a high biomass of small polychaete worms but a low biomass of large. The biomass of medium worms consumed by the different foragers was estimated to be very similar, as too was the biomass across all worm size classes consumed by mixed foragers. Despite these different foraging strategies consuming very different sizes of polychaete worms when the total biomass consumed is estimated it is the same across the three foraging modes, suggesting that none of these strategies is better than the others in the rate of food supply.

Foraging strategies exhibited by shorebirds can vary depending on factors such as sex, age, bill morphology, food availability, individual skills, and habitat type (Kohler et al. 2009, Nebel et al. 2005). Shorebirds may exhibit flexible foraging, a generalist feeding strategy in which a bird will continuously assess and adjust its foraging mode in response to its feeding conditions, or fixed foraging, a specific foraging strategy based on individual specialisation such as bill shape or innately acquired skills (Kohler et al. 2009, Kuwae et al. 2010). Oystercatchers (*Haematopus ostralegus ostralegus*) provide a good example of a shorebird in which a foraging mode is fixed based on individual specialisation. In this case the bill shape (pointed, chiselled or blunt) of an oystercatcher

determines prey choice and prey handling. Oystercatchers with a pointed bill feed on worms by probing the sediment, those with a chisel-shaped bill tend to feed on bivalves by stabbing the gap in the shells to cut the adductor muscle, and those with a blunt bill also tend to feed on bivalves but reach the shellfish meat by hammering the shells until they break (Kohler et al. 2009, van de Pol et al. 2009). In contrast, flexible foraging modes exist in Western Sandpipers, Sanderlings (*C. alba*), and Willets (*Tringa semipalmata*) (Green et al. 2014, VanDusen et al. 2012). These species routinely switch between visual and tactile foraging modes (Green et al. 2014). These foraging mode shifts tend to be in response to prey availability and habitat conditions (Dias et al. 2009, Fernandez and Lank 2008, Kuwae et al. 2010, Nebel and Thompson 2005). Tactile foraging is more likely to occur on soft substrates while visual foraging should be more common on firmer, coarser substrates (Fernandez and Lank 2008, Finn et al. 2008). Wrybills exhibit a flexible feeding strategy on the mudflats in the Firth of Thames.

The mixed foraging mode exhibited by Wrybills indicates that they are able to switch between foraging modes, rather than a foraging mode being specific to an individual. If there are alternative feeding strategies available to an animal it is expected that they should feed using the strategy that will achieve the highest intake rate (Kuwae et al. 2010). This means that when an animal has different foraging strategies available to them their foraging strategy should change in response to changes in prey availability or environmental conditions in order to get the highest intake rate possible (Kuwae et al. 2010). Shifts like this are seen in shorebirds that shift from a visual foraging strategy during the day to a tactile one at night in response to light levels (Kuwae et al. 2010). A shift between tactile and visual foraging occurs in Wrybills foraging on the mudflats in the Firth of Thames. In soft wet sediment they employ a tactile foraging method in which they consume a high number of small polychaete worms. On harder, sandier sediments they use a visual foraging method in which they consume a high biomass of large worms. In areas with a mixture of soft mud (often occurring in runnels) and sandy sediment Wrybills employ a mixed foraging mode where they use features of both the visual and tactile modes, in this foraging mode they consume similar biomasses of small, medium and large worms.

3.5.2 Diet Composition

Stable isotope analysis confirmed that the majority of the Wrybill diet is made up of polychaete worms with substantial overlap of signatures between polychaete worms and Wrybill faeces and blood. However, there was also evidence of biofilm feeding with some signature overlap in faeces

and mixing models revealing moderate and small dietary contributions in faeces and blood respectively. Biofilm feeding has been found in a number of small shorebird species including Western Sandpipers, Dunlins and Red-necked stints all of which utilise flexible foraging modes on mudflats as well as possessing distinctive tongue spines thought to play an important role in the uptake of biofilm from the surface of the sediment (Elner et al. 2005, Kuwae et al. 2008, Kuwae et al. 2012, Mathot et al. 2010). This is the first evidence of biofilm feeding in a non-scolopacid shorebird. Tongue spines have been found in plovers with Kentish Plovers (*Charadrius alexandrinus*), Lesser Sand Plovers (*C. mongolus*), and Grey Plovers (*Pluvialis squatarola*) all found to possess them (Elner et al. 2005, Kuwae et al. 2012). However, prior to this research no studies have been carried out to investigate whether biofilm is incorporated into the diet of species within the sub-family *Charadriinae* (containing Plovers), which are generally considered to be primarily visual feeders. There are a number of advantages that biofilm feeding could provide to shorebirds: a buffer to nutritional uncertainty, a way of reducing competition (both inter and intra-specific) for food, and it also provides an abundant source of energy which is immediately consumable (Kuwae et al. 2008). Biofilm can develop richly in areas of tidal flats with high mud and water content, areas which are certainly present in the Firth of Thames (Kuwae et al. 2008).

There is a clear difference in the signatures of the Wrybill feathers in comparison to the faeces and blood. There are two possible reasons for this: (1) it could be a real difference if the diet consumed by the birds during the moulting period (time of feather growth) was different to what was being consumed during the sampling period. Wrybills typically moult between December and the beginning of May, unless they are a juvenile, they will moult while at their wintering grounds (where they arrive from late December) (Davies 1997). The sampling period for stable isotope analysis was in mid-June therefore it is not implausible that the diet shifted between the moulting and sampling period. (2) It could be an artefact of fractionation. There are often consistent differences between the stable isotope ratios of feathers and blood even when they have been synthesised over the same time period (Bond and Jones 2009, Quillfeldt et al. 2008). Feathers tend to be enriched in both ^{13}C and ^{15}N in comparison to blood, although this appears to vary between species (Bond and Jones 2009, Evans Ogden et al. 2004, Quillfeldt et al. 2008). This enrichment is exactly what was seen in the Wrybill feathers. The most likely explanation for such enrichment is that the different protein sources found in blood (several proteins) and feathers (keratin) cause it or it comes about if endogenous reserves that have been stored long term are used in the production of feathers rather than resources directly from the diet (Evans Ogden et al. 2004, Quillfeldt et al. 2008).

When Wrybills exhibit the tactile foraging method in the soft, wet mud in the Firth of Thames they can be seen catching a high number of small worms (and very few large worms) however, a large proportion of foraging actions, most of which are bites or sluices, result in no obvious worm capture, instead mouthfuls of muddy sediment appear to be swallowed. These swallows with no obvious worm capture seem likely to be biofilm consumption by Wrybills. In addition to exhibiting a foraging mode that is seemingly suited to biofilm consumption, preliminary analysis of a Wrybill tongue has revealed structures along the edges and tip of the tongue as well as a channel through the middle of the tongue that may assist in the collection of biofilm from the mud surface (Figure 22). The tongue is concave above, almost U-shaped, and edged with a row of bristles on each side. These could plausibly be used to strain a mouthful of liquid mud and direct collected matter towards the back of the mouth. The structure of the bill may also aid biofilm feeding, with the inside curve of the bill and its slight opening allowing large amounts of sediment to be collected via the sluicing motion (Figure 1 middle). The prominent rear-facing denticles on the upper mandible that are likely to help secure polychaetes could also function to hold sediment-biofilm particles in place as they are moved along the channel in the tongue and into the pharynx (Elner et al. 2005).

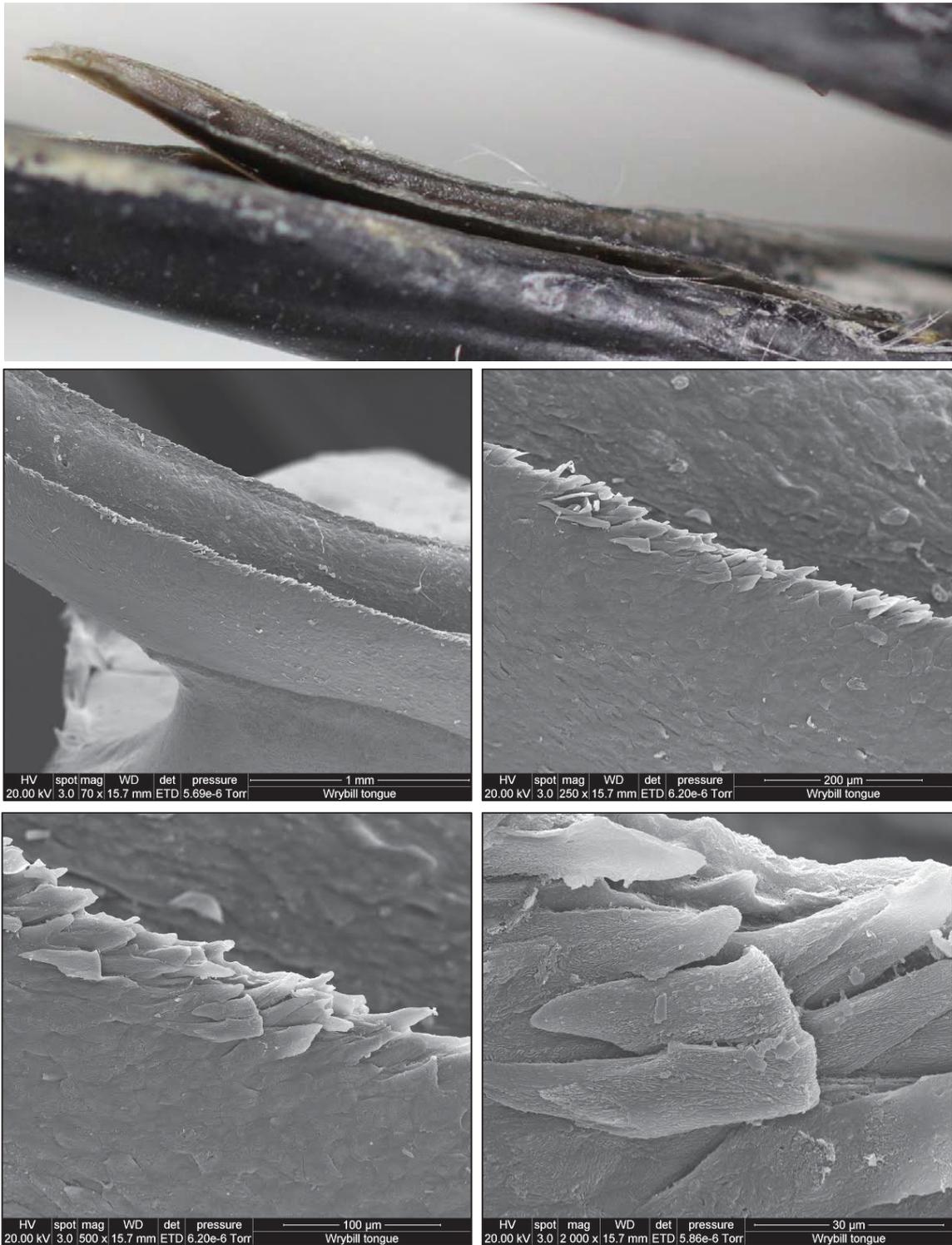


Figure 22. Close up images of a Wrybill tongue. The upper image shows the tongue *in situ*, and the row of bristles along each edge of the tongue. The lower four images are scanning electron microscope (SEM) images of the same tongue showing the bristles in more detail. Images: Upper, P. Battley; SEM, Manawatu Microscopy and imaging Centre, Massey University.

4 General Discussion

When Wrybills feed on the western tidal flats in the Firth of Thames they favour areas of the mudflat close to shore with soft mud and high polychaete biomass. Feeding Wrybills also exhibit a flexible foraging strategy, as they feed using a visual or tactile feeding mode or a mixture of the two. Wrybills are a fantastic species to study and get detailed foraging information from because they are so approachable; Wrybills can be videoed up close using just a handy-cam. Individual Wrybills appear to change foraging mode depending on sediment variables such as water content, mud, sand and gravel content, and prey availability. Tactile foraging tends to be exhibited in areas of the tidal flat close to shore with high mud and water content, low sand and gravel content and high polychaete abundance, whilst visual foraging tends to be exhibited in areas the reverse of this. Mixed foraging occurs in areas with features similar to those seen where tactile feeders are. From observations it is likely that these areas contain zones of raised sandy sediments broken up by runnels of soft muddy sediment high in water content, therefore as a Wrybill forages across such an area its feeding mode changes in relation to the changes in the sediment (and potentially the benthic invertebrates present). This sediment feature could not be conveyed through the sampling method used because it occurred in such constrained areas.

The first recorded sighting of a Wrybill was by the French Naturalists Quoy and Gaimard who were on the French exploring ship called 'Astrolab' when it visited New Zealand in 1827. They sighted Wrybills in small flocks on mudflats in the Hauraki Gulf (Oliver 1930, Sibson 1963). In 1872 when the first edition of History of the Birds of N.Z. was published by Buller there was very little known about the winter migration of Wrybills to the North Island. However, in 1888 when the second edition was published Buller was able to add that Wrybills were plentiful in the North Island during winter on the sandbanks at the mouth of the Kaipara Harbour, mudflats of Manukau Basin, in the Bay of Plenty and on beaches between Waikanae and Wanganui (Buller 1888). An idea of numbers in the Manukau Harbour, for the first time, were added in a footnote quoting a letter from Cheeseman "I have on some occasions seen as many as 200 or 300 together; but this is quite unusual, the flocks in that locality generally numbering from 10 to 20 birds" (Buller 1888). Buller published supplementary material in 1905 revealing more information about wintering Wrybills; in 1895 Captain Mair had discovered Wrybills at the Piako River mouth in the southern Firth of Thames stating that "here they are to be seen in thousands and are so tame that you may knock them over with a stick" (Sibson 1963). This reveals that back then the Firth of Thames was clearly one of the main wintering grounds

for Wrybills. At about the same time A. T. Pycroft reported that Wrybills were plentiful on the Kaipara mudflats. At the beginning of the twentieth century large numbers of wintering Wrybills had been discovered in areas that are still today their main wintering sites (Sibson 1963). Between 1956 and 1960 the numbers of Wrybills in their winter locations were estimated as follows: North of Kaipara, 100; Kaipara Harbour, 400–500; Manukau Harbour, 1500–1700; Firth of Thames, 2500–2600; and various other locations e.g. Bay of Plenty, Wellington Coast, Hawkes Bay, 50–100 (Sibson 1963). The modification of the tidal flats in the Firth of Thames during the late 1800s and early 1900s may have been the draw card for Wrybills as it created a more favourable location for wintering Wrybills compared to other locations. Sediment loads in the southern Firth of Thames increased between 1850 and 1920 following deforestation within the catchment and river-engineering work. It is estimated that 44 million m³ of mud was deposited (Swales et al. 2006). To put that into perspective, that is equivalent to approximately 300 years' worth of sediment out of the Waihou and Piako Rivers today (Swales et al. 2006). Sediment cores demonstrate the transition that occurred in the Firth of Thames as a result of this; the intertidal flats shifted from being made up of a mixture of silts and sands to being covered in a thick layer of homogenous mud (Swales et al. 2006). Given the preference of Wrybills for soft, muddy sediments (Chapter 2), this sedimentation could have enhanced the suitability of the Firth of Thames for Wrybills.

In recent years there appears to have been a shift in numbers between the two main wintering sites, the Firth of Thames and Manukau Harbour. The number of Wrybills spending winter in the Firth of Thames has never exceeded 4007 birds (in 1973) and since the 1970s the number of wintering Wrybills in the Firth of Thames has been gradually declining. At the same time as this decline in the Firth of Thames the number of Wrybills wintering in Manukau Harbour has been increasing, especially since the year 2000. This has resulted in Manukau Harbour becoming the most important wintering site for Wrybills in recent years. This shift could potentially relate to the decommissioning of the Mangere Sewage Ponds in 2002, that area is now soft tidal flats that may be providing improved feeding opportunities for Wrybills (Figure 23). The number of Wrybills in this area has increased from an average of 537 (maximum 900) in 1985–1995 to an average of 957 (maximum 1750) from 2000–2005.

Over the winter period an estimated 2000 Wrybills take up residence in the Firth of Thames (Auckland Regional Council 2007). In the area of western tidal flat sampled the maximum number of Wrybills seen in one area was 360 individuals, a small proportion of the Wrybills present in the Firth of Thames as a whole. The reason for the lower numbers on the western tidal flats is that a vast number of foraging Wrybills instead head to the southern mudflats as the tide recedes. These

southern tidal flats are composed of very thick mud and not easily accessible, therefore they were unsafe to walk on and sample. Given the large number of Wrybills that feed in this area it would be interesting to sample the benthic invertebrates, sediment types present in the area as well as the feeding modes exhibited by the Wrybills but this was not feasible during this study. However, the Wrybills counted on the western tidal flat were still about 20% of the Wrybills in the Firth of Thames and about 10% of the entire Wrybill population.



Figure 23. The Mangere Wastewater Treatment Plant oxidation ponds in the 1960s covering 600 hectares (left). The estuary following the decommissioning of the oxidation ponds in 2002 (right) (Dann 2013).

Further stable isotope refinement could provide a more definitive answer to the question of whether Wrybills are consuming biofilm. Although the stable isotope analysis revealed some overlap between biofilm and Wrybill faeces, the blood and feathers of the Wrybills were heavy in C^{13} which remained unexplained by the dietary samples collected. Further investigation should include microphytobenthos as a food source in the stable isotope analysis which could be a candidate of such heavy C^{13} (Tomohiro Kuwae, personal communication, May 22, 2015). Microphytobenthos is the assemblage of microorganisms (algae and photosynthetic bacteria typically diatoms and cyanobacteria respectively) on the sediment surface; when these algae and bacteria are associated with the sediment surface it is referred to as biofilm. Microphytobenthos can be extracted from the surface sediment (biofilm) by spreading the surface sediment samples on a tray in a layer approximately 5 mm deep, laying a nylon screen (65 μm mesh), placing pre-combusted glass wool on top of this and keeping the tray moist by spraying with filtered seawater and leaving in the dark at an ambient temperature overnight. This process causes the microphytobenthos to migrate into the

glass wool which should then be removed and kept dry until stable isotope analysis (Kuwae et al. 2008, Kuwae et al. 2012).

Future investigation should also involve the collection of more potential prey items to cover any food sources that are missing in this study particularly any that have high N^{15} values and C^{13} values (Tomohiro Kuwae, personal communication, May 22, 2015). One potential prey item that was not sampled here was small crustaceans however, the signatures of small amphipods and shrimp collected from Kakamatua Stream an estuarine stream in the Auckland region ($\delta^{13}C$ -23.65 to -21.9, $\delta^{15}N$ 9.36 to 11.53 and $\delta^{13}C$ -24.22 to -23.55 and $\delta^{15}N$ 9.07 to 9.91 respectively) do not match the signatures of Wrybill tissues but sampling in the Firth of Thames would still be worthwhile (Punchihewa and Krishnarajah 2013). Additionally, it would be beneficial to collect larger sample sizes of biofilm and polychaete worms. There can be a lot of variation in sources even if they are collected from the same area at the same time, therefore, the greater the sample size the better; sample sizes greater than 10 would be preferable (Phillips et al. 2014, Ward 2012).

The trophic enrichment factors used in this study were estimated based on those used in the literature. In order to be able to accurately quantify the trophic enrichment factor Wrybills would need to be placed on a controlled and isotopically constant diet for as long as it took the tissue of interest to turnover. For blood this is a matter of weeks (typically 12–15 days) however feathers reflect the isotopic ratios of the diet at the time they are grown (Bond and Jones 2009). To the best of our knowledge there are no captive Wrybills in New Zealand.

Investigation into the use of the area of decommissioned oxidation ponds by feeding Wrybills would provide better insight into use of wintering sites by Wrybills and into whether the shift in Wrybill numbers may be a result of this decommissioning. When the oxidation ponds were removed about 13 kilometres white-shell beaches were constructed and bird roosts (artificial shell islands) for the shorebirds were built (Loren 2013, Watercare 2010). These features provide favourable conditions for the shorebirds feeding here. Core sampling was undertaken in Manukau Harbour between 1995 and 2000 to monitor the effects of Mangere Wastewater Treatment Plant. Additional sampling was carried out in 2002, 2003 and 2007 following the removal of the sewage treatment ponds (Figure 23). This sampling revealed that after the removal of the oxidation ponds there was rapid re-colonisation by marine species and the number of species present increased between 2003 and 2007. The benthic community in the old oxidation pond area remain dominated numerically by pollution tolerant species but more sensitive species have started to colonise the area and are occurring in relatively high abundance (Kelly 2008). Improved roosting sites, shelter and changes in

the benthic invertebrate community may have led to this site in the Manukau Harbour being increasingly favoured by wintering Wrybills.

Only the daytime foraging activity of Wrybills was looked at in this study, therefore the foraging activity by Wrybills at night would be a good extension of this study. Night-time foraging activity is common and widespread amongst shorebirds and there are two hypotheses as to why it occurs: one is that it is required so that shorebirds can meet their daily energy requirements and the second is that shorebirds prefer to feed at night because it is safer or more profitable for them to do so; there has not been a shorebird found that forages only during the day. Some shorebirds switch from visual foraging during the day to tactile feeding at night while others retain visual foraging during the night due to superior nocturnal vision (McNeil et al. 1992, Rojas et al. 1999). Benthic invertebrates tend to have higher surface activity during the night therefore when shorebirds forage at night they can achieve a higher food intake (Esser et al. 2008, McNeil et al. 1992). Wrybills clearly adjust their foraging strategy in relation to environmental variables during the day so it would be expected that they also adjust it for foraging during the night. However, plovers usually retain visual foraging at night due to their large eyes and good eyesight. Therefore if Wrybills, like other plovers, retain excellent vision at night and the surface activity of benthic invertebrates is higher during the night in the Firth of Thames perhaps utilisation of the tactile foraging mode would not increase as expected, instead use of the visual foraging mode may increase (Esser et al. 2008, McNeil et al. 1992).

In future studies it would be worth investigating the presence of biofilm in Manukau Harbour and the biofilm seasonality in both the Firth of Thames and Manukau Harbour. Biofilm can be a predictable resource on estuarine tidal flats however, like any other living community, it will show natural variability. The biomass of microphytobenthos has been shown to vary over both temporal and spatial scales (short and long term) in relation to various environmental factors including: light, sediment, temperature, salinity, tides and exposure times, rain, nutrient availability and grazing intensity (Aberle-Malzahn 2004, Reyes 2013). In temperate regions the biomass, primary production and chlorophyll content of microphytobenthos generally shows spring or summer maximums (Aberle-Malzahn 2004). Variation is seen not only in the biomass but also at a taxonomic level within the microphytobenthos as well; particular algal groups have been shown to be dominant at different times of the year. Microphytobenthos is typically dominated by diatoms but during summer months the abundance of green algae and cyanobacteria can get particularly high (Aberle-Malzahn 2004). These studies have been carried out in temperate regions of the northern hemisphere and while patterns are likely to be the same in New Zealand that cannot be known for sure until detailed work is done. The presence, biomass, and composition of biofilm in the Firth of

Thames and Manukau Harbour is of greatest interest in terms of Wrybills from late summer through until late winter when Wrybills are present on their wintering grounds. It would be interesting to see whether the prevalence of the tactile foraging mode associated with biofilm feeding in Wrybills changes in relation to variability in the biomass or composition of the biofilm community.

Polychaete worm samples were collected using a standard core sampling technique; this was the best technique available to use at the time and it provided a quantitative measurement of polychaete abundance, revealing patterns across the tidal flat. However, core sampling does come with some disadvantages: benthic invertebrates that are capable of moving rapidly may be able to avoid the core sampler, the instantaneous sampling that is done using a core sampler does not account for the daily vertical and horizontal movement of benthic invertebrates within the sediment, and measuring prey availability for shorebirds with short bills that feed on polychaetes can be particularly difficult. Core sampling tends to provide data on the availability of benthic invertebrates for long-billed species such as Eurasian Oystercatchers (*Haematopus ostralegus*) and Eurasian Curlews (*Numenius arquata*) or shorebird species that feed mainly on molluscs such as Red Knots (*Calidris canutus*) however this type of sampling isn't as good for short-billed species that feed primarily on polychaetes in the top sediment layer because the polychaetes tend to escape into deeper layers when they are disturbed and they prey density value obtained from a 20 cm long core sample may not reflect what is actually accessible to shorter-billed species (Desholm et al. 1998, Esser et al. 2008). This problem can be overcome by sampling sediment very quickly (giving the invertebrates very little time to respond to the disturbance) at a depth corresponding to the bill length of the species of interest using a device called a sediment-plane (Desholm et al. 1998). A sediment plane consists of a metal plate with a handle on top and sampling box beneath it which is open at both ends. The box is pushed quickly through the sediment sampling to a depth i.e. 3 cm approximate to the depth to which small shorebirds feed (Desholm et al. 1998, Esser et al. 2008). This method is not only faster than core sampling but should also prevent the downwards movement of polychaetes and sample only what is available to the shorebird of interest. In comparison to core samples sediment plane samples had higher total abundance and biomass of benthic invertebrates in the upper layer (Desholm et al. 1998, Esser et al. 2008). Therefore, use of a sediment-plane device for sampling in the Firth of Thames could provide a better idea of the benthic invertebrates available to Wrybills, a short-billed shorebird. Additionally further understanding of how benthic invertebrates (in particular polychaete worms) respond to vibrations on the surface of the sediment would be useful in the long term; not only to understand sampling issues but also have a greater understanding of how the polychaete response may impact the movement of Wrybills following a worm capture.

Preliminary analysis of a Wrybill tongue revealed the presence of spines along the edges of the tongue as well as a channel down the middle of the tongue (Figure 22). The Wrybill tongue used for this analysis was that of a Wrybill found dead and subsequently frozen. This tongue was not in the best shape possibly due to degradation after death (tissue lysis of tongues can be extremely rapid) or damage during processing (especially the tip) (Elner et al. 2005). The basic structure of the Wrybill tongue appears similar to that of another plover, the Lesser Sand Plover (*Charadrius mongolus*), for which a photograph of the tongue tip in Kuwae et al. (2012) suggests the presence of spines along the edges of the tongue. All three plover species that had their tongues photographed (Lesser Sand Plover, Kentish Plover *Ch. alexandrinus* and Grey Plover *Pluvialis squatarola*) were categorised by Kuwae et al. as possessing tongue spines. The presence of spines in itself may therefore not necessarily be evidence of a morphological adaptation for biofilm feeding. Further detailed work of the structure of shorebird tongues (including the plovers and the Wrybill) would aid interpretation of the possible function of tongue spines across this group. Additionally close, slow motion footage of Wrybills feeding using the tactile feeding method (in which biofilm feeding is likely) would enhance the understanding of the technique that may be used to ingest biofilm and potentially provide detailed information about the bill and tongue actions used to collect it.

5 References

- Aberle-Malzahn, N. 2004. *The microphytobenthos and its role in aquatic food webs*, Kiel, Christian-Albrechts-Universität zu Kiel. PhD.
- Alves, J.A., W.J. Sutherland and J.A. Gill. 2011. Will improving wastewater treatment impact shorebirds? Effects of sewage discharges on estuarine invertebrates and birds. *Animal Conservation* **15**: 44-52.
- Anderson, M.G. 2003. *Investigations into shorebird community ecology: interrelations between morphology, behaviour, habitat and abiotic factors*, New Zealand, The University of Auckland. MSc.
- Auckland Regional Council. 2007. Population Biology and Foraging Ecology of Waders in the Firth of Thames - Update 2007. Auckland Regional Council Technical Publication 347.
- Battley, P., F., M. Poot, P. Wiersma, C. Gordon, Y. Ntiamoa-Baidu and T. Piersma. 2003. Social foraging by waterbirds in shallow coastal lagoons in Ghana. *Waterbirds* **26**: 26-34.
- BirdLife International. 2012. *Anarhynchus frontalis*. BirdLife International. Retrieved from <http://www.iucnredlist.org/details/22693928/0>.
- Blott, S.J. and K. Pye. 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms* **26**: 1237-1248.
- Bocher, P., F. Robin, J. Kojadinovic, P. Delaporte, R. P., C. Dupuy and P. Bustamante. 2014. Trophic resource partitioning within a shorebird community feeding on intertidal mudflat habitats. *Journal of Sea Research* **92**: 115-124.
- Bolduc, F. and A.D. Afton. 2004. Relationships between wintering waterbirds and invertebrates, sediments and hydrology of coastal marsh ponds. *Waterbirds* **27**: 333-341.
- Bond, A.L. and I.L. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. *Marine Ornithology* **37**: 183-188.
- Brownell, B. 2004. Muddy feet: Firth of Thames Ramsar Site. EcoQuest Education Foundation.
- Buller, W.L. 1873. *A History of the Birds of New Zealand*, London, UK, John Van Voorst, 1 Paternoster Row.
- Buller, W.L. 1888. *A History of the Birds of New Zealand*, London, England, The Author for the subscribers.
- Burton, P.J.K. 1972. Some anatomical notes on the Wrybill. *Notornis* **19**: 26-32.
- Chang, W. 2013. *R Graphics Cookbook*, California, USA., O'Reilly Media Inc.

- Colwell, M.A. 2010. *Shorebird Ecology, Conservation and Management*, Berkeley, University of California Press.
- Colwell, M.A. and S.L. Landrum. 1993. Nonrandom shorebird distribution and fine scale variation in prey abundance. *The Condor* **95**: 94-103.
- Cromarty, P. and D.A. Scott. 1995. A directory of wetlands in New Zealand- Waikato Conservancy. New Zealand Department of Conservation.
- Dann, C. 2013. Sewage, water and waste - Water pollution. Te Ara - the Encyclopedia of New Zealand. Retrieved from <http://www.TeAra.govt.nz/en/photograph/24465/waste-water-treatment-at-mangere>.
- Davies, S. 1997. Population structure, morphometrics, moult, migration, and wintering of the Wrybill (*Anarhynchus frontalis*). *Notornis* **44**.
- Desholm, M., A.M. Harder and K.N. Mouritsen. 1998. The sediment-plane: an alternative tool for estimating prey accessibility to tactilely feeding waders. *Wader Study Group Bulletin* **85**: 73-75.
- Dias, M.P., J.P. Granadeiro and J.M. Palmeirim. 2009. Searching behaviour of foraging waders: does feeding success influence their walking? *Animal Behaviour* **77**: 1203-1209.
- Dowding, J.E. 2013. Wrybill. In Miskelly, C.M. (ed.) New Zealand Birds Online. Retrieved from <http://nzbirdsonline.org.nz/species/wrybill>.
- Dowding, J.E. and S.J. Moore. 2006. Habitat networks of indigenous shorebirds in New Zealand. *Science for Conservation* **261**.
- Elnor, R.W., P.G. Beninger, D.L. Jackson and T.M. Potter. 2005. Evidence of a new feeding mode in western sandpiper (*Calidris mauri*) and dunlin (*Calidris alpina*) based on bill and tongue morphology and ultrastructure. *Marine Biology* **146**: 1223-1234.
- Esser, W., S. Vöge and K. Exo. 2008. Day-night activity of intertidal invertebrates and methods to estimate prey accessibility for shorebirds. *Senckenbergiana maritima* **38**: 115-122.
- Evans Ogden, L.J., K.A. Hobson and D.B. Lank. 2004. Blood isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) turnover and diet-tissue fractionation factors in captive Dunlin (*Calidris alpina pacifica*). *The Auk* **121**: 170-177.
- Fernandez, G. and D.B. Lank. 2008. Foraging behaviour of non-breeding Western Sandpipers *Calidris mauri* as a function of sex, habitat and flocking. *Ibis* **150**: 518-526.
- Finn, P.G., C.P. Catterall and P.V. Driscoll. 2007. Determinants of preferred intertidal feeding habitat for Eastern Curlew: A study at two spatial scales. *Austral Ecology* **32**: 131-144.
- Finn, P.G., C.P. Catterall and P.V. Driscoll. 2008. Prey versus substrate as determinants of habitat choice in a feeding shorebird. *Estuarine, Coastal and Shelf Science* **80**: 381-390.

- Fry, B. 2008. *Stable Isotope Ecology*, New York, USA, Springer Science + Business Media.
- Goss-Custard, J.D., D.G. Kay and R.M. Blindell. 1977. The density of migratory and overwintering Redshank, *Tringa totanus* (L.) and Curlew, *Numenius arquata* (L.) in relation to the density of their prey in south-east England. *Estuarine and Coastal Marine Science* **5**: 497-510.
- Goss-Custard, J.D. and M.G. Yates. 1992. Towards predicting the effect of saltmarsh reclamation feeding bird numbers. *Journal of Applied Ecology* **29**: 330-340.
- Granadeiro, J.P., C.D. Santos, M.P. Dias and J.M. Palmeirim. 2007. Environmental factors drive habitat partitioning in birds feeding in intertidal flats: implications for conservation. *Hydrobiologia* **587**: 291-302.
- Gratto-Trevor, C.L. 2000. *Marbled Godwit (Limosa fedoa)*. *The Birds of North America*, Philadelphia, Pennsylvania, The Birds of North America, Inc.
- Green, L., D.T. Blumstein and P. Fong. 2014. Macroalgal mats in a eutrophic estuary obscure visual foraging cues and increase variability in prey availability for some shorebirds. *Estuaries and Coasts* **38**: 917-926.
- Gurau, A. 2014. *The diet of the New Zealand long-tailed bat, Chalinolobus tuberculatus*, Palmerston North, Massey University. MSc.
- Hartman, R. 2013. Model Selection and Multi-Model Inference. Retrieved from <http://www.noamross.net/blog/2013/2/20/model-selection-drug.html>.
- Hay, J., R. 1984. *The behavioural ecology of the Wrybill plover, Anarhynchus frontalis*, Auckland, University of Auckland.
- Hobson, K.A. and R.G. Clark. 1992. Assessing avian diets using stable isotopes II: Factors influencing diet-tissue fractionation. *The Condor* **94**: 189-197.
- Hutton, F. 1873. Notes by Captain Hutton on Dr. Buller's "Birds of New Zealand," with the Author's Replies thereto. *Transactions- Zoology* **6**.
- Inger, R. and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. *Ibis* **150**: 447-461.
- Inger, R., A. Jackson, A. Parnell and S. Bearhop. 2010. Stable isotope analysis in R: *An ecologists guide*.
- Kelly, S. 2008. Environmental condition and values of Manukau Harbour. Prepared by Coast and Catchment Ltd. for Auckland Regional Council. Auckland Regional Council Technical Report 2009/112.
- Kohler, S., B. Bonnevie, C. McQuaid and S. Jaquemet. 2009. Foraging ecology of an endemic shorebird, the African Black Oystercatcher (*Haematopus moquini*) on the south-east coast of South Africa. *Estuarine, Coastal and Shelf Science* **84**: 361-366.

- Kuwaie, T., P.G. Beninger, P. Decottignies, K.J. Mathot, D.R. Lund and R.W. Elnor. 2008. Biofilm grazing in a higher vertebrate: The Western Sandpiper, *Calidris mauri*. *Ecology* **89**: 599-606.
- Kuwaie, T., E. Miyoshi, S. Hosokawa, K. Ichimi, J. Hosoya, T. Amano, T. Moriya, M. Kondoh, R.C. Ydenberg and R.W. Elnor. 2012. Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. *Ecology Letters*.
- Kuwaie, T., E. Miyoshi, S. Sassa and Y. Watabe. 2010. Foraging mode shift in varying environmental conditions by Dunlin *Calidris alpina*. *Marine Ecology Progress Series* **406**: 281-289.
- Lenhard, W. and A. Lenhard. 2015. Calculation of Effect Sizes. Retrieved from http://www.psychometrica.de/effect_size.html.
- Loren, A. 2013. Auckland's Secret Bird Sanctuary: Eighty species make coastline home. Retrieved from <http://www.stuff.co.nz/auckland/local-news/8163894/Aucklands-secret-bird-sanctuary>.
- Lunardi, V.O., R.H. Macedo, J.P. Granadeiro and J.M. Palmeirim. 2012. Migratory flows and foraging habitat selection by shorebirds along the northeastern coast of Brazil: The case of Baía de Todos os Santos. *Estuarine, Coastal and Shelf Science* **96**: 179-187.
- Mathot, K.J., D.R. Lund and R.W. Elnor. 2010. Sediment in stomach contents of Western Sandpipers and Dunlin provide evidence of biofilm feeding. *Waterbirds* **33**: 300-306.
- McNeil, R., P. Drapeau and J.D. Goss-Custard. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biological Reviews of the Cambridge Philosophical Society* **67**: 381-419.
- Nebel, S., D.L. Jackson and R.W. Elnor. 2005. Functional association of bill morphology and foraging behaviour in calidrid sandpipers. *Animal Biology* **55**: 235-243.
- Nebel, S. and G.J. Thompson. 2005. Foraging behaviour of western sandpipers changes with sediment temperature: implications for their hemispheric distribution. *Ecological Research* **20**: 503-507.
- Oliver, W.R.B. 1930. *New Zealand Birds*, Wellington, NZ, Fine Arts (N.Z) Ltd.
- Phillips, D.L., R. Inger, S. Bearhop, A.L. Jackson, J.W. Moore, A.C. Parnell, B.X. Semmens and E.J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology* **92**: 823-835.
- Pierce, R.J. 1979. Foods and feeding of the Wrybill (*Anarhynchus frontalis*) on its riverbed breeding grounds. *Notornis* **26**: 1-21.
- Pierce, R.J. 1985. Feeding methods of stilts (*Himantopus* spp.). *New Zealand Journal of Zoology* **12**: 467-472.

- Posey, M., C. Powell, L. Cahoon and D. Lindquist. 1995. Top down vs. bottom up control of benthic community composition on an intertidal tideflat. *Experimental Marine Biology and Ecology* **185**: 19-31.
- Potts, T.H. 1870. On the Birds of New Zealand. *Transactions and Proceedings of the New Zealand Institute* **2**: 40-78.
- Pukorokoro Miranda Shorebird Centre. 2015. Shorebirds at Miranda. Retrieved from <http://www.miranda-shorebird.org.nz/shorebirds-at-miranda>.
- Punchihewa, N.N. and S.R. Krishnarajah. 2013. Trophic Position of Two Mysid Species (Crustacea: Mysidacea) in an Estuarine Ecosystem in Auckland, New Zealand, Using Stable Isotopic Analysis. *American Journal of Marine Science* **1**: 22-27.
- Quillfeldt, P., L. Bugoni, R.A.R. McGill, J.F. Masello and R.W. Furness. 2008. Differences in stable isotopes in blood and feathers of seabirds are consistent across species, age and latitude: implications for food web studies. *Marine Biology* **155**: 593-598.
- Quinn, J.T. and D.J. Hamilton. 2012. Variation in diet of Semipalmated Sandpipers (*Calidris pusilla*) during stopover in the upper Bay of Fundy, Canada. *Canadian Journal of Zoology* **90**: 1181-1190.
- Reyes, A.J. 2013. *The "Secret Garden": Microphytobenthic biofilms and the foraging ecology of Calidridine Sandpipers*, Canada, Simon Fraser University. PhD.
- Riegen, A.C. and J.E. Dowding. 2003. The Wrybill *Anarhynchus frontalis*: a brief review of status, threats and work in progress. *Wader Study Group Bulletin* **100**: 20-24.
- Robertson, H.A., J.E. Dowding, G.P. Elliott, R.A. Hitchmough, C.M. Miskelly, C.F.J. O'Donnell, R.G. Powlesland, P.M. Sagar, R.P. Scofield and G.A. Taylor. 2013. Conservation Status of New Zealand Birds, 2012. New Zealand Department of Conservation.
- Robin, F., T. Piersma, F. Meunier and P. Bocher. 2013. Expansion into an Herbivorous Niche by a Customary Carnivore. *The Condor* **115**: 340-347.
- Rojas, L.M., R. McNeil, T. Cabana and P. Lachapelle. 1999. Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. *Brain, Behavior and Evolution* **53**: 29-43.
- Rose, M. and E. Nol. 2010. Foraging Behavior of Non-Breeding Semipalmated Plovers. *Waterbirds* **33**: 59-69.
- Santos, C.D., S. Saraiva, J.M. Palmeirim and J.P. Granadeiro. 2009. How do waders perceive buried prey with patchy distributions? The role of prey density and size of patch. *Journal of Experimental Marine Biology and Ecology* **372**: 43-48.
- Si, X., S.L. Pimm, G.J. Russell and P. Ding. 2014. Turnover of breeding bird communities on islands in an inundated lake. *Journal of Biogeography* **41**: 2283-2292.

- Sibson, R.B. 1963. A population study of the Wry-billed plover (*Anarhynchus frontalis*). *Notornis* **10**: 146-153.
- Spruzen, F.L., A.M.M. Richardson and E.J. Woehler. 2008. Influence of environmental and prey variables on low tide shorebird habitat use within the Robbins Passage wetlands, Northwest Tasmania. *Estuarine, Coastal and Shelf Science* **78**: 122-134.
- Stead, E.F. 1932. *The Life Histories of New Zealand Birds*, London, Search Publishing Company.
- Swales, A., R.G. Bell, R. Ovenden, C. Hart, M. Horrocks, N. Hermanspahn and R.K. Smith. 2006. Mangrove-Habitat Expansion in the Southern Firth of Thames: Sedimentation Processes and Coastal-Hazards Mitigation. National Institute of Water & Atmospheric Research Ltd. Environment Waikato Technical Report 2008/13.
- Tavares, P.C., R. McGill, J. Newton, E. Pereira, A. Duarte and R.W. Furness. 2009. Relationships between carbon sources, trophic level and mercury exposure in generalist shorebirds revealed by stable isotope ratios in chicks. *Waterbirds* **32**: 311-321.
- Turbott, E.G. 1970. The Wrybill: A feeding adaptation. *Notornis* **17**: 25-27.
- van de Pol, M., B.J. Ens, K. Oosterbeek, L. Brouwer, S. Verhulst, J.M. Tinbergen, A.L. Rutten and M. de Jong. 2009. Oystercatchers' bill shapes as a proxy for diet specialization: more differentiation than meets the eye. *Ardea* **97**: 335-347.
- VanDusen, B.M., S.R. Fegley and C.H. Peterson. 2012. Prey distribution, physical habitat features, and guild traits interact to produce contrasting shorebird assemblages among foraging patches. *PLoS One* **7**: e52694.
- Ward, E. 2012. Introduction to (Bayesian) Isotope Mixing Models. Northwest Fisheries Science Center. Retrieved from <https://afsuw.files.wordpress.com/2012/05/intro-to-mixing-models.pdf>.
- Watercare. AUCKLAND CITY COUNCIL. 2010. Watercare Coastal Walkway, Auckland, NZ. Watercare.
- Weimerskirch, H., D. Pinaud, F. Pawlowski and C.A. Bost. 2007. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *American Naturalist* **170**: 734-43.
- Woodley, K. 2012. *Shorebirds of New Zealand- Sharing the Margins*, Auckland, New Zealand, Penguin Books.
- Yates, M.G., J.D. Goss-Custard, S. McGrorty, K.H. Lakhani, S.E.A. Le, V.D. Durell, R.T. Clarke, W.E. Rispin, I. Moy, T. Yates, R.A. Plant and A.J. Frost. 1993. Sediment characteristics, invertebrate densities, and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology* **30**: 599-614.