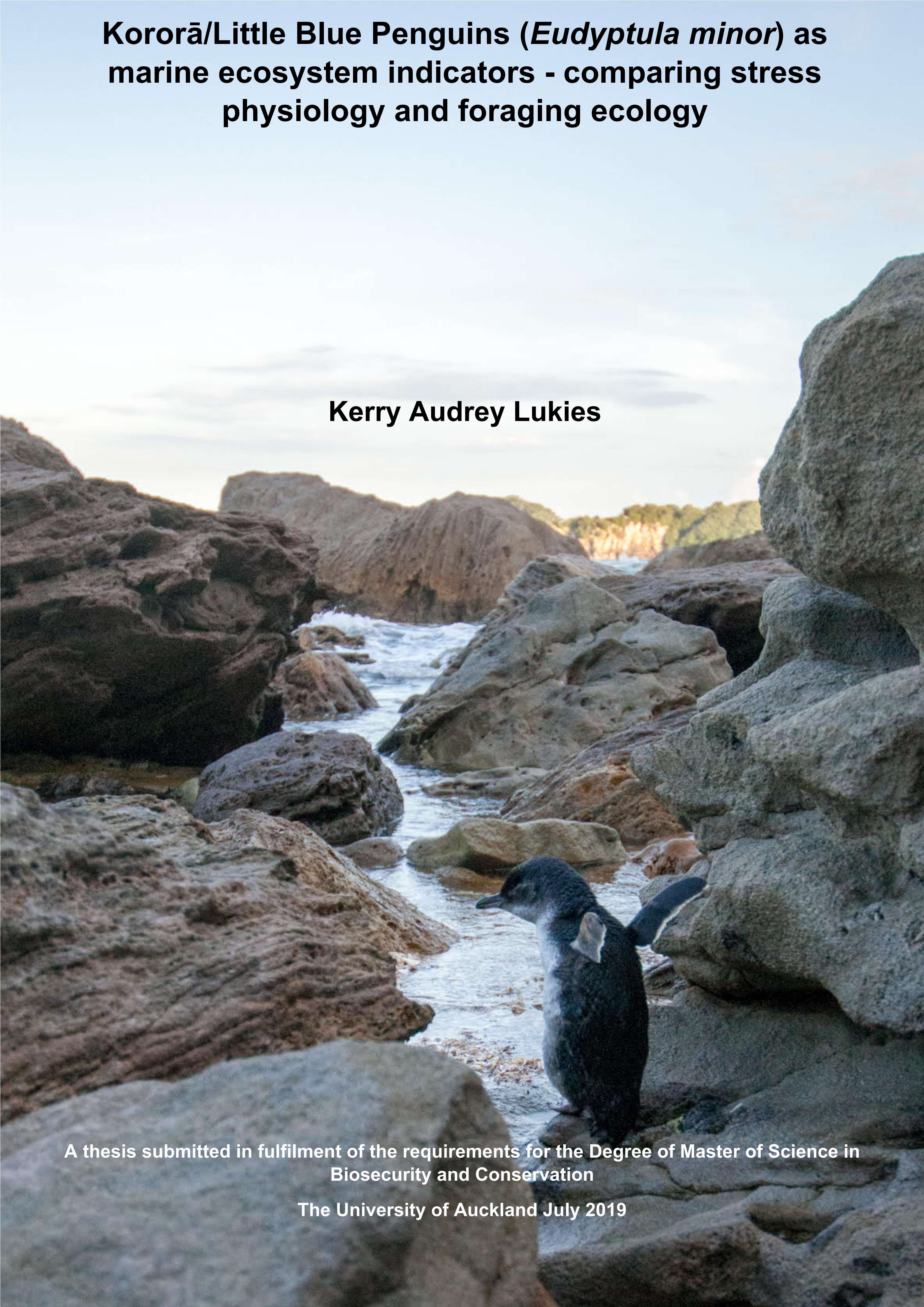
Kororā/Little Blue Penguins (*Eudyptula minor*) as marine ecosystem indicators - comparing stress physiology and foraging ecology



Kerry Audrey Lukies

A thesis submitted in fulfilment of the requirements for the Degree of Master of Science in Biosecurity and Conservation

The University of Auckland July 2019

Abstract

Using three study sites in the Hauraki Gulf, this study aimed to determine whether changes in foraging ecology and stress physiology were observed in kororā populations over time and space and whether these measurements could be used as indicators of marine ecosystem health. Kororā are inshore foragers and do not migrate following breeding, therefore they are reliant on local marine resources year-round and may act as a high-resolution marine indicator over a small spatial scale.

GPS tracking from Motu Muka during the breeding season revealed a foraging range of < 25 km. The tracking of kororā in the wider Hauraki Gulf provided insight into how individuals foraged in a marine environment with high human impact. Feather stable isotope analysis revealed kororā from Motu Muka foraged on a lower trophic level prey than the Otata or Tāwharanui populations during pre-moult foraging trips.

This study was the first to extract the stress hormone corticosterone from kororā feathers and to identify differences in the stress experienced by populations in the region. This method could provide a less-invasive monitoring tool in the conservation of kororā colonies. The combination of feather corticosterone with stable isotope analysis revealed nutritional stress may have been the reason behind elevated corticosterone in the Motu Muka population. Feather corticosterone was lower in contemporary kororā than in museum specimens collected in the region since 1934 but was irrelative to the prey trophic level. The use of museum specimens showed further trends in diet and broad foraging location over 113 years and indicated changes have occurred in the Hauraki Gulf marine food web over time.

Both temporal and spatial differences in physiology and foraging ecology reflected the contrasting environmental conditions experienced by each of the three colonies. This validated the integrated use of feather corticosterone, stable isotopes and tracking of kororā populations as measurements to monitor changes in marine ecosystem health. Further studies should seek to determine the causes behind the differences in stress physiology and foraging ecology among the colonies and over time through a region-wide monitoring program to link foraging ecology and stress physiology to breeding success.

He kororā, he tohu oranga

“The penguin is the sign of life”

Acknowledgements

I would like to start by thanking my supervisors Brendon Dunphy, Todd Landers and Jingjing Zhang. Thanks for all the advice, guidance, knowledge and proofreading that has gotten me through to the end, without you all, this project would not have been possible. A massive thanks to honorary supervisor, lab teacher and lead proofreader Edin Whitehead, this thesis would not be what it is without your guidance. I am also very grateful for all the amazing kororā photos that make my thesis look fancy.

Then to everyone who has helped me out in the field. Spencer McIntyre and Adelie Krellenstein, thanks for all of your help on Motu Muka catching penguins even though it was very stormy and we had to hike over the island twice each night, I could not have done it without you both. Chris Gaskin, James Ross and the rest of the Northern New Zealand Seabird Trust crew, thanks for everything you did to make my fieldwork possible over the past year, and for distracting me with other field work at the same time, often accompanied by snorkelling and gin. I look forward to continuing working with you to conserve the seabirds of the Hauraki Gulf.

To the Neureuter family whose passion for conservation is inspiring, thanks for letting me study the kororā on Otata and for all the fun trips over the past year. John Laurence and the Motuihe Island Trust, thanks for letting me spend time on Motuihe finding and monitoring the penguins, even though I didn’t end up including the data in this thesis. Matt Maitland and the Auckland Council, I appreciate your support of this project and I hope the results of this study benefit the kororā at Tāwharanui. To Evan Davies and DOC Whangarei, thanks for helping to arrange the Motu Muka/Lady Alice trip and for letting the conservation dogs wake us up in the morning after our long nights catching penguins.

I would like to thank Matt Rayner and the Auckland War Memorial Museum for letting me sample your kororā specimens for feather stress analysis, and for loaning me your stable isotope data, my thesis would not be half as interesting without it. To Daniel Thomas and Massey University, thanks for letting me collect feather samples from your kororā specimens, I hope you find the data they generated interesting. To Sarah Bury and NIWA, thanks for analysing the feather stable isotopes for this study. Also to Hendrik Schultz, thanks for teaching me to use ArcMap and helping me generate the maps of penguins tracks, it is much appreciated. I hope one day we get to work together studying penguins somewhere. I would also like to thank all the iwi whose rohe I have been privileged to work in.

Thanks to my family for all of your support throughout the many years it took me to get here, even if you don’t always know what it is that I do. To my partner Frank, thanks for being there through all the blood sweat and tears and reminding me to keep going and to do my best, I would not have been able to do this without your support.

Lastly, I would like to thank the stars of the show, the kororā themselves. Thanks for contributing to this project whether you wanted to or not. I hope this study will contribute to the conservation of your species and will help to ensure you remain the signs of life of the Hauraki Gulf.

Table of Contents

List of Figures

List of Tables

List of Plates

Chapter 1. General introduction

Plate 1.1. A kororā on Otata Island. Photo by Edin Whitehead, 2018.

1.1 Seabirds of the world

Seabirds are exquisitely adapted to a life at sea, needing to return to land only to breed (Croxall, 1987) or to moult (Borboroglu and Boersma, 2013). Waterproof feathers, webbed feet, hooked bills and salt-excreting glands are just some of the morphological traits that enable seabirds to spend their lives in the marine environment (Schreiber and Burger, 2001). There are approximately 370 species of seabirds in the world, making up just a fraction of the 10,500 bird species (IUCN, 2018). Seabirds differ in their life history characteristics to many terrestrial birds in that they are often long-lived, late to mature, have small clutches and are slow to develop (Croxall, 1987). These characteristics make seabirds particularly vulnerable to many threats, and one-third of all seabird species are classified as threatened (Croxall et al., 2012).

Seabirds range considerably in size and shape, from small storm petrels (~30g) to large albatross (~7kg) (Dunning Jr, 2007) and vary in their distribution from the tropics to polar regions (Schreiber and Burger, 2001). Seabirds transport marine nutrients to terrestrial environments through guano and eggshell deposition, which when combined with the burrowing behaviour of many species, aerates and enriches the soil encouraging plant growth (Smith et al., 2011). This nutrient cycling supports other plant and animal diversity and has led to seabirds being labelled as ecosystem engineers (Markwell and Daugherty, 2002; Smith et al., 2011). Accordingly, seabirds are a vital component of the ecosystems within which they reside.

1.1.1 Seabird foraging

Different foraging strategies are utilised by seabirds and vary according to their morphology, physiology and foraging habitat (Croxall, 1987). Seabirds have excellent vision and sense of smell, helping them to locate prey in often featureless habitats (Nevitt and Bonadonna, 2005). Some species forage across both marine and terrestrial environments (e.g. gulls) but the majority rely exclusively on marine resources (Shealer, 2002). Primary productivity in the ocean is driven by currents, temperature and the mixing of the water column (Miller, 2009). As such, productive areas are patchy in their distribution and readily shift, altering the distribution of seabird prey (Weimerskirch, 2007). Some seabirds have large foraging ranges which allow them to hunt for prey over a greater area (Bost et al., 2009). Others can dive deep into the water column, allowing them to exploit prey over greater depths than surface feeders (Croxall, 1987; Dunphy et al., 2015). For example, penguins dive deeper than any other seabird, and emperor penguins (*Aptenodytes forsteri*) can forage to depths of 343 m (Pütz and Cherel, 2005). The prey consumed by seabirds also differs considerably, from zooplankton consumed by storm petrels to large fish consumed by penguins, or carcasses scavenged by skua (Shealer, 2002). Despite their differences in foraging ranges, dive behaviour or prey preference, all seabirds need to be able to adjust their foraging strategies to cope with the unpredictability of marine environments (Mattern, 2001).

All seabirds are central place foragers during the breeding season and return to the nest after foraging (Orians 1979). Most seabirds share incubation and chick rearing duties equally between the sexes (Schreiber and Burger, 2001). While one parent tends to eggs or chicks, their partner forages before duties are alternated (Shoji et al., 2011). Foraging trips must be matched with the nest-bound partner’s ability to fast as a seabird may abandon the nest when their body condition is poor to prioritise their survival and future reproduction over their offspring (Shoji et al., 2011). When prey is scarce during breeding, for example, due to overfishing (Cury et al., 2011), climate change (Trathan et al., 2015) or natural environmental variation (Chambers et al., 2011), seabirds must increase their foraging effort which can result in longer foraging trips and an increased risk of nest desertion (Numata et al., 2000). This pattern was observed in Magellanic penguins (*Spheniscus magellanicus*) where decreased marine productivity was linked to a greater foraging range and subsequent nest failures (Boersma, 2008). The spatial constraint on foraging due to offspring provisioning means some seabirds rely heavily on locally abundant prey, therefore changes in the demography, foraging patterns or physiology of those populations can act as an early warning signal of declining local marine ecosystem health (Boersma 2008).

Our knowledge of seabird foraging has increased considerably with advancements in technology (Wilson et al., 1997). An array of tracking devices can be attached to seabirds to determine where they travel once they leave land (Quillfeldt et al., 2017). Tracking studies are a good way to collect information on free-living animals when following them is impossible (Ropert-Coudert et al., 2007). Information on seabird foraging can also be collected by sampling seabird tissues. Chemical signatures of prey species are synthesised into tissues such as blood, feathers and claws (Rubenstein and Hobson, 2004). Stable isotope analysis is the process that identifies the chemical signatures of prey trophic level in the tissues of the predators that consume them (Hobson et al., 1993). In seabirds, nitrogen isotopes provide information on the position of prey species within the marine food web and carbon isotopes indicate the approximate foraging location in relation to terrestrial carbon sources (Rubenstein and Hobson, 2004). Stable isotope analysis and the tracking of seabirds provides insight into how different species utilise marine environments (Inger and Bearhop, 2008). Knowing how and where seabirds forage can assist in the management and conservation of the many threatened or endangered seabird species (Croxall et al., 2012).

1.1.2 Seabirds as ecosystem indicators

Their reliance on the marine environment for food means seabirds can act as marine ecosystem indicators, with population fluctuations, foraging ecology and physiology reflecting changes in lower trophic levels caused by environmental and human impacts (Croxall, 1987). The nature of seabirds makes them comparatively easier to study: they are highly visible, often occur in large numbers, and are frequently accessible at breeding sites on land. These qualities mean using seabirds to measure ecosystem health may be logistically easier than identifying changes in marine environments such as fish stocks or primary productivity (Cairns, 1988; Einoder, 2009; Piatt et al., 2007). Measurements of seabird population parameters may reflect human-induced environmental changes such as climate change, overfishing, and pollution but it can be difficult to unpack anthropogenic changes to those attributed to natural environmental variation (Einoder, 2009; Mallory et al., 2010). Despite these difficulties, monitoring marine food webs through a seabird lens is increasingly used as an ecosystem-based approach to marine management (Parsons et al., 2008)

When using seabirds to assess ecosystem health, care must be taken to understand the physiological and behavioural norms of different species as each species responds differently to fluctuations in marine resource availability (Mallory et al., 2010; Piatt et al., 2007). Different morphologies, life histories and foraging behaviours determine whether a species makes a suitable marine ecosystem indicator (Einoder, 2009; Piatt et al., 2007). For example, food availability was weakly correlated to the reproductive parameters of common murre (*Uria aalge*) whereas it strongly impacted on black-legged kittiwake (*Rissa tridactyla*) populations (Piatt et al., 2007). Common murres were found to buffer low prey availability with extra foraging time without it impacting breeding success, whereas black-legged kittiwakes were already foraging at maximum capacity, thus could not allocate extra effort to acquiring prey (Piatt et al., 2007). In this instance, black-legged kittiwakes were a better indicator species as changes in their population size, reproductive success and physiology were more closely linked to changes in marine resource availability. However, such a comparison can only be uncovered via an integrative approach incorporating many parameters.

Determining how seabirds use marine ecosystems can help us understand how fluctuating oceanic conditions impact on different populations. Wide-ranging species reflect the marine health of a larger area and are less responsive to localised prey depletion than coastal species who rely on local prey availability and reflect changes over a smaller spatial scale (Cairns, 1988; Einoder, 2009; Parsons et al., 2008). Specialist foragers that rely on one prey type are more susceptible to changes in prey availability than species that can readily prey-switch (Einoder, 2009). For example, chinstrap penguins (*Pygoscelis antarcticus*) are heavily reliant on Antarctic krill (*Euphausia* superba) and have been experiencing population declines in response to changing environmental conditions in the Southern Ocean (Polito et al., 2015). Gentoo penguins (*Pygoscelis papua*) on the other hand consume a broader range of prey species and have experienced population increases (Polito et al., 2015). This example illustrates how seabird population parameters can reflect changes in prey availability and how some species can indicate the health of the marine environment in which they forage.

1.2 Penguins – *Spheniscidae*

Penguins are a group of flightless birds of the order *Sphenisciformes.* Penguins are most closely related to other marine birds, especially the *Procellariiformes* which include petrels and albatrosses (Bertelli and Giannini, 2005). They are the most threatened taxon of seabirds following albatrosses with more than half of the world's penguin species threatened and all of the temperate species in decline (Boersma, 2008). There are 17 species of penguins distributed throughout the Southern Hemisphere, reflecting their Gondwanan origins (Tambussi et al., 2005). Five species of the genera *Aptenodytes* and *Pygoscelis* are confined to continental Antarctica and the surrounding sub-Antarctic Islands (Borboroglu and Boersma, 2013). The six crested penguins are of the genus *Eudyptes* and are found on the Antarctic Peninsula, Sub-Antarctic islands and the lower reaches of mainland New Zealand and South America (Borboroglu and Boersma, 2013). *Megadyptes antipodes* is the sole species of its genus and breeds only on mainland New Zealand and the nearby Sub-Antarctic islands (Seddon et al., 2013). The four species of the genera *Spheniscus* live at low latitudes in warm terrestrial environments, but these are areas of cold currents with associated productive waters (Croxall and Lishman, 1987). The smallest of all penguin species is the kororā/Little Blue Penguin (*Eudyptula minor*) and is found throughout New Zealand and southern Australia. (Dann, 2013).

Penguins are well adapted to life in the ocean due to their evolution of wings into flippers (Croxall and Lishman, 1987; Tambussi et al., 2005) and it is due to their flightlessness that penguins are able to grow to a larger size than most flying seabirds (Croxall and Lishman, 1987). Unlike most flying seabirds, penguins are adapted to short-range foraging and bring back smaller but more frequent loads of food to the nest (Croxall and Lishman, 1987). Small, waterproof feathers interlock to trap air against the skin keeping penguins well insulated (Bertelli and Giannini, 2005). Their highly streamlined body shape and short legs reduce drag and allow for high speed and mobility when swimming (Croxall and Lishman, 1987).

1.3 Seabirds in New Zealand

One quarter of all seabird species breed in New Zealand, making the country a global seabird hotspot (Forest and Bird, 2014). Included in these are the tropicbirds (*Phaethontidae*), gannets and boobies (*Sulidae*), southern storm-petrels (*Oceanitidae*), shearwaters and petrels (*Procellariidae*), cormorants (*Phalacrocoracidae*), gulls and terns (*Laridae*), penguins (*Spheniscidae*), albatrosses (*Diomedeidae*), and skuas (*Stercorariidae*) (Birdlife International, 2019). This diversity is largely due to the productive oceans surrounding the country and the lack of native mammalian predators throughout much of its history (Gaskin and Rayner, 2013). New Zealand encompasses a range of different seabird habitats, from the sub-tropical Kermadec Islands where red-tailed tropicbirds (*Phaethon rubicauda*) are found, to the sub-Antarctic where penguins form breeding colonies into their thousands (Forest and Bird, 2014).

1.3.1 New Zealand Penguin diversity

Six species of penguin breed on the mainland and sub-Antarctic islands of New Zealand (Croxall and Lishman, 1987). On the sub-Antarctic islands of New Zealand live three of the six crested penguins, the southern rockhopper (*Eudyptes chrysocome*), erect-crested (*Eudyptes sclateri*) and Snares (*Eudyptes robustus*) penguins. In the South Island, the tawaki/Fiordland penguin (*Eudyptes pachyrhynchus*) can be found, along with the hoiho/yellow-eyed penguin (*Megadyptes antipodes*), the only extant species of the genus *Medadyptes* (Borboroglu and Boersma, 2013). The kororā/Little Blue Penguin (*Eudyptula minor*) is found throughout New Zealand (Dann, 2013).

1.3.2 The Hauraki Gulf as a seabird hotspot

Te Moananui ā Toi/Tīkapa Moana, or the Hauraki Gulf, encompasses both inshore waters and the continental shelf edge over 1.2 million hectares (Bassett et al., 2016). Within the Hauraki Gulf are 30 major island groups and 400 small islands and islets (Bassett et al., 2016). Many of these islands are pest-free and are refuges for native bird, reptile and invertebrate species (Buxton et al., 2016). The Hauraki Gulf is on the doorstep of Auckland, New Zealand's largest city, and is affected by the associated anthropogenic impacts such as increased sediment loading, pollution and high fishing effort (Hauraki Gulf Forum, 2018). Despite this, the Hauraki Gulf is home to 27 species of seabird which breed mainly on offshore islands (Gaskin and Rayner, 2013). The islands provide protection from introduced mammals and the proximity to pelagic feeding grounds for many species offer ample foraging opportunities (Buxton et al., 2016). Given this, the region is classified as an Important Bird Area (Forest and Bird, 2014) and the high diversity of seabirds makes the Hauraki Gulf a global seabird hotspot (Gaskin and Rayner, 2013).

1.4 Study species – Kororā/Little Blue Penguin (*Eudyptula minor*)

1.4.1 Morphology

Kororā are the smallest species of penguin weighing between 0.8 - 1.3 kilograms and reaching 33 centimetres in length (Dann, 2013). Feathers on the dorsal surface are medium to dark blue with white feathers on the underside. Towards moult, feathers become a dull brown/blue. The bill is dark grey with a hooked tip and webbed feet are pale-pink to white in colour. Males may be slightly heavier with longer bills than females (Arnould et al., 2004). Juveniles can be distinguished through their smaller bill size and brighter blue plumage, except immediately following moult where adults have new iridescent blue feathers (Dann, 2013).

1.4.2 Taxonomy

Kororā are the only extant species of their genus *Eudyptula*. The taxonomy of kororā is still in debate. Six distinct sub-species of kororā were identified by (Kinsky and Falla, 1976) based on morphometric data. These sub-species were the Australian Blue Penguin (*Eudyptula minor novaehollandiae*), Northern Blue Penguin (*Eudyptula minor iredalei*), Cook Strait Blue Penguin (*Eudyptula minor variabilis*), Southern Blue Penguin (*Eudyptula minor minor*), White-flippered Penguin (*Eudyptula minor albosignata*) and the Chatham Island Blue Penguin (*Eudyptula minor chathamensis*). Kororā is the Māori name for Little Blue Penguin as is used throughout this study for all six sub-species.

Banks et al. (2002) compared mitochondrial DNA from kororā across their range and found evidence of two distinct clades, one containing penguins from Australia and Otago and the other with penguins from the rest of New Zealand. The genetic and morphometric similarities observed in kororā from Australia and the Otago region suggest a back-dispersal event from Australia following the local extinction of kororā in the Otago region between 1500 and 1900 (Banks et al., 2002; Grosser et al., 2016; Grosser and Waters, 2015). Despite their geographical proximity, kororā from Southland, Stewart Island, and the West Coast are more morphometrically similar to those from the Cook Strait, rather than individuals from Otago (Banks et al., 2002). More recently, DNA barcoding of kororā by Peucker et al. (2009) and Waugh (2016) and morphological, behavioural and genetic evidence from Grosser et al. (2016) and Grosser and Waters (2015) further support the distinction between the two clades.

In the near future, two separate species of kororā may be recognised, the New Zealand taxon *Eudyptula minor* and the Australian/Otago taxon *Eudyptula novaehollandiae.* As the taxonomy currently stands, the penguins referred to in this study are the Northern Blue Penguin sub-species (*Eudyptula minor iredalei*) and the species considered as one taxon.

1.4.3 Distribution

Kororā are found throughout mainland New Zealand, Chatham Island, Stewart Island and southern Australia (IUCN, 2018). Kororā have been recorded as far south as the Snares Islands and as far north as Coffs Harbour, Australia (Marchant et al., 2006; Sagar et al., 2001). They are one of three penguin species to breed on mainland New Zealand and are the only penguins to breed in the North Island (Dann, 2013). In northern New Zealand, kororā are mainly found breeding on pest-free offshore islands (Figure 1.2), but can be found in small numbers on the mainland (Gaskin and Rayner, 2013; Landers, 2017).

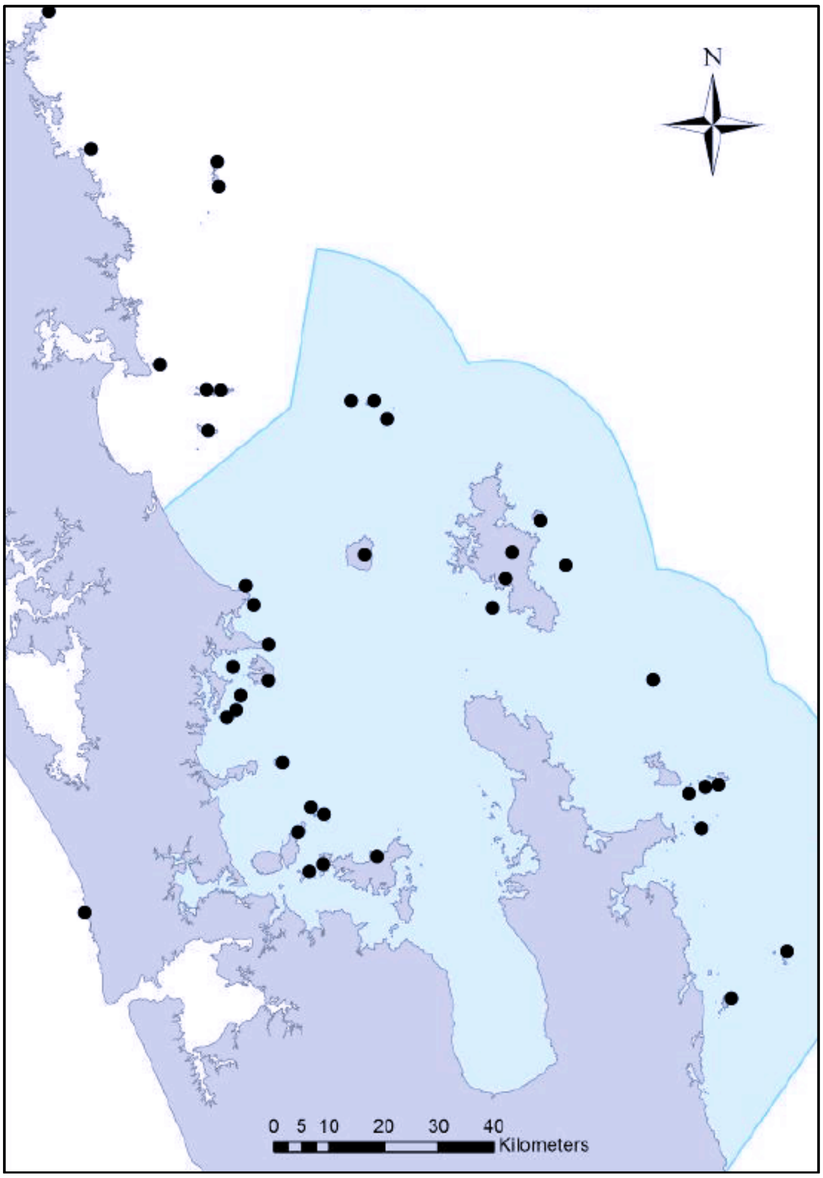


Figure 1.1. Map of Kororā/Little Blue Penguin (*Eudyptula minor iredalei*) breeding sites in the wider Hauraki Gulf of New Zealand.

1.4.4 Conservation

Kororā are a species of ‘Least Concern’ worldwide on the International Union for Conservation of Nature (IUCN) Red List with an estimated population of 470,000 mature individuals (IUCN, 2018). However, in New Zealand kororā are listed as ‘At Risk – Declining’ (Robertson et al., 2017) with a population estimate of 64,700 individuals (Mattern and Wilson, 2018). In New Zealand, little robust data exist for the population trends of many kororā colonies (Mattern and Wilson, 2018). Some populations appear to be decreasing e.g. parts of Banks Peninsula (Challies, 2015) and the West Coast (Heber et al., 2008) whereas others are increasing e.g. Oamaru (Agnew et al., 2014).

Should the distinction occur between the two clades, the conservation status of *Eudyptula minor* will likely change (Mattern and Wilson, 2018). Kororā are a taonga (sacred) species and have significant cultural and spiritual importance in New Zealand.

1.4.5 Threats

Threats to kororā are similar to those faced by many seabirds and are primarily anthropogenic in nature (Whitehead et al., 2019). Introduced mammals pose a major threat to kororā who are easily accessible in nests on the ground or in underground burrows (Dann, 2013). Rats (*Rattus spp.*), mustelids (*Mustela spp.*), cats (*Felis catus*) and dogs (*Canis lupus*) predate adults, chicks and eggs and have caused the decline or complete extermination of many populations (Challies, 2015; Perriman and Steen, 2000). Uncontrolled dogs attack penguins and are capable of digging nesting birds out of burrows (Dann, 1994). A review of kororā mortality in New Zealand found that dogs contributed to 14% of mortality events of necropsied individuals (Hocken, 2000) and foxes have single-handedly wiped out colonies in Australia (Stevenson and Woehler, 2007).

Coastal development, land clearance and other land use changes contribute to the degradation and destruction of kororā breeding and roosting habitat (Boersma, 2008). In addition, sedimentation from land development decreases water clarity which can reduce foraging ability (Trathan et al., 2015). Humans can directly disturb penguins by trampling breeding sites and preventing nest access (Klomp et al., 1991; Weerheim et al., 2003) and kororā can be hit by vehicles when returning to their nest after dark (Hocken, 2000).

Penguins spend more time in the marine environment than other seabirds, resulting in higher exposure to marine threats (Cannell, Campbell et al. 2016). Interactions with fisheries see kororā caught as bycatch (Crawford et al., 2017) or indirectly impacted through prey depletion (Klomp and Wooller, 1988). Kororā can be struck by recreational boats, causing trauma or sometimes death (Cannell et al., 2016). Marine habitats are polluted through sedimentation, chemical pollutants, effluent, plastic and oil products (Whitehead et al., 2019), and land-based pollutants such as trace metal contaminants have been found in kororā tissues (Cannell et al., 2016; Finger et al., 2015). An oil spill in Tauranga in 2015 caused the death of 89 kororā and coated another 383 individuals (Mattern and Wilson, 2018). In northern New Zealand, mass mortality of kororā are not uncommon (Crockett and Kearns, 1975) and the most recent mortality event in the region was caused by a severe storm in January 2018 (NIWA, 2018). Hundreds if not thousands of kororā were found wrecked along Auckland and Northland coastlines following the storm (Robson, 2018). Most individuals necropsied by Massey University had empty stomachs (Massey University Auckland, 2018), indicating they were unable to find sufficient food during or following the event.

An increase in the frequency and intensity of storms are predicted with climate change and will likely negatively affect kororā populations (Boersma and Rebstock, 2014). Extreme storm events were associated with decreased adult survival and nest visitation rates in Oamaru, resulting in decreased chick provisioning (Agnew et al., 2015). Storms increase turbidity in the ocean making it difficult for seabirds to find prey and can destroy nests through flooding and landslips (Trathan et al., 2015; Walker et al., 2014). Changes in marine productivity caused by climate change can shift the distribution of prey to cooler deeper waters or further south (Ramírez et al., 2017), which can be detrimental for kororā that rely on local prey availability year-round (Boersma, 2008). Changes in marine productivity may lead to a mismatch between peak primary productivity and the breeding season (Ramírez et al., 2017), a relationship that strongly correlates to fledgling success (Chiaradia et al., 2007).

1.4.6 Breeding Ecology

Kororā reach sexual maturity after two years and typically return to their natal colony (Dann and Cullen, 1990). Due to this high site fidelity, movement among colonies is infrequent but does sometimes occur (Kinsky, 1958; Overeem et al., 2008). Birds generally return to the same partner and nest each season (Rogers and Knight, 2006) where they construct a nest from twigs, sticks and debris (Mattern and Wilson, 2018). In New Zealand, kororā breed along the mainland coast and on offshore islands where they nest in burrows, caves, rock crevices, beneath vegetation or anthropogenic structures (Braidwood et al., 2011; Gaskin and Rayner, 2013). Kororā frequently nest within 25 m of the shore (Braidwood et al., 2011) but they can travel inland and be found nesting on tops of islands (Kinsky, 1958) and more than 500 m from shore (Van Rensburg, 2010). In parts of Australia and Otago, nests spaced two metres apart can form dense colonies into their thousands (Overeem et al., 2008; Stevenson and Woehler, 2007). Colonies in New Zealand are small compared to Australia, with most colonies 10 - 1000 pairs and nests are more widely spaced, forming loose colonies (Braidwood et al., 2011; Mattern and Wilson, 2018). Kororā are nocturnal on land, likely due to diurnal predators such as skua and giant petrels, so return after dusk and leave before dawn (Klomp et al., 1991). Individuals come ashore at night throughout the year and stay ashore longer as the breeding season approaches (Kinsky, 1958).

The breeding season in kororā varies across their geographical range and with changes in prey availability but typically occurs between the months of June and February in New Zealand (Dann, 2013). Egg laying begins as early as May in the

South Island where two eggs are laid and both parents alternate incubation and foraging (Agnew et al., 2014). Eggs are incubated for approximately 35 days before hatching and chicks are then guarded by alternate parents (Kinsky, 1958). Once chicks can thermoregulate unaided, usually at 2-3 weeks of age, both parents must forage at sea to meet the increased energetic demands of their offspring (Chiaradia and Kerry, 1999). Chicks then fledge at seven to eight weeks of age (Boersma, 2008; Chilvers, 2017). In both Australia and Otago, two clutches of eggs can be laid in one season, known as double brooding (Agnew et al., 2014). This differs from most of New Zealand where only one clutch is laid (Bull, 2000; Heber et al., 2008). Unlike other seabirds, kororā will not skip breeding when prey is scarce, but breeding may be delayed (Numata et al., 2000)

1.4.7 Diet and foraging behaviour

The diet of kororā varies geographically and across years (Chiaradia et al., 2003; Chiaradia et al., 2012; Fraser and Lalas, 2004; Gales et al., 1990; Klomp et al., 1991). Kororā are generalist foragers, and typically consume a diet of >70% small; shoaling fish followed by cephalopods (<5%) and a small number of crustaceans (Chiaradia et al., 2003; Flemming et al., 2013). Kororā forage in shallow coastal waters surrounding their colonies and visually search for prey from the water surface (Ropert-Coudert et al., 2006). Some studies suggest a difference in foraging strategy between the sexes with males diving deeper and for longer than females (Berlincourt and Arnould, 2014; Ropert-Coudert et al., 2007), but others have observed no difference (Hoskins et al., 2008).

Kororā are central place foragers during the breeding season and remain resident in the inshore marine environment surrounding their colony outside of breeding (Gales et al., 1988; McCutcheon et al., 2011). This differs from many high latitude penguin species, who migrate away from their breeding grounds to more productive waters following breeding (Borboroglu and Boersma, 2013). Foraging is less spatially constrained outside of breeding, but the inshore foraging strategy of kororā means they rely on prey availability in shallow coastal waters year-round (Boersma, 2008; Croxall and Lishman, 1987).

1.4.8 Moult

From one year of age, kororā undergo an annual moult where plumage is replaced (Dann, 2013). Old feathers get worn out and lose their insulation and waterproof properties, which can be critical for a bird that spends the majority of its time in the ocean (Reilly and Cullen, 1983). Feathers are replaced on land, and kororā typically return to the same burrow that they used during the breeding season (Kinsky, 1958). Penguins are unable to forage during moult due to a lack of waterproof plumage, therefore individuals can lose up to 46% of their body mass during this time (Gales et al., 1988). This weight reduction is accounted for during pre-moult foraging trips where kororā gorge themselves and greatly increase their body mass to survive weeks of fasting (Gales et al., 1988). The moulting process takes two to three weeks and occurs from December to March following breeding (Dann, 2013).

1.5 Stress physiology

1.5.1 Stress in vertebrates

Free-living animals regulate their physiology and behaviour based on predictable environmental variation such as seasons and the diurnal cycle (Wingfield and Silverin, 2002). Environmental stimuli let animals know when different life history stages should occur, such as breeding, migration or moult (Wingfield and Silverin, 2002). Stress is the interaction between a stimulus perceived as a threat and the individual experiencing the stimuli (Harvey et al., 1984). Whether real or perceived, a threatening stimulus triggers the bird’s stress response, allowing them to adjust their physiology and behaviour to increase their chance of survival (Sapolsky et al., 2000).

When a stress response is triggered in a vertebrate, the hypothalamic-pituitary-adrenal (HPA) axis in the brain is activated, releasing glucocorticoids, or stress hormones (Sapolsky et al., 2000; Wingfield and Silverin, 2002). While Cortisol is released in mammals and teleost species, corticosterone (CORT) is the primary glucocorticoid released by the adrenal gland of birds, reptiles, amphibians and rodents (Wingfield and Silverin, 2002).

The secretion of CORT is dependent on both extrinsic and intrinsic factors (Cottin et al., 2014). Extrinsic factors include severe weather, predator presence, food scarcity, resource competition and anthropogenic environmental changes (Sapolsky et al., 2000; Wingfield et al., 2017; Wingfield and Silverin, 2002). Conversely, intrinsic factors regulating CORT secretion include body condition and energy requirements (Cottin et al., 2014). If a stressor is powerful enough, normal activities such as migration, reproduction and foraging can be delayed or ceased as an animal enters an emergency life stage (Wingfield et al., 2017). Physiological adjustments made during the stress response include decreased appetite, reduced growth, suppressed immune function and the mobilisation of stored energy through gluconeogenesis (Sapolsky et al., 2000; Wingfield et al., 2017). During a stress response, an animal will allocate energy to survival, rather than normal behaviours, until the stressor has ceased and homeostasis is re-established (Romero, 2002).

The survival mechanisms caused by elevated CORT are beneficial in the short term as they allow individuals to mount a response and cope with stressors (Sapolsky et al., 2000). Acute stress may last for minutes or hours, whereas if a stressor is constant or frequent, CORT levels may remain elevated resulting in chronic stress (Sapolsky et al., 2000). When CORT levels are chronically elevated, for instance from food deprivation or severe weather, deleterious effects can occur such as reduced growth rates, decreased immune function and depressed cognition (Kitaysky et al., 2003). Long term exposure to a stressor can result in decreased fitness, reproduction, and increased mortality, all of which can contribute to a decrease in population size (Wingfield and Silverin, 2002). Corticosterone is released in greater amounts during unpredictable environmental variation, therefore by measuring stress hormones the environmental stressors experienced by wild-living individuals can be assessed (Fairhurst et al., 2015; Lamb et al., 2016). Corticosterone is circulated in the blood and deposited into new tissue growth, therefore the cumulative stress experienced by an individual during the tissue growth period can be measured by sampling blood, bones, feathers and claws.

1.5.2 Environmental and anthropogenic stress in seabirds

Both natural and human-induced environmental change can incite a stress response in seabirds (Sapolsky et al., 2000; Wingfield et al., 2017; Wingfield and Silverin, 2002). Normal activities such as foraging, reproduction and chick rearing may be impacted by the environmental changes caused by storms and other climatic events (Wingfield et al., 2017). For example, an increased stress response was observed in Magellanic penguins when high rainfall caused nest flooding and decreased the reproductive success of the population (Walker et al., 2014). Similarly, two severe El Niño weather events were responsible for the considerable population decline of Galapagos penguins (*Spheniscus mendiculus*) by causing a shift in marine productivity and decreasing the availability of prey (Vargas et al., 2006).

In both captive and free-living seabird populations, nutritional stress has been linked to increased levels of CORT, thus linking diet to survival and reproduction (Kitaysky et al., 2007; Kitaysky et al., 2010; Lamb et al., 2016). For example, increased food abundance resulted in decreased CORT levels for common guillemots (*Uria aalge*) (Kitaysky et al., 2007), rhinoceros auklets (*Cerorhinca moncerata*) (Will et al., 2014) and black-legged kittiwakes (*Rissa tridactyla*) (Kitaysky et al., 2003). The quality of prey items consumed is also important, and a decrease in CORT levels of common guillemots was associated with an increase in energy-rich larval cod (*Gadus morhua*) in the diet (Barrett et al., 2015). Seabird diet outside the breeding season influences body condition and reproductive success during breeding but is something we know little about as this is a difficult time to sample seabirds (Sorensen et al., 2009).

In times of food scarcity during the breeding season, chronically stressed seabirds may feed their chicks less to maintain their body condition and prioritise their survival, thus increasing the nutritional stress of the chicks (Wingfield and Silverin, 2002). While increased CORT levels may benefit chicks in the short term by increasing the chance of survival, chronic stress can negatively affect chick development. The long-term impacts of chronic stress during seabird development include reduced growth rates and cognitive ability which can cause diminished memory capacity when learning to forage (Kitaysky et al., 2003).

In addition to natural environmental variation, a stress response in seabirds can also be triggered by anthropogenic activities both in the terrestrial and marine environments (Alonso-Alvarez et al., 2007). Human presence can influence the stress response of several penguin species on land. For example, both yellow-eyed penguins and Fiordland crested penguins have been shown to temporarily abandon their nests in response to human presence (Ellenberg et al., 2015; Ellenberg et al., 2007). Similarly, fewer kororā nests were found in areas of the colony with high human presence compared to areas where human visitation was restricted, indicating less human presence was preferable (Giling et al., 2008). In marine environments, anthropogenic activities such as fishing can decrease prey availability and contribute to nutritional stress in seabirds (Bertrand et al., 2012). The reliance of seabirds on the marine environment for food and the link between physiology and prey availability means that measurements of stress hormones in seabirds can indicate the health of the marine environment in which they forage (Mallory et al., 2010).

1.6 Thesis Background

A recent study by Vickers (2017) of kuaka/common diving petrels (*Pelecanoides urinatrix urinatrix*) in the Hauraki Gulf saw spatial segregation of foraging behaviour between colonies with associated differences in physiology over smaller spatial scales than initially predicted. Kororā are more spatially constrained than common diving petrels and do not migrate during the non-breeding season, therefore they are reliant on local marine resources year-round (Boersma, 2008) and may serve as a higher resolution marine indicator. Given that the islands of the Hauraki Gulf are free of many terrestrial anthropogenic impacts such as land development and introduced mammals, this potentially reduces causative factors explaining physiological shifts among study colonies. Given this, the stress physiology and foraging ecology of kororā in the Hauraki Gulf is largely determined by the marine environment near their colonies.

Understanding how seabirds use marine ecosystems can help us understand how those ecosystems are changing over time and space. By tracking kororā, we can determine key foraging areas and movement corridors that can reflect the abundance and distribution of prey in the local marine environment. Foraging patterns can also be assessed through stable isotope analysis, and changes in the foraging location and broad prey trophic level act as additional indicators of shifts in marine productivity (Flemming and van Heezik, 2014). Prey abundance is tightly linked to physiology in seabirds, thus by measuring stress hormones, further inferences can be made of prey availability and marine ecosystem health (Kitaysky et al., 1999). This study aims to determine whether differences in the foraging ecology and stress physiology of kororā are observed over time and space and whether measurements of stable isotopes, stress hormones, and foraging characteristics can be used to indicate marine ecosystem health.

1.7 Study Aims

1. *To determine whether foraging behaviour differs among colonies in the wider Hauraki Gulf.*

2. *To assess whether the trophic level of prey and broad foraging location differs among contemporary colonies or over the last 113 years.*

3. *To determine whether the stress hormone corticosterone differs among contemporary colonies or over the last 85 years.*

1.8 Study sites

This study was carried out at three study sites within the wider Tīkapa Moana/Hauraki Gulf. Tāwharanui is a pest-free mainland sanctuary and Otata and Motu Muka are islands.

Otata, Noises Group

The Noises Island Group consist of four large islands and many offshore stacks and rocks 24 km northeast of Auckland. The island group has evidence of Māori occupation by Ngai Tai & Ngati Paoa (Monin, 1996) but is now managed by the Noises Islands Family Trust who contribute greatly to the conservation of the islands.

The largest of the four main islands is Otata (36°41'49.52"S, 174°58'24.56"E) (Figure 1.2), a 21.8 ha island covered in native forest. A fire in the 1920’s cleared most of the island of vegetation but it has since regenerated and is now fully forested with pohutukawa (*Metrosideros excelsa*) and karo (*Pittosporum crassifolium*) dominating the canopy and a dense understorey of kawakawa (*Piper excelsum*), mahoe (*Melicytus ramiflorus*) and houpara (*Pseudopanax lessonii*) (Cameron, 1998). The islands have been free of mammalian pests since 2002 and Otata supports many small seabird colonies alongside forest birds and invertebrates (Russell and Anderson, 2007). According to anecdotal evidence, the abundance of nesting kororā has declined since the 1970s (Sue Neureuter, pers. comm., 2018).

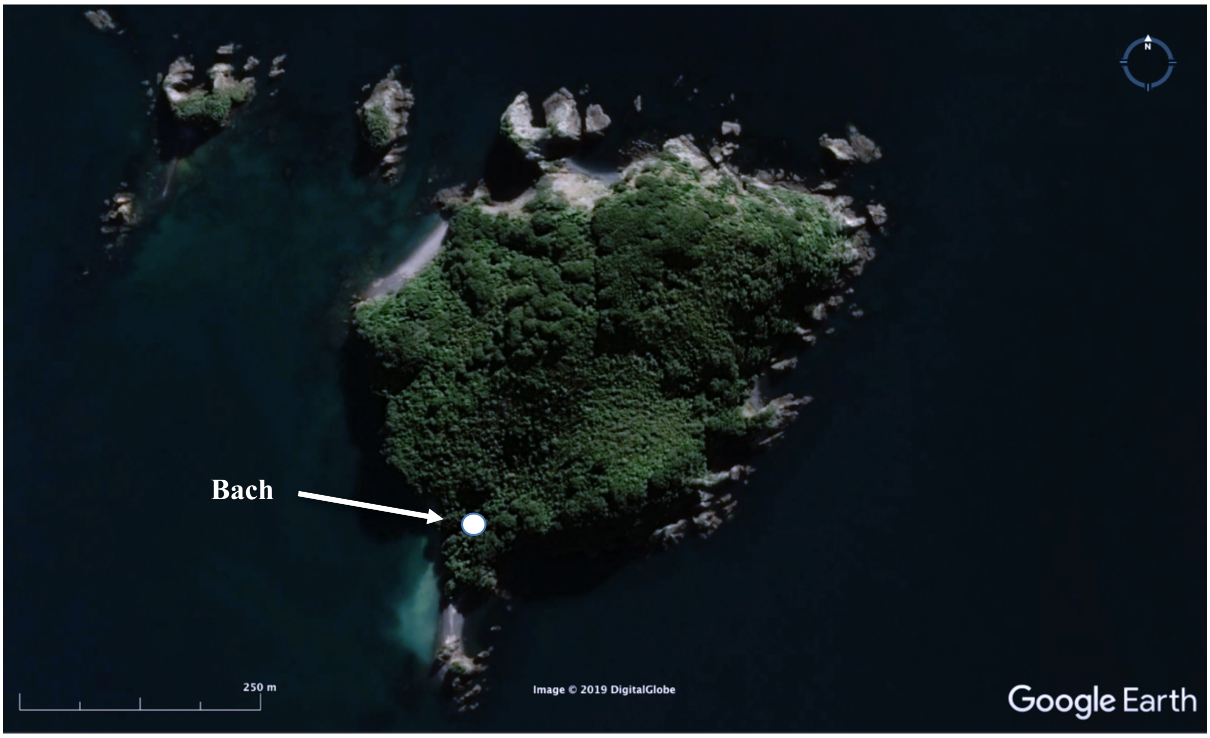


Figure 1.2. Map of Otata, Noises Island Group. Image from DigitalGlobe 2019.

Tāwharanui

Tāwharanui (36°21'50.16"S 174°51'36.71"E) (Figure 1.3) is a 588 ha pest-free mainland sanctuary located 90 km north of central Auckland on the Tāwharanui peninsula. The land has a history of Māori occupation before European farming began in 1870 (Auckland Council, n.d). Tāwharanui is now managed as a regional park by Auckland Council in collaboration with Tāwharanui Open Sanctuary Society Incorporated (TOSSI). In 2004, a 2.7 km predator proof fence was built to separate the park from the rest of the peninsula and create a sanctuary for biodiversity (Auckland Council, n.d). Tāwharanui contains a range of diverse landscapes with abundant rocky coastlines, sandy beaches, old growth forests, regenerating forest and pasture. In addition to remnant populations of ōi/grey-faced petrels (*Pterodroma gouldi)* and diving petrels, the park is involved in active seabird restoration and as such, artificial colonies of grey-faced petrel, pakaha/fluttering shearwater (*Puffinus gavia)* and takupu/Australasian gannets (*Morus serrator*) are found along the northern coast. Also found along the northern coast is a 400 ha marine reserve which was established in 2011 (Auckland Council, n.d).

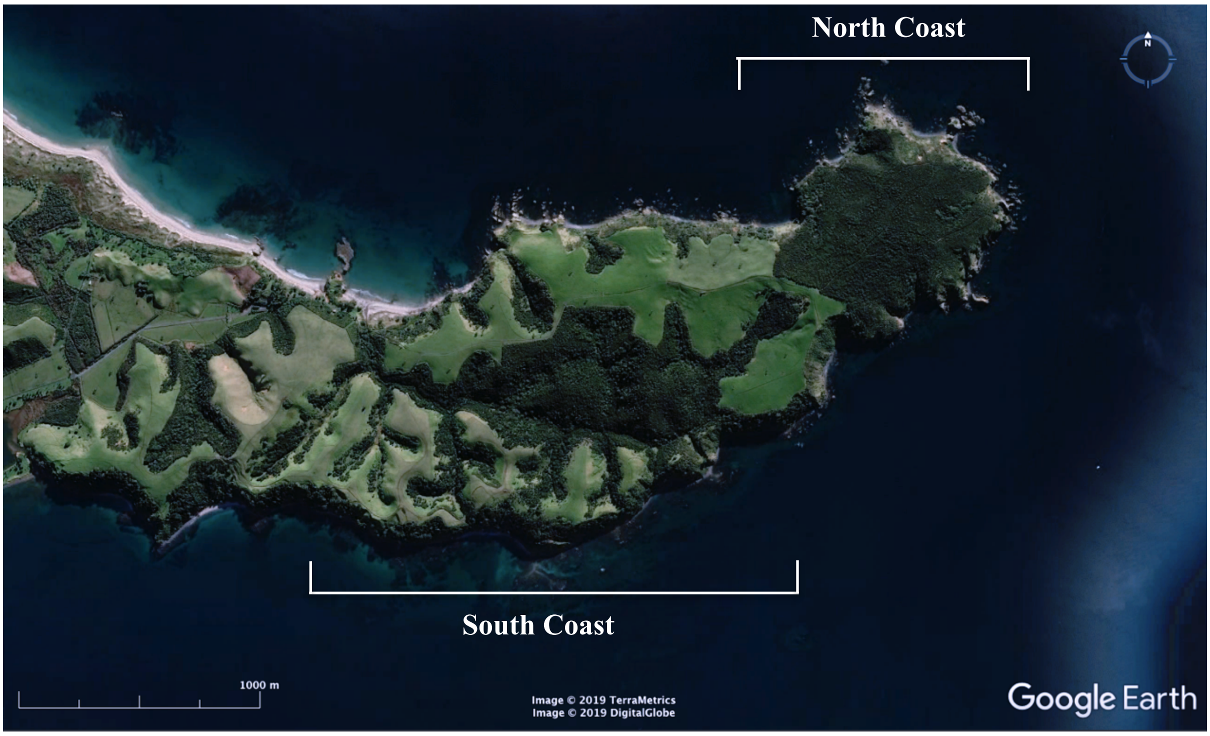


Figure 1.3. Map of Tāwharanui Regional Park. Image from DigitalGlobe 2019 and TerraMetrics 2019.

Motu Muka/Lady Alice Island

Motu Muka/Lady Alice Island (35°53'30.49"S 174°43'39.37"E) (Figure 1.4) is the largest of the Marotere/Chicken Islands group in northern New Zealand. The island is 138 ha and 169 m at its highest point. It has a history of both Māori and European settlement and land management practices have included the use of fires to clear vegetation and cattle farming (McCallum et al., 1984; Prickett, 1984). Motu Muka is in the rohe of Ngātiwai and has been managed as a scenic reserve since 1925 by the Department of Conservation.

The island is largely covered in coastal forest including pohutukawa (*Metrosideros excelsa*), puriri (*Vitex lucens*), ngaio (*Myoporum laetum*), karaka (*Corynocarpus laevigatus*) and kohekohe (*Dysoxylum spectabile*) (McCallum et al., 1984). Motu Muka was declared pest free in the 1990s and now supports large numbers of seabirds, forest birds and reptiles (Department of Conservation, 2019; Gaskin and Rayner, 2013).

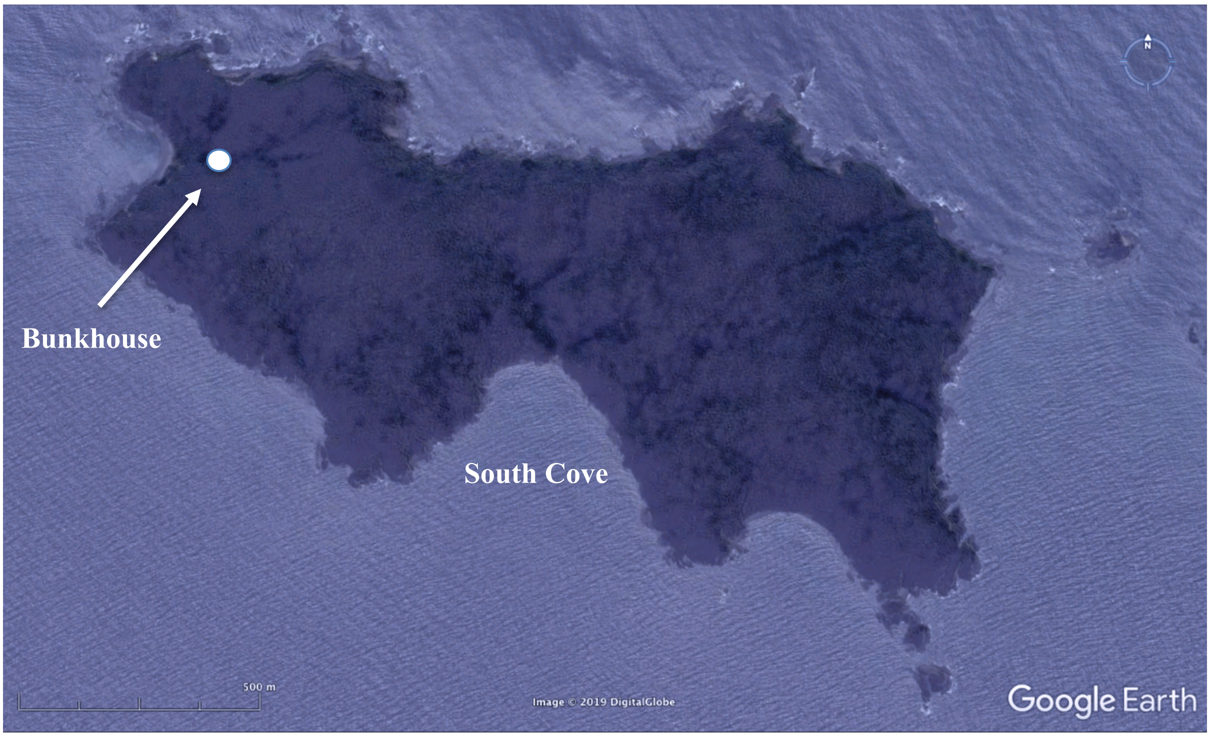


Figure 1.4. Map of Motu Muka/Lady Alice Island of the Marotere Islands. Image from DigitalGlobe 2019.

Otata is the smallest of the three sites (Figure 1.5) and supports a known population of 12 pairs of kororā scattered across the island, as well as pockets of grey-faced petrel burrows and sparse fluttering shearwater burrows. Tāwharanui is a much larger site but supports relatively few penguins, with a known population of 11 pairs in 2018. Similar to Otata, Tāwharanui has colonies of grey-faced petrels and fluttering shearwaters, in addition to common diving petrels. On Motu Muka, more than 40 kororā were observed coming ashore on one beach over the course of eight nights during the breeding season, making this a relatively abundant population of penguins in the Hauraki Gulf.

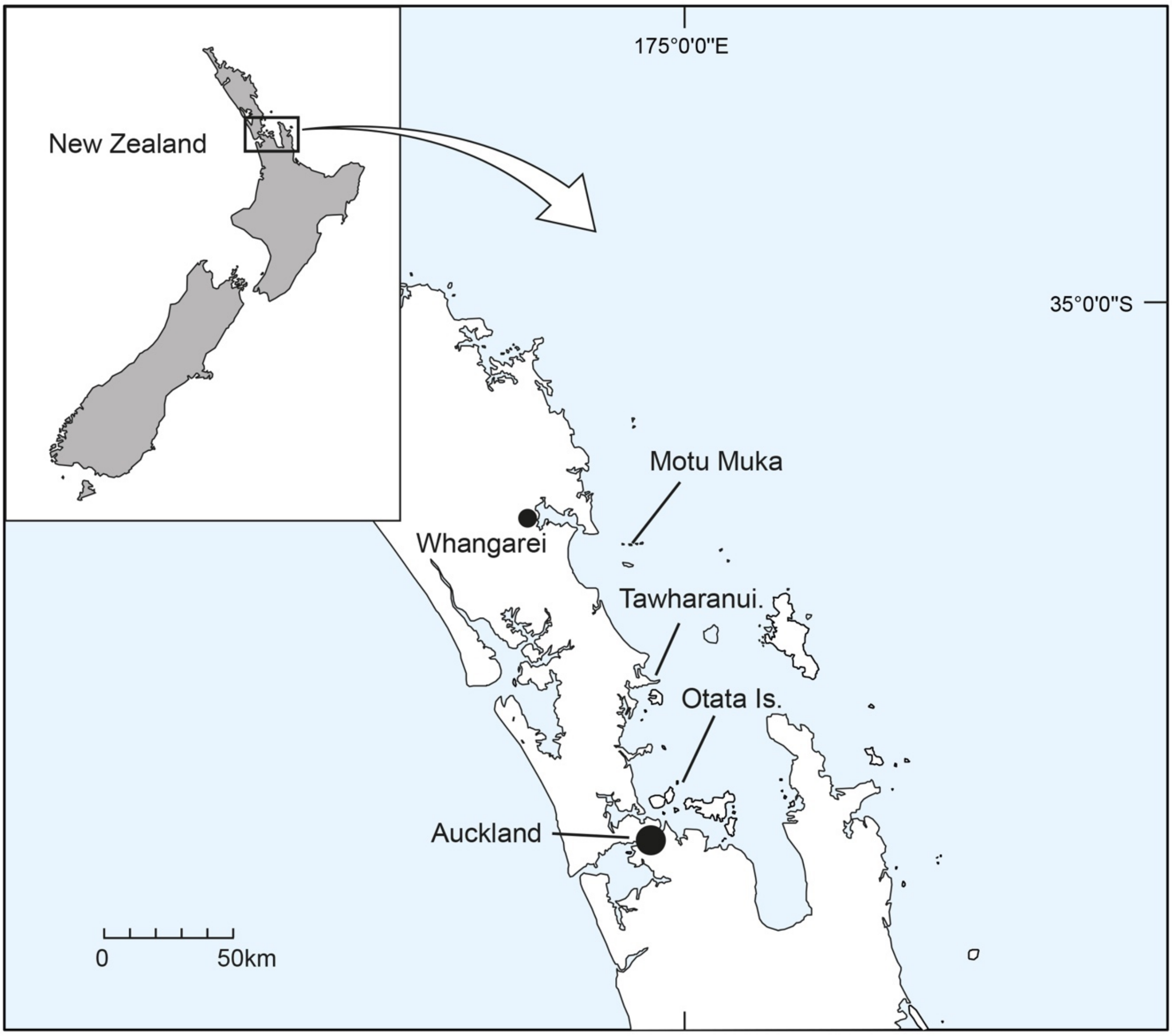


Figure 1.5 Map of the three study sites in the wider Hauraki Gulf.

1.9 Thesis structure

This thesis consists of three data chapters (Chapters 2 – 4), one introductory chapter (Chapter 1) and one general discussion chapter (Chapter 5).

Chapter 1 – Introduction

This chapter introduces seabirds, *Spheniscinae* and the *Eudyptula* genus in both global and New Zealand contexts. An overview of the current literature on kororā and avian stress physiology is provided along with the outline of this research.

Chapter 2 – Kororā foraging during the breeding season

The foraging patterns of kororā from Motu Muka are outlined. Trajectories, hotspots and characteristics of foraging during the breeding season were determined through GPS tracking.

Chapter 3 - Prey trophic level and foraging location as determined by feather stable isotopes

Prey trophic level and proxies of foraging locations are determined through feather stable isotopes and compared among colonies and to specimens from the Auckland War Memorial Museum and Massey University.

Chapter 4 - Feather corticosterone during the critical moult period

Feather corticosterone measures are compared among colonies and to specimens from the Auckland War Memorial Museum and Massey University. The relationship between feather corticosterone and foraging patterns is also assessed.

Chapter 5 – Discussion

The main findings of this study are summarised and integrated into a discussion regarding their application for the conservation of kororā, and directions for future research and management are considered.

All fieldwork for this thesis was conducted under The University of Auckland Ethics Approval permit AEC.001818, and Wildlife Act Authority from the New Zealand Department of Conservation 70910 - FAU and Auckland Council permit NS439.

Chapter 2. The foraging ecology of kororā during the breeding season

Plate 2.1. A kororā foraging in the Hauraki Gulf. Photo by Edin Whitehead, 2018.

2.1 Introduction

2.1.1 History of seabird tracking

Tracking studies are a useful way to collect information on free-living animals and overcome the challenges of directly observing marine species. Historically, at sea surveys were used to determine the spatial distribution of marine animals, but this can be a difficult method to observe animals that spend most of their time underwater (Bannasch et al., 1994). By understanding how seabirds utilise the marine environment, assessments can be made of how populations cope with environmental variability by making alterations to their foraging strategy (Boyd et al., 2014). Knowing how and where seabirds forage can assist in the management and conservation of the many threatened or endangered seabird species (Croxall et al., 2012). One way to identify key foraging areas at sea is by directly tracking them.

Tracking studies have helped increase our knowledge of seabird ecology throughout the world by helping us understand the movement patterns of the birds once they leave land (Wilson et al., 1997). Understanding how seabirds utilise the marine environment can help identify important ecological areas of high biodiversity and allows policymakers to make decisions on how those marine environments are managed, for example by deciding where to implement marine reserves or restrict damaging practices such as mining (Croxall et al., 2012). One tracking study of chinstrap penguins (*Pygoscelis antarcticus*) identified an overlap between the penguins' preferred krill foraging habitat and the Antarctic krill (*Euphausia* superba) fishery (Trathan et al., 2018). This led to the authors' suggestion that the krill fishery should avoid fishing in shallow coastal areas where competition with penguins would be greater. Other tracking studies have identified polar fronts and eddies as preferred foraging habitat for royal penguins (*Eudyptes schlegeli*) and macaroni penguins (*Eudyptes chrysolophus*) during the breeding season (Bon et al., 2015; Hull et al., 1997). Both of these studies helped highlight the ecological importance of oceanographic features in the Southern Ocean marine food web through the tracking of marine predators. Seabird tracking studies typically take place during the breeding season, when seabirds are required to return to their nest regularly which allows for device deployment and retrieval (Quillfeldt et al., 2017).

Three types of tracking devices are commonly used to track seabirds: Global Positioning System (GPS), Global Location Sensor (GLS), and Platform Transmitter Terminal (PTT) devices. PTT devices are bulky and have a medium resolution of 250 – 1500 m making them ideal for use on large species that travel great distances (Douglas et al., 2012). One benefit of PTT devices is the information collected by the devices is transferred directly to the ARGOS satellite network, meaning birds do not require recapturing for data retrieval (Douglas et al., 2012). GLS devices are small and lightweight which makes them ideal for use on small seabirds (Quillfeldt et al., 2017). However, the resolution of data derived from GLS devices is coarse (150 – 200 km) which means the devices can only determine long distances such as migration patterns (Phillips et al., 2004; Rayner et al., 2017). GPS devices are generally more expensive than both GLS and PTT devices and require recapturing the bird to retrieve data (Recio et al., 2011). Device selection depends on the study species and the spatial scale required for tracking and GPS devices have the benefit of fine-scale resolution data (< 10 m) which allows birds to be tracked over smaller spatial scales (Quillfeldt et al., 2017).

A GPS device is attached to the dorsal surface of a seabird and receives signals from orbiting GPS satellites, triangulating its position from the relative position of the satellites which allows the movement trajectory of the bird to be recorded. In New Zealand, GPS tracking studies have mainly focussed on medium-sized and large species, such as the tākapu/Australasian gannet (*Morus serrator*) (Ismar et al., 2011), tāiko/Westland petrel (*Procellaria westlandica*) (Waugh et al., 2018), takoketai/black petrel (*Procellaria parkinsoni*) (Zhang, 2016), hoiho/yellow-eyed penguin (*Megadyptes antipodes*) (Mattern et al., 2018a) and tawaki/Fiordland penguin (*Eudyptes pachyrhynchus*) (Mattern et al., 2018b). These studies have mainly determined how the different species utilise the marine environment during the breeding season.

Despite the wealth of information of at-sea behaviour garnered through tracking seabirds, there are considerations around the use of devices on the fitness of the animals that are being tracked as the loggers provide extra weight for the study animal to carry while moving. For flying birds, tracking devices weighing greater than 3% of an individual's body mass may negatively impact on foraging (Casper, 2009; Recio et al., 2011), thus this has been suggested as the upper limit of device weight. For swimming birds such as penguins, the cross-sectional area of a device is a more important measurement than weight as their streamlined body shape is compromised with the addition of an external instrument (Bannasch et al., 1994; Ropert-Coudert et al., 2007). It is because of these weight considerations that up until recently, only medium to large size species have been tracked using GPS and other types of tracking devices (Quillfeldt et al., 2017). With technological advances, these devices have become small enough to use on a wider range of seabird species. For example, kuaka/common diving petrel (*Pelecanoides urinatrix*) is a small petrel (weight 135 ± 8g) found breeding in the Hauraki Gulf, New Zealand (Vickers, 2017). The species was tracked using small GPS devices which showed for the first time that individuals travel 40 km from their nest during the breeding season (Zhang et al., 2019). While large species of penguins have been tracked for decades (Hull et al., 1997), it has only been recently that devices have become small enough to track the smallest species of penguin, the kororā (*Eudyptula minor)*.

2.1.2 Tracking and foraging ecology of kororā

Like other penguin species, preferential foraging habitats of kororā are areas of high primary productivity and include frontal zones, eddies, upwellings and river plumes in shallow coastal waters (Kowalczyk et al., 2015b; Poupart et al., 2017). Cold currents carry more nutrients which leads to greater marine productivity, increasing the distribution and abundance of prey species for marine top predators such as penguins (Croxall and Lishman, 1987). Marine productivity is a key determinant of breeding success in kororā, with the presence of upwellings, water current strength and seasonal changes in the distribution and abundance of prey species highly correlated to kororā fledgling rates (Chiaradia et al., 2007). Kororā are generalist foragers and commonly feed on small fish, squid and crustaceans (Flemming et al., 2013). For an in-depth description of kororā diet, see Section 3.1.2, Chapter 3.

The inshore foraging strategy of kororā means they rely on prey availability in shallow coastal waters year-round (Boersma, 2008; Croxall and Lishman, 1987). The small body size and associated anaerobic capacity of kororā limit their foraging to the top 50 m of the water column (Gales et al., 1990). Kororā are visual foragers and search for prey from the surface before diving in a "V" or "U" shape, or less commonly "W" shaped dive profile where they capture prey during the bottom phase (Berlincourt and Arnould, 2014; Cannell and Cullen, 1998; Chilvers, 2017). The foraging patterns of kororā change throughout their different life stages, with foraging trips more constrained during the breeding season (Hoskins et al., 2008).

Like other seabirds, kororā are central-place foragers during the breeding season (Orians, 1979). During egg incubation, one parent will forage during the day while the other remains on the nest (Kato et al., 2008). Foraging trips must be matched with their partner's ability to fast, as kororā will abandon the nest should their body condition decrease below a certain physiological threshold (Numata et al., 2000). Once the chicks hatch, they are guarded by alternate parents for 2 - 3 weeks until they can thermoregulate for themselves at which point both parents then forage at sea (Kato et al., 2008). The frequency with which chicks need to be fed limits the foraging range of kororā while guarding young chicks and individuals are usually restricted to one-day trips within 25 – 30 km of their nest site (Hoskins et al., 2008; Pelletier et al., 2014). In contrast to this commonly observed pattern, a recent study by Poupart et al. (2017) observed kororā from Malborough foraging far beyond this range with individuals travelling 102 km (± 69) during the breeding season in trips lasting > 2 days. These individuals were likely targeting more profitable patches of prey further from their nest to meet the increased energetic requirements of their growing chicks as well as themselves. This distant foraging strategy can indicate a lack of prey availability in the local marine environment immediately surrounding nest sites (Bethge et al., 1997).

Changes in foraging trip length during breeding can indicate changes in prey availability in the marine environment surrounding their colony (Flemming et al., 2013; Numata et al., 2000). The limited foraging range of kororā during the breeding season means prey can be depleted around large colonies, in a phenomenon dubbed “Ashmole's Halo” (Ashmole, 1963). If prey becomes scarce through the halo effect, or other factors such as weather events, overfishing or pollution, kororā must travel further from their nest to meet their nutritional requirements and those of their chicks. Prey scarcity during the breeding season can lead to the reduced body condition of adults, reduced growth rate in chicks and increased chick mortality (Chiaradia et al., 2010; Dann et al., 2000). The breeding season is a time when kororā are accessible on land and when their foraging range is constrained by chick provisioning, making this an ideal life stage to study how kororā utilise the local marine environment for foraging (Hoskins et al., 2008).

Most kororā tracking studies have been from Phillip Island, Australia, as a population of > 30,000 penguins reside there e.g. Berlincourt and Arnould (2014), Kato et al. (2008); Pelletier et al. (2014), Ropert-Coudert et al. (2007). In New Zealand, tracking studies have focused mainly on the Australian/Otago sub-species (*Eudyptula minor novaehollandiae*) with only a few studies on the New Zealand sub-species (*Eudyptula minor iredalei*) at e.g. Chilvers (2017), Mattern (2001), Numata et al. (2004), Poupart et al. (2017), Zhang et al. (2015). The bias in kororā tracking studies toward the Australian/Otago sub-species in New Zealand is likely due to large study colony of kororā in Otago, compared to the small, scattered populations of the New Zealand sub-species found throughout much of New Zealand (Mattern and Wilson, 2018). A pilot tracking study during the 2012 breeding season saw kororā from the Mokohinau Islands forage within 10 km of the colony in 1-2 day trips during early-September (Zhang, 2012). This has been the only tracking study of kororā in the Auckland/Northland region and therefore, there is comparatively scant information about the foraging patterns of kororā in northern New Zealand during the breeding season.

Tracking data can help identify key foraging areas and the movement corridors used by different seabird populations in unpredictable and heterogeneous marine environments (Zhang, 2016). The limited foraging range and reliance on local resources means changes in their foraging patterns of kororā over time or space can reflect shifts in local marine productivity (Kowalczyk et al., 2015b). Short, nearby foraging trips can indicate a healthy marine ecosystem with high prey availability compared to long, distant trips which can suggest prey is scarce (Hoskins et al., 2008)

2.1.3 Study significance

This is the first time kororā have been tracked from Motu Muka in the Marotere Islands and is only the second time kororā have been tracked in the wider Hauraki Gulf region, the first being that of Zhang (2012). This study enhances our knowledge of the foraging ecology of the New Zealand sub-species of kororā, and contributes to filling the knowledge gap of kororā foraging ecology in the wider Hauraki Gulf region, as identified by Mattern and Wilson (2018).

2.1.4 Aims

Considerable differences have been observed in the foraging trip length, range and distances travelled among kororā from Wellington, Motuara Island, Malborough Sounds and the Buller region (Poupart et al., 2017). This study aims to determine whether comparable differences are observed in the foraging patterns of kororā from different colonies in the wider Hauraki Gulf. The specific aims of this study are:

1. How do foraging patterns differ between study colonies?

2. What are the foraging characteristics of kororā in the wider Hauraki Gulf during the breeding season?

2.2 Materials and methods

2.2.1 Device set up

Measures of foraging behaviour were obtained using I-gotU GT120 GPS devices (Mobile Action Technology Inc., Taipei, Taiwan). To ensure a more secure mount on the bird, the devices were removed from their original plastic housing and sealed in 25.4 mm clear polyethylene terephthalate (‘PET’) heat-shrink tubing (Plate 2.1). This ensured the devices were smaller and lighter as well as waterproof. The devices including waterproof tape weighed approximately 25 g in air and had a physical dimension of 42 mm x 25 mm x 12 mm. The loggers weighed < 3% of the mean body weight (874.09 ± 20.39g) of kororā based on the upper limit of logger/body mass ratio recommended by (Wilson et al., 1997) and 5% of the frontal cross-sectional area (5,500 mm^2) (Lovvorn et al., 2001) of kororā, an important device requirement for swimming birds (Bannasch et al., 1994).

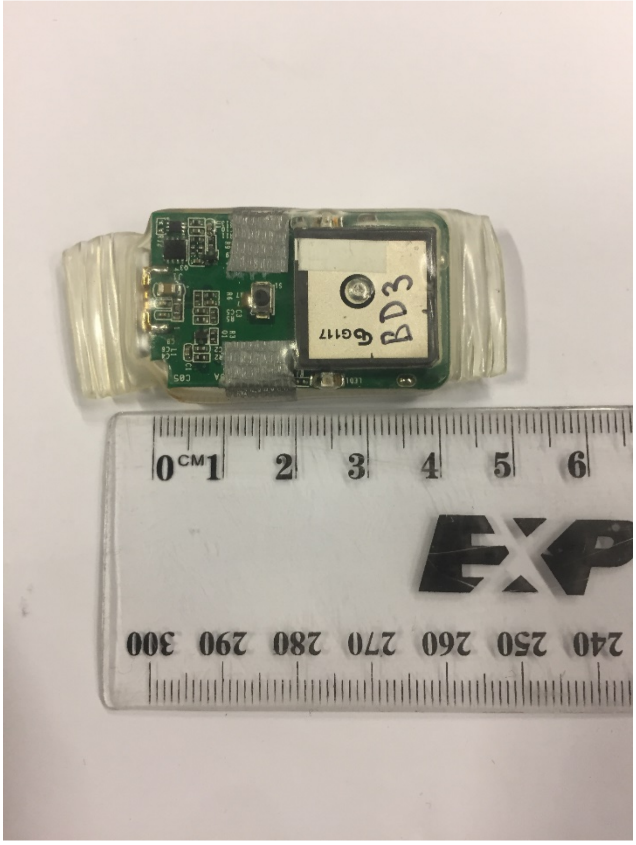


Plate 2.2. An I-GotU GT120 GPS device used to track kororā.

GPS devices were programmed to record a position fix once every two minutes starting at 5 am the following day to avoid battery depletion overnight when penguins were on land. The positional error of the GPS fixes averaged ± 10 m. A two-minute position fix was chosen as per Berlincourt and Arnould (2014) as opposed to one minute in Zhang (2016) in an attempt to record one complete foraging trip per individual before battery depletion.

2.2.2 Field method

Tracking was carried out at one site, Motu Muka/Lady Alice Island in the Marotere Islands group. For a full description of the study site, refer to Section 1.8, Chapter 1. Tracking was originally planned for three sites in the Hauraki Gulf to compare foraging patterns among colonies. Due to permitting delays, tracking was only performed at Motu Muka late in the breeding season.

GPS devices were deployed on 20 penguins over three consecutive nights in November 2018 at South Cove, on Motu Muka. Kororā were captured on the beach as they returned to land after dusk and fitted with GPS devices in a process that took < 10 minutes. Before deployment, morphometric measurements and feather samples were taken as per the methods in Section 3.2.1, Chapter 3.

Devices were attached to the lower dorsal surface with five to seven 1 cm strips of waterproof TESA® tape (No. 4651; Beiersdorf AG, Hamburg, Germany) as per the method used by (Wilson et al., 1997). Due to the streamlined body shape of kororā, the lower back was chosen for logger attachment to minimise drag (Bannasch et al., 1994). The strips were attached sticky side up beneath clusters of feathers and pulled tight over the top of the logger to hold it securely in place. The strips of tape were sealed together with superglue and another larger piece of tape fitted over the logger to streamline the attachment. This method enables the device to be removed while minimising feather damage (Wilson et al., 1997). Once processed, birds were marked with a non-toxic white paint mark on their head in either a vertical stripe, horizontal stripe or “X” to show which night they were caught and similarly had a single, double or long, thin strip of reflective tape attached to the tracker for easy identification under torchlight. Kororā were released where they were captured.

The sex of the kororā in this study was not determined as it was not deemed pertinent to the research question and because most studies on kororā foraging have found no difference in foraging trips between males and females (Chiaradia and Kerry, 1999; Hoskins et al., 2008; McCutcheon et al., 2011). No juveniles were equipped with GPS devices as only breeding aged individuals likely to have chicks were of interest. Due to the lack of study burrows on Motu Muka, it was unknown whether the penguins fitted with devices had chicks but at the time of tracking, penguins in study burrows at other Hauraki Gulf sites were in the late chick rearing stage (Dann, 2013).

GPS devices were deployed for 1-4 days and kororā equipped with GPS devices were re-captured on the beach at South Cove over the following eight nights. Devices were removed in a process that took < 3 minutes. Following device removal, kororā were re-weighed with a 2.5kg Pesola scale and released where they were captured. Of the 20 GPS devices deployed, 14 were retrieved. Six devices were not retrieved but will have either been washed off the bird when swimming or will have fallen off during moult which immediately follows the breeding season in kororā (Gales et al., 1988). One GPS device was corroded inside the heat-shrink casing indicating water leakage occurred and five loggers failed to work due to device error. A total of eight foraging tracks were recorded, which are summarised in Table 2.1.

2.2.3 Track analysis

A foraging trip was determined as the time the GPS turned on at 5 am to the time the penguin returned to the study site. All GPS track records were analysed using ArcMap 10.6.1 (Esri ArcMap, 2018) using the ‘spatial analysis’ package and RStudio software (R Core Development Team, 2018). The default Universal Transverse Mercator (UTM) coordinate system of the devices was transformed into the WGS84 ellipsoid and all location fixes that occurred over land were removed as only their at-sea behaviour was of interest.

As the GPS devices were scheduled to turn on at 5 am the day following attachment, many of the tracks began once the trip had already commenced, rather than when they left the colony. A point was added at the colony and points linearly interpolated between this location and the first position fix for all tracks. Additionally, some of the GPS devices ran out of battery while the penguin was still at sea (n = 6) so for these tracks, points were linearly interpolated between the last position fix and the colony. All recorded tracks (n = 8), complete and incomplete, were recorded in the following analyses.

2.2.3.1 Summary of the kororā foraging trips

To determine the maximum foraging distance, the Great Elliptic measurement tool on ArcMap was used to measure the distance from the colony to the furthest point tracked for each penguin (Table 2.1). The Great Elliptic measurement was used as opposed to Euclidian distance to match the spherical map projection. The R package '*geosphere*' (Hijmans et al., 2014) was used to calculate Great Circle Distance (spherical) between position fixes. From this, I was able to calculate the total distance travelled as the cumulative distance for each trip (in km). Given that six of the eight tracks were incomplete, the total distance travelled for these tracks is underestimated as it is unknown how much further the penguins travelled after battery depletion. The Great Circle Distance divided by the time between fixes provided information of the speed per track in m/sec which was then converted to km/hr. The distance to the first point and distance from the last point were excluded from the speed calculation as we did not know exact departure and arrival times. Any unrealistic speeds of greater than 2 m/sec were removed (Hoskins et al., 2008).

The trip duration tracked was the time elapsed between the first and last position fixes taken by the GPS device (i.e. the duration of the battery) whereas ‘trip duration until capture’ was the time elapsed between the first position fix and the minimum time of capture on the evening the GPS device was removed.

2.2.3.1 Trajectory map

The following spatial analyses were carried out in ArcMap 10.6.1. Point and line trajectories of the penguins were overlaid on the ArcMap Ocean_Basemap and each track was assigned a different colour (Figure 2.1). NIWA (2016) New Zealand Bathymetry Contours were added to see whether the ocean bathymetry was related to the penguin foraging trajectories.

2.2.3.3. Kernel density map

The spatial distributions of movement trajectories were determined by calculating kernel density using the ArcMap spatial analyst tool “kernel density”. Kernel density estimates the unknown probability distribution of a random variable based on sample points as determined by Worton (1989). Due to the small sample size there is likely a strong individual bias in the kernel distribution. The key areas where kororā movement was concentrated were assigned the following contours: the core area as a solid line (25% kernel UD), the focal area as dotted line (50% kernel UD) and the overall activity area as a dashed line (90% kernel UD).

2.3 Results

2.3.1 Foraging characteristics

Of the eight individuals tracked, only two were complete tracks (denoted by * in Table 2.1) due to the limited battery life of the devices and longer foraging trip length late in the breeding season. Individual 6 had the longest trip duration that was tracked (33.21 hours). The longest trip duration between the start of tracking and the time of recapture was 88 hours for the first kororā caught, individual 1. ‘Trip duration until capture’ assumes kororā were caught after only one foraging trip, which may not have been the case if kororā were missed when coming ashore. The topography of the beach meant most kororā were funnelled up a rock face so were unlikely to evade capture in this way. However, kororā may have come ashore after observations had concluded for the night, usually around 1.30 - 2.30 am.

Birds that were tracked for the entirety of their trips covered distances of around 41 km over the course of 16 hours. However, incomplete data sets suggest that penguins may travel considerably greater distances. The maximum distances from the colony were 15.81 km (individual 3) and 11.92 (individual 2) for the birds with complete tracks. For the six birds with incomplete tracks, the average maximum distance from the colony was 20.52 km and the total distance travelled varied between 42.55 and 75.01 km using the interpolated tracks that linked the first and last GPS fixes to the colony. The the maximum speed maintained by a bird over the course of its foraging trip was 2.7 km/h (individual 8) and the average travel speed of all birds combined was 2.0 (± 0.18) km/hr. All eight individuals were recaptured within 1-4 days.

Table 2.1. Foraging parameters of eight kororā/little blue penguins (*Eudyptula minor iredalei*) equipped with GPS devices at Motu Muka/Lady Alice Island during the 2018 breeding season. Trip duration tracked was the time elapsed between the first and last position fixes taken by the GPS device whereas trip duration until capture was the time elapsed between the first position fix and the time of recapture. * denotes complete foraging tracks.

Individual	Track colour	No. of fixes	Trip duration tracked (h)	Trip duration until capture (h)	Max distance from the colony (km)	Total distance travelled (km)	Speed (km/h)
1	red	*784*	28.85	88	21.80	75.01	1.71
2*	dark blue	307	15.96	16	11.92	40.58	2.35
3*	white	181	15.95	16	15.81	41.87	2.21
4	orange	704	29.46	40	23.23	64.49	1.32
5	grey	847	31.78	76	19.14	72.20	1.75
6	light blue	750	33.21	40	22.51	65.05	1.48
7	green	*442*	21.15	64	20.59	81.59	2.48
8	yellow	263	10.06	16	15.90	42.55	2.70
Mean (±SEM)		**534.75 (±93.93)**	**23.30 (±3.07)**	**44.50 (±10.13)**	**18.86 (±1.40)**	**60.42 (±5.82)**	**2.00 (±0.18)**

2.3.2 Foraging direction

All eight kororā headed in a westerly direction from the study site of Motu Muka toward the mainland and spent most of their time in the ocean near the coast with a depth < 50 metres (Figure 2.1). A red star shows the kororā colony at South Cove on Motu Muka. The trajectories of individuals 2 (dark blue) and 3 (white) were one-day foraging trips where the batteries recorded the entire trip. The trajectory of individual 8 (yellow) was also a one-day foraging trip but the battery ran out at sea mid-afternoon, as can be seen with a straight line interpolating the minimum distance between the last position fix and the colony. Individual 7 (green) travelled the longest cumulative distance of 81.59 km and was recaptured after 64 hours, although the tracking device only recorded position fixes for 21.15 hours. This particular device turned off between

9 pm and 5 am and missing position fixes during this time were linearly interpolated. Individual 4 (orange) travelled the furthest distance from the colony into the shallow coastal waters of Bream Bay at a distance of 23.23 km from Motu Muka.

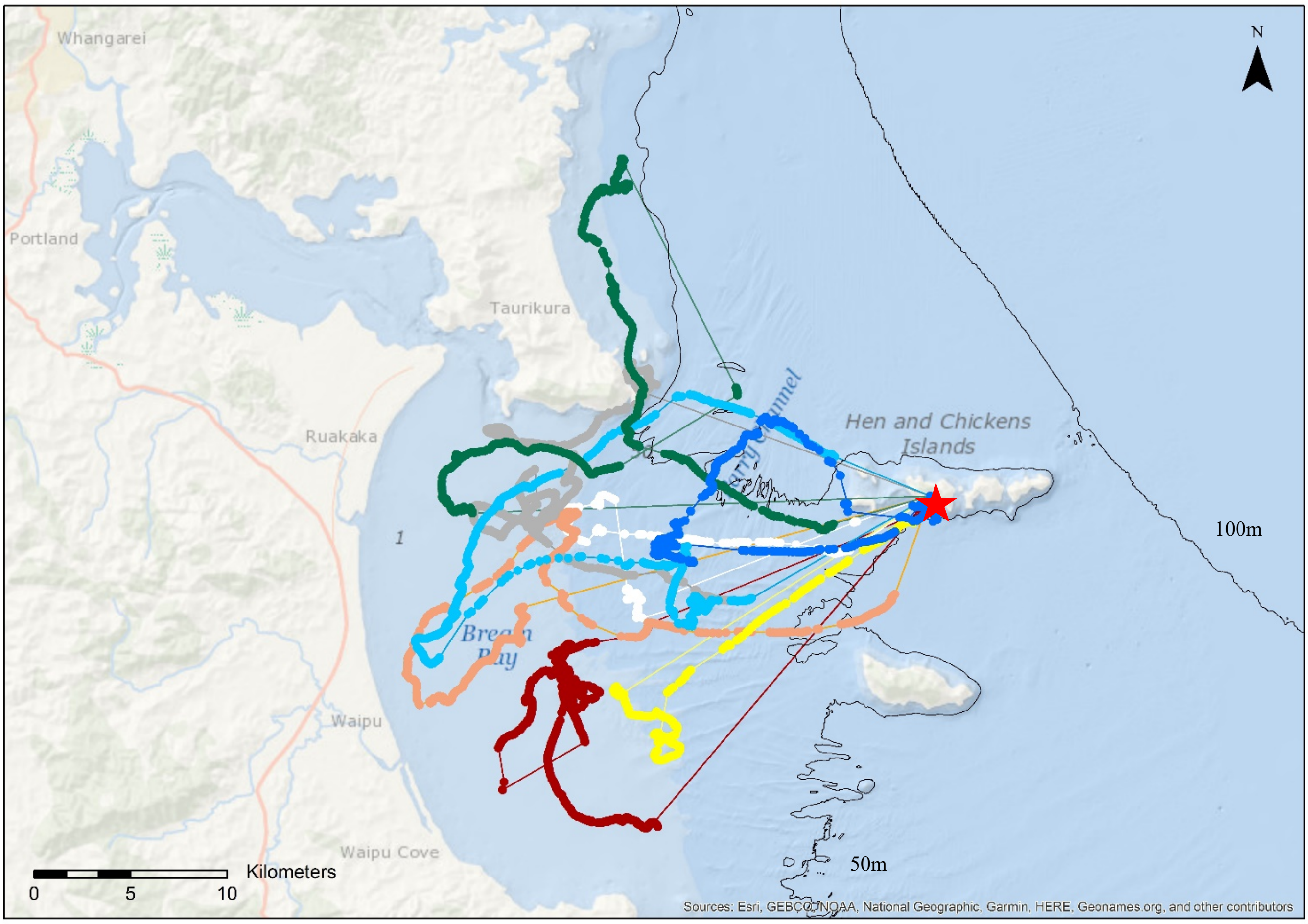


Figure 2.1. Foraging trajectories of eight kororā/little blue penguins (*Eudyptula minor iredalei*) from Motu Muka/Lady Alice Island during the 2018 breeding season as recorded by GPS data loggers. The nominal sampling interval of the loggers was 1 fix every 2 minutes. Colours represent tracks of different individuals. The location of the penguin colony is indicated by a red star. 50m depth contours given. Sources of the background map: Esri, GEBCO NOAA, National Geographic, Garmin, HERE. Geonames.org and other contributors.

2.3.3 Foraging hotspots

The overall foraging area (90% kernel UD; dashed line) shows pockets of activity ranging from Ocean Beach in the north to Waipu Cove in the south and a small patch immediately South of Motu Muka (Figure 2.2). Both 50% (dotted line) and 25% (solid black line) kernel UD occurred in water < 50 m depth.

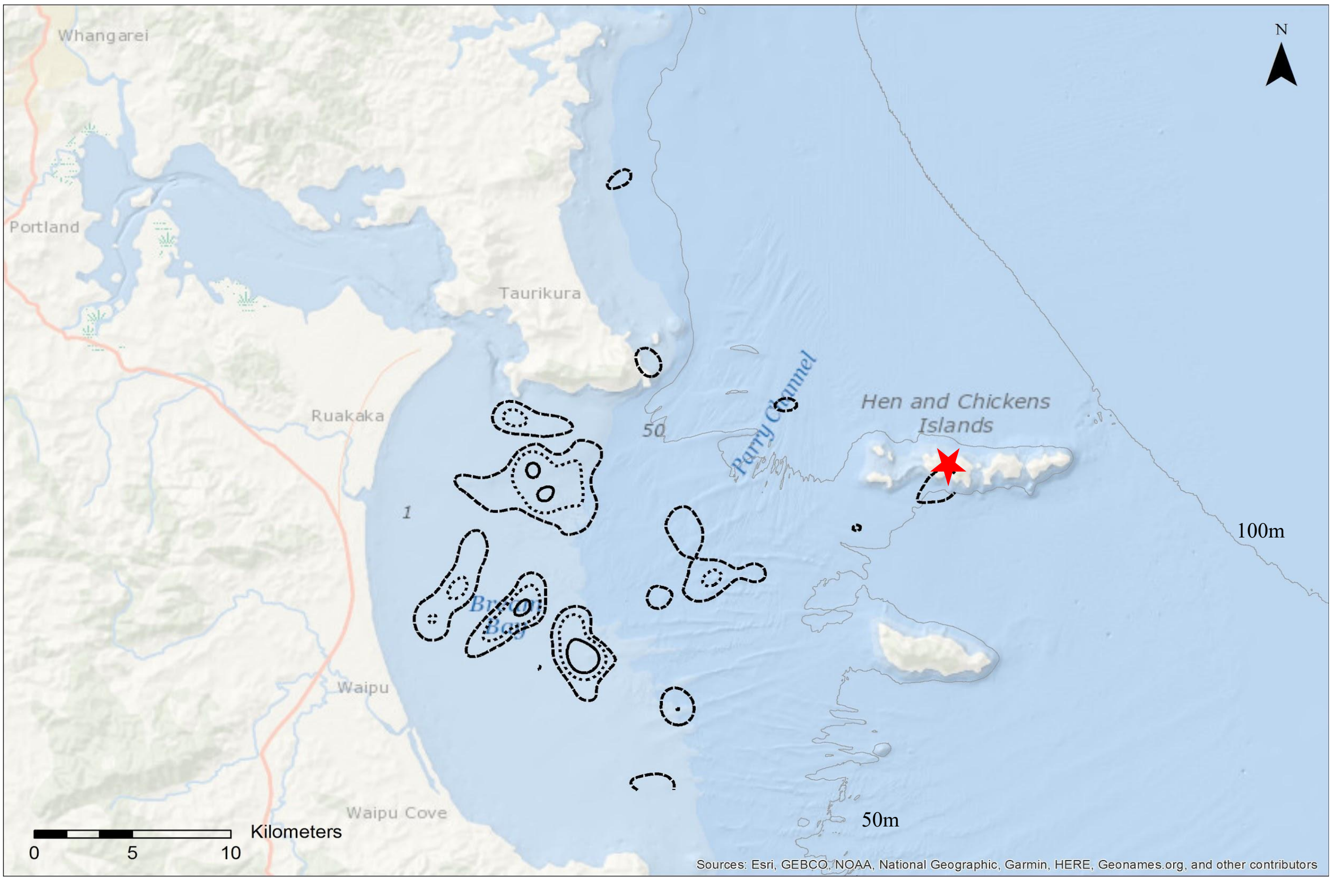


Figure 2.2. Kernel Density Analysis of eight kororā/little blue penguins (*Eudyptula minor iredalei*) tracks from Motu Muka/Lady Alice Island during the 2018 breeding season as recorded by GPS data loggers. The core area (solid line; 25% kernel UD), focal area (dotted line; 50% kernel UD) and overall activity area (dashed line; 90% kernel UD) are represented. The location of the penguin colony is indicated by a red star. 50m depth contours given. Sources of the background map: Esri, GEBCO NOAA, National Geographic, Garmin, HERE. Geonames.org and other contributors.

2.4 Discussion

How kororā utilise the marine environment in the wider Hauraki Gulf is relatively unknown, as only one other tracking study has occurred in the region by Zhang (2012) on the Mokohinau Islands. Given this, the information gained from this study has helped fill the knowledge gap of the foraging patterns of kororā in northern New Zealand as identified by Mattern and Wilson (2018). The limited foraging range and reliance on local resources means changes in the foraging behaviour of kororā can indicate changes in prey availability near to nesting sites (Flemming et al., 2013). As well as indicating the abundance and availability of prey near the Marotere Islands during the breeding season, the information gained from this study can help inform where at-sea protection could benefit the population of Motu Muka.

This study aimed to determine whether any spatial segregation patterns were observed in kororā foraging in the wider Hauraki Gulf as this has been observed in the region by common diving petrels (Vickers, 2017; Zhang et al., 2019) and among kororā colonies in Wellington and the South Island (Poupart et al., 2017). Unfortunately, this study was only able to track kororā from one site in the wider Hauraki Gulf due to permit delays.

2.4.1 Foraging characteristics

The foraging ranges, travel distances and trip durations of kororā in this study were comparable to those reported for kororā elsewhere in New Zealand and in Australia (Hoskins et al., 2008; Pelletier et al., 2014; Zhang et al., 2015). Kororā in this study travelled further from the colony for longer than individuals from the Mokohinau Islands in 2012 (Zhang, 2012). These differences were likely due to the different stages of chick-rearing duties and associated foraging trip lengths (Hoskins et al., 2008) in early September (Zhang, 2012) and late November (this study), or due to variation in marine productivity among the sites or across years (Chiaradia and Nisbet, 2006). The time elapsed between the start of tracking and the time of capture acted as a proxy for foraging trip length and varied between 1 - 4 days in this study. Foraging trips lengths during the breeding season have been shown to vary between 1-7 days depending on chick age and environmental conditions (Chiaradia and Nisbet, 2006). The maximum distance tracked from the colony was within the 30 km radius determined by Hoskins et al. (2008); Pelletier et al. (2014); Zhang et al. (2015) and the total distance travelled (60.42 ± 5.82 km) was within the range of other chick rearing birds in November (28 – 213 km) as discussed by Poupart et al. (2017).

The foraging trips observed in this study suggest sufficient prey may have been available within 25 km of the colony for those individuals tracked. It is possible, however, that individuals equipped with trackers who did not return during the study period were on longer, more distant foraging trips and were unable to capture sufficient quantities of prey in the local marine environment surrounding Motu Muka (Bethge et al., 1997). The effort expended on foraging trips is highly linked to breeding success with higher foraging effort related to a decreased fledgling rate (Chiaradia et al., 2007). Juvenile birds that are adequately provisioned have a greater body condition and a higher chance of survival into adulthood than those with increased nutritional stress (Kitaysky et al., 2010). This has been observed in a recent study by (Ainley et al., 2018), who showed that juvenile Adelie penguins (*Pygoscelis adeliae*) with greater body mass at fledging were more likely to return to breed than those of lower weights. Due to a lack of study burrows in this study fledging weights were unable to be obtained, which may have provided more information on prey availability in the shallow marine environment surrounding Motu Muka. In areas of low prey availability, higher foraging effort has been observed with kororā diving deeper and for longer than in areas of high prey availability (Chilvers, 2017). Similarly, Poupart et al. (2017) found that kororā in the Malborough region that spent longer foraging, travelled further from the nest and travelled a greater distance produced fewer chicks in 2014 than in 2015 where foraging effort was lower.

2.4.2 Foraging direction and hotspots

All of the kororā tracked in this study foraged in the shallow coastal waters of Bream Bay to the west of Motu Muka where the water depth is less than 50 m. Previous studies of kororā dive depth using Time-Depth Recorders (TDR) have shown the majority of prey captures occur along the seafloor (Ropert-Coudert et al., 2006). The maximum seafloor depth of 60 m throughout much of the wider Hauraki Gulf means most of the region is shallow enough for kororā to forage throughout the entire water column without exceeding their physiological limit (Chilvers, 2017). In areas of gentle sloping bathymetry such as Oamaru, kororā forage up to 30 km from their nest during the breeding season which differs to penguins from the Queen Charlotte Sounds, where the steep bathymetry sees kororā foraging much closer to shore, travelling just 9 km from their nests (Chiaradia et al., 2007).

The focal foraging area of kororā (50% kernel UD) likely receives increased nutrient loading from the Hātea River and Whangarei Harbour. Kororā have been shown to preferentially forage near river mouths and estuarine plumes where high levels of Chlorophyll-a, lower salinity and sea surface temperature aggregate prey (Kowalczyk et al., 2015b; Poupart et al., 2017). Turbidity also appeared to benefit kororā foraging to an extent, but focal foraging areas were shown to have lower turbidity than home ranges (95% kernel UD) suggesting prey was easier to capture in less turbid waters (Kowalczyk et al., 2015b). Little is known about what influences the distribution of kororā prey species in the Hauraki Gulf, but Bream Bay is a known spawning ground for mohimohi/pilchard (*Sardinops sagax*) (Paul and Parkinson, 2001) and is also one of the few places in New Zealand the species is caught in large quantities by the bait fishery (Paul, 2014).

2.4.3 Summary

This study successfully tracked kororā from Motu Muka during the 2018/2019 breeding season and highlighted the importance of the shallow coastal environment within 25 km of the colony for the individuals tracked. The results showed all individuals travelled in a westerly direction away from the colony and all foraging hotspots were in water depths of < 50 m near Bream Bay. Foraging trip length, distance travelled and maximum distance from the colony differed among individuals. While this study was unable to determine spatial differences in foraging patterns among sites in the wider Hauraki Gulf, it can serve as a baseline for the foraging pattern of kororā from Motu Muka during the breeding season.

Chapter 3. Prey trophic level and foraging location as determined by feather stable isotopes

Plate 3.1. A kororā at Tawharanui. Photo by Edin Whitehead, 2018.

3.1 Introduction

3.1.1 Stable isotopes as proxies for seabird diet and foraging location

Determining how seabirds use marine ecosystems can help us understand how fluctuating oceanic conditions impact seabird populations (Cherel and Hobson, 2007) and is heavily reliant on appropriate means to unpick these relationships. Three types of markers that may be useful for tracking animal movements, and thus how seabirds utilise the marine environment, include extrinsic, biological, and biogeochemical markers (Rubenstein and Hobson, 2004). Extrinsic markers involve directly tracking animals by attaching devices to them (Chapter 2), or through the use of remote sensing data. Extrinsic markers are the most commonly used because they provide precise data on animal movement (Quillfeldt et al., 2017). Biological markers, such as genetic, behavioural and morphological variation, can be used to identify individuals from the same population over large spatial scales (Rubenstein and Hobson, 2004). Biogeochemical markers, such as trace elements and stable isotopes, can indirectly show us where an animal has been foraging and on the trophic level of prey consumed (Inger and Bearhop, 2008). The most common stable isotopes analysed in seabird diet studies are carbon and nitrogen, with stable carbon isotope values ($\delta^{13}C$) indicating the foraging location and stable nitrogen isotope values ($\delta^{15}N$) acting as a proxy for the trophic position of prey items (Hobson et al., 1993). Measurements of $\delta^{15}N$ (the ratio between light ^{14}N and heavy ^{15}N nitrogen isotopes) escalate in a predictable stepwise fashion as they move up the food web, increasing 3 - 5‰ with each trophic level (Post, 2002). Higher trophic level prey is generally of better nutritional value, thus the trophic level consumed can indicate the availability of quality prey items (Ainley et al., 2018). Stable isotopes are resistant to radioactive decay and are heavier than their common forms due to added neutrons, which allows them to be tracked through the food web (Inger and Bearhop, 2008).

Stable isotopes present in prey species are synthesised into the tissues of predators that consume them, tissues such as blood, hair, feathers and nails (Inger and Bearhop, 2008). Blood is metabolically active and reflects the diet of the predator over a period of a few weeks (Cherel et al., 2005a). Keratinised tissues (e.g. feathers) and bones are inert once grown, thus the stable isotopes of prey species consumed during the weeks to months of tissue growth remain present in those structures until they are replenished (Inger and Bearhop, 2008). In terrestrial environments, plants have different photosynthetic pathways, which are reflected in their $\delta^{13}C$ values (Hobson et al., 1993). In the marine environment, inshore coastal ecosystems with greater terrestrial input have higher $\delta^{13}C$ compared to pelagic environments where carbon is mainly derived from phytoplankton fixation (Post, 2002). Measurements of $\delta^{13}C$ (the ratio between light ^{12}C and heavy ^{13}C carbon isotopes) do not change as they move through food webs, indicating the geographical origin of the prey species (Rubenstein and Hobson, 2004). Accordingly, by looking at $\delta^{15}N$ and $\delta^{13}C$ in seabird tissues, inferences can be made about the dietary trophic level and foraging range of these predators.

Conventional diet studies in seabirds have used a stomach flushing technique (lavaging) to identify the prey species consumed by seabirds e.g. Flemming et al. (2013). While this approach allows prey to be recognised at a species level, identification often requires specialist knowledge and often overestimates the proportion of fish in the diet of the seabird, while underestimating the proportion of crustaceans due to their lack of indigestible hard parts (Flemming and van Heezik, 2014). Stomach flushing provides a snapshot of what seabirds have consumed over the past hours or days, but this method can be stressful for the individual and deprives chicks of a meal if performed during the breeding season (Inger and Bearhop, 2008). Stable Isotope Analysis (SIA) using blood and feather samples is an alternative way to look at the diet of marine megafauna and is a non-destructive sampling method increasingly used in studies of seabird migration routes, resource partitioning and foraging plasticity (Bearhop et al., 2002; Cherel and Hobson, 2007). Feathers are easy to sample with less specialist knowledge required, and sampling is less invasive than stomach flushing (Cherel et al., 2005).

Most diet studies take place during the breeding season, as this is when seabirds are accessible on land (Chiaradia et al., 2003; Chiaradia et al., 2012; Flemming et al., 2013; Fraser and Lalas, 2004). This can be problematic in the sense that sampling feathers indicates the diet at the time of feather growth, which may differ from that of the breeding season (Kowalczyk et al., 2015a). Nonetheless, long-term trends in foraging can be seen through SIA of feathers, and thus can be used to monitor shifts in marine ecosystem health over long temporal scales (Fleming et al., 2018). Stable isotopes remain unchanged over time, therefore comparisons can be made between the foraging patterns of extant individuals and museum specimens. This was seen in a change of the rockhopper penguins (*Eudyptes chrysocome*) foraging locations over time by Hilton et al. (2006), with penguins in the 1870s foraging closer to shore as determined through higher $\delta^{13}C$ values than those in the 1990s, who foraged further offshore. Similarly, a shift in the prey trophic level of glaucous-winged gulls (*Larus glaucescens*) was observed through feather SIA, with gulls in the 1860s feeding on higher trophic level prey than those in the 2000s (Blight et al., 2015). Changes in isotopic niches indicate a shift in the feeding location and the trophic level of prey species, and thus by observing these shifts, inferences of the fluctuations in marine resource availability can be made (Blight et al., 2015).

3.1.2 Kororā foraging during the pre-moult period

Kororā are generalist foragers, and typically consume a diet of >70% small, shoaling fish followed by cephalopods (<5%) and a small number of crustaceans (Chiaradia et al., 2003; Flemming et al., 2013). The size range of prey items is between 15 – 100 mm (Fraser and Lalas, 2004). The majority of kororā diet studies have taken place in South Australia during the breeding season e.g. Chiaradia et al. (2003); Chiaradia et al. (2016); Kowalczyk et al. (2014), where mohimohi/pilchard (*Sardinops sagax*), kokowhawha/anchovy (*Engraulis australis*), manga/barracouta (*Thyrsites atun*) and squid were identified as popular food items. In the South Island of New Zealand, kurahina/Graham's gudgeon (*Grahamichthys radiata*), slender sprat (*Sprattus antipodum*), ahuru (*Auchenoceros punctatus*) and wheketere/arrow squid (*Nototodarus sloanii*) are important components of the kororā diet (Flemming et al., 2013; Fraser and Lalas, 2004). Only one study has assessed the diet of kororā in the

Hauraki Gulf and found that fish made up 85.71% of the diet, followed by cephalopods (42.86%), copepods (35.71%) and other crustaceans (14.29%) (Geurts, 2006). Anchovy and one species of cephalopod (likely arrow squid) made up the largest proportion of the diet at 21.88% and 18.75% of the diet respectively. These species were followed by fish type A, either yellow-eyed mullet (*Aldrichetta forsteri*) or lantern fish (*Myctophidae*) (15.63%), copepods (15.63%) and fish type B, likely goby (*Parioglossus spp.*) at 12.5% (Geurts, 2006). Other studies of kororā foraging ecology in the Hauraki Gulf include two studies of feather stable isotopes by Geurts (2006) at Tiritiri Matangi and McKenzie (2011) at Tiritiri Matangi and Kawau island, and one tracking study at the Mokohinau Islands (Zhang, 2012). Given that most studies of kororā diet have occurred during the breeding season, little is known about their foraging behaviour during the pre-moult period.

Outside of the breeding season, kororā remain resident in the inshore marine environment surrounding their nesting site and regularly return to land during this time (Gales et al., 1988; McCutcheon et al., 2011). It is at this time kororā prepare for the next breeding season, which includes undergoing an annual post-breeding moult, a two to three week period where new feather growth occurs (Kinsky, 1958). Old feathers get worn out and lose their insulation and waterproofing properties, which can be critical for a bird that spends the majority of its time in the ocean (Reilly and Cullen, 1983). As kororā are not waterproof during moult, they are unable to forage at sea and can lose up to 46% of their body mass (Gales et al., 1988). Accordingly, moult is a stressful time for penguins because they are unable to forage and new feather growth creates high energetic demands, thus this is when the body condition is often at its lowest and high mortality rates occur (Klomp and Wooller, 1988; Mortimer and Lill, 2007). Outside of the breeding season, kororā are less spatially constrained in their foraging patterns and can exploit patches of prey that are usually beyond their reach when they are provisioning chicks (Chiaradia et al., 2012). Like other seabirds e.g. Leach’s storm petrel (*Oceanodroma leucorhoa*) (Fairhurst et al., 2015), kororā forage more broadly in the non-breeding season (Kowalczyk et al., 2015a). During pre-moult foraging trips kororā gorge themselves and greatly increase their body mass to survive weeks of fasting (Gales et al., 1988; Klomp and Wooller, 1988). Analysis of feather stable isotopes is a novel way to determine the foraging patterns of kororā outside of the breeding season.

3.1.3 Spatial and temporal comparisons of foraging

Stable isotopes in penguin feathers reflect the broad foraging location and prey trophic level consumed during pre-moult foraging trips which are between December and March in New Zealand (Dann, 2013). The synchronised moult strategy of kororā means that stable isotopes in feathers are comparable over time and space, as all individuals grow their plumage at the same time of year and typically moult at the same colony where they breed (Kinsky, 1958). It is because kororā remain resident near their colonies year round that changes in the feather stable isotopes of kororā can shed some information on the distribution and abundance of prey, and thus marine productivity, during the pre-moult foraging period (Bortolotti et al., 2008; Kowalczyk et al., 2015a).

3.1.4 Study significance

This study is significant as it is the first stable isotope analysis of kororā feathers from Motu Muka, Tāwharanui and Otata and the most recent comparison of stable isotopes from museum specimens to contemporary individuals Given that few studies have examined the diet and foraging locations of kororā in the wider Hauraki Gulf e.g. Geurts (2006); McKenzie (2011); Zhang (2012), this study contributes further information on the foraging ecology of kororā in the region

3.1.5 Aims

This study aims to determine whether the prey trophic level and broad foraging locations of kororā in the wider Hauraki Gulf are different among colonies or whether they have changed over time. This study also aims to fill knowledge gaps of the foraging ecology of kororā outside of the breeding season and in the New Zealand sub-species. The specific aims of this study are to determine:

1. Are differences observed in the diet and foraging location among three colonies of kororā in the wider Hauraki Gulf?

2. Has the diet and general foraging location of kororā in the Hauraki Gulf changed over time?

3.2 Materials and Methods

3.2.1 Field method

Feathers samples were collected from both live and dead individuals at Motu Muka/ Lady Alice Island (n = 37), Tāwharanui (n = 11) and Otata (n = 11) in November and December 2018. For full descriptions and maps of field sites, see Section 1.8, Chapter 1.

Individuals were captured by hand either on the nest or intercepted when returning from a foraging trip. On Motu Muka, birds were caught at South Cove and measurements, feather collection and GPS attachment (Section 2.2.2, Chapter 2) carried out in the open on the rocky outcrop above the beach. Due to low numbers, at Tāwharanui birds were captured at multiple sites along both the north and south coast, and on Otata birds were captured at a range of locations in the vicinity of the bach.

At each of the study sites, birds were placed in a dark-coloured cotton bag to minimise stress. In total, eight feathers were collected from the breast of the bird where six feathers were for used in feather corticosterone analysis (Chapter 4) and two for stable isotope analysis. Feathers were stored in a labelled ziplock bag for later analyses. Morphometric measurements were also taken. Processing lasted < 3 minutes and kororā were released where they were captured. Individuals sampled from the above field sites were compared to necropsied wild birds collected during 2015 – 2018 (n = 12; Massey University) and specimens from the Auckland War Memorial Museum (AWMM) spanning 1905 to 1977 (n = 17). Specimens from both Massey and AWMM were collected from a range of locations in the Hauraki Gulf, thus do not reflect one particular site.

The sex of the kororā in this study were not determined as it was not deemed pertinent to the research question, and as no difference in kororā diet has been observed between males and females (Chiaradia et al., 2012; Pelletier et al., 2014). No juveniles were sampled for SIA as feather growth occurred at a different time of year so isotopic values were incomparable. Juveniles were determined by iridescent blue plumage and smaller bill size (Dann, 2013).

3.2.2 Lab method

Due to financial constraints, not all kororā feather samples were analysed for stable isotopes. Randomly selected samples from each group were as follows: Motu Muka (n = 20), Tāwharanui (n = 5), Otata (n = 7) and all samples from Massey University necropsy specimens (n = 12). Data of feather stable isotopes from museum specimen kororā were shared with me by the Auckland War Memorial Museum but were analysed at the same lab using an identical method.

Kororā feather samples (n = 44) were sent to the National Institute of Water and Atmospheric Research (NIWA) for stable isotope analysis. Lipids were removed before analysis as these contain carbon but no nitrogen and therefore bias the isotopic ratio (Bearhop et al., 2002). Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) were analysed from kororā feather samples using an AS200 LS autosampler and NA 1500N (Fisons Instruments, Rodano, Italy) elemental analyser combustion furnace connected to a DELTA^{Plus} continuous flow, isotope ratio mass spectrometer (Thermo-Fischer Scientific, Bremen, Germany) by the NIWA Environmental Stable Isotope Laboratory in Wellington. Operational details are outlined in Rayner et al. (2016) with the exception that δ^{13}C values were calibrated against a CO_2 reference gas, relative to the international standard Carrara Marble NSB-19 (National Institute of Standards and Technology (NIST), Gaithersberg, MD, USA). This was calibrated against the original Pee Dee Belemnite (PDB) limestone standard and was then corrected for ^{17}O. Carbon isotope data were corrected via a two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid; certified δ^{13}C = -26.39 ± 0.09‰) and NIST 8542 (IAEA-CH-6 Sucrose; certified δ^{13}C = -10.45 ±0.07 ‰). A two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid; certified δ^{15}N = -4.52 ± 0.12‰) and IAEA-N-2 (ammonium sulphate: certified δ^{15}N = +20.41 ± 0.2‰) was applied to δ^{15}N data. DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $C_6H_{13}NO_2$, Lot 127H1084, Sigma, Australia) was run every ten samples to check analytical precision and enable drift corrections to be made if necessary. Additional international standards NIST 8574 (USGS41 L-glutamic acid; certified δ^{13}C = +37.63 ±0.10‰ and δ^{15}N = +47.57 ±0.22‰), NIST 8547 (IAEA-N1 ammonium sulphate; certified δ^{15}N = +0.43 ±0.04‰) were run daily to check isotopic accuracy. Repeat analysis of standards produced data accurate to within 0.25‰ for both δ^{15}N and δ^{13}C, and precision of better than 0.32‰ for δ^{15}N and 0.24‰ for δ^{13}C. Isotope ratios are reported in (δ) notation as parts per thousand (‰).

The δ^{13}C for all feather samples were corrected for the Suess effect, which adjusts for a temporal decline in carbon values due to an increase in atmospheric carbon caused by anthropogenic activities (Suess, 1955). δ^{13}C was not corrected for changes in aquatic CO_2 as Bond and Lavers (2014) showed these were within the bounds of analytical error in stable isotope analysis.

3.2.3 Statistical Analyses

3.2.3.1 Spatial differences in the foraging pattern of kororā

A one-way analysis of variance (ANOVA) was used to compare the means of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes among the three sites and to specimens from Massey University and the AWMM. A Shapiro-Wilk normality test confirmed the data met the assumptions of normality. A multiple pair-wise comparison among the groups was conducted using the Tukey post-hoc significant difference test.

3.2.3.2 Trends of feather stable isotopes over a 113-year period

Furthermore, second-order polynomial regression models were fitted to identify significant associations between $\delta^{13}C$ and $\delta^{15}N$ and years. Results are presented as means ± Standard Error of the Mean (SEM) unless otherwise indicated.

The statistical analyses were performed in R version 3.4.1 (R Core Development Team, 2018).

3.3 Results

The mean body weight for all individuals was 892.38 ± 27.61g. Isotopic niches of the kororā groups are shown in Figures 3.1 and 3.2 and a time series of the data can be seen in Figure 3.3. Differences in $\delta^{13}C$ ($F_{(4,56)} = 93.07$, p-value <0.001), and $\delta^{15}N$ ($F_{(4,56)} = 5.326$, p-value = 0.001) were observed among the five groups.

3.3.1 Differences in foraging among colonies

Auckland War Memorial Museum specimens had significantly higher levels of $\delta^{13}C$ than all other groups (Figure 3.1), indicating those individuals foraged further inshore than the contemporary kororā sampled. Individuals from Motu Muka foraged further offshore (lower $\delta^{13}C$) than specimens from Massey University (Adj p-value = 0.000), and Otata (Adj p-value = 0.002). The difference in $\delta^{13}C$ between Tāwharanui and Massey was also significant (Adj p-value = 0.039) as individuals from Tāwharanui had lower carbon values than Massey specimens which indicated a further offshore foraging location in the Tāwharanui group. Motu Muka had significantly lower $\delta^{15}N$ values than AWMM (Adj p-value = 0.032), Massey (Adj p-value = 0.011) and Otata (Adj p-value = 0.016) indicating individuals foraged on lower trophic level prey during pre-moult foraging trips (Figure 3.1). No difference in $\delta^{15}N$ was observed between samples from Motu Muka and Tāwharanui (Adj p-value > 0.05).

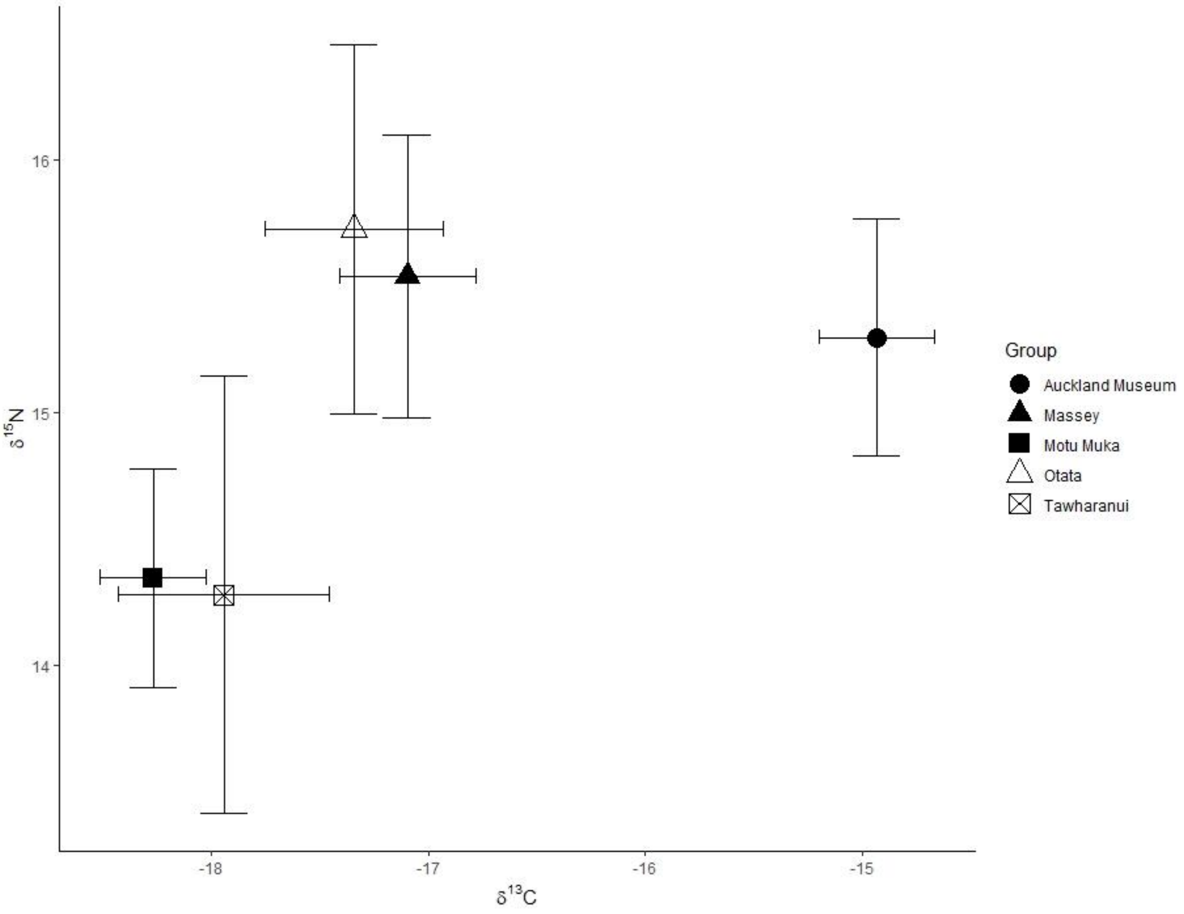


Figure 3.1. Stable isotope signatures (δ15N and δ13C) of modern and museum feather samples from Kororā/Little Blue Penguin (Eudyptula minor iredalei) in the wider Hauraki Gulf. Depicted are museum specimens (1905 - 1977), Massey University necropsy specimens (2015-2018), Motu Muka (2018), Otata (2018) and Tāwharanui (2018). Values are shown as means ± Standard Error of the Mean (corrected for the Suess effect) for modern and museum samples.

The isotopic niches of each of the groups are shown in Figure 3.2. Massey and AWMM had wide confidence intervals with individual isotope values scattered across a wider range which reflected the greater spatial distribution of the sample origins. Motu Muka had the smallest niche, followed by Tāwharanui and Otata. The isotopic niches of AWMM samples overlapped with those from Massey, but contemporary kororā and historic kororā showed a reasonable amount of segregation. Motu Muka, Tāwharanui and Otata ellipses fell mostly within the 90% confidence interval of Massey samples.

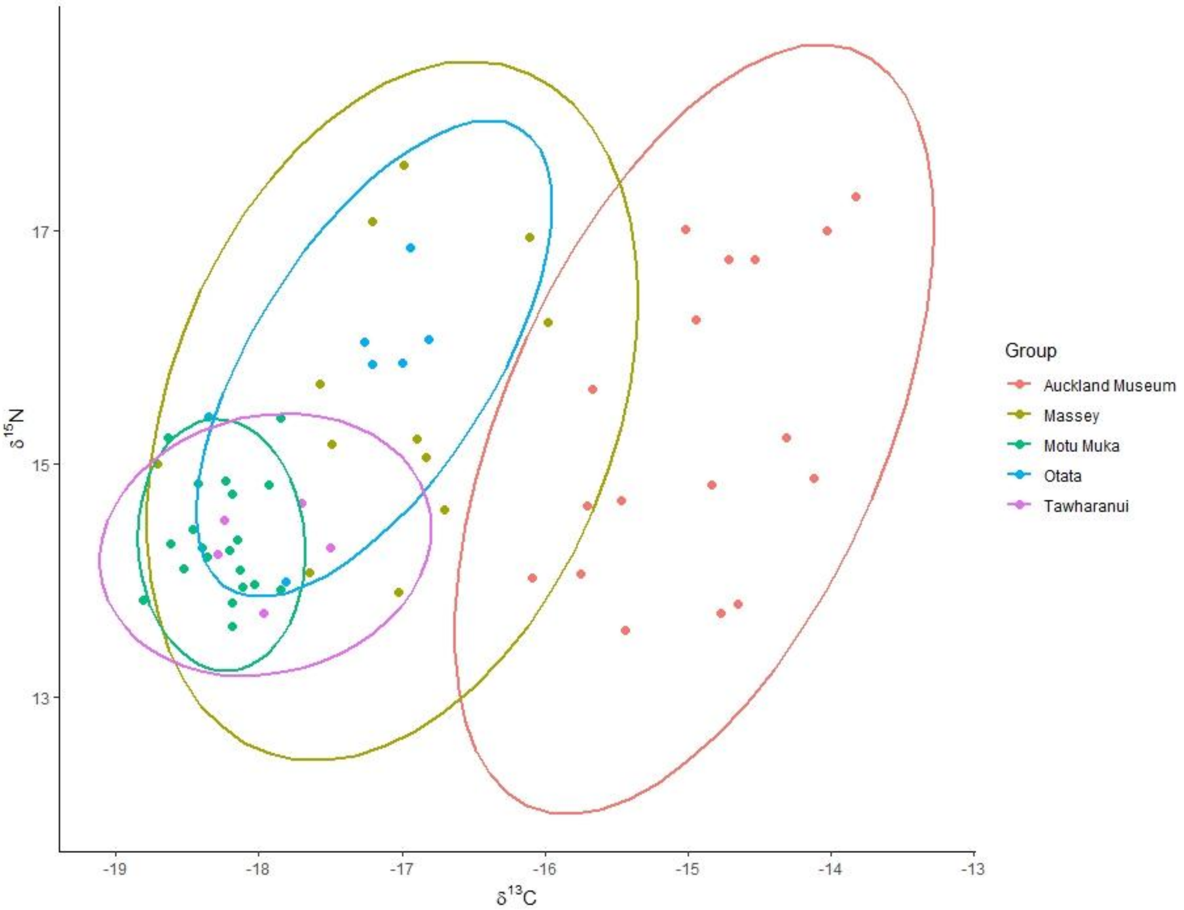


Figure 3.2. Isotope values ($\delta^{15}N$ and $\delta^{13}C$ corrected for the Seuss effect) of modern and museum feather samples from kororā/Little Blue Penguin (*Eudyptula minor iredalei*) in the wider Hauraki Gulf. Depicted are museum specimens (1905 – 1977), Massey University necropsy specimens (2015-2018), Motu Muka (2018), Otata (2018) and Tāwharanui (2018). Ellipses are shown as 90% confidence intervals.

The mean isotopic values of kororā sampled, Hauraki Gulf fish species and prey items from the South Island are shown in Table 3.1 for reference.

Table 3.1. Mean stable isotopic values (δ15N and δ13C corrected for the Seuss effect) of kororā/little blue penguin (*Eudyptula minor iredalei*), and potential prey items from the South Island and Hauraki Gulf fish species.

Species	**$\delta^{15}N$**	**$\delta^{13}C$**	**Location Collected**	**Source**
Kororā (AWMM)	15.3	-14.94	Various Hauraki Gulf Locations	AWMM
Kororā (Massey)	15.54	-17.1	Various Hauraki Gulf Locations	This study
Kororā (Motu Muka)	14.34	-18.27	Motu Muka	This study
Kororā (Tāwharanui)	14.28	-17.94	Tāwharanui	This study
Kororā (Otata)	15.73	-17.34	Otata	This study
Blue Maomao (*Scorpis violacea*)	11.9	-	Hauraki Gulf	Pinkerton et al. 2015
Butterfish (*Odax pullus*)	10.9	-	Hauraki Gulf	Pinkerton et al. 2015
Parore (*Girella tricuspidata*)	13.6	-	Hauraki Gulf	Pinkerton et al. 2015
Red Moki (*Cheilodactylus spectabilis*)	13.9	-	Hauraki Gulf	Pinkerton et al. 2015
Snapper (*Pagrus auratus*)	14.7	-	Hauraki Gulf	Pinkerton et al. 2015
Sweep (*Scorpis lineolate*)	13.4	-	Hauraki Gulf	Pinkerton et al. 2015
Isopod	8.0	-	Hauraki Gulf	Pinkerton et al. 2015
Red Cod (*Pseudophycis bachus*)	14.0	-18.3	Banks Peninsula, Oamaru, Stewart Island	Flemming and van Heezik 2014
Slender Sprat	13.0	-18.7	Banks Peninsula, Oamaru, Stewart Island	Flemming and van Heezik 2014
Graham's Gudgeon	13.3	-18.5	Banks Peninsula, Oamaru, Stewart Island	Flemming and van Heezik 2014
Arrow squid	12.2	-18.8	Banks Peninsula, Oamaru, Stewart Island	Flemming and van Heezik 2014
Stomatopod larvae	10.0	-20.1	Banks Peninsula, Oamaru, Stewart Island	Flemming and van Heezik 2014

3.3.2 Trends of feather stable isotopes over a 113-year period

Two models were built to explain carbon and nitrogen isotope values from the year 1905 to 2018. For the carbon data, the linear regression model explained 59.25% of the variation in the carbon isotope values across years. However, a second-order polynomial regression model explained 78.88% of the variation. Also, the coefficients of the second-order polynomial regression model were all shown to be significant. Furthermore, the third-order polynomial regression model explained 78.86% of the variation with no significant coefficients. Thus, a second-order polynomial regression model is written as:

$$C = -2.42 \times 10^{3} + 2.469\ \text{Year} - 6.342 \times 10^{-4}\ \text{Year}^{2}$$

was used to interpret the carbon isotope values across years (Figure 3.3a). Carbon isotope values remained relatively constant between 1905 and 1980 before decreasing sharply to 2018.

For the nitrogen data, a second-order polynomial regression model was shown to explain 4.935% of the variation, which was better than both linear and third-order polynomial regression models, which explained 0% and 4.221%, respectively. The second-order polynomial model is written as:

$$N = -1.092 \times 10^{3} + 1.126\ \text{Year} – 2.86 \times 10^{-4}\ \text{Year}^{2}$$

and may be used to interpret the nitrogen data as depicted in Figure 3.3b. Notice that little change can be seen in nitrogen isotopes from 1905 to 2018, as this second-order polynomial model only explains 4.935% of the variation which is much lower compared to the previous second-order polynomial regression model for carbon isotope values (explains 78.86% of variation).

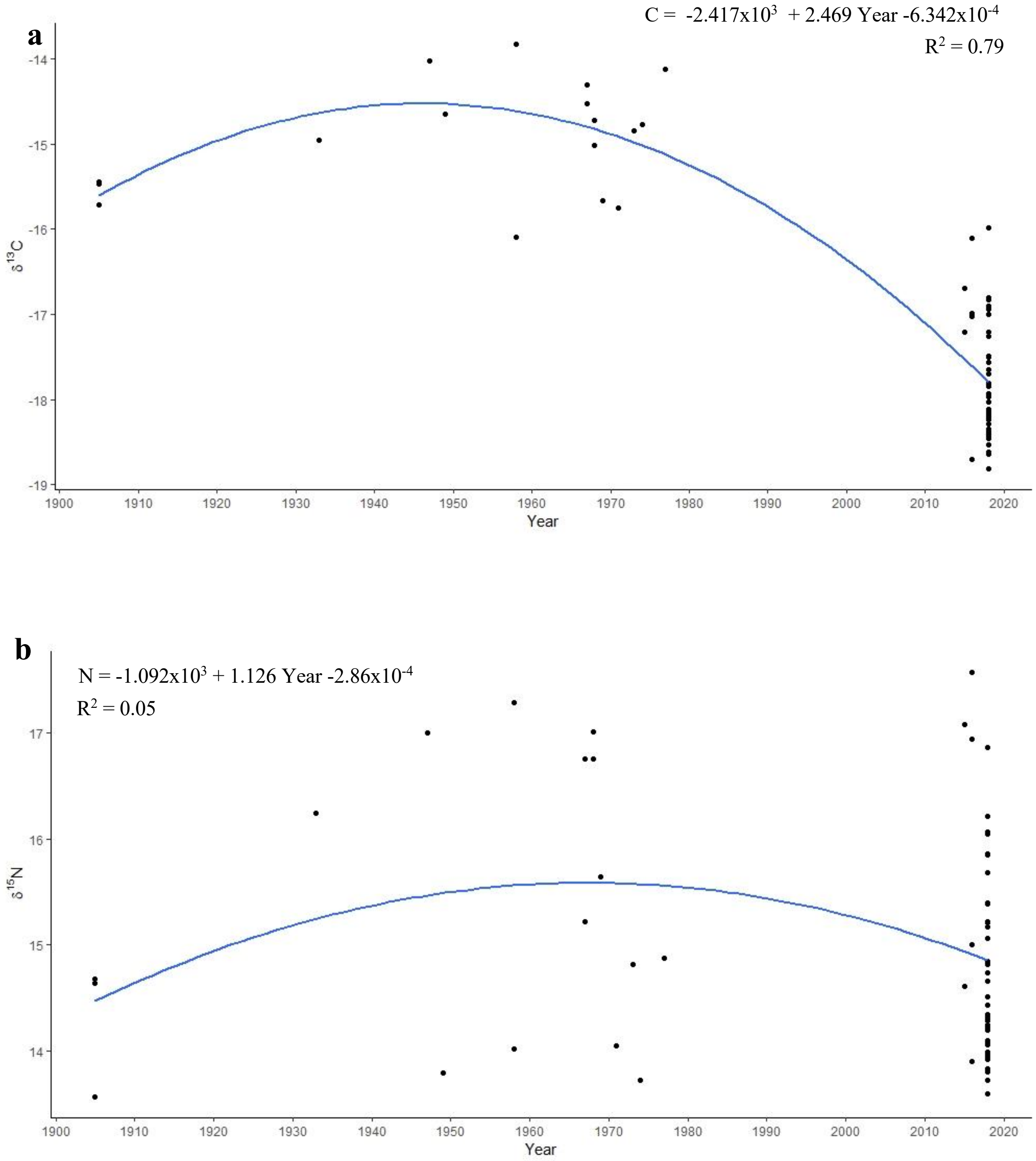


Figure 3.3. Trends of **a**) δ^{13}C and **b**) δ^{15}N over time from kororā/little blue penguins (*Eudyptula minor iredalei*) in the wider Hauraki Gulf. Shown are raw isotopic measurements (δ^{13}C corrected for the Suess effect).

3.4 Discussion

This chapter aimed to determine whether differences in broad foraging location or prey trophic level were observed in the diet of kororā both among sites in the Hauraki Gulf and over time (from 1905 to 2018). From kororā feather samples taken from three sites in the wider Hauraki Gulf in 2018, significant spatial differences were observed between $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Temporal variation in isotope values between contemporary penguins and museum specimens were also observed.

3.4.1 Differences in foraging among colonies

Natural variation in marine productivity among the sites may be one reason that spatial differences in prey trophic level and broad foraging location were observed in this study. Primary productivity varies across the Hauraki Gulf and with it the distribution of higher trophic level prey such as zooplankton, invertebrates and fish (Zeldis and Willis, 2015). Similar zooplankton composition was found at sites sampled near Otata and Tāwharanui by (Zeldis and Willis, 2015) in January and February 1997, but this differed to species found at a site north of Motu Muka. The difference in zooplankton compositions among the sites likely correlated to differences in prey trophic level and broad foraging location of kororā in this study, as individuals may have adapted their foraging patterns to match marine productivity.

A severe storm occurred in northern New Zealand during January 2018, around the time the kororā in this study were in the pre-moult/moult phase (NIWA, 2018). Turbid water caused by storms can make it difficult for visual predators such as penguins to find prey, and increased energy is expended when foraging during increased wind and wave intensity (Trathan et al., 2015). Following this storm event, hundreds of kororā were found wrecked on Auckland and Northland coastlines (Robson, 2018) and most of those necropsied by Massey University had empty stomachs (Massey University Auckland, 2018), indicating they were unable to find sufficient food. This event may have led to kororā foraging more opportunistically during the 2018 feather growth period. The storm would likely have impacted all three study colonies equally, so any decline in trophic level would have been comparable among sites, but trophic levels may have been higher for all extant individuals in the absence of the storm.

Differences observed in $\delta^{15}N$ between feather samples from Motu Muka and Otata suggests kororā from Motu Muka were foraging on a prey species with a slightly lower trophic level during the pre-moult period in 2018 (Figure 3.1). This was surprising considering the geographical locations of the sites. Otata is located 20 km from downtown Auckland and in a marine environment predicted to have enhanced anthropogenic inputs compared to Motu Muka, located 40 km southeast of Whangarei city where the land use of the surrounding catchment and lower human population would arguably suggest a healthier marine environment (Putland et al., 2017; Seers and Shears, 2015). Auckland Museum and Massey had wide isotopic niches compared to the other three groups (Figure 3.2) which are likely due to the wide geographical sampling of the specimens in each of these groups.

The $\delta^{15}N$ range observed in this study (13.5 – 16.5‰) is consistent with a mixed diet of fish, squid and crustaceans (Table 3.1). The prey trophic level in this study was either consistent with or lower than the mean trophic levels of kororā from other Hauraki Gulf sites in earlier years. The mean trophic level of prey consumed by kororā from Tiritiri Matangi in 2005 was 15.45‰ (Geurts, 2006) and was within the range observed in this study. Individuals from Kawau Island in 2010 and Tiritiri Matangi in 2011 had mean prey trophic levels of 15.7‰ and 17.0‰ respectively (McKenzie, 2011) indicating kororā were feeding on a slightly more fish based diet on average in 2010 and 2011 from those sites than the individuals in this study. It is important to note that one trophic level is 3 – 4‰ $\delta^{15}N$ so the prey trophic levels discussed above are all within a similar fish-based diet range. No isotopic references exist for prey species of kororā within the Hauraki Gulf but $\delta^{15}N$ in the South Island varied between 13.3 and 14.0‰ for fish species (Table 3.1.), 12.2‰ for arrow squid and 10.0‰ for stomatopod larvae (Flemming and van Heezik, 2014). The trophic levels of prey in this study were comparable to the kororā diet at Motuara Island, Banks Peninsula and Oamaru in the

South Island, Stewart Island, and Matiu/Somes Island in the North Island (Chilvers, 2017; Flemming and van Heezik, 2014). Geurts (2006) identified that fish made up >80% of the kororā diet during the 2005 breeding season at Tiritiri Matangi and fish species included anchovy, yellow-eyed mullet, lantern fish, goby, sardine and hoka/red cod (*Pseudophycis bachus*). Anchovy made up the greatest proportion of the diet (27.03%). No pilchard was found in the stomach contents by Geurts (2006), despite its presence in the Hauraki Gulf and pilchard (*Sardinops neopilchardus*) having been identified as the preferred prey species of kororā in southern Australia (Chiaradia et al., 2003). Geurts (2006) suggested this may have been due to competition with commercial fishing or more efficient predators, as pilchard are common prey items for both Australasian gannets (*Morus serrator*) and common dolphins (*Delphinus delphis*) in the Hauraki Gulf (Burgess, 2006; Robertson, 1992).

Competition with commercial fisheries at Motu Muka is a possible reason for the lower $\delta^{15}N$ levels. A geographical overlap occurs between the pilchard commercial fishery in northeastern New Zealand and the foraging range of kororā from Motu Muka (see Figure 2.1 and 2.2, Chapter 2), and this geographical overlap potentially creates competition for small bait fish. With a mean size range of 10 cm at two years of age (Fisheries New Zealand, 2018), both pilchard and anchovy are the optimal size for kororā consumption (Flemming et al., 2013). Pilchard and anchovy are found in the Hauraki Gulf, although little is known about their abundance or distribution due to a lack of stock assessments for either species (Fisheries New Zealand, 2018). A commercial fishery for pilchard developed in north-eastern New Zealand in the 1990s and has landed up to 1,290 t of bait fish per year (Fisheries New Zealand, 2018). While the fishery primarily targets pilchard, they are often associated with other shoaling fish species and multiple fish species caught together as ‘pilchard’ (Fisheries New Zealand, 2018). This competition for small bait fish could be a reason that kororā from Motu Muka feed on lower trophic level prey compared to the Otata population, where commercial trawling and Danish seine fishing is prohibited (Klomp and Wooller, 1988; Paul, 2014). Competition between fisheries and a polar penguin species has been discussed by Trathan et al. (2018), where chinstrap penguins (*Pygoscelis* antarcticus) compete with the Krill fishery for Antarctic krill (*Euphausia superba*), a key food resource during the breeding season when the penguins foraging range is restricted by chick rearing. Similarly, a comparison of foraging effort between two colonies of African penguin (*Spheniscus demersus*) identified longer pre-moult foraging trips from the colony where higher human fishing effort occurred when compared to a colony with no fishing effort (Harding, 2014). Bertrand et al. (2012) provide further evidence for the direct prey depletion caused by fisheries, with Peruvian boobies (*Sula variegate*) increasing their foraging range as anchovy fishing activity increased.

An alternative explanation for the lower trophic level of prey consumed by kororā from Motu Muka is the relatively high density of kororā and other seabirds on the island resulting in prey depletion. The idea of both intraspecific and interspecific competition for prey are discussed further in Sections 4.4.1 and 4.4.3 in Chapter 4. Finally, one thing that cannot be discounted are the low sample sizes at Tāwharanui and Otata, brought about by low numbers of birds on these islands.

Unsurprisingly, kororā from Otata (inner-Hauraki Gulf site for this study) had a more enriched carbon signature than individuals from Tāwharanui (mid-Hauraki Gulf) and Motu Muka (outer-Hauraki Gulf), with values reflecting their respective geographic locations on the continental shelf. While no direct comparisons can be made between this study and that of Geurts (2006) due to sampling occurring at different sites and in different years, the study mentioned above can act as a reference for prey trophic level and foraging locations for kororā in the Hauraki Gulf. Of the two years sampled by Geurts (2006), only the 2005 feather $\delta^{13}C$ data was comparable to the results of this study. Feathers from kororā from Tiritiri Matangi in 2004 yielded a $\delta^{13}C$ range between -16.5 and -14.5‰ Geurts (2006), compared to -19 and -16.5‰ for contemporary penguins in this study. This indicates Tiritiri Matangi kororā may have been foraging in a marine environment further inshore in 2004 when compared with the populations in this study. However, the $\delta^{13}C$ values in 2005 from Tiritiri Matangi were comparable to those observed in this study, and ranged from -18.5 to -16.5‰, indicating kororā were foraging further offshore the following year. Kororā from four sites in the South Island (Motuara Island, Banks Peninsula, Oamaru, Stewart Island) and one in the North Island (Matiu/Somes Island) appear to have foraged at a similar distance from the coast to individuals in this study, with carbon values ranging from -19.4 to -17.2‰ (Chilvers, 2017; Flemming and van Heezik, 2014). This may be biased however, due to the decrease in $\delta^{13}C$ with an increase in latitude (Rubenstein and Hobson, 2004).

3.4.2 Trends of feather stable isotopes over a 113-year period

The $\delta^{13}C$ values of kororā remained relatively constant from 1905 to 1980 as seen in Figure 3.3a before decreasing from 1980 to 2018, indicating that either 1) the foraging location of kororā has shifted from an inshore, benthic environment to a more offshore, pelagic environment, or 2) the environmental baseline has changed since the 1980s. In the marine environment, $\delta^{13}C$ is influenced by phytoplankton growth and a decrease of $\delta^{13}C$ in the feathers of high trophic level seabirds could be attributed to declining primary productivity in the marine environment. Without historical isotopic data from other marine organisms within the Hauraki Gulf over a comparable time scale, it is impossible to tell whether the environmental baseline has changed e.g. as seen by Blight et al. (2015). However, we would expect a shifting environmental baseline to decline more linearly than that observed in this study, therefore these data more likely reflect a change in the foraging location of kororā since the 1980s.

It is possible that kororā in the Hauraki Gulf historically foraged in more enriched, inshore locations than contemporary conspecifics which would result in lower $\delta^{13}C$ over time. This has been observed in marbled murrelets *(Brachyramphus marmoratus*) where the foraging location of pre-breeding individuals changed following the decline of the Pacific sardine (*Sardinops sadax*) fishery in the 1940s which meant they had to forage further from the colony (Becker and Beissinger, 2006). Decreased $\delta^{13}C$ in thin-billed prions (*Pachyptila belcheri*) was also observed over 80 years and it was suggested this was caused by a shift in moulting grounds to higher latitudes (Cherel et al., 2014). Unlike the thin-billed prions, the results of this study do not indicate a shift in moulting grounds, as kororā tend to moult where they breed and do not migrate outside of the breeding season (Kinsky, 1958).

Interestingly, the diet of kororā in the Hauraki Gulf during the pre-moult period has not changed considerably over the last 113 years, with $\delta^{15}N$ values consistent with the generalist diet of fish, cephalopods and crustaceans observed throughout their geographic range (Figure 3b). This suggests the increased anthropogenic activities in the Hauraki Gulf over time (Hauraki Gulf Forum, 2018) have not altered prey availability for kororā or that there is less competition for prey than there was historically. Pinkerton et al. (2015) suggest the latter, as the number of seabirds, cetaceans, seals, sharks and other large fish in the Hauraki Gulf have reduced considerably since human occupation. This reduced competition may be the reason the prey trophic level has not changed over time, as kororā have moved up the marine food web.

Stable isotope analysis is useful in determining broad shifts of diet over spatial and temporal scales, but it cannot distinguish between different species of a similar trophic level (Flemming and van Heezik, 2014). While it appears the diet of kororā in the Hauraki Gulf has not changed over time, it is possible that kororā have switched between similar trophic level prey, for example from pilchard to red cod, over the last 120 years with a change in the food web. Kororā can prey switch to cope with unpredictable marine productivity, as was observed when a major die-off of pilchard and anchovy occurred throughout South Australia and New Zealand in the 1990s (Chiaradia et al., 2003). As the preferred prey species of kororā in South Australia, the sudden decline of pilchard caused penguin populations to switch to juvenile red cod, barracouta and blue warehou (*Seriolella brama*), a change that could not be detected from stable isotopes alone (Chiaradia et al., 2003). With the advent of emerging eDNA technologies where prey items within the scat are starting to be identified with increasing resolution (Carroll et al., 2019), such shifts may be more readily identifiable in future.

3.4.3 Summary

Both spatial and temporal differences were observed in the foraging location and prey trophic level of kororā from the wider Hauraki Gulf. Spatiotemporal differences may be due to altered marine food webs, natural environmental variation, competition for prey or other factors. As marine ecosystems change over time and space, the foraging patterns, population size and reproductive success of marine megafauna such as seabirds can show shifts in the availability and abundance of prey species within that marine ecosystem. While natural variation occurs in the marine environment, anthropogenic activities such as pollution, the removal of top predators and climate change are altering the marine food web at unprecedented rates, which can be detrimental for species such as kororā that rely on local prey availability year-round (Boersma, 2008). The temporal differences in $\delta^{13}C$ show that contemporary kororā foraged further offshore than museum specimens collected prior to 1980, indicating the distribution or abundance of prey has shifted over time. This study showed that the foraging patterns and trophic levels of prey consumed by kororā during pre-moult foraging have changed over time and space, and these results help validate the use of feather SIA to assess fine-scale shifts in marine ecosystem health. This study has contributed to filling the knowledge gap of kororā foraging outside of the breeding season and in the wider Hauraki Gulf.

Chapter 4. Feather corticosterone during the critical moult period

Plate 4.1. Kororā specimens from Auckland War Memorial Museum sampled for feather stress hormones.

4.1 Introduction

4.1.1 Measurements of corticosterone in avian species

Corticosterone (CORT) in plasma is commonly used as a measurement of avian stress in conventional stress response studies. The stress response of a bird is generally determined by capturing a bird during the breeding season, taking an initial blood sample before re-sampling at set intervals while the bird is restrained in a box or bag e.g. Chilvers et al. (2016); Cockrem et al. (2009); Cockrem et al. (2017); Whitehead (2018). The initial sample acts as a proxy for baseline stress and subsequent samples are the acute response to the stress of being handled. Blood samples must be taken immediately when using this method to determine baseline stress, as CORT increases within approximately three minutes in response to being handled (Cockrem, 2007). Sampling plasma CORT is a snapshot of how stressed a bird is at the time of blood sampling, which does not reflect baseline stress over the entire breeding season (Bortolotti et al., 2008). Therefore, to access CORT levels over a longer temporal scale, this hormone needs to be measured in tissues that take longer to synthesise, such as feathers.

Compared to plasma CORT, feather CORT is a less invasive method to obtain a measure of stress hormones in birds and is a relatively new method developed by Bortolotti et al. (2008). CORT in the circulatory system is deposited continuously into new feather growth in birds and reflects the cumulative stress experienced by birds during the days to weeks of feather synthesis (Romero and Fairhurst, 2016). Feather CORT has been found to accurately reflect HPA activity in the red-legged partridge (*Alectoris rufa*) and was concluded that feather CORT is a useful measure of cumulative stress levels (Bortolotti et al., 2008). Sampling feathers is less invasive than blood sampling, and less intensive training is required, making it a relatively easy collection method in stress hormone analysis (Romero and Fairhurst, 2016). Feathers may be collected from live or dead birds, or those that have naturally moulted, meaning the collection process does not necessitate capturing live animals which can be a stressful event in itself (Bortolotti et al., 2008; Romero and Fairhurst, 2016).

If the non-breeding movements of a species are known, feather CORT can be compared among locations and can reflect the environmental conditions such as prey availability or weather events experienced by different individuals during the non-breeding season (Fairhurst et al., 2017). This overcomes the time constraints imposed by taking blood samples from multiple distant populations in the same breeding season e.g. as shown by Lamb et al. (2016). Feather CORT remains stable over time, therefore temporal comparisons can be made between the cumulative stress of extant individuals and museum specimens (Bortolotti et al., 2008; Romero and Fairhurst, 2016). Few studies have compared feather CORT in museum specimens, but one found no relationship between feather CORT and time in Leach’s storm-petrel (*Oceanodroma leucorhoa*) (Fairhurst et al., 2015). By comparing feather CORT in birds over time and space, inferences can be made of how birds respond to environmental variation through changes in their cumulative stress (Wingfield et al., 2017; Wingfield and Silverin, 2002).

4.1.2 The relationship between stress physiology and foraging ecology

Combining CORT and stable isotope analysis (Chapter 3) of feathers can retrospectively study relationships between foraging ecology and stress physiology of an individual during the non-breeding period (Fairhurst et al., 2015). This unique combination can assess whether stress is explained by prey trophic level ($\delta^{15}N$) or broad foraging location ($\delta^{13}C$). Foraging locations can act as a proxy for foraging effort which can reflect the availability of prey near the colony (Fairhurst et al., 2015). Higher trophic level prey is usually of better nutritional value, thus contributing to a better body condition (Ainley et al., 2018). Understanding this relationship can help explain how the foraging patterns outside the breeding season influence reproductive success during breeding (Sorensen et al., 2009). If a bird has poor body condition due to nutritional stress e.g. from low quality or quantity prey, they may not have the energy reserves to produce eggs, survive long periods without feeding during egg incubation, or be able to meet chick provisioning requirements (Kitaysky et al., 2007). Chronically stressed birds may feed their chicks less to maintain their body condition and prioritise their survival, thus increasing the nutritional stress of the chicks in times of food scarcity (Wingfield and Silverin, 2002). Combining stable isotopes with feather CORT measurements is an increasingly common technique to collect information about local environmental conditions, for example, prey availability, and assesses how individuals physiologically respond to those conditions (Fairhurst et al., 2015; Fairhurst et al., 2017; Fairhurst et al., 2013).

4.1.3 The stress response in kororā

Nearly all studies of stress in kororā have taken place during the breeding season e.g. Cockrem et al. (2017); Long (2017); Lowe (2009); Ogle (2018), with only a few occurring outside of the breeding season e.g. Chilvers et al. (2016). Of these studies, only one has assessed the stress response of kororā in the Hauraki Gulf (Lowe, 2009). All of the above studies have measured plasma CORT, and one other study has measured the glucocorticoid in kororā droppings (Sherwen and Fanson, 2015). All of these studies found little variation in the initial (first sample taken from a captured bird) CORT measurements but considerable variation was observed in the stress response within individuals. In general, plasma CORT peaked between 30 to 60 minutes of restraint before gradually decreasing over several hours. None of these studies analysed feather CORT, which represents the baseline and response to stressors during the moult period (Bortolotti et al., 2008). To my knowledge, the only examination of feather CORT in penguins is by Barbosa et al. (2013) who found differences in feather CORT levels between gentoo penguin (*Pygoscelis papua*) colonies with varying levels of human visitation. Given this, the current literature regarding feather CORT is biased toward flying seabirds which differ considerably in their moult strategy to penguins.

Moulting is a critical and stressful time because kororā are unable to forage without waterproof plumage and can lose up to 46% of their body mass during this time (Gales et al., 1988). Additionally, new feather growth creates high energetic demands, thus this is when the body condition is often at its lowest and high mortality rates occur

(Klomp and Wooller, 1988; Mortimer and Lill, 2007). If penguins do not gain sufficient energy stores during pre-moult foraging trips, they may not survive the two to three week period of fasting or may have reduced foraging efficiency after moult due to muscle wastage (Cooper, 1978). The stress response in penguins is suppressed during moult (Holberton et al., 1996) as elevated CORT negatively impacts on feather growth (Romero and Fairhurst, 2016). The ratio of heterophils to lymphocytes in blood, another measure of stress in birds, was lower during moult than any other life stage for kororā, showing the downregulation of stress during this time (Mortimer and Lill, 2007). It was only during the final phase of moult in king penguins (*Aptenodytes patagonicus*) that CORT increased, mobilising stored energy to assist with the final feather growth phase (Holberton et al., 1996).

4.1.4 Spatial and temporal comparisons of environmental stress through feather corticosterone

Feather CORT reflects the individual’s body condition during the feather growth period (Wingfield and Silverin, 2002), and body condition during moult is determined by the accumulation of sufficient energy stores in the weeks before moult (Cherel et al., 2005). The synchronised moult strategy of penguins suggests that measurements of feather CORT are comparable over time and space, as all individuals grow their plumage at the same time of year and typically moult at the same colony where they breed (Kinsky, 1958). By monitoring spatiotemporal changes in kororā feather CORT, some inferences can be made of fine-scale changes in local environmental conditions as kororā remain resident in the inshore waters near their nest site year-round and rely on local prey availability (Kinsky, 1958). It is because of this reliance on the local marine environment that changes in the feather CORT of kororā can shed some information on how individuals respond to local environmental perturbation over the feather growth period (Barbosa et al., 2013). Measurements of feather CORT can indicate individual fitness and the likelihood of reproductive success, thus influencing the demography of seabird populations (Kitaysky et al., 2007; Lamb et al., 2016). Given this, feather CORT is an important measurement of the environmental stress experienced by kororā populations in the Hauraki Gulf and may provide information on the decline of the species (Robertson et al., 2017).

4.1.5 Study significance

Previous studies of how kororā respond to stressful stimuli have mainly assessed plasma CORT during the breeding season; and most studies have occurred at Phillip Island, Australia or Otago, New Zealand. To my knowledge, this is the first time feather CORT has been analysed in kororā. This study is the first to use a multi-colony approach to analysing CORT of kororā in the Hauraki Gulf, and to compare contemporary kororā feather CORT to museum specimens. This study contributes to filling the knowledge gap of the stress physiology of kororā outside of the breeding season, and in the wider Hauraki Gulf.

4.1.6 Aims

This study aims to determine whether measurements of stress hormones increased or decreased over time or among colonies in the Hauraki Gulf given the year-round reliance of kororā on local marine environments. In addition, it aims to determine whether age, status or foraging patterns were related to measurements of corticosterone. This study also aims to fill knowledge gaps of the stress experienced by kororā populations outside of the breeding season and in the New Zealand sub-species. The specific aims of this study are to determine:

1. Is feather corticosterone higher in kororā from the inner Hauraki Gulf than the outer Hauraki Gulf?

2. Has feather corticosterone in kororā changed over time?

3. Does feather corticosterone differ between age and status?

4. Is feather corticosterone linked to diet and foraging location as determined through stable isotope analysis?

4.2 Materials and Methods

4.2.1 Field method

For the field method of feather collection, refer to Section 3.2.1, Chapter 3.

Not all individuals sampled in the field were included in the analysis of feather CORT due to limitations on lab equipment, therefore the samples used in this analysis were from Motu Muka/Lady Alice Island (n = 18), Tāwharanui (n = 11) and Otata (n = 11). These were compared to necropsied wild birds collected during 2015 – 2018 (n = 12; Massey University) and specimens from the Auckland War Memorial Museum (AWMM) spanning 1933 to 2003 (n = 22). Specimens from both Massey and AWMM were collected from a range of locations in the Hauraki Gulf, thus do not reflect samples of penguins from one particular site.

In addition, kororā feather samples analysed for stable isotopes and feather CORT were not necessarily from the same individuals, therefore only individuals sampled for both feather CORT and stable isotopes were included in this comparison (n = 44).

The sex of the kororā in this study was not determined as it was not deemed pertinent to the research question and because no sex-specific differences in baseline CORT levels were observed in kororā by Cockrem et al. (2017). Feathers samples were collected from both live and dead individuals and both adult and juveniles. Juveniles were determined by iridescent blue plumage and smaller bill size (Dann, 2013).

4.2.2 Corticosterone extraction

Feather CORT was extracted based on the methods of Lamb et al. (2016). A trial run of different feather weights (9 - 15 mg) was used to optimise the ELISA assay. Four feathers (9.1 – 10.8 mg) was the minimum amount required to generate results within the bounds of a four-parameter logistic curve which validated the sample size. Given this, four feathers were analysed for each individual bird. The calamus was removed from the feather and each feather measured to the nearest mm and weighed to the nearest 0.000g before being cut into small pieces (< 5 mm^2) and the entire sample transferred to an individually labelled 15mL falcon tube. Feather weights were later used to standardise the CORT concentrations.

Each falcon tube had 4mL of HPLC-grade methanol (Sigma-Aldrich, product #67-56-1) added and lids were replaced to limit evaporation. The samples were sonicated in a water bath (30 min at 23°C), followed by overnight shaking in a water bath at 50°C at 100 rpm. After centrifuging tubes at 4000 rpm for 5 min, the methanol extract was carefully pipetted into a second individually labelled 15 mL falcon tube. Feather remnants were rinsed twice, each time with 2 mL of methanol and incubated for at least 6 hours in the shaking water bath before methanol was added to the extraction sample totalling 8 mL for four feathers. All feathers were extracted in the same batch to minimise differences in the extraction method. The methanol extract tubes were placed in a 50 °C water bath overnight to evaporate in a fume hood under air. The extracted residue was reconstituted in 200ul of Assay Buffer from the Enzo LifeSciences Corticosterone ELISA kit (ADI-091-907, New York, United States of America) and vortexed to resuspend the residue.

4.2.3 Corticosterone quantification

Analysis of feather samples for CORT was performed using an ENZO LifeSciences Corticosterone ELISA kit following the included directions but modified by using a 1:8

dilution (50µl of sample + 300 µl diluted assay buffer). This modification was to ensure feather CORT measurements were within the limits of detection of the kit given the limited feather material from museum specimens. Samples were read in duplicate in two 96 well plates with a mass spectrometer. A four-parameter logistic curve validated the use of the ELISA kit with serial dilutions of the standards of known CORT concentration parallel to the standard curve for both plates ($R^2 = 0.99$ for each plate). In total, feather CORT was measured in 74 individuals. Feather CORT measurements were corrected for total feather weight (mg) as per Lamb et al. (2016) and measurements of feather CORT expressed as pg mg^{-1}.

4.2.4 Statistical Analyses

4.2.4.1 Differences in feather corticosterone among colonies

The means of feather CORT concentration were compared among all samples (n = 40) collected from Motu Muka, Tāwharanui, and Otata. To do this, a one-way analysis of variance (ANOVA) was performed, followed by a Tukey post-hoc test to compare among groups. A Shapiro-Wilk normality test confirmed the assumptions of normality. Results are shown visually in the form of bar plots with error bars.

4.2.4.2 Differences in feather corticosterone between age and status

A two-way ANOVA was used to compare the status (Alive, n = 31; Dead, n = 21) of each individual penguins age (Adult, n = 38; Juvenile, n = 14) to the CORT measurement of contemporary penguins (2015 – 2018), followed by a Tukey post-hoc test to compare among groups. The normality assumptions were not met, thus this data was log transformed. Results are shown visually in the form of bar plots with error bars.

4.2.4.3 Trends in feather corticosterone over a 85 year period

The means of feather CORT concentration were compared among feather samples collected from Motu Muka, Tāwharanui and Otata and to specimens from Massey

University (n = 12) and the AWMM (n = 22). To do this, a one-way ANOVA was performed, followed by a Tukey post-hoc test to compare among groups. A Shapiro-Wilk normality test confirmed the assumptions of normality. Results are shown visually in the form of bar plots with error bars.

Linear regression was used to examine the association between feather CORT and years the feather samples were collected. Data were presented in a time-series graph.

4.2.4.4 The link between stress physiology and foraging ecology

Linear regression analysis was used to examine the association between feather CORT and both the broad foraging location ($\delta^{13}C$) and prey trophic level ($\delta^{15}N$). Due to the violation of the normality assumptions, the feather CORT measurements had to be logarithm transformed for the linear regression model, and therefore, the statement about the effects of the foraging location ($\delta^{13}C$) and prey trophic level ($\delta^{15}N$) on the feather CORT measurement are multiplicative in nature and are expressed in percentage terms.

Results are presented as means ± Standard Error of the Mean (SEM) unless otherwise indicated. P-values are considered significant if <0.05. The statistical analyses were performed in R version 3.4.1 (R Core Development Team, 2018).

4.3 Results

4.3.1 Differences in feather corticosterone among colonies

The mean body weight for live individuals was 879.69 ± 21.59 g. Feather CORT observed in this study reflects CORT secretion by kororā from Otata, Tāwharanui and Motu Muka between January and March 2018. Significant differences in feather CORT were observed among live penguins from the three study sites ($F_{(2,28)} = 7.459$, p-value

= 0.003) (Figure 4.1). Feather CORT at Motu Muka was higher than both Tāwharanui (Adj p-value = 0.044) and Otata (Adj p-value = 0.003), suggesting that individuals from Motu Muka had elevated baseline and integrated stress levels during the moult period in comparison to the other two sites. No difference was observed between Otata and Tāwharanui (adj p-value > 0.05).

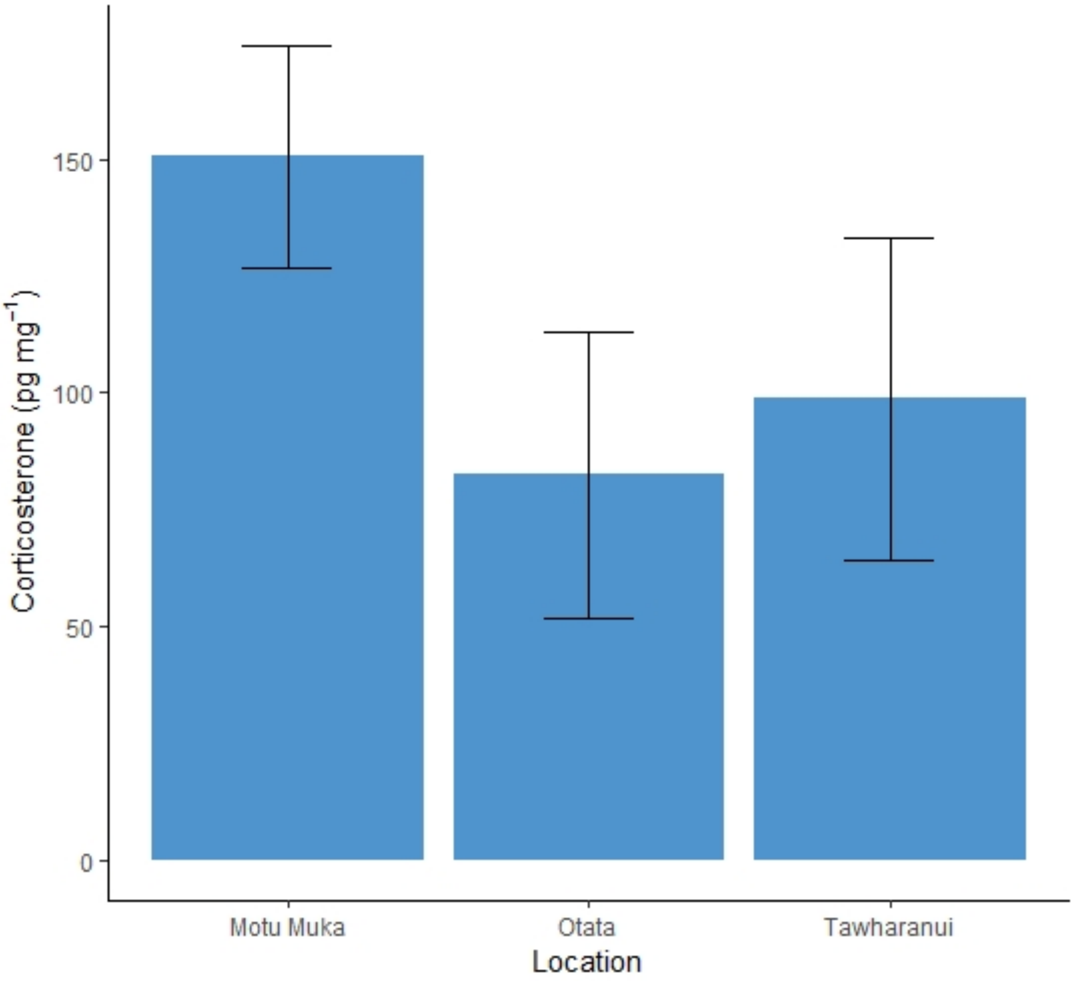


Figure 4.1. Feather corticosterone values from contemporary kororā/little blue penguin (*Eudyptula minor iredalei*) sampled from the wider Hauraki Gulf during the 2018 breeding season. Values are means ± standard error of the mean

4.3.2 Differences in feather corticosterone between age and status

A significant interaction effect was found between Age (Adult vs. Juvenile) and Status (Alive vs. Dead) for kororā from Otata, Tāwharanui and Motu Muka ($F_{(1,36)} = 7.87$, p-value = 0.008). Feathers of live adults had CORT levels 2.4 times higher than dead adults whereas feathers of dead juveniles had CORT levels 1.5 times higher than live juveniles. Live adults were 1.63 times more stressed than live juveniles and no significant interaction was observed between dead adults and dead juveniles (Figure 4.2).

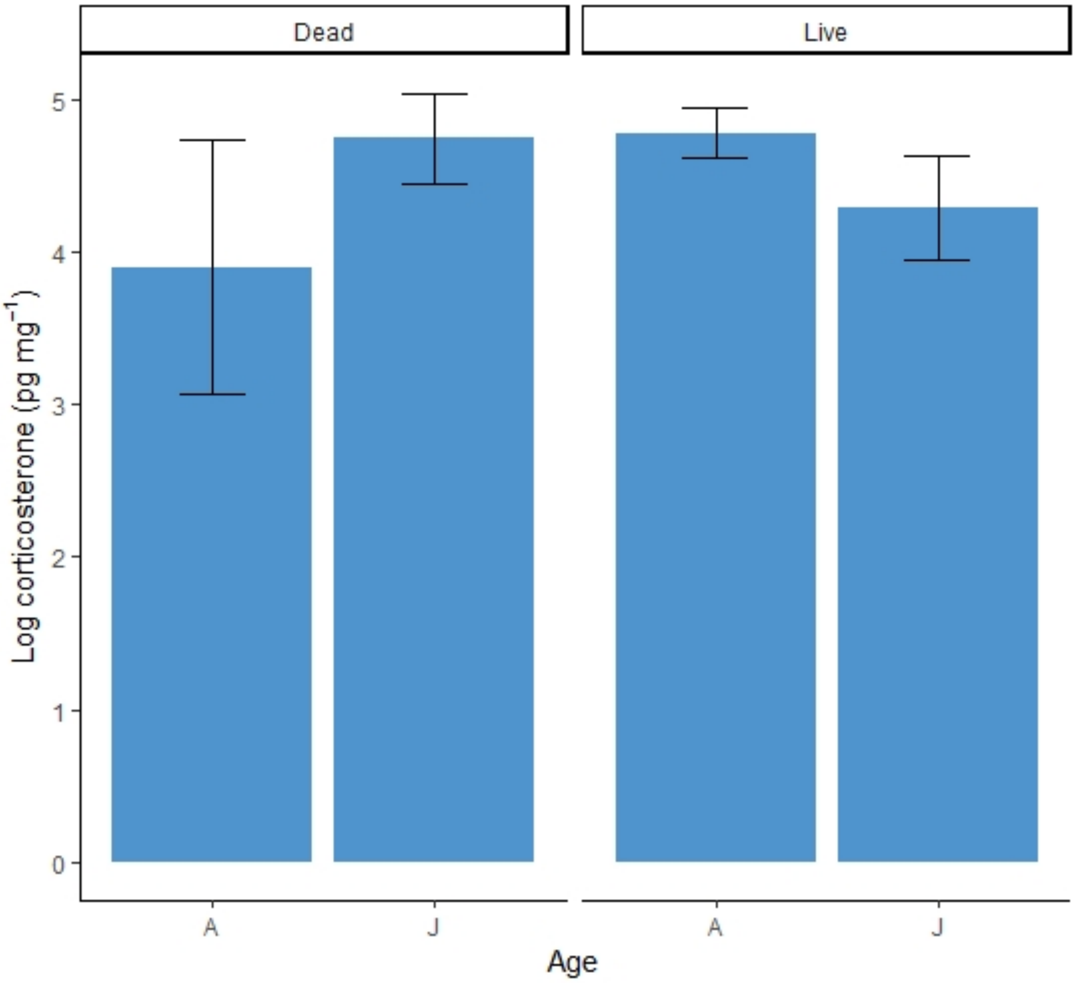


Figure 4.2. Interaction of log feather corticosterone values from live and dead, adult and juvenile kororā/little blue penguin (*Eudyptula minor iredalei*) sampled from the wider Hauraki Gulf during the 2018 breeding season. Values are log means ± standard error of the mean.

4.3.3. Trends in feather corticosterone over an 85 year period

Significant differences in feather CORT were observed among the five groups ($F_{(4,69)} = 9.656$, p-value < 0.001) (Figure 4.3). Feather CORT was higher in kororā from AWMM than all other groups (Massey – Adj p-value = 0.005; Motu Muka – Adj p-value = 0.021; Tāwharanui - Adj p-value = 0.000; Otata - Adj p-value = 0.000), indicating penguins historically had higher feather CORT levels than contemporary conspecifics. No difference was observed among any of the other groups (Adj p-value >0.05).

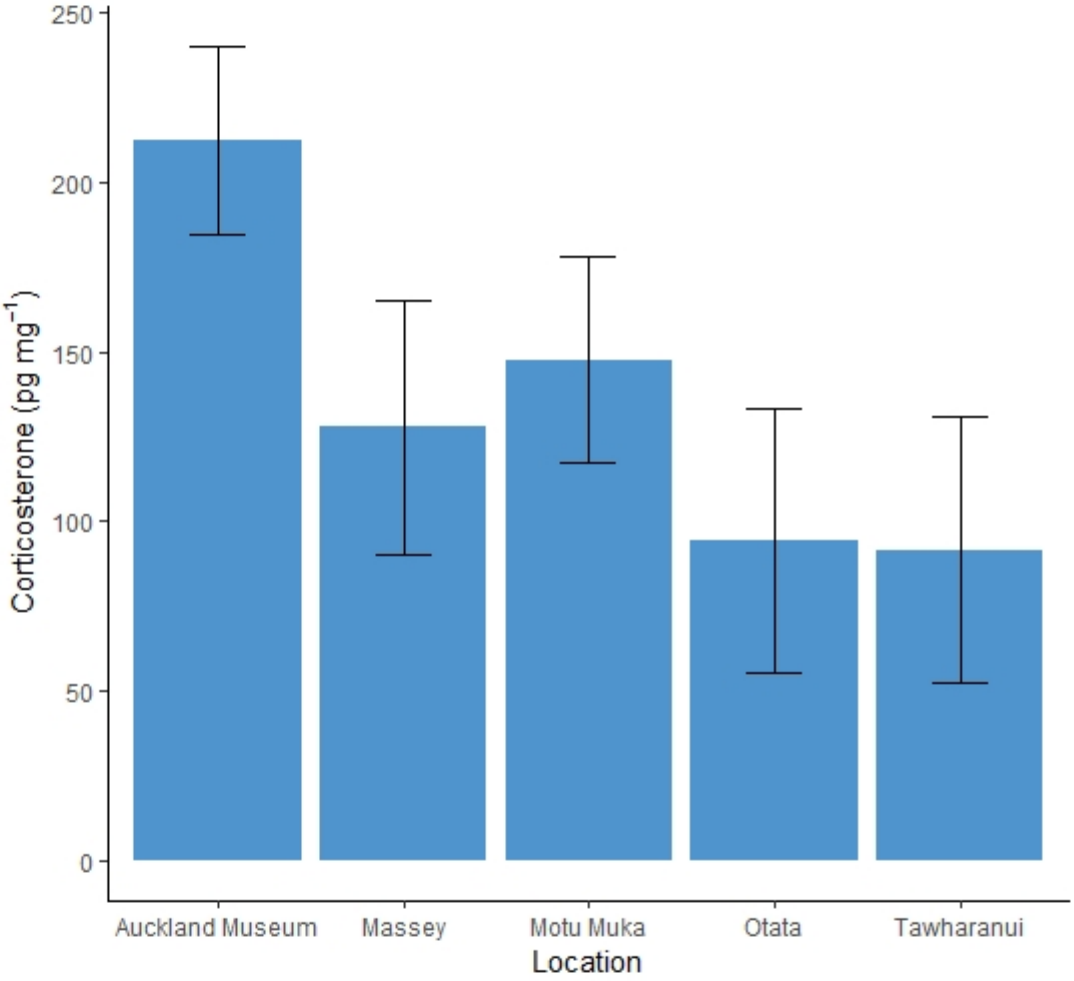


Figure 4.3. Feather corticosterone values from contemporary and museum feather samples from kororā/little blue penguin (*Eudyptula minor iredalei*) in the wider Hauraki Gulf. Depicted are museum specimens (1933 - 2003), Massey University necropsy specimens (2015-2018), Motu Muka, Otata and Tāwharanui (2018). Values are means ± standard error of the mean.

A statistically significant negative linear relationship was identified (p-value = < 0.01, $R^2 = 0.36$) between feather CORT and year (Figure 4.4). Feather CORT levels declined over an 86 year period (slope = -1.8763 ± 0.2921). For every one year increase, CORT levels have decreased by 1.88 pg mg^{-1}.

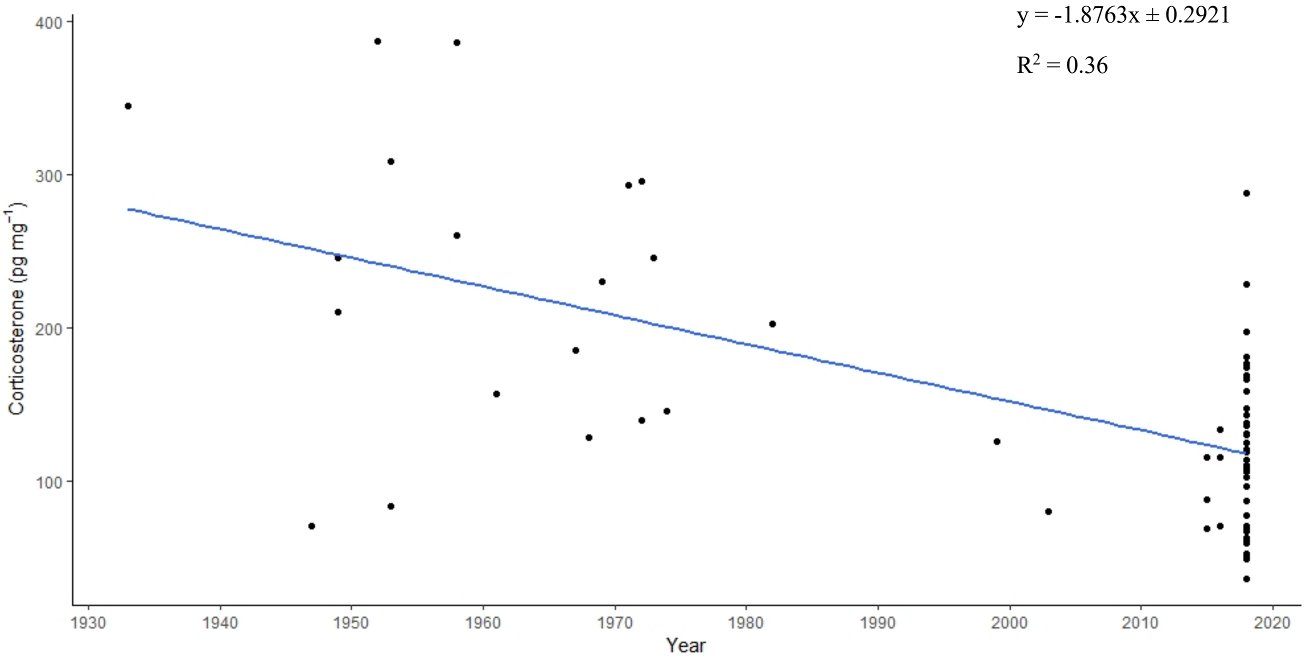


Figure 4.4. Feather corticosterone measurements over time from contemporary and museum feather samples from kororā/little blue penguin (*Eudyptula minor iredalei*) in the wider Hauraki Gulf. Depicted are museum specimens (1933 - 2003), Massey University necropsy specimens (2015-2018), Motu Muka, Otata and Tāwharanui (2018).

4.3.4 The link between stress physiology and foraging ecology

A statistically significant positive linear relationship (p-value = 0.0192, $R^2 = 0.10$) was identified between logarithm transformed feather CORT measurements and foraging location ($\delta^{13}C$) (Figure 4.5). For every one-unit increase in $\delta^{13}C$, feather CORT increased by 0.128 (± 0.05247) in the logarithm scale or increased by 13.63% after back-transformation.

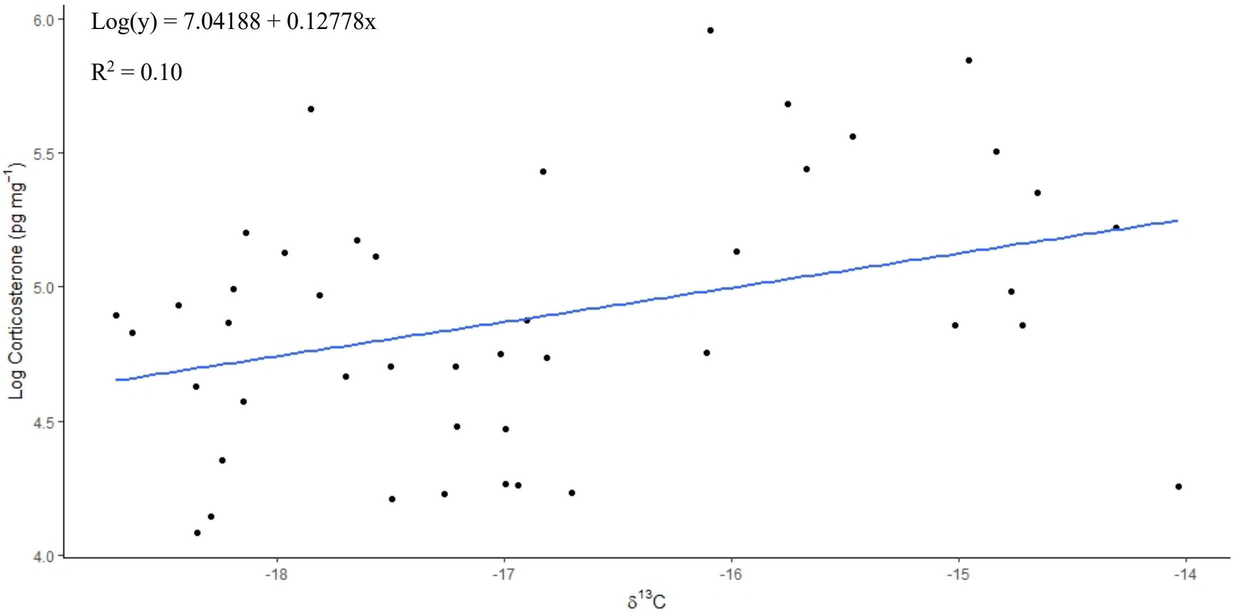


Figure 4.5. Log feather corticosterone measurements in relation to broad foraging location ($\delta^{13}C$) of modern and museum feather samples (1933 – 2018) from kororā/little blue penguin (*Eudyptula minor iredalei*) in the wider Hauraki Gulf.

A very weak negative linear relationship (p-value = 0.0548, R^2 = 0.06) was found between logarithm transformed feather CORT measurements and trophic level of prey ($\delta^{15}N$) (Figure 4.6). For every one-unit increase in $\delta^{15}N$, feather CORT decreased by 0.128 (± 0.06488) in logarithm scale, or by 12.03% after back-transformation.

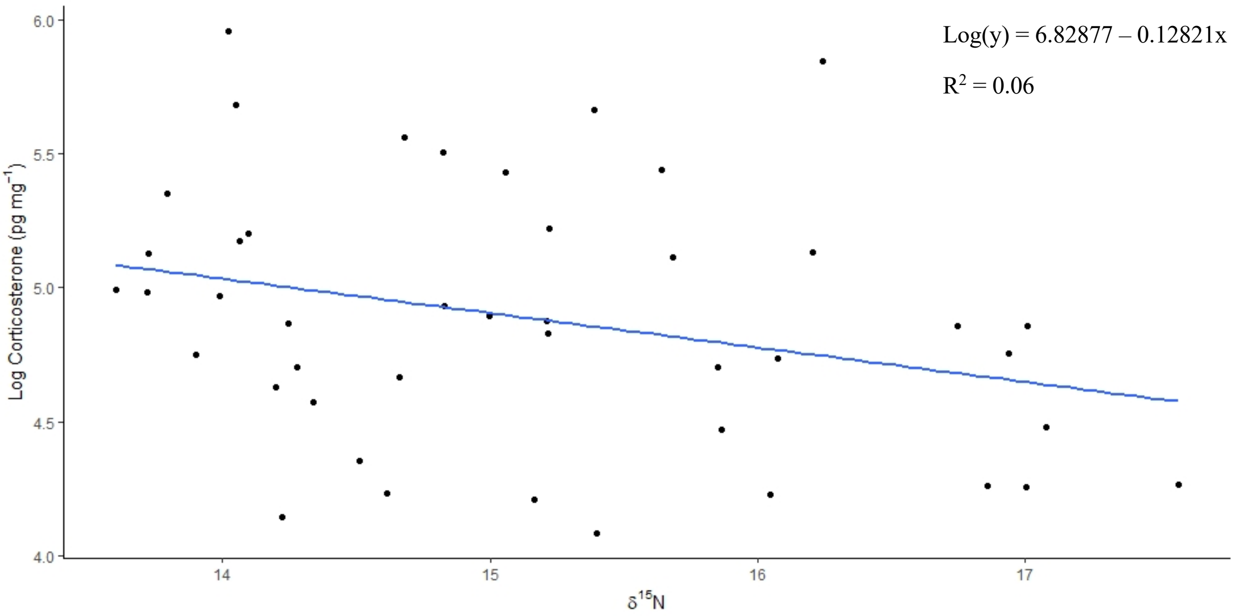


Figure 4.6. Log feather corticosterone measurements in relation to prey trophic position ($\delta^{15}N$) of modern and museum feather samples (1933 – 2018) from kororā/little blue penguin (*Eudyptula minor iredalei*) in the wider Hauraki Gulf.

4.4 Discussion

This study aimed to determine whether measurements of stress hormones increased or decreased over time or among kororā colonies in the Hauraki Gulf or whether age, status or foraging patterns were related to measurements of corticosterone. The feather CORT in this study reflected the environmental conditions the study birds experienced during the post-breeding moult. Significant differences were observed among feather CORT values taken from three sites in the wider Hauraki Gulf in 2018. There was also temporal variation in feather CORT between contemporary penguins and museum specimens.

4.4.1 Differences in feather corticosterone among colonies

Spatial differences in feather CORT were observed among the colonies (Figure 4.1), but these differences were not in the expected direction, as Motu Muka (outer-Hauraki

Gulf) had higher feather CORT than both Otata (inner-Hauraki Gulf) and Tāwharanui (mid-Hauraki Gulf). This was surprising considering the geographical locations of the sites. Otata is located 20 km from downtown Auckland and in a marine environment predicted to have enhanced anthropogenic inputs compared to Motu Muka, located 40 km southeast of Whangarei city where the land use of the surrounding catchment and lower human population would arguably suggest a healthier marine environment (Putland et al., 2017; Seers and Shears, 2015).

Increased competition for burrows represents a potential explanation for kororā from Motu Muka exhibiting higher feather CORT levels than both Tāwharanui and Otata, where fewer burrow-nesting species occur at lower densities. Kororā burrows are frequently found amongst ōi//grey-faced petrel (*Pterodroma gouldi*) colonies in the Hauraki Gulf, and the two species are known to compete for nesting sites (Friesen et al., 2016). Given this, it is likely that kororā on Motu Muka compete with grey-faced petrels and toanui/flesh-footed shearwaters (*Puffinus carneipes)*, and to a lesser extent the smaller little shearwaters (*Puffinus assimilis haurakiensis)*, fluttering shearwaters and titi/pycroft's petrels (*Pterodroma pycrofti)* for burrows during the moult period. Similarly, the presence of tuatara in high abundance on Motu Muka could initiate a stress response during the feather growth period due to the predatory nature of the reptile and the vulnerability of kororā during moult. Tuatara have predated eggs of Fairy Prions (*Pachyptila turtur*) with which they cohabit in burrows (Walls, 1978), and may be viewed as a threat by kororā.

Greater intraspecific competition for prey for kororā from Motu Muka due to the relatively large population size may be the cause of higher feather CORT levels. Feather CORT is often related to nutritional stress in seabirds (Lamb et al., 2016; Will et al., 2014) and nutritional stress may increase with more competition for food. Kororā in dense colonies compete with conspecifics for food resources, and density-driven food shortages have been found to limit kororā populations during the breeding season (Dann and Norman, 2006). A correlation between colony size and body mass was observed in kororā, where small colonies (~200 individuals) weighed considerably more (1136 ± 49 g) during the breeding season than those in large colonies (>35,000 individuals; 853 ± 53 g), indicating individuals in larger colonies had higher nutritional stress (Dann and Norman, 2006). Given this, it may be that less competition for prey items at the smaller colonies of Tawaharanui and Otata resulted in decreased nutritional stress and lower feather CORT values.

The higher feather CORT measurements observed at Motu Muka may also have been caused by prey scarcity during pre-moult foraging trips, resulting in fewer energy reserves during the moult period. The accumulation of sufficient energy reserves during pre-moult foraging ensures kororā will survive the fasting period of two to three weeks on land (Kinsky, 1958). Poor body condition from the consumption of less energy-dense prey during pre-moult foraging trips was observed in African penguins (*Spheniscus demersus*), where individuals that failed to accumulate sufficient energy stores were found to have high mortality levels post-moult, as muscle atrophy occurred during moult and they were unable to forage effectively afterwards (Cooper, 1978). It is worth noting that while feather CORT levels were higher at Motu Muka, the sampled penguins were still alive in the breeding season following feather growth so poor body condition was not enough to cause mortality. In addition to the resident penguin population, Motu Muka also supports large numbers of other burrow-nesting species including five species of Procellariiformes (Gaskin and Rayner, 2013) and the predatory reptile tuatara (*Sphenodon punctatus*). The high abundance of kororā and other seabirds at Motu Muka likely increases competition for food and resources both on land and in the marine environment.

Finally, one thing that cannot be discounted are the low sample sizes at Tāwharanui and Otata, brought about by low numbers of birds on these islands.

4.4.2 Difference in feather corticosterone between age and status

The higher feather CORT values of dead juveniles in this study potentially reflected nutritional stress before fledging (Figure 4.2). Nutritional stress in seabird chicks can lead to decreased fitness and an increase in mortality (Kitaysky et al., 2003) and reduced population recruitment can occur if too few individuals survive to adulthood (Kitaysky et al., 2007). Similar to the results of this study, higher feather CORT was observed in brown pelican (*Pelecanus occidentalis*), chicks that died after fledging than in live chicks (Lamb et al., 2016). Elevated feather CORT has also been associated with a decreased provisioning rate (Lamb et al., 2016; Lodjak et al., 2015) and a nutritionally poor diet (Kitaysky et al., 1999), either of which may have been the cause of high feather CORT in dead juveniles in this study. It is possible that even though the juveniles in this study survived until fledging, they may have died as a result of the negative impacts of chronic stress on development, such as reduced cognition when learning how to forage (Kitaysky et al., 2003).

The higher feather CORT values of live adults than live juveniles (Figure 4.2) in this study may have resulted from a severe storm event that occurred during January 2018 in northern New Zealand (NIWA, 2018) as storm events are known to cause CORT upregulation (Fairhurst et al., 2015). Adult kororā in this study would have been in the pre-moult foraging stage or have already commenced moult (Kinsky, 1958), thus the elevation in CORT triggered by the storm event would have been synthesised into new feather growth (Bortolotti et al., 2008). This event would have occurred before the breeding season the juveniles in this study hatched, thus the storm event would not have been reflected in juvenile feather growth. Following this storm event, hundreds of kororā were found wrecked on Auckland and Northland coastlines (Robson, 2018) and most of those necropsied by Massey University had empty stomachs (Massey University Auckland, 2018), indicating they were unable to find sufficient food.

While no studies have explicitly studied the impact of storm events on CORT in kororā, higher plasma CORT levels were observed in Magellanic penguins when high rainfall caused nest flooding and decreased the reproductive success of the population (Walker et al., 2014). Similarly, the population of Galapagos penguins (*Spheniscus mendiculus*) decreased by 77% following severe El Niño weather events in 1982 and 1997 and had still not recovered by 2004, which shows the long term negative impact of unpredictable environmental perturbation on temperate penguin species (Vargas et al., 2006). Severe weather events in South Australia have caused kororā to breed later (Chambers, 2004) and have caused flooding and other damage to kororā burrows, resulting in decreased fledging rate (Ross et al., 1996).

Plate 4.2. Otata Island during the January 2018 storm event that flooded many kororā nests near the coast. Photo by Rod Neureuter, 2018.

An increase in severe weather events is predicted with climate change and predicted variation in weather patterns are stronger ocean currents, sea level rise, ocean acidification, increased frequency and intensity of storm events (Chambers et al., 2011). The unpredictable weather patterns caused by climate change in future will likely cause increased stress responses in kororā as individuals adapt their behaviour and physiology to cope with the perturbations. Assessments of how kororā have coped with previous environmental variation and other stressors can be made by measuring feather CORT in museum specimens.

4.4.3 Trends in feather corticosterone over an 85 year period

Temporal differences in feather CORT were observed between contemporary and museum specimens (Figure 4.3), with individuals sampled in 2018 having lower feather CORT values (117.56 ± 7.98 pg mg^{-1}) than pooled museum specimens (212.39 ± 20.46 pg mg^{-1}). The decrease in feather CORT over time in this study (Figure 4.4) was surprising considering the increase in anthropogenic inputs into the Hauraki Gulf marine ecosystem since the 1930s due to an increased human population in the region (Hauraki Gulf Forum, 2018). In addition to the intraspecific competition discussed in section 4.4.1 of this Chapter, there is some evidence that a decrease in interspecific competition may have occurred in the Hauraki Gulf over the last century.

Pinkerton et al. (2015) suggest that the reduced biomass of marine megafauna in the Hauraki Gulf since human occupation has led to seabirds filling the ecological niche left by large fish, cetaceans and seals. The reduction in interspecific competition for prey items with cetaceans is a possible reason why kororā feather CORT in this study declined over time. Common (*Delphinus delphis*) and Bottlenose dolphins (*Tursiops truncatus*) are two cetacean species found in the Hauraki Gulf and prey items for these dolphin species have been identified as small fish, squid and crustaceans (Meynier et al., 2008), indicating an overlap in prey preference with kororā. Cetaceans in the Hauraki Gulf have declined in biomass considerably since human occupation, and their importance in the Hauraki Gulf marine food web has decreased from the 7th most important predators in 1950 to the 21st most important in 2016 (Pinkerton et al., 2015). In the Antarctic, the removal of cetaceans and large fish through overfishing has resulted in larger colonies of Adelie penguins as competition for prey has declined (Ainley et al., 2018), showing the impact of a decrease of large predators on penguin populations. New Zealand fur seals (*Arctocephalus forsteri*) feed on similar prey to kororā (Carey, 1992) but this species was locally extinct in the Hauraki Gulf by the 1500s due to human harvest, thus they would not have contributed to competition for prey items with kororā in the early 1900s (Pinkerton et al., 2015).

The decline in feather CORT over time in this study may be due to reduced competition for prey items with large fish due to human harvest, which can benefit seabirds by increasing the abundance of small prey items (Pinkerton et al., 2015). The biomass of large fishes such as sharks, tamure/snapper (*Pagrus auratus*), and araara/trevally (*Caranx lutescens*) in the Hauraki Gulf has decreased by 86%, 83% and 86% respectively since human occupation largely due to the industrial fishing practices that began in the 1950s (Pinkerton et al., 2015). This may have further contributed to a reduction in competition for small shoaling fish over the time scale observed in this study. Evidence of interspecific competition between large fish and seabirds has been seen between the flathead fish (*Platycephalus speculator*) and two species of small seabird; the little pied cormorant (*Phalocrocorax melanoleucos*) and little black cormorant (*Phalocrocorax sulcirostris*) with all three species feeding on similar sized bait fish and crustaceans (Humphries et al., 1992).

The reduction in competition with conspecifics and other seabirds for prey items is a possible reason why kororā feather CORT is lower in contemporary penguins than in museum specimens. It is due to the decrease in biomass of other marine megafauna that seabirds are now considered the top marine predator in the Hauraki Gulf in terms of biomass (Pinkerton et al., 2015). Takupu/Australasian gannets (*Morus serrator*), kawau tikitiki/spotted shags (*Stictocarbo punctatus punctatus*), tara/white fronted terns (*Sterna striata*) and tarapunga/red-billed gulls (*Larus scopulinus*) have all declined in the region since 1940 (Frost, 2017; Frost and Taylor, 2018). Although no population surveys exist for kororā over the period of this study, anecdotal evidence suggests populations were much higher in the past than they are currently (Chris Gaskin pers. comm., 2018). Fluttering shearwater, flesh footed shearwater, rako/Buller's shearwater (*Puffinus bulleri*), takahikare/white-faced storm petrel (*Pelagodroma marina maoriana*) and titi/cook's petrel (*Pterodroma cookii*) have all been found to forage on baitfish in the Hauraki Gulf, providing some evidence of a diet overlap between these procellariform species and kororā (Gaskin, 2017). The removal of large predators over time has undoubtedly altered the marine food-web of the wider Hauraki Gulf (Pinkerton et al., 2015). The trophic cascade caused by this food web alteration may have ultimately benefitted kororā by reducing the number of species and abundance of individuals competing for small shoaling fish and squid.

4.4.4 The link between stress physiology and foraging ecology

The positive relationship between feather CORT and foraging location ($\delta^{13}C$) in this study (Figure 4.5) showed that foraging location during pre-moult foraging trips did likely influence feather CORT. Feather CORT was higher in kororā foraging closer to shore than in individuals foraging further offshore, suggesting offshore environments provided better foraging during the pre-moult period than inshore marine environments. Kororā target high-fat prey items during pre-moult foraging trips (Gales et al., 1988) and it is possible the distribution of prey may have been higher offshore during pre-moult foraging. The opposite result was found in Dupont's larks (*Chersophilus duponti*), where feather CORT decreased with an increase in $\delta^{13}C$ and it was suggested this was caused by the agricultural land use surrounding lark habitat. No relationship between feather CORT and foraging location was identified in northern gannets (*Morus bassanus*) or Leach's storm-petrel (Fairhurst et al., 2015; Fairhurst et al., 2017). Unlike Leach's storm-petrels, kororā do not migrate away from their breeding grounds outside of the breeding season, thus feather CORT reflects local environmental conditions experienced during the moult period at the same location that breeding occurs.

The weak relationship identified between feather CORT and prey trophic level ($\delta^{15}N$) in this study (Figure 4.6) shows the broad trophic level of prey did not strongly correlate to feather CORT. This result was interesting given the link between nutritional stress and CORT (Lamb et al., 2016; Will et al., 2014) and suggests that variation in feather CORT may have been caused by resource competition rather than diet. However, individuals from Motu Muka were found to forage on a lower trophic level prey and further offshore (Figure 3.1, Chapter 3) and had higher feather CORT than birds from Otata and Tāwharanui, which implies that diet and feather CORT may be linked for the population sampled at Motu Muka. A stronger link between diet and feather CORT was identified by Fairhurst et al. (2015), where a negative relationship between prey trophic level and feather CORT was observed in Leach's storm-petrels. Conversely, no relationship was observed between prey trophic level and feather CORT in northern gannets (Fairhurst et al., 2017).

4.4.5 Summary

The feathers used in this study spanned an 85 year period and provided a unique perspective in assessing long term trends in feather CORT and stable isotopes. This was the first evidence of a link between stress physiology and foraging ecology in kororā as determined by stable isotopes. Both spatial and temporal differences were observed in measurements of feather CORT in kororā from the wider Hauraki Gulf. Spatiotemporal differences may be due to severe weather, competition, nutritional stress or other factors. With fewer penguins and other large marine megafauna due to anthropogenic changes to the marine environment, individuals may face less competition for food and nesting sites at the smaller colonies of Otata and Tāwharanui, and in contemporary populations when compared to museum specimens. Reduced competition seems a likely reason for the temporal decline in feather CORT. While reduced competition appears to benefit these smaller populations of kororā through lower feather CORT levels, small populations may be less resilient to severe environmental perturbations due to reduced genetic diversity and subsequent population fitness (Couvet, 2002; Jamieson et al., 2006). Fine-scale changes in the environmental conditions experienced by kororā during the moult period can be observed in measurements of feather CORT but the causes behind the variation in this study require further unpicking.

5. General Discussion

Plate 5.1. A kororā on the Poor Knights Islands. Photo by Edin Whitehead, 2018.

5.1 Synthesis of chapters

The research undertaken in this thesis has expanded overall knowledge of kororā ecology and stress physiology and has direct implications for kororā conservation in New Zealand, as well as highlighted areas that need further research. This study aimed to determine whether changes in foraging ecology and stress physiology were observed in kororā populations over time and space and whether these measurements could be used as indicators of marine ecosystem health.

The tracking component of this study was unfortunately constrained in its spatial extent. Nonetheless, I was able to show where kororā from one site foraged during the breeding season, whereas the stable isotopes and corticosterone in the feathers of kororā reflected the environmental conditions experienced by individuals during the pre-moult/moult period from all three sites. The inconsistencies between the timing of the different measurements meant direct correlations between tracking and stable isotope analysis or feather corticosterone could not be made. However, the environmental conditions experienced by birds outside of the breeding season influence their body condition and the likelihood of reproductive success during breeding (Sorensen et al., 2009), thus the foraging ecology and stress physiology during the pre-moult/moult period likely influenced how kororā foraged during breeding.

The foraging ranges, durations and distances corresponded with other kororā tracking studies throughout New Zealand and Australia during the breeding season (Hoskins et al., 2008; Pelletier et al., 2014; Zhang et al., 2015). The tracking component of this study highlighted the importance of the inshore coastal environment near the Motu Muka colony for the individuals tracked. Conversely, carbon stable isotopes in feathers indicated individuals were foraging offshore during pre-moult foraging trips earlier in the year. The discrepancy in foraging locations may have tracked the different energetic requirements of individuals during breeding and pre-moult (Kowalczyk et al., 2015a) or may have been due to temporal variation in prey availability (Weimerskirch, 2007).

Of the contemporary kororā populations, Motu Muka had the highest stress measurements during moult which, when combined with lower prey trophic level, provided some evidence of nutritional stress during pre-moult foraging for those individuals. This may have been due to inter and intraspecific competition for prey due to the high abundance of seabirds on Motu Muka (Dann and Norman, 2006), or due to other factors such as human fishing effort resulting in the reduced abundance or distribution of higher trophic level prey (Bertrand et al., 2012). The broad trophic level of prey did not strongly correlate to feather corticosterone over time in the Hauraki Gulf suggesting that variation in feather corticosterone may have been caused by resource competition rather than diet. Combining stable isotopes with feather corticosterone measurements is a novel technique to collect information about local environmental conditions and assesses how individuals physiologically respond to those conditions (Fairhurst et al., 2013).

5.2 Novel research – filling knowledge gaps and providing insight into historical responses

Most tracking studies have occurred in Australia or Otago, and very few have tracked the New Zealand sub-species of kororā (*Eudyptula minor iredalei*). This study is the first to track kororā from the Marotere/Hen and Chickens Islands and is the second time they have been tracked in the wider Hauraki Gulf region. The kororā in this study foraged up to twice as far and for twice as long than those in Zhang (2012) from the Mokohinau Islands. This difference may have been due to the different stages of chick-rearing duties and associated foraging trip lengths in early September (Zhang, 2012) compared to late-November (this study).

As kororā are spatially restricted foragers, this tracking study has provided a unique insight into their habitat use around an area of potentially high human degradation (Whangarei harbour), with implications for the productivity of this population over time. The kororā from Motu Muka breed on a predator free island and are exposed to few threats when on land. However, in the marine environment surrounding their colony their foraging efforts may be hindered by boat traffic, sedimentation and high fishing effort, all of which may contribute to decreased prey availability and higher stress levels in the population (Barbosa et al., 2013). These tracking data, along with those of Zhang (2012), can act as a baseline for future foraging studies of kororā in the wider Hauraki Gulf during the breeding season.

This was the first analysis of stable isotopes in kororā feathers from Motu Muka, Tāwharanui and Otata, and the most recent comparison of stable isotopes between contemporary kororā and museum specimens for the wider Hauraki Gulf. The findings of this study showed for the first time that the fish-based diet consumed by kororā has remained constant since 1905 whereas the broad foraging ranges during pre-moult foraging trips have shifted further offshore. This study provided the first combination of stable isotopes and feather CORT derived from kororā feathers. Combining these two measurements informs our perception of how the Hauraki Gulf marine food web has changed over time with offshore shifts in productivity detected and the possibility that decreased densities of megafauna may be linked to lower stress in kororā.

This study also developed an assay for analysing CORT in feathers of kororā, which is a first as far as I know. Moreover, this acts as a baseline for feather stress analysis in kororā and is the first to assess changes in feather corticosterone over time for the species. While there have been previous studies of stress hormones in kororā, these have largely focused on corticosterone in plasma in response to capture and handling during the breeding season e.g. Cockrem et al. (2017).

5.3 How this study may improve seabird conservation implications

The novel and less-invasive feather CORT method for measuring stress in kororā can be used to monitor the stress experienced by a population. Corticosterone is an important measurement of the environmental stress experienced by kororā populations in the Hauraki Gulf and may provide information on the decline of the species (Robertson et al., 2017). Sampling feathers is less intensive than blood sampling, with little specialist knowledge required so it can be a simple monitoring technique to implement (Cherel et al., 2005). It was through this method that I identified a population of kororā in the Hauraki Gulf that experienced greater stress than two other colonies. From this, future studies can work to uncover the causes behind the spatial differences in stress hormones in an urban region where mass mortality of penguins is common (Crockett and Kearns, 1975).

The method of combining stable isotopes and stress hormones from feathers can provide insight into whether changes in the physiology of a seabird population are linked to food supply or whether they may be caused by other factors (Fairhurst et al., 2013). This method could be utilised in other inshore foraging penguins e.g. hoiho/yellow-eyed penguin (*Megadyptes antipodes*) to detect whether the stress experienced by individuals is linked to local prey availability, which could be useful in implementing protection measures for the endangered species.

Should the two clades of kororā be recognised as distinct species in the future, this study could provide useful baseline information of the foraging ecology and stress physiology for the conservation management of *Eudyptula minor*.

5.4 How this study helps utilise seabirds as indicators of the marine environment

The reliance of seabirds on the marine environment means that their foraging ecology and stress physiology reflects the state of the marine environment in which they forage (Mallory et al., 2010). The small foraging range and heavy reliance on local resources make kororā particularly sensitive to changes in marine resource distribution (Flemming et al., 2013) and changes in the foraging ecology and stress physiology of kororā can reflect fine scale shifts in local environmental conditions (Chilvers, 2017; Kowalczyk et al., 2015a).

Kororā in this study foraged within 25 km from their colony during the breeding season which indicated sufficient prey was available to those individuals in the local marine environment. Had they foraged further than the 30 km radius identified in other studies e.g. Pelletier et al. (2014); Zhang et al. (2015), this may have indicated reduced prey availability, as prey scarcity has been linked to increased foraging effort in kororā (Flemming et al., 2013; Numata et al., 2000; Poupart et al., 2017).

Stable isotope analysis showed the fish-based diet of kororā in this study remained stable over time despite a change in the broad foraging location. This suggests that the monitoring of nitrogen isotopes in kororā tissues could potentially act as an indication of changes in fish stocks. Nutritional stress is often reflected in the body condition (Kato et al., 2008) and physiology of kororā (Mortimer and Lill, 2007). Given this, changes in the stress physiology of kororā can be indicative of marine resource availability.

5.5 Implications of study findings

The shallow coastal environment was identified as an important foraging habitat during the breeding season whereas the shift in pre-moult foraging locations over time suggests that such environments may have been more productive pre-1980 than at present. Given this, ecosystem management plans could focus on reducing negative impacts on coastal marine environments to ensure kororā can forage near their colonies throughout the year. For example, increased sediment loadings from terrestrial environments may be transported into coastal ecosystems with an increase in rainfall events as forecast with climate change (Trathan et al., 2015). Sediment plumes in marine environments reduce the foraging efficiency of kororā and can cause nutritional stress (Kowalczyk et al., 2015b) so councils could work to minimise the amount of sediment entering marine environments to reduce the negative impacts of high rainfall events on kororā foraging, especially around colonies with higher stress measurements.

The identification of fish as an important dietary component to kororā over time can help inform management decisions regarding the bait fish species consumed by kororā. In New Zealand no stock assessments have been made for many species of baitfish including pilchard and anchovy (Fisheries New Zealand, 2018), therefore it is only assumed that stocks are being fished sustainably. Sustainably managing fish stocks in the Hauraki Gulf would help ensure kororā populations can allocate their energy to reproduction and chick rearing instead of high foraging effort (Poupart et al., 2017) which could increase the population of kororā in the Hauraki Gulf.

Declining populations of kororā and other marine megafauna in the Hauraki Gulf appears a likely cause for the lower stress hormone levels for both contemporary kororā and individuals from Tāwharanui and Otata compared to museum specimens and extant individuals from Motu Muka. The lower densities of kororā at Otata and Tāwharanui (~12 pairs each) had significantly lower stress hormones than Motu Muka where a larger population of kororā (20+ pairs) exists alongside five other species of burrowing seabirds. While smaller populations appear to benefit those individuals physiologically, such populations are less resilient to unpredictable environmental variation due to their reduced genetic diversity and decreased population fitness (Couvet, 2002; Jamieson et al., 2006). Given this, management strategies such as seabird restoration should aim to restore kororā populations to a density where stress effects are not an issue. Restoring kororā to a medium density throughout multiple sites, rather than scattered pockets of high and low density populations, may increase genetic diversity resilience of the overall population of kororā in the Hauraki Gulf.

Identifying healthy or degraded marine ecosystems through a seabird lens can be useful in marine spatial planning and can inform marine ecosystem management (Einoder, 2009). For example, marine ecosystems where seabird foraging effort is high and stress hormones elevated could indicate where resource extraction should be minimised to improve ecosystem health. Similarly, the information gathered from seabird foraging ecology and stress physiology could inform where terrestrial inputs into marine ecosystems have the biggest impact on marine megafauna, and thus marine food webs, and where mitigation measures should be put in place. As kororā reflect changes over a scale often < 30 km, these marine environments are often are located within the bounds of local councils, which means mitigation measures are potentially easier to implement than for species that cross regional, national or international boundaries.

5.6 Future directions

Given the time constraint for this study, the information gathered presents a snapshot in time of the foraging ecology and stress physiology of kororā from the wider Hauraki Gulf. Repeated sampling across years and study sites would build a greater picture of how foraging ecology and stress physiology change with fluctuations in environmental conditions and would determine whether the results of this study were part of a broader pattern of change.

Recently installed artificial nest boxes throughout the Hauraki Gulf could be utilised in a region-wide monitoring program to link foraging ecology and stress physiology to breeding success, an important measurement of seabird population health (Kitaysky et al., 2007). Seabirds frequently prioritise their body condition over that of their chicks (Wingfield and Silverin, 2002) so the stress physiology, fledging success and body condition of chicks may be more indicative of changes in marine ecosystems than that of adults alone (Kitaysky et al., 2010). By assessing the stress physiology of chicks from different colonies, we could assess whether the costs of nutritional stress in parents are transferred to chicks and whether measurements of stress are related to population demography of kororā in the Hauraki Gulf.

Through repeated sampling of kororā foraging ecology over time and space, assessments could be made of how individuals adjust their foraging strategy to cope with changes in the marine environment. Additionally, by comparing the results of this study to feathers grown in 2019, some assessment could be made of how the January 2018 storm influenced kororā foraging through the trophic level of prey consumed. For example, if kororā had higher $\delta^{15}N$ values in 2019 than in 2018, this could reflect difficult foraging conditions caused by the storm. Similar assessments could be made of how the storm influenced stress hormones with additional feather sampling over time.

Future studies would benefit from combining GPS tracking devices with time-depth recorders (TDR) to generate further information on foraging effort by assessing range and depth together. This would provide a greater indication of foraging behaviour and would provide further evidence of marine resource availability in the wider Hauraki Gulf. The combination of tracking and TDR devices has been used to determine differences in foraging patterns among kororā colonies from central and southern New Zealand by Chilvers (2017), and to establish the foraging behaviour of hoiho/yellow-eyed penguin (*Megadyptes antipodes*) (Mattern et al., 2007) and Snares penguins (*Eudyptes robustus*) (Mattern et al., 2018).

The development of isoscapes in the Hauraki Gulf and throughout New Zealand would be useful in determining the foraging patterns of many marine species through stable isotope analysis. More specifically, by determining the isotopic composition of kororā prey species in the wider Hauraki Gulf such as small shoaling fish and arrow squid, the trophic level and foraging locations determined from stable isotope analysis would be more precise. As it stands, isotopic values of kororā prey items are derived from prey species in the South Island and carbon isotopes may reflect the higher latitude. Understanding the trophic position and geographic location of prey species in the Hauraki Gulf would allow for a better understanding of the local marine food web.

5.7 Limitations

Due to permitting delays, the earliest I was able to commence tracking was in late-November when chicks are typically older and parents spend longer away from the nest (Kato et al., 2008). This meant some kororā were on longer foraging trips and did not return to the colony during the study period. Additionally, device batteries ran out on the longer foraging trips, meaning I was only able to record full tracks for two individuals. Most studies track kororā for one day early in the breeding season to minimise the impact of tracker attachment and to ensure trackers are retrieved (Chilvers, 2017).

The low numbers of kororā at Tāwharanui and Otata late in the chick-rearing phase meant tracking was not feasible, thus tracking was only achieved at Motu Muka as this was the largest colony. Only tracking kororā at one site meant I was unable to make spatial comparisons among the three study sites to match the physiological assessments, which may have shown differences in foraging patterns associated with prey availability and abundance throughout the wider Hauraki Gulf.

The breeding status of kororā in this study was unknown due to a lack of study burrows. Having birds in study burrows would have made them easier to access than intercepting penguins returning to their nest after a foraging trip. Having accessible birds would have allowed me to correlate foraging ecology and stress physiology to reproductive success, an important measure of marine resource availability in seabirds (Fairhurst et al., 2015). New artificial nest boxes on several islands within the Hauraki Gulf will help future studies to avoid this limitation.

5.8 Conclusions

The differences in prey trophic level, broad foraging location and stress physiology of kororā show that measurements of corticosterone and stable isotopes in feathers do change with variations in local marine ecosystems over both space and time. In addition, the small foraging range and reliance on local marine resources throughout the year makes kororā sensitive to changes in local resource availability in the marine environment surrounding their colony. By monitoring changes in the foraging ecology and stress physiology of colonies in addition to population parameters, kororā can act as indicators for marine environments over small spatial scales. This study aimed to determine whether kororā reflected marine ecosystem health, but further research is needed to determine the causes behind the differences in foraging ecology and stress physiology observed in this study.

The Hauraki Gulf is home to 27 species of seabird which all rely on healthy marine ecosystems for survival (Gaskin and Rayner, 2013). Their breeding sites are mainly pest-free islands protected by the conservation estate, but they are offered little protection in the marine environment where they spend most of their lives. Understanding how seabirds use marine ecosystems, and how they respond to changes in those environments, is critical for protecting them. It is up to individuals, communities, councils, and governments to ensure the Hauraki Gulf marine environment continues to support such an extraordinary seabird diversity and that the Hauraki Gulf remains a global seabird hotspot.

Plate 5.2. The author holding her first kororā

Reference List

Agnew, P., Houston, D., Lalas, C., & Wright, J. (2014). Variation in reproductive performance of Little Penguins (Eudyptula minor) attributable to double brooding. *Journal of ornithology, 155*(1), 101-109.

Agnew, P., Lalas, C., Wright, J., & Dawson, S. (2015). Variation in breeding success and survival of little penguins Eudyptula minor in response to environmental variation. *Marine Ecology Progress Series, 541*, 219-229.

Ainley, D. G., Dugger, K. M., La Mesa, M., Ballard, G., Barton, K. J., Jennings, S., . . . Schmidt, A. (2018). Post-fledging survival of Adélie penguins at multiple colonies: chicks raised on fish do well. *Marine Ecology Progress Series, 601*, 239-251.

Alonso-Alvarez, C., Munilla, I., López-Alonso, M., & Velando, A. (2007). Sublethal toxicity of the Prestige oil spill on yellow-legged gulls. *Environment International, 33*(6), 773-781.

Arnould, J. P., Dann, P., & Cullen, J. (2004). Determining the sex of Little Penguins (Eudyptula minor) in northern Bass Strait using morphometric measurements. *Emu, 104*(3), 261-265.

Ashmole, N. P. (1963). The regulation of numbers of tropical oceanic birds. *Ibis, 103*(3), 458-473.

Auckland Council. (n.d). Tawharanui - Our History, . In *Pamphlet*. Auckland, New Zealand: Auckland Council.

Banks, J. C., Mitchell, A. D., Waas, J. R., & Paterson, A. M. (2002). An unexpected pattern of molecular divergence within the blue penguin (Eudyptula minor) complex. *Notornis, 49*(1), 29-38.

Bannasch, R., Wilson, R. P., & Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental Biology, 194*(1), 83-96.

Barbosa, A., De Mas, E., Benzal, J., Diaz, J. I., Motas, M., Jerez, S., . . . Lauzurica, P. (2013). Pollution and physiological variability in gentoo penguins at two rookeries with different levels of human visitation. *Antarctic Science, 25*(2), 329-338.

Barrett, R. T., Erikstad, K. E., Sandvik, H., Myksvoll, M., Jenni-Eiermann, S., Kristensen, D. L., . . . Vikebø, F. (2015). The stress hormone corticosterone in a marine top predator reflects short-term changes in food availability. *Ecology and evolution, 5*(6), 1306-1317.

Bassett, I. E., Cook, J., Buchanan, F., & Russell, J. C. (2016). Treasure Islands: biosecurity in the Hauraki Gulf marine park. *New Zealand Journal of Ecology, 40*(2), 250-266.

Bearhop, S., Waldron, S., Votier, S. C., & Furness, R. W. (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and biochemical zoology, 75*(5), 451-458.

Becker, B. H., & Beissinger, S. R. (2006). Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology, 20*(2), 470-479.

Berlincourt, M., & Arnould, J. P. (2014). At-sea associations in foraging little penguins. *PLoS One, 9*(8), e105065.

Bertelli, S., & Giannini, N. P. (2005). A phylogeny of extant penguins (Aves: Sphenisciformes) combining morphology and mitochondrial sequences. *Cladistics, 21*(3), 209-239.

Bertrand, S., Joo, R., Smet, C. A., Tremblay, Y., Barbraud, C., & Weimerskirch, H. (2012). Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology, 49*(5), 1168-1177.

Bethge, P., Nicol, S., Culik, B., & Wilson, R. (1997). Diving behaviour and energetics in breeding little penguins (Eudyptula minor). *Journal of Zoology, 242*(3), 483-502.

Birdlife International. (2019). New Zealand Seabirds, (Online database). Retrieved from http://datazone.birdlife.org/species/results?cty=152&cri=&fam=0&gen=0&spc=&cmn=&bt=&rec=N&vag=N&stsea=Y&wat=&aze=. Retrieved 6th June, 2019, from International Union for the Conservation of Nature http://datazone.birdlife.org/species/results?cty=152&cri=&fam=0&gen=0&spc=&cmn=&bt=&rec=N&vag=N&stsea=Y&wat=&aze=

Blight, L. K., Hobson, K. A., Kyser, T. K., & Arcese, P. (2015). Changing gull diet in a changing world: A 150-year stable isotope (δ13C, δ15N) record from feathers collected in the Pacific Northwest of North America. *Global Change Biology, 21*(4), 1497-1507.

Boersma, P. D. (2008). Penguins as marine sentinels. *Bioscience, 58*(7), 597-607.

Boersma, P. D., & Rebstock, G. A. (2014). Climate change increases reproductive failure in Magellanic penguins. *PLoS One, 9*(1), e85602.

Bon, C., Della Penna, A., d'Ovidio, F., Arnould, J. Y., Poupart, T., & Bost, C.-A. (2015). Influence of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands. *Movement ecology, 3*(1), 32-43.

Bond, A. L., & Lavers, J. L. (2014). Climate change alters the trophic niche of a declining apex marine predator. *Global Change Biology, 20*(7), 2100-2107.

Borboroglu, P. G., & Boersma, P. D. (Eds.). (2013). *Penguins: natural history and conservation*. Seattle, USA: University of Washington Press.

Bortolotti, G. R., Marchant, T. A., Blas, J., & German, T. (2008). Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Functional Ecology, 22*(3), 494-500.

Bost, C.-A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.-B., Guinet, C., . . . Weimerskirch, H. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems, 78*(3), 363-376.

Boyd, C., Punt, A. E., Weimerskirch, H., & Bertrand, S. (2014). Movement models provide insights into variation in the foraging effort of central place foragers. *Ecological modelling, 286*, 13-25.

Braidwood, J., Kunz, J., & Wilson, K. (2011). Effect of habitat features on the breeding success of the blue penguin (Eudyptula minor) on the West Coast of New Zealand. *New Zealand Journal of Zoology, 38*(2), 131-141.

Bull, L. (2000). Fidelity and breeding success of the blue penguin Eudyptula minor on Matiu-Somes Island, Wellington, New Zealand. *New Zealand Journal of Zoology, 27*(4), 291-298.

Burgess, E. A. (2006). *Foraging ecology of common dolphins (Delphinus sp.) in the Hauraki Gulf, New Zealand: a thesis presented in fulfilment of the requirements for the degree of Master of Science (Zoology), Massey University, Albany, New Zealand.* (Master's thesis). Massey University,

Buxton, R. T., Jones, C. J., Lyver, P. O. B., Towns, D. R., & Borrelle, S. B. (2016). Deciding when to lend a helping hand: a decision-making framework for seabird island restoration. *Biodiversity and conservation, 25*(3), 467-484.

Cairns, D. (1988). Seabirds as indicators of marine food supplies. *Biological oceanography, 5*(4), 261-271.

Cameron, E. (1998). Bot Soc trips to the Noises (Hauraki Gulf) and an updated species list. *Auckland Botanical Society Journal, 53*(1), 25-35.

Cannell, B., Campbell, K., Fitzgerald, L., Lewis, J., Baran, I., & Stephens, N. (2016). Anthropogenic trauma is the most prevalent cause of mortality in Little Penguins, Eudyptula minor, in Perth, Western Australia. *Emu-Austral Ornithology, 116*(1), 52-61.

Cannell, B. L., & Cullen, J. (1998). The foraging behaviour of little penguins Eudyptula minor at different light levels. *Ibis, 140*(3), 467-471.

Carey, P. W. (1992). Fish prey species of the New Zealand fur seal (Arctocephalus forsteri, Lesson). *New Zealand Journal of Ecology, 16*(1), 41-46.

Carroll, E., Gallego, R., Sewell, M., Zeldis, J., Ranjard, L., Ross, H., . . . Constantine, R. (2019). Multi-locus DNA metabarcoding of zooplankton communities and scat reveal trophic interactions of a generalist predator. *Scientific reports, 9*(1), 281.

Casper, R. M. (2009). Guidelines for the instrumentation of wild birds and mammals. *Animal behaviour, 78*(6), 1477-1483.

Challies, C. N. (2015). Predation of white-flippered penguins (Eudyptula minor albosignata) by ferrets (Mustela furo) in Harris Bay, Banks Peninsula, New Zealand. *Notornis, 62*, 202-208.

Chambers, L. E. (2004). Delayed breeding in Little Penguins–evidence of climate change? *Australian Meteorological Magazine, 53*(1), 13-19.

Chambers, L. E., Devney, C. A., Congdon, B. C., Dunlop, N., Woehler, E. J., & Dann, P. (2011). Observed and predicted effects of climate on Australian seabirds. *Emu-Austral Ornithology, 111*(3), 235-251.

Cherel, Y., Connan, M., Jaeger, A., & Richard, P. (2014). Seabird year-round and historical feeding ecology: blood and feather δ13C and δ15N values document foraging plasticity of small sympatric petrels. *Marine Ecology Progress Series, 505*, 267-280.

Cherel, Y., & Hobson, K. A. (2007). Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series, 329*, 281-287.

Cherel, Y., Hobson, K. A., Bailleul, F., & Groscolas, R. (2005). Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. *Ecology, 86*(11), 2881-2888.

Cherel, Y., Hobson, K. A., & Hassani, S. (2005a). Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiological and biochemical zoology, 78*(1), 106-115.

Chiaradia, A., Costalunga, A., & Kerry, K. (2003). The diet of little penguins (Eudyptula minor) at Phillip Island, Victoria, in the absence of a major prey—Pilchard (Sardinops sagax). *Emu-Austral Ornithology, 103*(1), 43-48.

Chiaradia, A., Forero, M. G., Hobson, K. A., & Cullen, J. M. (2010). Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey. *ICES Journal of Marine Science, 67*(8), 1710-1720.

Chiaradia, A., Forero, M. G., Hobson, K. A., Swearer, S. E., Hume, F., Renwick, L., & Dann, P. (2012). Diet segregation between two colonies of little penguins Eudyptula minor in southeast Australia. *Austral Ecology, 37*(5), 610-619.

Chiaradia, A., & Nisbet, I. (2006). Plasticity in parental provisioning and chick growth in little penguins Eudyptula minor in years of high and low breeding success. *Ardea - Wageningen, 94*(2), 257 - 270.

Chiaradia, A., Ramírez, F., Forero, M. G., & Hobson, K. A. (2016). Stable isotopes (δ13C, δ15N) combined with conventional dietary approaches reveal plasticity in central-place foraging behavior of little penguins Eudyptula minor. *Frontiers in Ecology and Evolution, 3*, 154.

Chiaradia, A., Ropert-Coudert, Y., Kato, A., Mattern, T., & Yorke, J. (2007). Diving behaviour of Little Penguins from four colonies across their whole distribution range: bathymetry affecting diving effort and fledging success. *Marine Biology, 151*(4), 1535-1542.

Chiaradia, A. F., & Kerry, K. R. (1999). Daily nest attendance and breeding performance in the little penguin Eudyptula minor at Phillip Island, Australia. *Marine Ornithology, 27*, 13-20.

Chilvers, B., Finlayson, G., Candy, E., Sriram, A., Morgan, K., & Cockrem, J. (2016). Corticosterone stress hormone responses in oil rehabilitated and non-rehabilitated little penguins. *Marine Pollution Bulletin, 113*(1-2), 312-315.

Chilvers, B. L. (2017). Comparison of New Zealand's little blue penguins, Eudyptula minor, diving behaviour. *Polar Biology, 40*(10), 1965-1974.

Cockrem, J. F. (2007). Stress, corticosterone responses and avian personalities. *Journal of ornithology, 148*(2), 169-178.

Cockrem, J. F., Barrett, D. P., Candy, E. J., & Potter, M. A. (2009). Corticosterone responses in birds: individual variation and repeatability in Adelie penguins (Pygoscelisadeliae) and other species, and the use of power analysis to determine sample sizes. *General and comparative endocrinology, 163*(1-2), 158-168.

Cockrem, J. F., Candy, E. J., Barrett, D. P., Agnew, P., & Potter, M. A. (2017). Individual variation and repeatability of corticosterone responses of little penguins (Eudyptula minor) sampled in two successive years at Oamaru, New Zealand. *General and comparative endocrinology, 244*, 86-92.

Cooper, J. (1978). Moult of the Black-footed penguin. *International Zoo Yearbook, 18*(1), 22-27.

Cottin, M., MacIntosh, A. J., Kato, A., Takahashi, A., Debin, M., Raclot, T., & Ropert-Coudert, Y. (2014). Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. *Marine Ecology Progress Series, 496*, 249-262.

Couvet, D. (2002). Deleterious effects of restricted gene flow in fragmented populations. *Conservation Biology, 16*(2), 369-376.

Crawford, R., Ellenberg, U., Frere, E., Hagen, C., Baird, K., Brewin, P., . . . Pompert, J. (2017). Tangled and drowned: a global review of penguin bycatch in fisheries. *Endangered Species Research, 34*, 373-396.

Crockett, D., & Kearns, M. (1975). Northern little blue penguin mortality in Northland. *Notornis, 22*, 69-72.

Croxall, J. P. (Ed.) (1987). *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge, United Kingdom: Cambridge University Press.

Croxall, J. P., Butchart, S. H., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International, 22*(1), 1-34.

Croxall, J. P., & Lishman, G. S. (1987). The food and feeding ecology of penguins. In J. P. Croxall (Ed.), *Seabirds, feeding ecology and role in marine ecosystems* (pp. 101-133). Cambridge, United Kingdom: Cambridge University Press.

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W., . . . Paleczny, M. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science, 334*(6063), 1703-1706.

Dann, P. (1994). The abundance, breeding distribtuion and nest sites of Blue Penguins in Otago, New Zealand. *Nortonis, 41*(3), 157-166.

Dann, P. (2013). Little Penguin (Eudyptula minor). In P. G. Borboroglu & P. D. Boersma (Eds.), *Penguins: natural history and conservation* (pp. 305 - 319). Seattle, USA: University of Washington Press.

Dann, P., & Cullen, J. (1990). Survival, patterns of reproduction, and lifetime reproductive output in Little Blue Penguins (Eudyptula minor) on Phillip Island, Victoria, Australia. In L. Davis & J. Darby (Eds.), *Penguin biology* (pp. 63-84). San Deigo, California, USA: Academic Press Inc.

Dann, P., & Norman, F. (2006). Population regulation in Little Penguins (Eudyptula minor): the role of intraspecific competition for nesting sites and food during breeding. *Emu-Austral Ornithology, 106*(4), 289-296.

Dann, P., Norman, F. I., Cullen, J., Neira, F. J., & Chiaradia, A. (2000). Mortality and breeding failure of little penguins, Eudyptula minor, in Victoria, 1995–96, following a widespread mortality of pilchard, Sardinops sagax. *Marine and Freshwater Research, 51*(4), 355-362.

Department of Conservation. (2019). Taranga (Hen) Island restoration project. Retrieved from https://www.doc.govt.nz/our-work/taranga-hen-island-restoration-project/

Douglas, D. C., Weinzierl, R., C. Davidson, S., Kays, R., Wikelski, M., & Bohrer, G. (2012). Moderating A rgos location errors in animal tracking data. *Methods in Ecology and Evolution, 3*(6), 999-1007.

Dunning Jr, J. B. (Ed.) (2007). *CRC handbook of avian body masses* (2nd ed.). Boca Raton, Florida, USA: CRC press.

Dunphy, B., Taylor, G., Landers, T., Sagar, R., Chilvers, B., Ranjard, L., & Rayner, M. (2015). Comparative seabird diving physiology: first measures of haematological parameters and oxygen stores in three New Zealand Procellariiformes. *Marine Ecology Progress Series, 523*, 187-198.

Einoder, L. D. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research, 95*(1), 6-13.

Ellenberg, U., Edwards, E., Mattern, T., Hiscock, J. A., Wilson, R., & Edmonds, H. (2015). Assessing the impact of nest searches on breeding birds–a case study on Fiordland crested penguins (Eudyptes pachyrhynchus). *New Zealand Journal of Ecology, 39*(2), 231-244.

Ellenberg, U., Setiawan, A. N., Cree, A., Houston, D. M., & Seddon, P. J. (2007). Elevated hormonal stress response and reduced reproductive output in Yellow-eyed penguins exposed to unregulated tourism. *General and comparative endocrinology, 152*(1), 54-63.

Esri ArcMap. (2018). ArcMap 10.6.1. Computer Software.

Fairhurst, G. D., Bond, A. L., Hobson, K. A., & Ronconi, R. A. (2015). Feather-based measures of stable isotopes and corticosterone reveal a relationship between trophic position and physiology in a pelagic seabird over a 153-year period. *Ibis, 157*(2), 273-283.

Fairhurst, G. D., Champoux, L., Hobson, K. A., Rail, J.-F., Verreault, J., Guillemette, M., . . . Soos, C. (2017). Feather corticosterone during non-breeding correlates with multiple measures of physiology during subsequent breeding in a migratory seabird. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 208*, 1-13.

Fairhurst, G. D., Vögeli, M., Serrano, D., Delgado, A., Tella, J. L., & Bortolotti, G. R. (2013). Can synchronizing feather-based measures of corticosterone and stable isotopes help us better understand habitat–physiology relationships? *Oecologia, 173*(3), 731-743.

Finger, A., Lavers, J. L., Dann, P., Nugegoda, D., Orbell, J. D., Robertson, B., & Scarpaci, C. (2015). The Little Penguin (Eudyptula minor) as an indicator of coastal trace metal pollution. *Environmental pollution, 205*, 365-377.

Fisheries New Zealand. (2018). *Fisheries Assessment Plenary, May 2018: stock assessments and stock status: Volume 2: Hake to Pilchard*. Wellington, New Zealand.: Fisheries New Zealand

Fleming, A. H., Kellar, N. M., Allen, C. D., & Kurle, C. M. (2018). The utility of combining stable isotope and hormone analyses in marine megafauna research. *Frontiers in Marine Science, 5*, 338.

Flemming, S. A., Lalas, C., & van Heezik, Y. (2013). Little penguin (Eudyptula minor) diet at three breeding colonies in New Zealand. *New Zealand Journal of Ecology, 37*(2), 199.

Flemming, S. A., & van Heezik, Y. (2014). Stable isotope analysis as a tool to monitor dietary trends in little penguins E udyptula minor. *Austral Ecology, 39*(6), 656-667.

Forest and Bird (Ed.) (2014). *New Zealand Seabirds: Important Bird Areas and Conservation*. Wellington, New Zealand: The Royal Forest & Bird Protection Society of New Zealand.

Fraser, M. M., & Lalas, C. (2004). Seasonal variation in the diet of blue penguins (Eudyptula minor) at Oamaru, New Zealand. *Notornis, 51*(1), 7-15.

Friesen, M. R., Ross, J. R., Maitland, M., & Gaskin, C. P. (2016). First record of a petrel species killed by penguins: outcome of competition for artificial nesting boxes. *Notornis, 63*, 109-112.

Frost, P. G. (2017). *Population status and trends of selected seabirds in northern New Zealand*. Retrieved from Wellington, New Zealand:

Frost, P. G., & Taylor, G. A. (2018). The status of the red-billed gull (Larus novahollandiae scopulinus) in New Zealand, 2014-2016. *Notornis, 65*(1), 1-13.

Gales, R., Green, B., & Stahel, C. (1988). The energetics of free-living little penguins Eudyptula-Minor (Spheniscidae), during molt. *Australian Journal of Zoology, 36*(2), 159-167.

Gales, R., Williams, C., & Ritz, D. (1990). Foraging behaviour of the little penguin, Eudyptula minor: initial results and assessment of instrument effect. *Journal of Zoology, 220*(1), 61-85.

Gaskin, C. (2017). *Procellariiformes associating with shoaling fish schools – northern New Zealand* Retrieved from Wellington, New Zealand:

Gaskin, C., & Rayner, M. J. (2013). *Seabirds of the Hauraki Gulf: natural history, research and conservation*. Auckland, New Zealand: Auckland Council.

Geurts, J. L. (2006). *The feeding and breeding ecology of little blue penguins (Eudyptula minor) from Tiritiri Matangi Island, New Zealand: a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in Conservation Ecology, Massey University.* (Master's thesis). Massey University,

Giling, D., Reina, R. D., & Hogg, Z. (2008). Anthropogenic influence on an urban colony of the little penguin Eudyptula minor. *Marine and Freshwater Research, 59*(7), 647-651.

Grosser, S., Rawlence, N. J., Anderson, C. N., Smith, I. W., Scofield, R. P., & Waters, J. M. (2016). Invader or resident? Ancient-DNA reveals rapid species turnover in New Zealand little penguins. *Proceedings of the Royal Society B: Biological Sciences, 283*(1824).

Grosser, S., & Waters, J. M. (2015). Development and characterisation of 20 novel microsatellite markers for the little blue penguin (Eudyptula minor) using next-generation sequencing. *Conservation genetics resources, 7*(1), 143-145.

Harding, C. T. (2014). *Tracking African penguins (Spheniscus demersus) outside of the breeding season: Regional effects and fishing pressure during the pre-moult period.* (Doctoral Dissertation). University of Cape Town,

Harvey, S., Phillips, J., Rees, A., & Hall, T. (1984). Stress and adrenal function. *Journal of Experimental Zoology, 232*(3), 633-645.

Hauraki Gulf Forum. (2018). *State of our Gulf 2017 Hauraki Gulf/Tikapa Moana/Te Moana-nui-a-Toi State of the Environment Report 2017* (192721663X). Retrieved from Auckland, New Zealand

Heber, S., Wilson, K. J., & Molles, L. (2008). Breeding biology and breeding success of the blue penguin (Eudyptula minor) on the West Coast of New Zealand's South Island. *New Zealand Journal of Zoology, 35*(1), 63-71.

Hijmans, R. J., Williams, E., & Vennes, C. (2014). Geosphere: spherical trigonometry. R package version 1.3-11. In.

Hilton, G. M., Thompson, D. R., Sagar, P. M., Cuthbert, R. J., Cherel, Y., & Bury, S. J. (2006). A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin Eudyptes chrysocome. *Global Change Biology, 12*(4), 611-625.

Hobson, K. A., Alisauskas, R. T., & Clark, R. G. (1993). Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *The Condor, 95*(2), 388-394.

Hocken, A. (2000). Cause of death in blue penguins (Eudyptula m. minor) in North Otago, New Zealand. *New Zealand Journal of Zoology, 27*(4), 305-309.

Holberton, R. L., Helmuth, B., & Wingfield, J. C. (1996). The corticosterone stress response in gentoo and king penguins during the non-fasting period. *The Condor, 98*(4), 850-854.

Hoskins, A. J., Dann, P., Ropert-Coudert, Y., Kato, A., Chiaradia, A., Costa, D. P., & Arnould, J. P. (2008). Foraging behaviour and habitat selection of the little penguin Eudyptula minor during early chick rearing in Bass Strait, Australia. *Marine Ecology Progress Series, 366*, 293-303.

Hull, C. L., Hindell, M. A., & Michael, K. (1997). Foraging zones of royal penguins during the breeding season, and their association with oceanographic features. *Marine Ecology Progress Series, 153*, 217-228.

Humphries, P., Hyndes, G. A., & Potter, I. C. (1992). Comparisons between the diets of distant taxa (teleost and cormorant) in an Australian estuary. *Estuaries, 15*(3), 327-334.

Inger, R., & Bearhop, S. (2008). Applications of stable isotope analyses to avian ecology. *Ibis, 150*(3), 447-461.

Ismar, S. M., Phillips, R. A., Rayner, M. J., & Hauber, M. E. (2011). Geolocation tracking of the annual migration of adult Australasian Gannets (Morus serrator) breeding in New Zealand. *The Wilson Journal of Ornithology, 123*(1), 121-125.

IUCN. (2018). Eudyptula minor: Birdlife International:. In *The IUCN Red List of Threatened Species 2018: e.T22697805A132603951*: International Union for the Conservation of Nature.

Jamieson, I. G., Wallis, G. P., & Briskie, J. V. (2006). Inbreeding and endangered species management: is New Zealand out of step with the rest of the world? *Conservation Biology, 20*(1), 38-47.

Kato, A., Ropert-Coudert, Y., & Chiaradia, A. (2008). Regulation of trip duration by an inshore forager, the little penguin (Eudyptula minor), during incubation. *The Auk, 125*(3), 588-593.

Kinsky, F. (1958). The Northern Blue Penguin (Eudyptula minor Novaehollandiae) in Wellington Harbour. *Proceedings (New Zealand Ecological Society)*(6), 12-15.

Kinsky, F., & Falla, R. A. (1976). A subspecific revision of the Australasian blue penguin (Eudyptula minor) in the New Zealand area. *Records National Museum of New Zealand, 1*(7), 105 - 126.

Kitaysky, A., Kitaiskaia, E., Piatt, J. F., & Wingfield, J. (2003). Benefits and costs of increased levels of corticosterone in seabird chicks. *Hormones and behavior, 43*(1), 140-149.

Kitaysky, A., Piatt, J. F., & Wingfield, J. (2007). Stress hormones link food availability and population processes in seabirds. *Marine Ecology Progress Series, 352*, 245-258.

Kitaysky, A., Wingfield, J., & Piatt, J. F. (1999). Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology, 13*(5), 577-584.

Kitaysky, A. S., Piatt, J. F., Hatch, S. A., Kitaiskaia, E. V., Benowitz-Fredericks, Z. M., Shultz, M. T., & Wingfield, J. C. (2010). Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology, 24*(3), 625-637.

Klomp, N., Meathrel, C., Wienecke, B., & Wooller, R. (1991). Surface nesting by little penguins on Penguin Island, Western Australia. *Emu-Austral Ornithology, 91*(3), 190-193.

Klomp, N., & Wooller, R. (1988). Diet of little penguins, Eudyptula minor, from Penguin Island, western Australia. *Marine and Freshwater Research, 39*(5), 633-639.

Kowalczyk, N. D., Chiaradia, A., Preston, T. J., & Reina, R. D. (2014). Linking dietary shifts and reproductive failure in seabirds: a stable isotope approach. *Functional Ecology, 28*(3), 755-765.

Kowalczyk, N. D., Chiaradia, A., Preston, T. J., & Reina, R. D. (2015a). Fine-scale dietary changes between the breeding and non-breeding diet of a resident seabird. In *Royal Society open science* (Vol. 2).

Kowalczyk, N. D., Chiaradia, A., Preston, T. J., & Reina, R. D. (2015b). Selective foraging within estuarine plume fronts by an inshore resident seabird. *Frontiers in Marine Science, 2*, 42.

Lamb, J. S., O'Reilly, K. M., & Jodice, P. G. (2016). Physical condition and stress levels during early development reflect feeding rates and predict pre-and post-fledging survival in a nearshore seabird. *Conservation physiology, 4*(1).

Landers, T. J. (2017). *Muriwai Beach to Te Henga (Bethells) 2016 grey-faced petrel and little penguin survey* (1988529743). Retrieved from Auckland, New Zealand:

Lodjak, J., Mägi, M., Rooni, U., & Tilgar, V. (2015). Context-dependent effects of feather corticosterone on growth rate and fledging success of wild passerine nestlings in heterogeneous habitat. *Oecologia, 179*(4), 937-946.

Long, K. H. (2017). *The time course of corticosterone responses in kororā (little penguin, Eudyptula minor): a thesis presented in partial fulfilment of the requirements of the degree of Master of Science in Zoology at Massey University.* (Master's thesis). Massey University,

Lovvorn, J., Liggins, G. A., Borstad, M. H., Calisal, S. M., & Mikkelsen, J. (2001). Hydrodynamic drag of diving birds: effects of body size, body shape and feathers at steady speeds. *Journal of Experimental Biology, 204*(9), 1547-1557.

Lowe, M. I. (2009). *The effect of conservation management on Little Blue Penguins (Eudyptula minor) on North Island, New Zealand: a thesis presented in partial fulfilment of the requirements for the degree of Masters of Science in Conservation Biology at Massey University, Auckland, New Zealand.* (Master's thesis). Massey University,

Mallory, M. L., Robinson, S. A., Hebert, C. E., & Forbes, M. R. (2010). Seabirds as indicators of aquatic ecosystem conditions: A case for gathering multiple proxies of seabird health. *Marine Pollution Bulletin, 60*(1), 7-12.

Marchant, S., Higgins, P. J., Ambrose, S. J., & Steele, W. K. (Eds.). (2006). *Handbook of Australian, New Zealand & Antarctic birds* (Vol. 7). Oxford, UK: Oxford University Press.

Markwell, T. J., & Daugherty, C. H. (2002). Invertebrate and lizard abundance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. *Ecoscience, 9*(3), 293-299.

Massey University Auckland. (2018). *Massey University Auckland Seabird Necropsy Data*.

Mattern, T. (2001). *Foraging Strategies and Breeding Success in the Little Penguin, Eudyptula Minor: A Comparative Study Between Different Habitats: a Thesis Submitted for the Degree of Master of Science in Zoology of the University of Otago, Dunedin, New Zealand.* (Master's thesis). University of Otago Dunedin, New Zealand, Dunedin, New Zealand.

Mattern, T., Ellenberg, U., Houston, D. M., & Davis, L. S. (2007). Consistent foraging routes and benthic foraging behaviour in yellow-eyed penguins. *Marine Ecology Progress Series, 343*, 295-306.

Mattern, T., Ellenberg, U., Houston, D. M., & Davis, L. S. (2018). Like clockwork-nest attendance patterns and foraging behaviour of Snares penguins Eudyptes robustus as a function of daylength and oceanography. *PeerJ Preprints, 6*, e26653v26651.

Mattern, T., McPherson, M., Ellenberg, U., van Heezik, Y., & Seddon, P. (2018a). High definition video loggers provide new insights into behaviour, physiology, and the oceanic habitat of marine top predators. *PeerJ Preprints, 5*(e2765v1).

Mattern, T., Pütz, K., Garcia-Borboroglu, P., Ellenberg, U., Houston, D. M., Long, R., . . . Seddon, P. J. (2018b). Marathon penguins–Reasons and consequences of long-range dispersal in Fiordland penguins/Tawaki during the pre-moult period. *PLoS One, 13*(8), e0198688.

Mattern, T., & Wilson, K.-J. (2018). Little (blue) penguin/kororā. *New Zealand penguins-current knowledge and research priorities*, 36 - 72.

McCallum, J., Bellingham, P., Hay, J., & Hitchmough, R. (1984). The birds of the Chickens Islands, northern New Zealand. *Tane, 30*, 105-124.

McCutcheon, C., Dann, P., Salton, M., Renwick, L., Hoskins, A., Gormley, A., & Arnould, J. (2011). The foraging range of Little Penguins (Eudyptula minor) during winter. *Emu, 111*(4), 321-329.

McKenzie, F. R. K. (2011). *The foraging ecology of Little Penguin (Eudyptula minor) on Tiritiri Matangi Island: a thesis submitted in partial fulfilment of the requirements of Master of Science in Conservation Biology, Massey University, Auckland.* (Master's thesis). Massey University,

Meynier, L., Stockin, K., Bando, M., & Duignan, P. (2008). Stomach contents of common dolphin (Deiphinus sp.) from New Zealand waters. *New Zealand Journal of Marine and Freshwater Research, 42*(2), 257-268.

Miller, C. B. (2009). *Biological oceanography*. Oregon, USA: John Wiley & Sons.

Monin, P. (1996). The islands lying between Slipper Island in the south-east, Great Barrier Island in the north and Tiritiri-Matangi in the north-west: Report for the Waitangi Tribunal on the Hauraki Gulf Islands. *Wai, 406*(7).

Mortimer, L., & Lill, A. (2007). Activity-related variation in blood parameters associated with oxygen transport and chronic stress in little penguins. *Australian Journal of Zoology, 55*(4), 249-256.

Nevitt, G. A., & Bonadonna, F. (2005). Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biology Letters, 1*(3), 303-305.

NIWA. (2018). January 2018 New Zealand Storm (2018-01-04). Retrieved from https://hwe.niwa.co.nz/event/January_2018_New_Zealand_Storm. Retrieved May 18th, 2019 https://hwe.niwa.co.nz/event/January_2018_New_Zealand_Storm

Numata, M., Davis, L. S., & Renner, M. (2000). Prolonged foraging trips and egg desertion in little penguins (Eudyptula minor). *New Zealand Journal of Zoology, 27*(4), 277-289.

Numata, M., Davis, L. S., & Renner, M. (2004). Growth and survival of chicks in relation to nest attendance patterns of little penguins (Eudyptula minor) at Oamaru and Motuara Island, New Zealand. *New Zealand Journal of Zoology, 31*(3), 263-269.

Ogle, S. (2018). *The development of the corticosterone stress response of kororā (little penguin, Eudyptula minor) chicks in response to frequent handling: a thesis presented in partial fulfilment of the requirements of the degree of Master of Science in Physiology at Massey University.* (Master's thesis). Massey University,

Orians, G. H. (1979). On the theory of central place foraging. *Analysis of ecological systems*, 157-177.

Overeem, R. L., Peucker, A. J., Austin, C. M., Dann, P., & Burridge, C. P. (2008). Contrasting genetic structuring between colonies of the World's smallest penguin, Eudyptula minor (Aves: Spheniscidae). *Conservation genetics, 9*(4), 893-905.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., & Reid, J. B. (2008). Seabirds as indicators of the marine environment. *ICES Journal of Marine Science, 65*(8), 1520-1526.

Paul, L. (2014). *History of, and trends in, the commercial landings of finfish from the Hauraki Gulf, 1850-2006* (047842373X). Retrieved from Wellington, New Zealand:

Paul, L., & Parkinson, D. (2001). *Pilchard (Sardinops neopilchardus) biology and fisheries in New Zealand, and a review of pilchard (Sardhops, Sardina) biology, fisheries, and research in the main world fisheries*. Retrieved from Wellington, New Zealand:

Pelletier, L., Chiaradia, A., Kato, A., & Ropert-Coudert, Y. (2014). Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia, 176*(2), 399-408.

Perriman, L., & Steen, H. (2000). Blue penguin (Eudyptula minor) nest distribution and breeding success on Otago Peninsula, 1992 to 1998. *New Zealand Journal of Zoology, 27*(4), 269-275.

Peucker, A. J., Dann, P., & Burridge, C. P. (2009). Range-wide phylogeography of the little penguin (Eudyptula minor): evidence of long-distance dispersal. *The Auk, 126*(2), 397-408.

Phillips, R., Silk, J., Croxall, J., Afanasyev, V., & Briggs, D. (2004). Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series, 266*, 265-272.

Piatt, J. F., Sydeman, W. J., & Wiese, F. (2007). Introduction: seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series, 352*, 199-204.

Pinkerton, M. H., MacDiarmid, A., Beaumont, J., Bradford-Grieve, J., Francis, M., Jones, E., . . . Nodder, S. (2015). *Changes to the Food-web of the Hauraki Gulf During a Period* *of Human Occupation: A Mass-balance Model Approach* (1776650514). Retrieved from Wellington, New Zealand:

Polito, M. J., Trivelpiece, W. Z., Patterson, W. P., Karnovsky, N. J., Reiss, C. S., & Emslie, S. D. (2015). Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of Pygoscelis penguins. *Marine Ecology Progress Series, 519*, 221-237.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology, 83*(3), 703-718.

Poupart, T. A., Waugh, S. M., Bost, C., Bost, C.-A., Dennis, T., Lane, R., . . . Wilson, K.-J. (2017). Variability in the foraging range of Eudyptula minor across breeding sites in central New Zealand. *New Zealand Journal of Zoology, 44*(3), 225-244.

Prickett, N. (1984). An archaeological survey of the Chickens Islands (Marotere), New Zealand. *Tane, 30*, 177-197.

Putland, R., Constantine, R., & Radford, C. (2017). Exploring spatial and temporal trends in the soundscape of an ecologically significant embayment. *Scientific reports, 7*(1), 5713.

Pütz, K., & Cherel, Y. (2005). The diving behaviour of brooding king penguins (Aptenodytes patagonicus) from the Falkland Islands: variation in dive profiles and synchronous underwater swimming provide new insights into their foraging strategies. *Marine Biology, 147*(2), 281-290.

Quillfeldt, P., Engler, J. O., Silk, J. R., & Phillips, R. A. (2017). Influence of device accuracy and choice of algorithm for species distribution modelling of seabirds: a case study using black-browed albatrosses. *Journal of avian biology, 48*(12), 1549-1555.

R Core Development Team. (2018). R Foundation for Statistical Computing; Vienna, Austria: 2014.

Ramírez, F., Afán, I., Davis, L. S., & Chiaradia, A. (2017). Climate impacts on global hot spots of marine biodiversity. *Science Advances, 3*(2), e1601198.

Rayner, M., Carlile, N., Priddel, D., Bretagnolle, V., Miller, M., Phillips, R., . . . Torres, L. (2016). Niche partitioning by three Pterodroma petrel species during non-breeding in the equatorial Pacific Ocean. *Marine Ecology Progress Series, 549*, 217-229.

Rayner, M. J., Taylor, G. A., Gaskin, C. P., & Dunphy, B. J. (2017). Seasonal activity and unpredicted polar front migration of northern New Zealand Common Diving Petrels (Pelecanoides urinatrix). *Emu-Austral Ornithology, 117*(3), 290-298.

Recio, M. R., Mathieu, R., Denys, P., Sirguey, P., & Seddon, P. J. (2011). Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. *PLoS One, 6*(12), e28225.

Reilly, P., & Cullen, J. (1983). The little penguin Eudyptula minor in Victoria, IV: moult. *Emu, 83*(2), 94-98.

Robertson, D. (1992). Diet of the Australasian gannet Morus serrator (GR Gray) around New Zealand. *New Zealand Journal of Ecology, 16*, 77-77.

Robertson, H., Baird, K., Dowding, J., Elliott, G., Hitchmough, R., Miskelly, C., . . . Scofield, R. (2017). Conservation status of New Zealand birds, 2016. New Zealand threat classification series 19. *Wellington: Department of Conservation*.

Robson, S. (2018, 11 April). Hundreds of blue penguins die off, starved by La Niña. *Radio New Zealand*. Retrieved from https://www.rnz.co.nz/news/national/354729/hundreds-of-blue-penguins-die-off-starved-by-la-nina

Rogers, T., & Knight, C. (2006). Burrow and mate fidelity in the little penguin Eudyptula minor at Lion Island, New South Wales, Australia. *Ibis, 148*(4), 801-806.

Romero, L. M. (2002). Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and comparative endocrinology, 128*(1), 1-24.

Romero, L. M., & Fairhurst, G. D. (2016). Measuring corticosterone in feathers: strengths, limitations, and suggestions for the future. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 202*, 112-122.

Ropert-Coudert, Y., Kato, A., Wilson, R. P., & Cannell, B. (2006). Foraging strategies and prey encounter rate of free-ranging Little Penguins. *Marine Biology, 149*(2), 139-148.

Ropert-Coudert, Y., Knott, N., Chiaradia, A., & Kato, A. (2007). How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep Sea Research Part II: Topical Studies in Oceanography, 54*(3-4), 415-423.

Ross, G., Weaver, K., & Greig, J. (1996). The status of Australia's seabirds: proceedings of the National Seabird Workshop, Canberra 1–2 November 1993. *Canberra: Biodiversity Group, Environment Australia*.

Rubenstein, D. R., & Hobson, K. A. (2004). From birds to butterflies: animal movement patterns and stable isotopes. *Trends in ecology & evolution, 19*(5), 256-263.

Russell, J., & Anderson, S. (2007). Birds of Motuhoropapa I, Noises Group, Hauraki Gulf, North Is, New Zealand. *Notornis, 54*, 197-200.

Sagar, P. M., Tennyson, A. J., & Scofield, R. P. (2001). Birds of the Snares Islands, New Zealand. *Notornis, 48*, 1-40.

Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine reviews, 21*(1), 55-89.

Schreiber, E., & Burger, J. (2001). Seabirds in the marine environment. In *Biology of marine birds* (pp. 19-34): CRC Press.

Seddon, P., van Heezik, Y., Ellenberg, U., Borboroglu, P., & Boersma, P. (2013). Yellow-eyed penguin. *Penguins: natural history and conservation*, 91-100.

Seers, B. M., & Shears, N. T. (2015). Spatio-temporal patterns in coastal turbidity–long-term trends and drivers of variation across an estuarine-open coast gradient. *Estuarine, Coastal and Shelf Science, 154*, 137-151.

Shealer, D. A. (2002). Foraging behavior and food of seabirds. *Biology of marine birds*, 137-177.

Sherwen, S. L., & Fanson, K. V. (2015). Validation of an assay to measure glucocorticoid metabolites in the droppings of little penguins (Eudyptula minor). *Journal of Zoo and Aquarium Research, 3*(4), 134-136.

Shoji, A., Elliott, K. H., Aris-Brosou, S., Crump, D., & Gaston, A. J. (2011). Incubation patterns in a central-place forager affect lifetime reproductive success: scaling of patterns from a foraging bout to a lifetime. *PLoS One, 6*(3), e17760.

Smith, J., Mulder, C., & Ellis, J. (2011). Seabirds as ecosystem engineers: nutrient inputs and physical disturbance. In (pp. 27-55): Oxford Univ. Press Inc.

Sorensen, M. C., Hipfner, J. M., Kyser, T. K., & Norris, D. R. (2009). Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology, 78*(2), 460-467.

Stevenson, C., & Woehler, E. J. (2007). Population decreases in little penguins Eudyptula minor in southeastern Tasmania, Australia, over the past 45 years. *Marine Ornithology, 35*, 71-76.

Suess, H. E. (1955). Radiocarbon concentration in modern wood. *Science, 122*(3166), 415-417.

Tambussi, C. P., Reguero, M. A., Marenssi, S. A., & Santillana, S. N. (2005). Crossvallia unienwillia, a new Spheniscidae (Sphenisciformes, Aves) from the late Paleocene of Antarctica. *Geobios, 38*(5), 667-675.

Trathan, P. N., García-Borboroglu, P., Boersma, D., Bost, C. A., Crawford, R. J., Crossin, G. T., . . . De La Puente, S. (2015). Pollution, habitat loss, fishing, and climate change as critical threats to penguins. *Conservation Biology, 29*(1), 31-41.

Trathan, P. N., Warwick-Evans, V., Hinke, J. T., Young, E. F., Murphy, E. J., Carneiro, A. P. B., . . . Godø, O. R. (2018). Managing fishery development in sensitive ecosystems: identifying penguin habitat use to direct management in Antarctica. *Ecosphere, 9*(8), e02392.

Van Rensburg, M. (2010). *Parasitism, disease and breeding ecology of little blue penguins (Eudyptula minor) on Tiritiri Matangi Island, New Zealand.* (Master's thesis). Massey University,

Vargas, F. H., Harrison, S., Rea, S., & Macdonald, D. W. (2006). Biological effects of El Niño on the Galápagos penguin. *Biological Conservation, 127*(1), 107-114.

Vickers, S. I. (2017). *Comparing the Foraging Locations and Stress Physiology of Common Diving Petrels, Pelecanoides Urinatrix Urinatrix, Between Colonies in the Hauraki Gulf.* (Master's thesis). University of Auckland,

Walker, B. G., Boersma, P. D., & Wingfield, J. C. (2014). The glucocorticoid stress response in Magellanic Penguins (Spheniscus magellanicus): comparing within and between breeding seasons, by age and colony, after fighting, and with other penguin species. *Canadian Journal of Zoology, 93*(2), 123-131.

Walls, G. (1978). The influence of the tuatara on fairy prion breeding on Stephens Island, Cook Strait. *New Zealand Journal of Ecology, 1*, 91-98.

Waugh, J. (2016). DNA barcodes highlight two clusters within the little penguin (Eudyptula minor): time to reassess species delineation? *Nortonis, 63*, 66-72.

Waugh, S. M., Griffiths, J. W., Poupart, T. A., Filippi, D. P., Rogers, K., & Arnould, J. Y. (2018). Environmental factors and fisheries influence the foraging patterns of a subtropical seabird, the Westland Petrel (Procellaria westlandica), in the Tasman Sea. *The Condor: Ornithological Applications, 120*(2), 371-387.

Weerheim, M. S., Klomp, N. I., Brunsting, A. M., & Komdeur, J. (2003). Population size, breeding habitat and nest site distribution of little penguins (Eudyptula minor) on Montague Island, New South Wales. *Wildlife Research, 30*(2), 151-157.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography, 54*(3-4), 211-223.

Whitehead, E. (2018). *Age-related Physiological Change and Population Stress Variability in Grey-faced Petrels.* (Master's thesis). University of Auckland,

Whitehead, E., Adams, N., Baird, K., Bell, B., Borrelle, S., Dunphy, B., . . . Russell, J. (2019). *Threats to Seabirds of Northern Aotearoa New Zealand*. Retrieved from Auckland, New Zealand:

Will, A. P., Suzuki, Y., Elliott, K. H., Hatch, S. A., Watanuki, Y., & Kitaysky, A. S. (2014). Feather corticosterone reveals developmental stress in seabirds. *Journal of Experimental Biology, 217*(13), 2371-2376.

Wilson, R. P., Pütz, K., Peters, G., Culik, B., Scolaro, J. A., Charrassin, J.-B., & Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin (1973-2006), 25*(1), 101-106.

Wingfield, J. C., Pérez, J. H., Krause, J. S., Word, K. R., González-Gómez, P. L., Lisovski, S., & Chmura, H. E. (2017). How birds cope physiologically and behaviourally with extreme climatic events. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1723), 20160140.

Wingfield, J. C., & Silverin, B. (2002). Ecophysiological studies of hormone-behavior relations in birds. In *Hormones, brain and behavior* (pp. 587-647): Elsevier.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology, 70*(1), 164-168.

Zeldis, J., & Willis, K. (2015). Biogeographic and trophic drivers of mesozooplankton distribution on the northeast continental shelf and in Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research, 49*(1), 69-86.

Zhang, J. (2012). *Foraging trajectories of Little Blue Penguins from Mokohinau Islands*. Unpublished data.

Zhang, J. (2016). *Modelling animal movement in heterogeneous environments: from statistical inferential models to individual-based models.* (Doctoral thesis). University of Auckland,

Zhang, J., O'Reilly, K. M., Perry, G. L., Taylor, G. A., & Dennis, T. E. (2015). Extending the functionality of behavioural change-point analysis with k-means clustering: a case study with the little penguin (eudyptula minor). *PLoS One, 10*(4), e0122811.

Zhang, J., Rayner, M., Vickers, S., Landers, T., Sagar, R., Stewart, J., & Dunphy, B. (2019). GPS telemetry for small seabirds: using hidden Markov models to infer foraging behaviour of Common Diving Petrels (Pelecanoides urinatrix urinatrix). *Emu-Austral Ornithology, 119*(2), 126-137.