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Population ecology and foraging behaviour of yellow-eyed penguins in New Zealand's subantarctic Auckland Islands

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

Doctor of Philosophy in Veterinary Science and Ecology
Massey University, Manawatū, New Zealand.

Christopher George Muller
2022

Abstract

Penguins and other seabirds rely on healthy, functioning marine systems, and are vulnerable to human-induced changes. Accurate long-term monitoring of a threatened species' population size and trend is therefore important for conservation management.

The endangered yellow-eyed penguin (*Megadyptes antipodes*) is found only in New Zealand waters, with separate northern (mainland New Zealand and offshore islands) and southern (subantarctic) breeding populations. The northern population is declining, believed to be due to threats at sea including direct mortality, as well as changes to food supply, and the effects of climate change. The southern population was previously estimated to comprise at least 60% of the species. Despite this, the subantarctic has been little studied, with one previous population estimate at the Auckland Islands in 1989, two at Campbell Island, and no recent data or measurement of population trends. To address this data gap, this research studied the population and foraging behaviour (diving, foraging location, and diet) of breeding yellow-eyed penguins on Enderby Island, Auckland Islands, from 2015–2017.

The first step for this research was locating cryptic yellow-eyed penguin nests hidden in thick vegetation, as ground searches are inefficient, time-consuming, and potentially hazardous for researchers in subantarctic terrain. I utilised a drone fitted with a novel multi-frequency VHF receiver which located nests in only 3% of the time for traditional search methods, facilitating my other research.

Next, I defined methods for surveying populations in the subantarctic, and estimated a mean of 577 breeding pairs at the Auckland Islands, although the population and number of breeders fluctuated annually, and may have declined since 1989. My foraging research showed that 62% of foraging trips, and over 86% of all southern yellow-eyed penguin dives were pelagic (mid-water), unlike the predominantly benthic (seabed) dives of the northern population. Maximum dive depth was 134 m for benthic dives, and 115 m for pelagic dives, which is deeper than many northern penguins dive. The proportion of pelagic dives increased during La Niña years, likely influenced by climate conditions and prey availability. Foraging distance also varied, with a maximum distance of 47 km from shore, further than many northern birds travel. Foraging area size was greater for females and for pelagic foragers, although benthic foragers travelled further from shore on average. Diet also varied, and during El Niño conditions comprised lower trophic level prey, which were more benthic, and found closer to shore than during La Niña years. Diet results showed some individuals maintained consistent foraging behaviour, although foraging plasticity was also evident. Some individuals changed their foraging behaviour between years, and even within a breeding season.

Variable breeding success in the subantarctic, along with variable foraging behaviour and diet suggests that prey availability is likely limiting the southern population in some years. Prey availability is therefore expected to be a major influence on survival and breeding success in the future, particularly if the effects of climate change become more pronounced.

Dedication

For the penguins

Acknowledgements

Life has a way of throwing curve balls from time to time, and – to adapt an old army saying – no plan survives first contact with adversity. This PhD definitely didn't go according to plan, although that was the fault of a health bomb, not the PhD or the plan.

The project turned out to be very much a marathon rather than a sprint, and I am grateful to a great many people for their assistance to get this thesis over the line.

Supervisors

I am indebted to my supervisors for their unwavering support. Thank you Louise and Phil for your understanding and assistance throughout the course of this PhD. Thanks for having faith in my abilities, and giving me scope to plan my own fieldwork, including adding all the additional tech toys I could dream up.

Louise – thanks for being a great role model of a remote field scientist and team leader, and especially for my many past fieldwork opportunities in the subantarctic. That experience definitely set me up for this PhD. Thanks for all of your support and encouragement over the years.

Phil – thanks for providing a great example of an ecologist and bird scientist, and in particular for your wise counsel, your kind and generous encouragement, and your legendary proof-reading skills!

This PhD was not without tribulations, and at times the prognosis looked grim, but it is due to both of your support and understanding that I have been able to carry on. Most of all, thank you for allowing me scope find my own way through at my own pace. Without your belief in me, this thesis would not have survived to see the light of day!

Co-authors

Thanks to my co-authors at the University of Canterbury's Wireless Research Centre; Fred Samandari, Kelvin Barnsdale, Zane Barker, and Josh McCullough. Thanks for agreeing to collaborate with me on developing an aerial tracking system for wildlife, and for letting me disappear off to the subantarctic with the prototype, and your drone! Thanks also for your hard work and commitment to refining and improving the technology since then, it has been a pleasure working with you.

Thanks to my co-authors on the foraging research; Andre Chiaradia, Yan Ropert-Coudert, and Akiko Kato. Your generous loan of technology greatly expanded and improved the scope of my research.

Thanks also to the subantarctic researchers who I collaborated with on other species while at the Auckland Islands, including Barry Baker, Graham Parker, Kalinka Rexer-Huber, Graeme Elliot, Kath Walker, Emily Kay, Colin Miskelly, Rodney Russ and many others back on the mainland.

Advice and Review

Thanks to Peter Moore and John Darby for generously sharing your expansive penguin knowledge and expertise.

Peter – thank you for sharing your subantarctic research, including unpublished dive data, and for reviewing most (all?) of my papers. Thanks also for demonstrating my first experience of subantarctic research science on Campbell Island all those years ago.

John – thank you for reviewing my thesis discussion, and for your helpful suggestions on my research. Thanks for being a great example of a consummate penguin expert, and an inspiration to young scientists.

Thanks also to the other anonymous reviewers who offered helpful suggestions to improve the papers which ultimately became my research chapters.

Thanks to Mel Young for always being ready to chat about penguins, and to Phil Seddon, Yolanda van Heezik, and all of the other yellow-eyed penguin scientists for welcoming a stray Massey student into the hoiho research community.

Funding and logistics

A huge thankyou to Simon Childerhouse and Blue Planet Marine for generously sharing equipment and logistics. Subantarctic research survives on cooperation and collaboration between research groups, and the opportunity to lead the sea lion and fur seal teams was also extremely valuable financial support for an impoverished grad student.

Thanks to the Department of Conservation for supporting my research, including permits, logistics, and providing historical data. Particular thanks to the staff at the Southern Islands Area office, and the Quarantine Store for helping to process our mountains of field equipment, and always with a smile.

Thanks to Massey University for awarding a PhD scholarship to support my research. Also to the following for providing scholarships and additional funding in support of my studies (in chronological order); Massey School of Vet Science Research Fund, Wildbase Research Trust Scholarship, Freemasons Charity Scholarship, Birds New Zealand Research Fund, Massey University Foundation Grant, Bailey Bequest Bursary, Joan Berry Fellowships in Veterinary Science (awarded but not presented), Massey Pūtea Tautoko – Doctoral Financial Support Grant, and Julie Alley Bursary.

Special thanks are also due to the Massey Ecentre, Massey Ventures, the Innovate competition at The Factory, the Central Economic Development Agency, and to Callaghan Innovation for their business advice and funding assistance to commercialise the drone-tracking methods from Chapter Two. I am proud to say the technology is now available to assist other wildlife biologists with their conservation research at www.AltitudeConservation.com

Fieldwork assistance

Huge thanks to Dani Sijbranda for fieldwork assistance, including long hours of nest searches, penguin catching, and vet skills collecting and processing blood samples. Thanks for your cheerful attitude despite the weather. Your skill at baking breads was also much appreciated!

Thanks also to Emily Kay, Shannon Taylor and Aditi Sriram for helping with chick weighing, and for introducing us Kiwis to Australia Day celebrations.

Thanks to Jo Hiscock for organising the Yellow-eyed penguin counting trips to the Auckland Islands, and to all of the DOC staff and Yellow-eyed penguin volunteers for the early starts and long hours you put in counting penguins. A special shout-out to Sharon Kast for your commitment to every trip!

Thanks also to the film crews for sharing an insight into your world, including Ritchie Robinson, Kina Scollay, and especially to Bill Morris for many evenings of companionship amidst our hectic schedules.

Thanks to the many other subantarctic researchers and professionals who made this research such a great experience.

Technical assistance

Thanks to Stu Cockburn for developing and providing technical assistance with the automatic PIT tag reader, and to Tim Prebble for additional assistance.

Thanks to Jim Fyfe, Mel Young, and Iain Graham for lending other vital field equipment. Also to Trudi Webster, Dave McFarlane and Sue Murray from the Yellow-eyed penguin Trust.

Thanks to Mel Young and Dave Houston for sharing your previous Enderby nest location data. It was a great help to identify where to start looking for nests!

Thanks to Yolanda van Heezik for sharing raw chick weights from the mainland for comparison.

Thanks to Colin Hunter from Sirtrack, and Kevin Lay from Wildlife Computers for advice, equipment, and assistance with tracking technology.

Thanks also to Debbie Hill and Bridey White for help with Massey stuff.

Skippers

Thanks to all of the skippers for providing safe passage for us and all of our gear to the "Furious Fifties" and back during the course of this research;

Steve Kafka and the crew of Evohe,
Henk Haazen and the crew of Tiama,
Mick Fogg and the captain and crew of L'Austral,
Captain and crew of HMNZS Otago.

Thanks also to all the captains and crew who offered hot meals and showers on their way past the island!

Family

Many thanks to my family, including my Mum, Dad, brother and sisters, and to my adopted French family. Thanks for your ongoing support and encouragement during the long processes of fieldwork, analysis, and write-up. Thanks for being ok with me skipping numerous family Christmases to hang out with the penguins, and spending many more hours glued to a computer. And thanks for only occasionally asking "how long until you finish?" I appreciate all of your love and encouragement when I was in hospital, and while I got back on my feet again.

Particular thanks to my parents for instilling my sense of independence and self-reliance, along with an overriding interest and passion for science and nature. Thanks also to my Dad for proof reading this entire thesis!

Massive thanks to Rebecca French. This thesis would not have been possible without you. Whether you were crawling through impenetrable subantarctic scrub with me during hailstorms, or staying by my side during those long weeks in hospital, I am grateful for your unwavering support. Thanks for teaching your awesome R skills, for enduring many months of getting beaten up by penguins, and sacrificing three summers in the name of cold and damp fieldwork. I can't think of anyone else I would rather be abandoned on a desert island with.

Thanks for being such an important part of my PhD, and my life.

The future is in our hands.

Special thanks and many treats to Dusty and Tonks for being great study buddies.

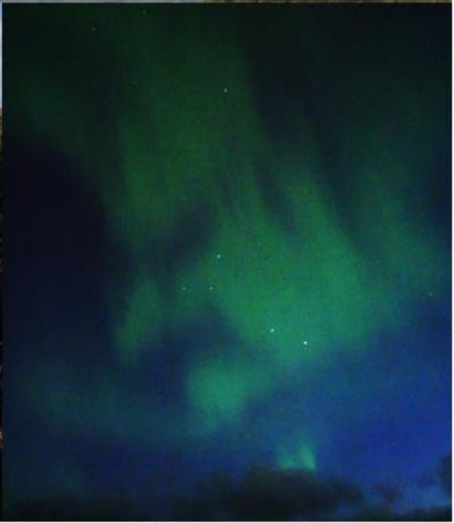
Last, but by no means least, thanks to the penguins, without whose help none of this would have been possible.









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As my primary supervisor, Louise provided overall guidance and helped shape my research questions and methods. Louise supported my Massey PhD scholarship, as well as other grant, permit, and Animal Ethics applications. She provided financial support for field equipment and logistics. Louise reviewed all parts of this thesis and is a co-author of all chapters.

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As my secondary academic supervisor, Phil made important contributions to my study design and interpretation of results, including helpful comments on research chapters. Phil also assisted with field equipment and funding applications. He reviewed all parts of this thesis and is a co-author of all chapters.

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Zane Barker (University of Canterbury, Spatial Engineering Research Centre)

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Fred Samandari (University of Canterbury, Spatial Engineering Research Centre)

Fred assisted with the development of aerial VHF tracking equipment used for nest location. Fred is a co-author of Chapter 2.

Johanna Hiscock (Department of Conservation, Southern Islands)

Johanna assisted with DOC permits and logistics for the Auckland Island penguin transit counts. Johanna is a co-author of Chapter 3.

Andre Chiaradia (Phillip Island Nature Parks, Conservation Department)

Andre provided GPS tracking equipment and gave advice on the analysis of spatial data. Andre is a co-author of Chapter 5.

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Chapter details

Explanation

This section contains the author information, acknowledgments, and other associated details for each of the chapters which are published as scientific papers (Chapters 2–6). Author contact details have been updated to be correct at the time of writing, so some may differ from previously published information.

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CGM conceived and designed the experiments, carried out the fieldwork, analysed the data, and wrote the paper. RKF assisted with fieldwork and data collection, and data analysis. KPB, ZB, and JM developed the UAV system (hardware and software) with input from CGM and oversight and funding from FS. BLC and PFB provided funding, general oversight, and assisted with ecological aspects of the project. All authors reviewed the paper and gave final approval for publication.

Conflicts of interest statement

The authors declare that they have no conflicts of interest.

Data availability statement

Summarised data supporting the findings of this study are available in the Supplementary Materials section.

Declaration of funding

Funding was provided by a Massey University PhD Scholarship, Massey University Research Funding, Institute of Veterinary Animal and Biomedical Sciences Post-graduate studies grant, Birds NZ grant, and Freemasons Charity scholarship.

Acknowledgments

We thank four anonymous reviewers for their helpful suggestions to improve this paper.

Fieldwork was carried out under the New Zealand Department of Conservation Wildlife Act (39214-FAU) and Massey University animal ethics (MUAEC 14/67) approval, and with the approval of Ngāi Tahu iwi. Funding was provided by a Massey University PhD Scholarship, Massey University Research Funding, Institute of Veterinary Animal and Biomedical Sciences Post-graduate studies grant, Birds NZ grant, and Freemasons Charity scholarship. Thanks to the following for supplying additional, equipment, logistics, and other assistance: Department of Conservation; Wildlife and Ecology Group, Massey University; Spatial Engineering Research Centre, University of Canterbury; Yellow-eyed Penguin Trust; Blue Planet Marine; Phillip Island Nature Park; Ponant Expeditions.

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Conflicts of interest statement

The authors declare no conflict of interest.

Data availability statement

Summarised data supporting the findings of this study are available in the Supplementary Materials section.

Acknowledgements

We thank reviewers Peter Moore, Colin Miskelly, and Alan Tennyson for their helpful suggestions to improve this paper. Field work was carried out under DOC Wildlife Act (39214-FAU) and Massey University animal ethics permits (MUAEC 14/67), and with the approval of Ngāi Tahu iwi. Grants were provided by a Massey University PhD Scholarship, Massey University Research Funding, and Institute of Veterinary Animal and Biomedical Sciences post-graduate studies grant. Thanks to the following for supplying additional funding, equipment, logistics, and other assistance: DOC; Wildlife and Ecology Group, Massey University; Yellow-eyed Penguin Trust; Blue Planet Marine; Birds New Zealand; Freemasons Charity; and Ponant Expeditions. Thanks to Juzah Zammit-Ross, Sarah Crump, Danielle Sijbranda, and the many DOC yellow-eyed penguin survey volunteers for contributing to data collection, and to Steve Kafka and the crew of “Evohe” for safe passage to the subantarctic and back. Thanks also to Stu Cockburn and Tim Prebble for technical assistance with the autologger, and Dave Houston for GIS assistance.

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Conflicts of interest statement

The authors declare no conflict of interest.

Data availability statement

Summarised data supporting the findings of this study are available in the Supplementary Materials section.

Acknowledgements

Fieldwork was carried out under DOC Wildlife Act (39214-FAU) and Massey University animal ethics permits (MUAEC 14/67), and with the approval of Ngāi Tahu iwi. Thanks to Mel Young, Thomas Mattern, and Peter Moore for information on mainland diving, and Peter Moore for providing data from Campbell Island, as well as to Danielle Sijbranda for assistance in the field. We thank three anonymous reviewers for their helpful suggestions to improve this paper. Funding was provided by a Massey University PhD Scholarship, Massey University Research Funding, an Institute of Veterinary Animal and Biomedical Sciences postgraduate studies grant, and Birds New Zealand Research Fund. Thanks to the Freemasons Charity for additional funding, and to the following for supplying equipment, logistics, and other assistance: Jo Hiscock and DOC Southland, Wildlife and Ecology Department of Massey University, Yellow-eyed Penguin Trust, Blue Planet Marine, Ponant Expeditions. Thanks to Steve Kafka and the crew of "Evohe" for safe passage to the subantarctic and back.

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Conflicts of interest statement

The authors declare no conflict of interest.

Data availability statement

Summarised data supporting the findings of this study are available in the Supplementary Materials section.

Acknowledgements

We thank Peter Moore and two anonymous reviewers for their helpful suggestions to improve this paper. Fieldwork was carried out under DOC Wildlife Act (39214-FAU) and Massey University Animal Ethics Permits (MUAEC 14/67), and with the approval of Ngāi Tahu iwi. Thanks to Mel Young and Thomas Mattern for information on mainland diving, and to Peter Moore for information on Campbell Island diving. Thanks also to Danielle Sijbranda for assistance in the field. Funding was provided by a Massey University PhD Scholarship, Massey University Research Funding, and Institute of Veterinary Animal and Biomedical Sciences / School of Veterinary Science Postgraduate studies grant, Birds New Zealand Research Fund, and Freemasons Charity. Thanks also to the following for supplying equipment, logistics, and other assistance: Jo Hiscock, DOC Southland; Wildlife and Ecology Group Massey University; Yellow-eyed Penguin Trust; Blue Planet Marine; Phillip Island Nature Parks; Sirtrack; and Ponant Expeditions. Thanks to Steve Kafka and the crew of "Evohe" for safe passage to the subantarctic and back.

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Conflicts of interest statement

The authors declare no conflict of interest.

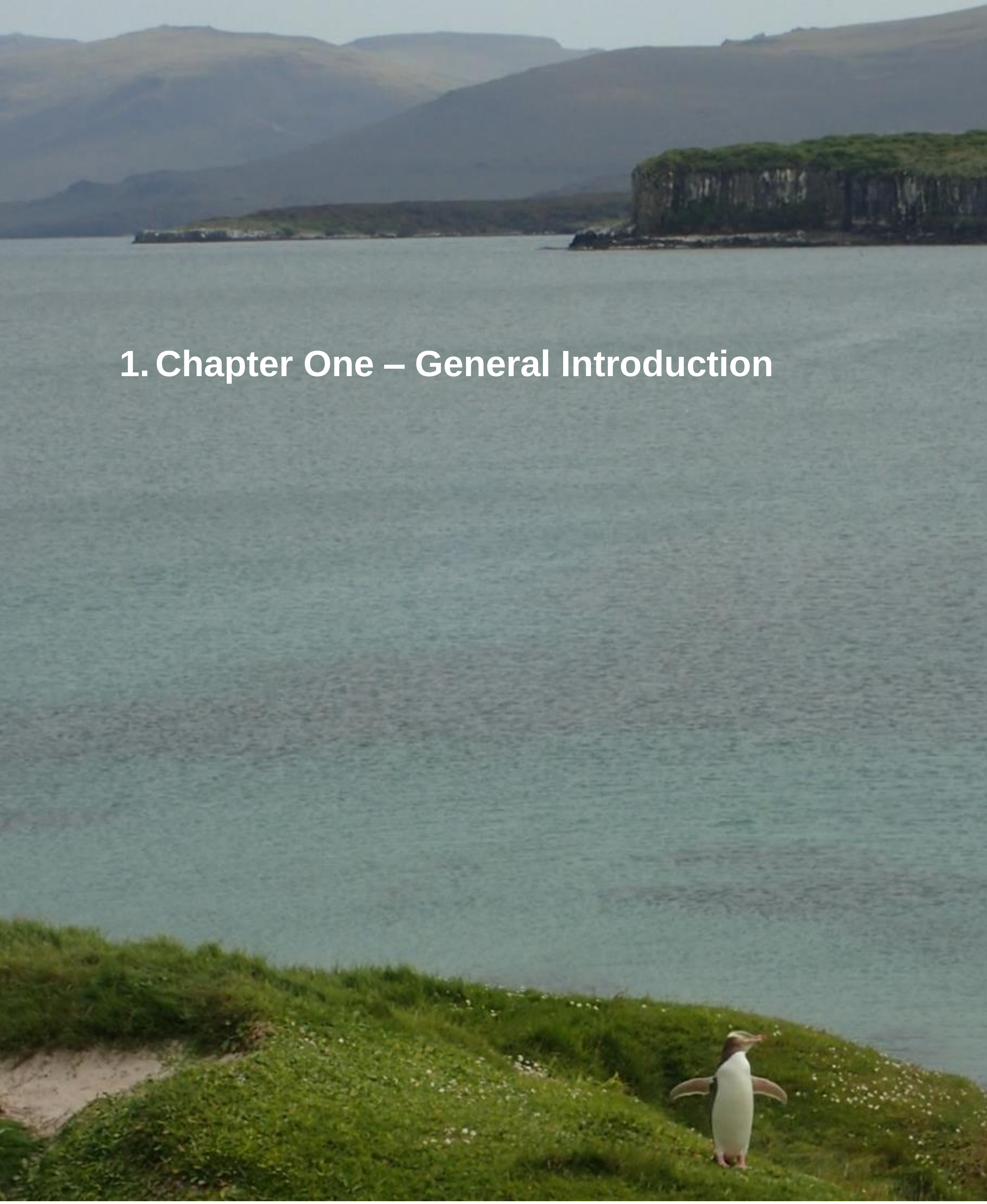
Data availability statement

Summarised data supporting the findings of this study are available in the Supplementary Materials section.

Acknowledgements

We thank John M. Baxter, Peter Moore and one anonymous reviewer for their helpful suggestions to improve this paper. Fieldwork was carried out under DOC Wildlife Act (39214-FAU) and Massey University animal ethics permits (MUAEC 14/67), and with the approval of Ngāi Tahu iwi. Grants were provided by a Massey University PhD Scholarship, Massey University Research Funding, Institute of Veterinary, Animal and Biomedical Sciences Post-graduate studies grant, and Birds New Zealand Research Fund. Thanks to Danielle Sijbranda for veterinary assistance, to Anjana Rajendram for isotope analysis, and to the following for supplying additional funding, equipment, logistics, and other assistance: Jo Hiscock; DOC; Ecology Dept, Massey University; Yellow-eyed Penguin Trust; Blue Planet Marine; Birds NZ; Freemasons Charity, Ponant Expeditions. Thanks to Steve Kafka and crew of “Evohe” for safe passage to the subantarctic and back.

1. Chapter One – General Introduction



1.1 Overview

This introductory chapter discusses the background literature that is required for the reader to understand the context and significance of my research, and represents the state of background knowledge at the time the thesis was planned, as this is when my research questions were formulated. It describes the physical marine environment, and introduces seabirds and penguins, including the yellow-eyed penguin (*Megadytpes antipodes*). Next, it gives some background on general population biology and foraging ecology, including diving behaviour and diet, and methods for their measurement. Following that, it introduces the population status and behavioural ecology of yellow-eyed penguins, particularly in their subantarctic range, and explains the rationale for my research. Finally, it outlines the contents and aims of my thesis.

1.2 The physical environment

1.2.1 Marine ecosystems

Often referred to as “The Blue Planet”, 69% of the Earth’s surface is covered in salt water (Perlman 2016), and in the oceans, organisms face considerably different environmental conditions compared to terrestrial ecosystems. The marine environment consists of benthic (ocean bottom) and pelagic (mid water) environments. The epipelagic zone extends from the sea surface to a depth of 200 m, which is the maximum depth at which there is sufficient light to support photosynthesis (Webber and Thurman 1991). The pelagic environment is further divided into provinces, with the neritic (coastal) province extending from shore and encompassing water over the continental shelf to a depth of 200 m (Webber and Thurman 1991), and is the location of many coastal marine communities.

The primary producers of marine food webs are phytoplankton which provide food for primary and secondary carnivores including zooplankton, cephalopods, fish, seabirds, and marine mammals, and including complex predator-prey relationships within food webs (Webber and

Thurman 1991). The productivity of phytoplankton, and therefore zooplankton, is primarily influenced by sunlight, nutrients, and sea temperature (Webber and Thurman 1991, Hunt et al. 2001). Primary productivity varies according to the duration and intensity of solar radiation, and therefore can be predicted to some extent by latitude. However, nutrients can also vary in space and time due to the effects of ocean currents, stratification, bathymetry, terrestrial inputs, and dynamic inputs from weather and sea surface temperature (SST) (Hunt et al. 2001). Consequently, the number and distribution of many prey species including phytoplankton, zooplankton, cephalopods and fish vary in time and space. For marine predators, this means their food supply may be relatively predictable at certain times and locations, but at other times prey species are often sparsely or patchily distributed in space, and their availability may be intermittent or highly seasonal (Mackas et al. 2001, Murphy et al. 2001).

1.2.2 The Southern Ocean

The Southern Ocean surrounds the Antarctic continent, and at its northern extent is loosely defined by the Antarctic Convergence marking the transition between cold Antarctic surface water and warmer subantarctic water (Foster 1984). Currents in the Southern Ocean are characterised by a westerly flow of air and water within the Antarctic Convergence, but an easterly flow within the Antarctic Divergence zone immediately adjacent to the continent (Knox 2006).

The circumpolar front between Antarctic and subantarctic water is characterised by steep gradients in sea-surface temperature, salinity, and weather conditions. These environmental changes result in areas of upwelling and abrupt changes in phytoplankton abundance, and therefore also in the distribution of zooplankton, and secondary consumers including pelagic bird species and other marine predators (Knox 2006). Many nektonic, or free-swimming prey display diel patterns as they migrate from deeper daytime depths of around 200–500 m to near the surface at night (Foxton and Roe 1974, Hopkins 1987), as well as seasonal patterns arising from phytoplankton blooms in summer (Foster 1984), and contributing an important part of the diet of many subantarctic seabirds. Seabirds perform an important ecosystem role as major predators of zooplankton, krill, and fish, with approximately 25% of all known seabird species breeding in the Southern Ocean, and foraging nearby (Knox 2006). Since seabirds require land areas to breed, the subantarctic islands form an important part of the breeding biology of this unique Southern Ocean avifauna community.

1.2.3 Oceanic variability and climate change

The El Niño Southern Oscillation (ENSO) is a global weather phenomenon which influences rainfall, temperature, and wind patterns (Null 2019), and measures an anomalous warming and cooling of sea surface temperatures in the Pacific Ocean, resulting from atmospheric pressure differences (Mullan 1995). The ENSO is defined by the Southern Oscillation Index (SOI) which measures the difference in mean sea level pressure between Darwin and Tahiti (standardised by the long term pressure difference mean and divided by the long term standard deviation) (Mullan 1995, Null 2019). El Niño conditions represent negative SOI values, when warmer water moves up the west coast of South America, preventing the upwelling of the Humboldt Current which normally stimulates local productivity in marine systems (Weichler et al. 2004). Conversely, La Niña conditions represent positive SOI values and result in the opposite effect, with cooler water moving up the South American coast. La Niña conditions, in particular, can disrupt biological systems across the Pacific Ocean (Moore and Wakelin 1997, Perriman et al. 2000). In New Zealand, El Niño conditions generally result in cooler SST and terrestrial temperatures, with more rainfall in some regions, whereas La Niña is often warmer (Gordon 1986, Mullan 1995).

Changes in sea surface temperatures (SST) or oceanographic shifts that affect SST, such as the El Niño-Southern Oscillation, are a major factor influencing environmental variability, and also seabird productivity (Gregg et al. 2003, Lewison et al. 2012). Changes in SST can influence changes affecting whole food webs (Trenberth and Fasullo 2007) with significant implications for seabirds (Lewison et al. 2012). Major population crashes and breeding failures have been documented for many seabird species, including penguins, as a result of changing environmental conditions (Boersma 2008, Mallory et al. 2009). Expected environmental effects due to climate change make this an important influencer of future seabird population stability (Collins et al. 2013).

1.3 New Zealand's subantarctic islands

1.3.1 Overview

New Zealand's subantarctic islands (Figure 1.1) include a total land area of 76,458 ha, with a marine area covering 1.4 million ha, and are up to 870 km from the South Island, making this one of New Zealand's remotest protected natural areas, and including some of the world's least-modified islands. World Heritage status applies to the marine environment out to 12 nautical miles (22.22 km) from each group (UNESCO 2017).

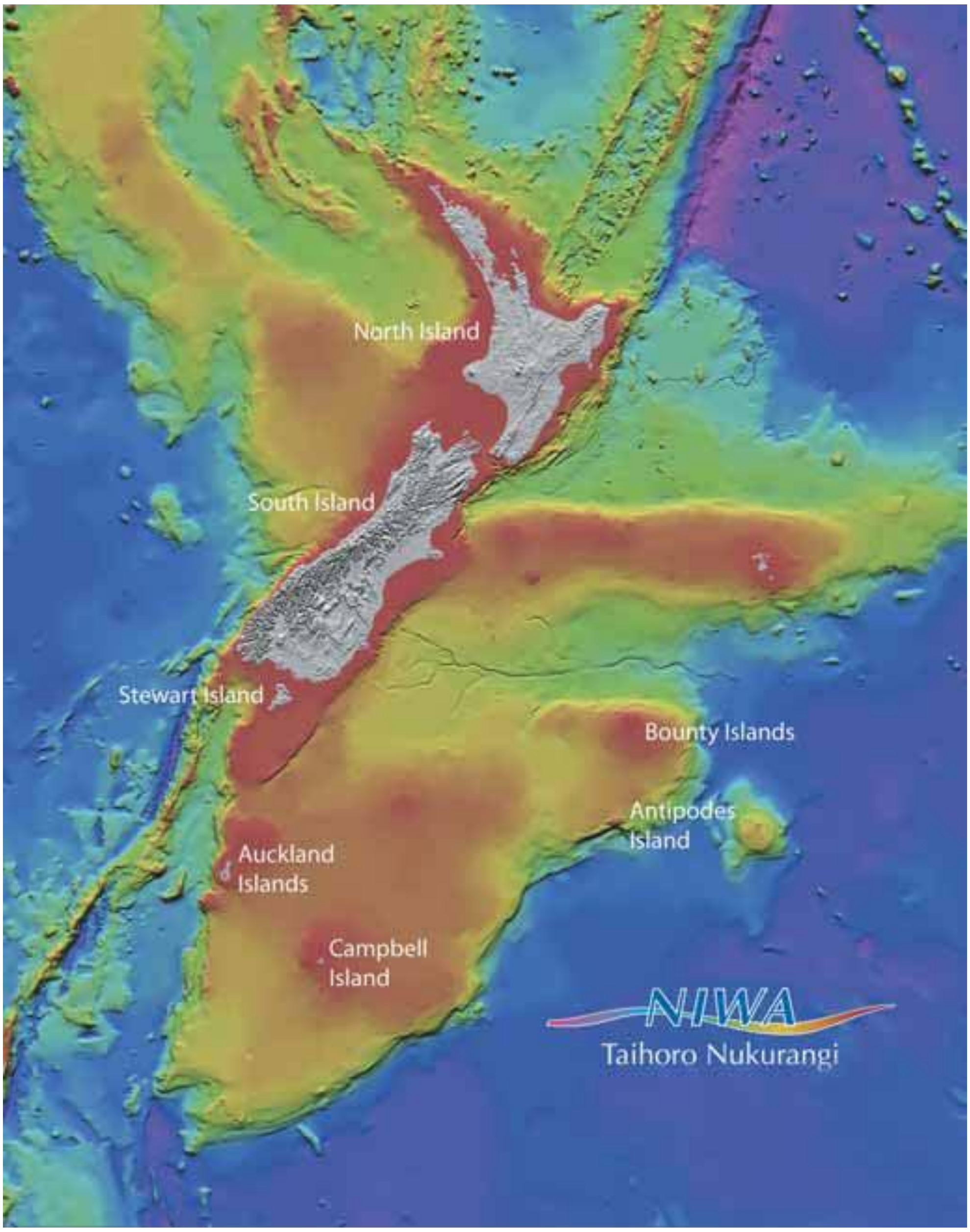


Figure 1.1 Map of New Zealand and subantarctic islands. Colours show bathymetry, from shallow water depth (red) to deep (purple). Source: NIWA.

The islands lie between the Antarctic and Subtropical Convergence zones and the surrounding seas are highly productive, leading to correspondingly high biodiversity, wildlife population densities and endemism (Department of Conservation 1998). While all of the New Zealand subantarctic islands are located on the Pacific Tectonic Plate (Department of Conservation 1998), the different geological history and age of each island group, and their geographical isolation from mainland New Zealand and from each other has led to a unique biodiversity with distinctive plants, birds, invertebrates, marine mammals, fish and marine algae including numerous endemic species (UNESCO 2017).

Between them, New Zealand's subantarctic islands support the most diverse community of breeding seabirds in the Southern Ocean, with 10–15% of the world's seabirds breeding there (Department of Conservation 1998). These include 41 different species of seabirds, eight of which breed nowhere else in the world, including three species of shag (Auckland Island (*Leucocarbo colensoi*), Campbell Island (*Leucocarbo campbelli*), and Bounty Island (*Leucocarbo ranfurlyi*)), three species of albatross (southern royal (*Diomedea epomophora*), Antipodean (*D. epomophora antipodensis*), and Gibson's (*D. antipodensis gibsoni*)), and two species of penguin (erect-crested (*Eudyptes sclateri*), and eastern rockhopper (*E. chrysocome filholi*) (Department of Conservation 2006, Miskelly et al. 2020). The islands support major populations of 10 of the world's 22 species of albatross, and 11 species of penguin have been recorded there, with three species breeding regularly including yellow-eyed penguins (Department of Conservation 1998). In addition, king (*Aptenodytes patagonicus*), royal (*E. schlegeli*), gentoo (*Pygoscelis papua*), and chinstrap (*P. antarctica*) penguins frequently visit, and while they nest on other subantarctic islands they do not breed in the New Zealand subantarctic (Department of Conservation 2006). More than 97% of the world's population of New Zealand sea lion (*Phocarctos hookeri*) breed there, and the marine environment provides critical breeding areas for the southern right whale (*Eubalaena australis*). Land birds also display a surprising diversity in the limited land area available, with a large number of threatened endemics (Department of Conservation 2016, UNESCO 2017). The plant life of the subantarctic islands is recognised for its diversity, special forms and unique communities. The Snares Islands, along with Adams and Disappointment Islands in the Auckland Islands archipelago are some of the last areas in the world where vegetation is unmodified by humans or introduced animals (Department of Conservation 1998).

1.3.2 The Auckland Islands

Geography

The Auckland Islands (*Motu Maha* or *Maungahuka*) archipelago lies 465 kilometres (290 miles) south of New Zealand's South Island (50.7°S 166.1°E), (Figure 1.2).

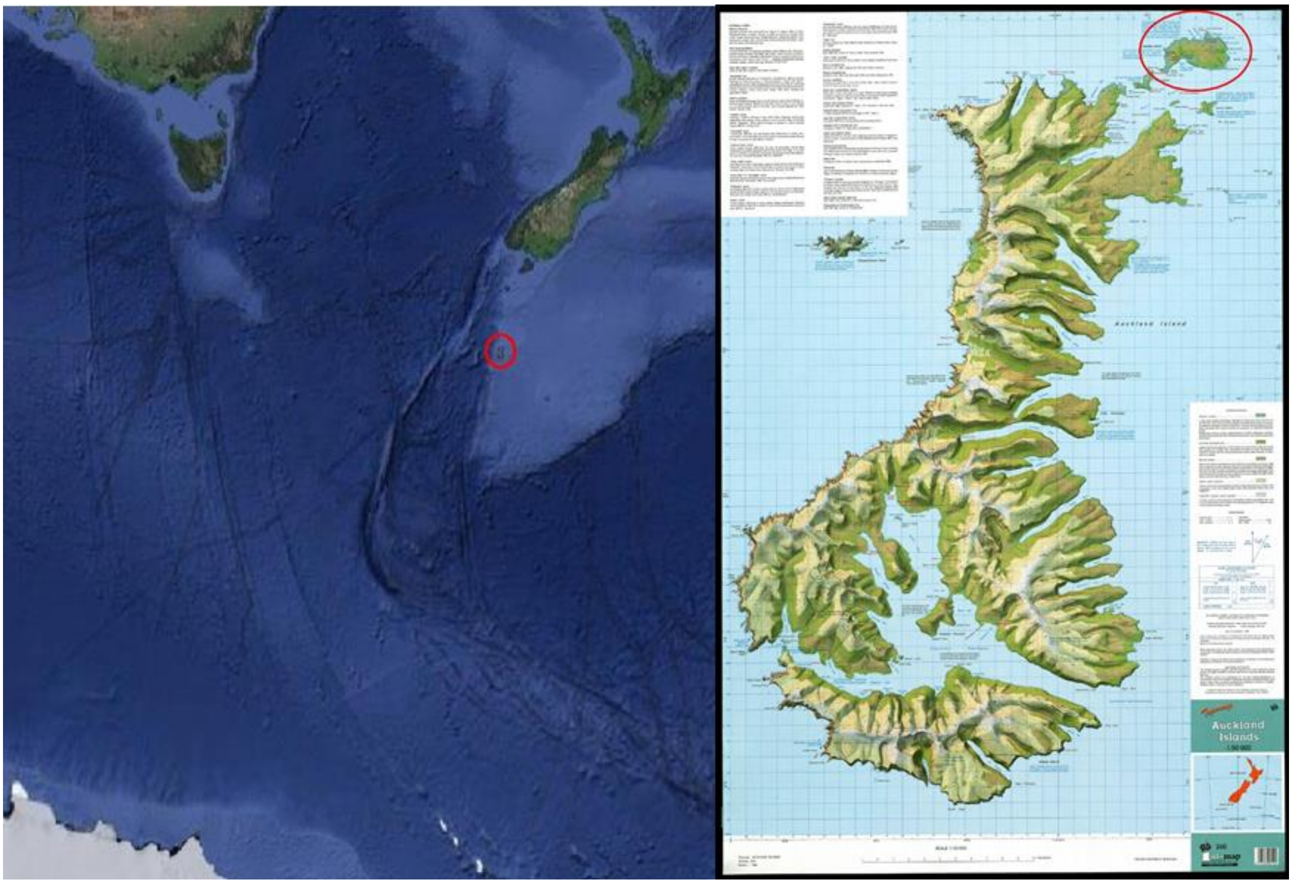


Figure 1.2 Auckland Islands location map (left), Source: Google Maps; and inset Auckland Islands topomap (right), showing the location of Enderby Island in the north-east (circled), Source: NZ Topomaps.

The Auckland Islands archipelago has a combined land area of 625 km^2 (240 sq mi). It includes the main Auckland Island (51,000 ha), Adams Island (10,120 ha), Enderby Island (710 ha) and several smaller islands including Disappointment Island, Ewing Island, Rose Island, Dundas Island and Green Island, plus smaller rock outcrops (Higham 1991). The Auckland Islands are located on the undersea Campbell Plateau, formed from the eroding cones of two 12-million-year-old Miocene volcanoes (Denison and Coombs 1977). Carnley Harbour is the centre of one caldera, and Disappointment Island the other (with the 300 m high western cliffs of Auckland Island all that remains of its crater rim), and many peninsulas and fjords formed by lava flows from these two vents (Peat et al. 2006).

Weather

The Auckland Islands are located in the region of the "Roaring Forties" where westerly winds and cold fronts are strong and frequent. Maximum air temperature generally ranges from 10–16 ^{O}C in summer, and 4–10 ^{O}C in winter (Peat et al. 2006). Shipwrecked sailors described miserable weather including incessant gales, constant hail, snow, and pelting rain (Raynal 1874). The climate was also blamed for the failure of historic whaling and farming ventures at the Auckland Islands (Peat et al. 2006).

Habitat

The Auckland Islands are dominated by peat soils, with vegetation around coastal areas of the Auckland Islands predominantly southern rātā (*Metrosideros umbellata*) forest, continuing to an altitude of around 50 m above sea level in most areas, but forming a canopy around half the height it reaches on the mainland (Godley 1965). Around Ross Harbour the introduced tree daisy *Olearia lyallii* dominates, and in some sheltered areas the world's southernmost tree fern *Cyathea smithii*, and the tree fuchsia *Fuchsia excorticata* can be found (Peat et al. 2006). At higher altitudes the forest gives way to shrubland comprising *Dracophyllum, Coprosma, Myrsine, Ozothamnus, Pseudopanax* and *Hebe*. Above 300 m tussock grasslands of

Chionochloa antarctica occur, interspersed with megaherbs such as *Pleurophyllum*, and giving way to ground-hugging fellfield vegetation above 450 m altitude (Godley 1965, Peat et al. 2006).

Human history

The Auckland Islands were discovered by Europeans in 1806, and were visited by sealers and whalers, with a number of shipwrecks and castaways also present for short periods in the 19th century. In 1842 a group of Māori and Moriori from the Chatham Islands established a settlement on Auckland Island, and in 1849 the European settlement of Hardwicke was founded in Port Ross on Auckland Island, which also included land clearance for farming on Enderby Island. All settlements were abandoned by 1853 (Peat et al. 2006). The islands currently have no permanent human inhabitants, but research huts administered by the Department of Conservation are present on Enderby and Adams Islands, with smaller huts for occasional use on Dundas Island, and Dees Head in Port Ross on Auckland Island. Commercial fishing boats trawl and long-line around the Auckland Islands, particularly in the waters to the north and east, and vessels sometimes shelter in Port Ross (Ministry of Primary Industries 2018a). Tour boats carrying up to 200 passengers visit in the summer months, with guests usually going ashore on Enderby Island, and sometimes also conducting Zodiac tours and day walks on Auckland Island.

Protection

The five New Zealand subantarctic island groups have each been identified as National Reserves, which acknowledges “values of national or international significance” (section 13 Reserves Act 1977). The islands are also covered by additional protective legislation including the Wildlife Act 1953, the Wild Animal Control Act 1977, the Resource Management Act

1991, the Marine and Coastal Area (Takutai Moana) Act 2011, the Marine Mammals Protection Act 1978, and the Fisheries Act 1996. The existing no-take marine reserve and marine mammal sanctuary around the Auckland Islands, and similar reserves around Campbell, Antipodes, and Bounty Islands are managed by the Department of Conservation.

1.3.3 Enderby Island

Enderby Island (50°29′45″S 166°17′44″E) lies 1 km to the north-east of Auckland Island, and is low-lying with a maximum elevation of 43 m above sea level, compared to the 659 m summit of nearby Auckland Island (LINZ 2020). Enderby Island is comparatively small at 695 ha, representing around 1% of the land area of the archipelago (LINZ 2020). The weather can be very changeable with frequent squalls bringing high winds and driving rain (Eden 1955), and precipitation on an average of 300 days per year (Higham 1991). Enderby Island is partially sheltered by the larger Auckland Island to the west, and subsequently has a milder climate (Peat et al. 2006). Nevertheless, wind gusts average more than 35 knots for 280 days per year, and the temperature ranges from 5 to 12 ºC with occasional snowfall any time of the year. Sunshine averages only 660 hours per year (Higham 1991).

Vegetation on Enderby Island includes a narrow band of rātā forest and scrub (including *Cassinia vauvilliersii, Myrsine,* and *Hebe* spp.) in the east and south. The centre of the island consists primarily of low herbs and cushion plants, interspersed with small gullies of scrub. The exposed west and north areas of the island are dominated by tussocks (including *Poa litorosa*, *P. foliosa and P. breviglumis,* and *Agrostis magellanica*); and close to the northern cliffs only salt- and wind-tolerant megaherbs (such as *Bulbinella rossii* and *Anisotome latifolia*) grow. Subantarctic megaherbs are also present in other areas, with *B. rossii,* and *Stilbocarpa polaris* the most common (Godley 1965). The vegetation of the island, particularly Sandy Bay, has been significantly modified through burning for agriculture and by introduced mammals (Taylor et al. 1970, Higham 1991).

Enderby Island was cleared for farming in the 19th century and previously hosted numerous introduced species, with pigs released in 1807 and 1867, rabbits in 1865, cattle in 1894, and mice accidentally introduced, probably before 1840 (Taylor 1971, Russell et al. 2020). These species all either died out naturally, or were eradicated by 1993, leading to the re-establishment of native plants (Torr 2002). Enderby Island is now free from introduced vertebrates, and has remained free of mammalian carnivores throughout its history. This is in contrast to the main Auckland Island which currently has a number of introduced mammalian pest species including mice (*Mus musculus*), cats (*Felis catus*), and feral pigs (*Sus scrofa*) (Russell et al. 2018), which are all known to depredate eggs, chicks, and nesting seabirds (Challies 1975, Dilley et al. 2016). These neighbouring islands could therefore provide an interesting comparison of the effects of mammalian predation on breeding success for yellow-eyed penguins and other seabirds. Since Auckland Island includes considerably more land area than any of the outlying islands in the group, any future removal of pest animals could therefore open up large areas of suitable habitat for breeding seabirds to use, and positively affect population growth.

As a pest-free island, Enderby is an important breeding area for a number of land and seabird species and subspecies, many endemic to the Auckland Islands, including the Auckland Island shag (*Leucocarbo colensoi*), Auckland Island snipe (*Coenocorypha aucklandica aucklandica*), Auckland Island teal (*Anas aucklandica*), Auckland Island banded dotterel (*Charadrius bicinctus exilis*), and Auckland Island tomtit (*Petroica macrocephala marrineri*), and is a key breeding site for the yellow-eyed penguin (*Megadyptes antipodes*) (BirdLife International 2019, French et al. 2020).

1.4 Penguin biology

1.4.1 General seabird ecology

Seabirds forage at sea, relying on marine ecosystems for nutrition for themselves and their chicks, but they breed on land, relying on terrestrial ecosystems for courtship, nesting, and moulting (Diamond and Devlin 2003). Seabird species vary greatly in their morphology and foraging methods, however, most taxa have a similar life history and breeding cycle due to their shared need to forage at sea, where prey availability is variable in space and time (Williams 1995, Gaston 2004). Some, such as terns and storm petrels are adapted to surface feeding, while albatross and shearwaters feed on or just below the surface, and penguins dive to greater depths to forage (Mackas et al. 2001, Murphy et al. 2001, Gaston 2004). Unlike freshwater birds which include many diving herbivores and insectivores, these food sources are less commonly used by birds foraging in the marine environment (Higgins and Davies 1996). Seabirds more commonly specialise as scavengers, planktivores, and marine predators which frequently catch live fish, cephalopod, and crustacean prey (Gaston 2004). One of the most specialised marine birds are penguins, which have traded flight in exchange for becoming dedicated diving predators, with larger penguin species able to dive to depths in excess of 500 m to capture live prey (Borboroglu and Boersma 2013).

1.4.2 Penguin ecology

Penguins began evolving from flying seabirds from around 71 million years ago during the Cretaceous period (Baker et al. 2006, Borboroglu and Boersma 2013), and adapted to a dedicated marine lifestyle more than 60 million years ago when they evolved a streamlined body shape and lost the ability to fly (Ksepka and Clarke 2010). The most recent common ancestor of modern penguins is thought to be around 20 million years old, and most of the major groups of extant penguins had diverged by 11–16 million years ago, radiating out of

Antarctica (Subramanian et al. 2013). This coincides with the drop in Antarctic temperatures beginning around 12 million years ago, suggesting a likely link between climatic conditions and penguin evolution (Subramanian et al. 2013). The extant penguin fauna includes 18 species in six genera, and their distribution is limited to the southern hemisphere, from Antarctica to the tropics, likely constrained by warmer water around the equator (Borboroglu and Boersma 2013, Subramanian et al. 2013).

Penguins are flightless, foraging for live prey under the sea surface. As wings become more efficient for swimming they become less efficient for flying, and vice versa (Elliott et al. 2013) requiring a trade-off for diving seabirds using their wings for propulsion. Although swimming theoretically uses more energy than flying (Elliott and Gaston 2009), penguin wings are modified into highly-adapted flippers which are more efficient for diving and underwater locomotion than can be achieved by any flying seabirds, whether using their wings or feet for propulsion (Elliott et al. 2013). Additionally, being able to dive to greater depths allows access to a wider prey assemblage than is available to other seabirds.

Penguins are considerably heavier than diving seabirds such as auks occupying similar niches in the northern hemisphere, since they no longer need to maintain a light bodyweight for flying (Gaston 2004). In addition to improving swimming efficiency, larger body size allows a lower surface-area to volume ratio which minimises heat loss to the surroundings in colder climates, requiring less energy to keep warm and allowing slower metabolism and lower energy intake requirements (Williams 1995). A larger body size, and energy savings from using wings exclusively for underwater propulsion suggests that the evolution of flightlessness allowed penguins to exploit colder and otherwise inhospitable polar regions. This is assisted in ice-breeding species such as emperor penguins by the development of huddling behaviour, and a circulatory counter-current exchange system to minimise heat loss to the environment, and to warm blood returning from extremities before it enters the core (Knox 2006).

Most penguins are colonial breeders, forming breeding aggregations in coastal areas close to the sea during a summer breeding season (Borboroglu and Boersma 2013). Breeding and foraging commonly belong to either sedentary or migratory strategies. Sedentary species (including yellow-eyed and gentoo penguins) remain in the general vicinity of their breeding area year-round, whereas migratory species (including many *Eudyptes* penguins) forage off-shore for extended periods over winter (Croxall and Davis 1999, Davis and Renner 2003). Migratory species may begin the breeding season with large body reserves, but may also have a shorter breeding season with more extended fast periods, due to the need to return sooner to areas with more abundant prey (Croxall and Davis 1999, Davis and Renner 2003). Larger penguin species generally have a slower life-history with a greater age at first-breeding, lower fecundity, and greater adult survival (Williams 1995, Davis and Renner 2003).

Penguins face a range of threats globally, including warming climate, habitat loss, human disturbance, pollution, and negative interactions with fisheries (Borboroglu and Boersma 2013, Ropert-Coudert et al. 2019), with populations of 11 of the 18 extant penguin species currently declining (BirdLife International 2018). The Antarctic breeding species – Adélie (*Pygoscelis adeliae*), and emperor penguins (*Aptenodytes forsteri*) – are well-studied, and known to face threats related to climate change (Barbraud and Weimerskirch 2001, Croxall et al. 2002, Jenouvrier et al. 2009b). However, many species living in temperate areas closer to human interference face greater immediate threats (Ropert-Coudert et al. 2019). For example, the Galapagos (*Spheniscus mendiculus*), African (*S. demersus*), erect-crested, northern rockhopper (*Eudyptes moseleyi*), and yellow-eyed penguin are all classified as Endangered (BirdLife International 2020, IUCN 2021). Population crashes including declines of up to 90% in some breeding areas have been documented in numerous species, including Humbolt and Galapagos (Borboroglu and Boersma 2013), rockhopper (Cunningham and Moors 1994, Pütz et al. 2003, Cuthbert et al. 2009), African (Crawford et al. 2015), and yellow-eyed penguins (Ellenberg and

Mattern 2012, Mattern et al. 2017). *Megadyptes* (yellow-eyed penguin) and all seven *Eudyptes* (crested penguin) species are listed as vulnerable or endangered (IUCN 2021), meaning these two closely-related genera therefore require particular conservation attention.

1.4.3 New Zealand penguins

Of the six extant genera of penguins worldwide, three are found in New Zealand waters (*Eudyptes* (crested penguins), *Megadyptes* (yellow-eyed penguins), and *Eudyptula* (little or blue penguins)), with many endemic species and sub-species. Members of two other genera (*Aptenodytes* (large penguins) and *Pygoscelis* (brush-tailed penguins)) are found in New Zealand's Antarctic territory (Borboroglu and Boersma 2013).

The genus *Eudyptes* radiated in the last 8 million years, giving rise to the six species of crested penguins: southern (*Eudyptes chrysocome*) and northern rockhopper, erect-crested, Fiordland crested (*E. pachyrhynchus*), and Snares crested penguin (*E. robustus*). These all breed either in New Zealand or its subantarctic islands, while the macaroni penguin (*E. chrysolophus*) and closely-related royal penguin (*Eudyptes schlegeli*) are vagrants to New Zealand (Borboroglu and Boersma 2013, Baker et al. 2017). *Eudyptes* is the most prolific penguin genus with a combined total of over 28 million breeding pairs (Shirihai et al. 2002). Crested penguins display distinctive speciation within the genus with different breeding behaviour, vocalisations, and plumage between the different species, including those inhabiting the South Island and subantarctic islands of New Zealand (Jouventin et al. 2006). The *Megadyptes* genus is thought to have separated from *Eudyptes* penguins around 11–15 million years ago (Baker et al. 2006, Subramanian et al. 2013). *Megadyptes* penguins are restricted to New Zealand, and the genus contains one extant species, the yellow-eyed penguin. The New Zealand mainland was previously occupied by a closely-related yellow-eyed penguin species (*M. waitaha*) which was extirpated following Polynesian settlement in New Zealand (Boessenkool et al. 2009a, Collins et al. 2014). Modern yellow-eyed penguins are believed to have expanded their range from the subantarctic to mainland New Zealand only in the last few hundred years, following the extinction of *M. waitaha*, and coinciding with significant reductions in the populations of pinniped predators on the mainland (Boessenkool et al. 2009a, Collins et al. 2014).

Most species of *Eudyptes* penguins breed in the open in dense colonies, often on rocky slopes above the shoreline. However, two New Zealand endemic species are an exception: Snares crested penguins nest under forest canopy, and Fiordland crested penguins nest in isolation or in small or loosely-defined colonies in the forest, or in small caves (Warham 1975). The yellow-eyed penguin is also a non-colonial breeder, nesting individually in the forest out of visual range of other nests (Darby et al. 1990).

Eudyptes and *Megadyptes* penguins typically feed on lower trophic level prey, including krill, small fish and squid (Clausen and Pütz 2002), and are therefore vulnerable to changes in local primary productivity (Devney et al. 2009). Being flightless, penguins are less mobile and have a more restricted foraging range than other flying seabirds. Penguins display limited phenotypic plasticity in response to prey shortages, making them important as environmental indicators (Grémillet and Charmantier 2010), but also enhancing their vulnerability to the consequences of global climate change and effects on prey availability (Canale and Henry 2010). Large scale declines are evident in many *Eudyptes* species, and rockhopper penguins are classified as Vulnerable. The yellow-eyed penguin is also declining, and listed as Endangered (BirdLife International 2010), making New Zealand penguins an important focus for conservation.

1.4.4 Study species, the yellow-eyed penguin (*Megadyptes antipodes*)

The yellow-eyed penguin (hoiho in Māori) (Figure 1.3) is one of the larger penguin species, standing around 65 cm tall, with a mean adult weight between 4.2 and 8.5 kg (Marchant and Higgins 1990, Seddon et al. 2013), making it the fourth-largest penguin behind the emperor, king, and gentoo (Borboroglu and Boersma 2013). While the sexes look alike, there is a small degree of sexual dimorphism with males generally larger than females in weight and morphometrics (Darby et al. 1990), allowing measurement of the head and foot to be used for sexing of individuals (Setiawan et al. 2004).

Figure 1.3 Nesting yellow-eyed penguin on Enderby Island. Photo: C. G. Muller

Yellow-eyed penguins are endemic to southern New Zealand, with a distribution restricted to the south-east coast of the South Island / *Te Wai Pounamu*, (including coastal Otago and Southland), and offshore islands including Stewart Island / *Rakiura* and nearby Codfish Island / *Whenua Hou* (the northern population). A separate breeding population (the southern population) encompasses the subantarctic Auckland Islands / *Motu Maha* (including the main

Auckland Island, as well as Enderby and other offshore islands), and Campbell Island / *Motu Ihupuku* (Darby et al. 1990, Marchant and Higgins 1990, Seddon et al. 2013) (Figure 1.1). Breeding is discussed in more detail in Chapter 3, including a detailed map of breeding areas (Figure 3.2). Yellow-eyed penguin distribution corresponds to the presence of continental shelf feeding areas and land areas where the mean summer temperatures are less than 16.5 ^{O}C (Smith and Lewis-Smith 1987). The South Island distribution also relates to the former extent of coastal podocarp-hardwood forests, believed to be the penguin's traditional nesting habitat (Darby et al. 1990).

Breeding is restricted in geographical range and numbers, with population estimates as few as 4000 breeding adults (2000 nesting pairs), or around 6000 to 7000 adults in total (McKinlay 2001, Department of Conservation 2019), although accurate figures are available only for the mainland breeding population, and some offshore islands. Estimates for the South Island are around 800 nests, or 2,200 individuals (McKinlay 2001). The Auckland Islands are thought to represent approximately 27 to 32% of the total yellow-eyed penguin population, and previous population estimates suggest that Enderby Island accounts for up to 63% of the Auckland Islands population (Moore 1990). Despite the suspected low number of founders, low contemporary migration rates (<2%), and relatively low genetic variability in the South Island population (Boessenkool et al. 2009a, Boessenkool et al. 2009b), nevertheless around 40% of yellow-eyed penguins globally were believed to breed on and around the New Zealand mainland (McKinlay 2001). An updated southern (subantarctic) population estimate is investigated in Chapter 3.

The low genetic diversity of South Island yellow-eyed penguins is likely affected by strong fluctuations in population size and high variance in reproductive success, and the loss of genetic diversity and increased levels of inbreeding due to population bottlenecks or small population sizes may have reduced the mean population fitness and adaptive potential (Allendorf and

Leary 1986, Lande and Shannon 1996, Frankham et al. 2002, Keller and Waller 2002). The long-term viability of this species on the mainland and offshore islands may be compromised by reduced adaptive potential (Boessenkool et al. 2010).

Yellow-eyed penguins have recently been re-classified from ‘Nationally Threatened’ to ‘Nationally Endangered’ under the New Zealand Threat Classification System due to extreme fluctuations in population size (Robertson et al. 2013, Robertson et al. 2017) and are classified as ‘Endangered’ on the International Union for the Conservation of Nature (IUCN) Red List (BirdLife International 2020).

1.4.5 General threats

Recent stocktake reports show the mainland (South Island) yellow-eyed penguin population is undergoing serious decline due to successive poor breeding seasons and ongoing higher than average adult mortality (Couch-Lewis et al. 2016, Department of Conservation 2020a). Populations on offshore islands including Stewart and Codfish islands are also thought to be declining (Mattern and Wilson 2018). Concerns include changes to the marine environment, interaction with fisheries, predation (on land and at sea), disease, and disturbance to breeding areas from human activities, including unregulated tourism, habitat modification, and other disturbance, with declines in breeding populations and even breeding site abandonment on the mainland around Otago as a result (McClung et al. 2004, Couch-Lewis et al. 2016). Despite recent conservation measures, yellow-eyed penguin population sizes have continued to be highly unstable over recent decades (McKinlay 2001, Moore 2001, Couch-Lewis et al. 2016). Ongoing demographic instability has been attributed to changes in food supply (van Heezik and Davis 1990), climatic variations (Peacock et al. 2000), eco-tourism disturbance and disease epidemics (Gill and Darby 1993, Couch-Lewis et al. 2016).

Forest clearance on the South Island has resulted in a lack of suitable breeding sites and a major reduction of the northern population from their former range (Darby et al. 1990). On mainland New Zealand, the current distribution of yellow-eyed penguins is a result of terrestrial habitat destruction and modification, including for farmland, and compounded by terrestrial predation and disease outbreaks (Alley et al. 2004). Introduced exotic mammalian predators have played a dramatic role in the decline and extinction of many endemic fauna in New Zealand (Clout 2001, Blackburn et al. 2004, Duncan and Blackburn 2004), but intense conservation efforts have resulted in the eradication or control of predators in some localised mainland and offshore areas. By the 1980s, non-native predators (primarily mustelids and cats) introduced to the mainland by Europeans in the late 19th century had caused major egg and chick predation of yellow-eyed penguins (Darby et al. 1990) and prompted the implementation of intensive predator trapping around breeding areas.

The yellow-eyed penguin is one of the penguin species most sensitive to human disturbance (McClung et al. 2004, Ellenberg et al. 2007, Ellenberg et al. 2009). While nests are usually hidden from sight, adults are nevertheless prone to human disturbance when transiting to and from the sea. Research from the South Island suggests that yellow-eyed penguin nesting is incompatible with continuous disturbance such as tourism. Reduced breeding productivity, lower fledgling weights and increased hormonal stress responses have all been recorded for the species at sites exposed to tourism (Roberts and Roberts 1973, Wright 1998, McClung et al. 2004, Ellenberg et al. 2007, Ellenberg et al. 2009).

Mortality due to fisheries bycatch is an ongoing problem, particularly for the inshore set net fishery (Couch-Lewis et al. 2016, Mattern and Wilson 2018). Multiple birds have been reported drowned in a single net (Ellenberg and Mattern 2012), with as many as 12 reported bycatch incidents per year (Darby and Dawson 2000). Other indirect fisheries impacts include bottom trawls which can alter the benthic habitat and affect the foraging success of yellow-eyed penguins (Darby and Dawson 2000, Browne et al. 2011). However, despite the risk identified by negative interactions with fisheries, incomplete data and a lack of observer coverage prevents reliable measurement of fisheries-related mortality (Mattern et al. 2017), with less than 2% of gill net vessels monitored (Richard et al. 2015).

Disease is also a recurring issue for the northern population. In 1990 over 150 adult yellow-eyed penguins died during a mass-mortality event on the Otago peninsula. A cause of death was not established but was thought to be due to a toxic diatom (Gill and Darby 1993). In 2008–09, mass-mortality events were documented on the mainland, and disease-related mortality was identified in the subantarctic (Argilla 2015). In 2013, a mass mortality event, also believed to be a toxic agent, killed around 70 adult and juvenile yellow-eyed penguins on the Otago Peninsula (Gartrell et al. 2017). Later that year, low food supply had left penguins emaciated and unable to moult without intervention and supplementary nutrition. In December 2015 up to 50 yellow-eyed penguins chicks died, attributed to a combination of high temperatures, disease, and barracuda attacks on foraging parents (Gartrell et al. 2017). Tourism disturbance was also cited as a contributing factor. Fewer than 190 breeding pairs were counted on the Otago coast in the 2015–16 season, down from nearly 500 in 2012. In addition, diphtheria has been responsible for the death of yellow-eyed penguin chicks on the mainland (Alley et al. 2004, Alley et al. 2017).

Changes in environmental conditions can affect prey species, with diet quality predicted to decrease for many marine species due to climate change (Worm et al. 2006, Cury et al. 2011). Climate change is a significant contributor to the yellow-eyed penguin decline in the northern population, and may be responsible for a shift in the primary prey species available to penguins, with consequences for reproductive success, including chick starvation (Browne et al. 2011, Ellenberg and Mattern 2012), and facilitating disease outbreaks at mainland locations (Mattern and Wilson 2018). An increase in the frequency and severity of storms and severe weather events is also expected with climate change (Collins et al. 2013). Storms can reduce the foraging ability of penguins, including for several days after the event (Barreau et al. 2021), and may affect breeding success as well (Saraux et al. 2016). While climate change is likely a major factor in the northern population decline, other threats including fisheries interactions, pollution and human disturbance are all considered significant contributors (Mattern and Wilson 2018).

Yellow-eyed penguins have a range of natural predators. While these are not expected to result in population declines in isolation, when combined with other anthropogenic threats they may hinder recovery or exacerbate declines of vulnerable populations. New Zealand sea lions breed in the subantarctic, and in small numbers on the South Island and Stewart Island. Sea lions are known occasionally to take yellow-eyed penguins, including on shore near mainland breeding colonies (Lalas et al. 2007) and in the subantarctic (pers. obs.), which has the potential to threaten the viability of smaller breeding areas as a result. Sea lions have also been documented taking rockhopper penguins (Strange 1982, Raya Rey et al. 2012, Morrison 2015). Yellow-eyed penguins also share their distribution range with fur seals (*Arctocephalus* spp.), orcas (*Orcinus orca*) and leopard seals (*Hydrurga leptonyx*), all of which are known to take various species of penguins (Charbonnier et al. 2010, Pitman and Durban 2010, Reisinger et al. 2011), although predation has not been documented for yellow-eyed penguins. A variety of large predatory fish species including sharks and barracuda are also present in the local marine environment, and are suspected of causing injury and possible death at sea for yellow-eyed penguins and other small penguin species. Around 55 yellow-eyed penguins were injured from suspected barracuda attacks in early 2015 (Argilla 2015, Couch-Lewis et al. 2016).

Known and suspected terrestrial predators of adults and chicks include a number of introduced mammal species – feral pigs, dogs (*Canis familiaris*), domestic and feral cats, mustelids (*Mustela* spp.), rats (*Rattus* spp.) and mice – as well as traffic and direct human interference.

In some areas trampling by livestock (primarily cattle) has been an issue (Couch-Lewis et al. 2016). These species are all present on the mainland, and on some offshore and subantarctic islands.

Potential avian predators include northern giant petrels (*Macronectes halli*) and brown skuas (*Catharacta antarctica lonnbergi*), although skuas are most likely a threat to eggs and chicks rather than adults. Northern giant petrels have been observed killing smaller penguins including adult northern rockhoppers at sea (Ryan et al. 2008), as well as eastern rockhopper penguins around Campbell Island (Morrison 2015). An ongoing, localised population decline of eastern rockhopper penguins on Campbell Island is being driven in part by high rates of predation on adults by sea lions, as well as on eggs by skuas (Morrison 2015), although there is no indication of a similar effect on yellow-eyed penguins. Forest nesting appears to be a successful adaptation to minimise nest exposure to seabird predators as both rockhopper species restrict themselves to marine and coastal habitats and do not venture under the forest canopy where yellow-eyed penguins nest (pers. obs.).

Threats to yellow-eyed penguins have been identified, and conservation recommendations developed into a recovery plan (Taylor 2000, McKinlay 2001, Department of Conservation 2020b). While habitat protection, restoration, and terrestrial pest control efforts have improved as a result (Webster 2018), fisheries impacts remain a problem for the northern population (Ellenberg and Mattern 2012, Crawford et al. 2017, Mattern and Wilson 2018), as do unregulated visitor access and depredation by uncontrolled domestic dogs (M. J. Young, pers. comm.).

1.4.6 Threats in the subantarctic

The full range of marine predators are present in the subantarctic, and although predation rates on yellow-eyed penguin at sea are unknown, it is reasonable to assume some occurs. Individual sea lions have also been observed killing a small number of penguins on land on Enderby Island (pers. obs.). Avian predators including skuas and giant petrels are present, but not thought to be a major predator of nests due to the yellow-eyed penguin's forest-nesting habits. Introduced terrestrial predators were likely a greater threat in the past, and rats were known to attack yellow-eyed penguin chicks on Campbell Island before they were eradicated (Amey and Moore 1995). The history of introduction and eradication of terrestrial predators is described in more detail in the Auckland Islands section below, but since most subantarctic islands are now pest-free, with the notable exception of the main Auckland Island, terrestrial predation is likely secondary to other threats in the region.

No disease epidemics or mass mortality events have been reported in the southern population, although there is much less monitoring undertaken there. A high prevalence of *Leucocytozoon* spp. was found on Enderby Island, and was associated with chick deaths (Argilla et al. 2013). High parasite pathogen loads were also found on Enderby Island, including a novel *Eimeria* species which causes coccidiosis (Kay et al. 2022a), and *Plasmodium* spp. which cause avian malaria (Kay et al. 2022b), although these did not appear to correlate with elevated chick mortality rates. Nesting success (which covered the period of the parasite research) is explored in more detail in Chapter 3.

Disturbance to the southern population is a cause of concern for the Department of Conservation, given the possibility of reduced breeding success or nest abandonment documented in the northern population as a result of tourism (McClung et al. 2004). This includes the possibility of disturbance to nesting and transiting birds. Mitigation measures include a "no-stopping area" for all personnel where penguins are known to transit, and restrictions in landing permits and schedule times for tour vessels, limiting their time ashore to exclude the main penguin commute times in the morning and evening (Department of Conservation 2016). However, while the current 5 m minimum distance for tourists to approach wildlife in the subantarctic is too close to prevent disturbance to yellow-eyed penguins (French et al. 2019), disturbance caused by tourism does not appear to affect breeding success (French 2018).

Little is known about population trends or diet in the southern population, nor how these may be affected by climate change. More research is needed, not only into yellow-eyed penguin population dynamics, but also to identify prey species and how their distribution may change in time and space.

Population estimates for the southern population are lacking or out of date for many locations, making it difficult to know the current status of the southern yellow-eyed penguin breeding population, or current threats. The population is believed to be larger and more stable than the northern population and is therefore widely considered an insurance population for the species (Couch-Lewis et al. 2016, Boersma et al. 2020). However, there are insufficient data to be able to confirm population size or trends, and many population estimates are several decades out of date. Furthermore, the low rate of migration between the southern and northern populations makes it unlikely that any re-colonisation would occur naturally. Up-to-date research is therefore required on yellow-eyed penguin population biology and breeding success in the subantarctic.

1.4.7 Yellow-eyed penguin breeding behaviour

Yellow-eyed penguins are a long-lived species, breeding up to the age of 25 years in the wild (Young 2014) although by 10 years a significant sex skew is apparent, with males outnumbering females two to one (Marchant and Higgins 1990). Age at first breeding is an average of 2.6 years in females, and 4.3 years in males (Richdale 1957), although breeding success is lower for inexperienced breeders (Richdale 1957, Williams 1995). Adults are sedentary, staying close to their breeding area throughout the year and do not migrate during the non-breeding period (Darby et al. 1990). Nest locations are typically in coastal forest or scrub, with overhead cover from vegetation or other available features (Darby et al. 1990). Unlike colonial breeding penguins, yellow-eyed penguins do not form rookeries. They congregate in areas of suitable breeding habitat, building solitary nests which are usually out of visual contact with their neighbours (Jouventin 1982, Darby 1985).

Breeding occurs from late September through to March throughout their range, with a lag of approximately two weeks in the subantarctic (Moore 1990). Usually, two eggs are laid in late September with synchronous incubation by both parents for a period of 39 to 51 days (Seddon 1989). Adults undertake only short (1–3 days) foraging trips away from the breeding areas during incubation (Marchant and Higgins 1990). Eggs usually hatch 6–7 weeks later in November. Unlike in some *Eudyptes* penguins, both eggs are a similar size and both usually hatch (Darby et al. 1990). Both adults brood and feed the chicks. Once chicks hatch they are guarded at the nest by one adult while the other forages, with this guard stage lasting approximately six weeks. In the post-guard stage of chick rearing, both adults make daily trips to sea as the energy demands of their chicks increase (van Heezik 1990c). Chicks reach adult weight in mid to late January and then moult to juvenile plumage before fledging. Fledging is at a mean age of 105 days in February, after which adults moult; see Figure S1.1 for a timeline. Juvenile survival to recruitment is low, with Richdale (1957) estimating survival to be 26% overall, with a range of 10–45% for all cohorts. Recent analysis of the percentage of juveniles surviving to adulthood indicates a decline over time to 18.8% overall, with fewer than 13.7% of individuals attempting to breed at least once (Stein 2013). Annual chick production can vary between pairs and years (Marchant and Higgins 1990), but the average is 1.4 chicks per pair per season (Moller et al. 1995). Annual survival of adult breeding yellow-eyed penguins on the mainland has been shown to range from 48–91% in different breeding seasons, depending on conditions (Lalas et al. 2007). Therefore, the survival of both juveniles and adults remains an important factor affecting long-term population stability.

1.5 Population biology

1.5.1 Measuring population dynamics

The majority of seabirds, including penguins, are K-selected, being long-lived and slow growing animals with a low reproduction rate (Diamond and Devlin 2003, Borboroglu and Boersma 2013). Consequently, they are vulnerable to any factors which may affect adult survival, as well as any reduction in breeding success or the survival of chicks to recruitment age (Cairns 1988, Ricklefs 1990, Purvis et al. 2000). Therefore, reproductive success is likely limited by a combination of factors such as prey availability, marine-based stochasticity, extreme weather events, and the performance of individual breeders, including age-related competence (Forslund and Pärt 1995, Fowler 1995, Wendeln and Becker 1999, Moreno 2003). The interaction of these factors is also relevant, and long-term studies are required to provide sufficient detail, particularly for factors relating to parental condition which may be variable (Moreno 2003). Population estimates are needed to provide a baseline, and to gauge the impact of these factors on species survival.

Population estimates require counting or estimating population abundance, with the size of a population indicating its success, and determining, in part, its vulnerability to extinction. Measuring population dynamics requires quantifying the numbers of individuals, as well as births, deaths, immigration, and emigration, and is ideally done using a population census of as many age cohorts as possible (Chapman and Reiss 1999). If not all of the individuals in a population are easily counted at the same time, then a smaller sub-group can be counted and this number used to generate an estimate for the entire population (Chapman 1951).

Population monitoring is necessary to quantify a population's size and trend over time and involves the ongoing collection of population information at different times, with the aim of detecting a change between counts (Dowding 2012). In many cases, determining an accurate measure of a population first requires an accurate knowledge of its distribution, including individuals' home range, or the extent of areas used by a population for breeding. Variability in distribution may also indicate changes in the population, including contraction or expansion in numbers, as well as changes in the suitability of the habitat, or other population pressures (Chapman and Reiss 1999). Regular population monitoring is important for wildlife conservation and management, particularly for long-lived species where some population changes may not be evident for longer time periods. Changes in population abundance can also be used to assess the impact of threats and environmental changes, as well as the effectiveness of any management actions (Purvis et al. 2000, Witmer 2005, Lindenmayer and Likens 2009). Two commonly-used population monitoring methods include demographic and numeric monitoring. For avian research, demographic monitoring involves the estimation of survival rates (including of different age classes and/or genders) and productivity. Demographic studies can be labour-intensive, as they frequently require capturing and marking birds for repeated re-sighting or re-capture. As a result, demographic studies often involve a smaller subset of the total population, or its spatial distribution (Dowding 2012). Numeric measures involve census counts, indices, and estimations of density and abundance. These are often undertaken at larger scales than demographic studies, and may be less precise, but methods may be combined for greater efficiency (Dowding 2012).

1.5.2 Monitoring seabird populations

Population estimates are commonly conducted for seabirds during the breeding season when adults and chicks can be reliably found on shore (Diamond and Devlin 2003), where they are more easily accessible to researchers. When monitoring seabirds, it is important to determine the number of breeding adults, as this represents the current state of the breeding population. This is often achieved by means of colony counts (Hutchinson 1980, Trathan 2004, Baker et al. 2020). Wherever possible, it is also important to measure productivity, or the number of offspring produced by each pair, as this will affect future population growth. The survival of chicks provides an important measure of a population's stability and can vary greatly due to external factors including climate and weather, predation, food availability, and nest attendance by the adults (Dowding 2012). In addition, chick survival, measured by the number and condition of fledglings produced by a population, is an important measure of future population trends. A poor breeding season may have ongoing repercussions for future population stability as a depleted age cohort moves through the age classes to become the future breeding population (Chapman and Reiss 1999).

If resources allow, additional demographic data measuring the survival rate of different age classes (eggs, chicks, juveniles, and adults) are valuable (Lindenmayer and Likens 2009). Survival data provide valuable information on pressures which may be affecting different parts of the population, since declines in the survival rate of any individual age class may result in an overall population decrease over time. Measuring survivorship may be more difficult for some age classes, as this requires identifying and monitoring known individuals over a longer period of time (Lindenmayer and Likens 2009). Data on diet and foraging behaviour are also useful as these can inform on trends in foraging success, as well as possible links between the physical environment and breeding success, which can help to identify reasons for population declines (Witmer 2005).

1.5.3 Yellow-eyed penguin nest location

Accurate long-term monitoring of a breeding population is important to determine population trends and the effectiveness of ongoing management measures to increase the population. Locating nests is therefore important for monitoring breeding success. Efficiencies enabling earlier nest location allow monitoring and other dependent research to begin as soon as possible.

Yellow-eyed penguin nests can be difficult to locate. Unlike colonial-breeding species, yellow-eyed penguins build solitary nests up to 1 km inland hidden within coastal forest and scrub, making nests difficult and time-consuming to find (Darby et al. 1990, Ellenberg and Mattern 2012). Nests are commonly located in dense vegetation, with over 90% of them built against vegetation stems, logs, embankments or rocks which adds to their concealment. Nest density varies with vegetation type, with lower densities in open forest and high densities in scrub. Most nests in the northern population are shielded from the sun by undergrowth to avoid heat stress (Seddon and Davis 1989), further adding to their cryptic nature.

Nest searching is labour-intensive. The usual method requires manual searches of an area to look for nest sign including visual detection of adult birds, tracks, chick vocalisations, and latrine smell (Hegg et al. 2012). Manual searching is therefore time-consuming, and success is dependent on the experience level of searchers, requiring teams to include at least one experienced searcher for best efficiency (Hegg et al. 2012). Individual searches are not particularly effective (with a single search team expected to find a maximum of 88% of nests in an area), therefore two independent search teams are recommended for maximum efficacy, requiring many personnel (Hegg et al. 2012). Independent search teams can be a difficult and time-consuming technique to utilise in some areas due to vegetation, logistics and safety concerns. Nest searching can therefore be expected to require additional time and effort in many locations due to accessibility, vegetation, searcher availability and experience, and other factors. Alternative nest search techniques are needed in order to find nests with a high degree of accuracy and precision, and some methods have been trialled.

Trained detection dogs can potentially locate species more efficiently than researchers and have the ability to cover large areas quickly. Detection dogs can also have higher rates of detection than traditional survey methods (Harrison 2006, MacKay et al. 2008, Nussear et al. 2008, Goodwin et al. 2010). However, at the time of my fieldwork there were no detection dogs in New Zealand trained and certified to detect yellow-eyed penguins. There would also be logistical and permitting difficulties for a dog to be able to work in the subantarctic, including quarantine issues, and being able to work safely alongside sea lions and other fauna present there.

A number of technologies exist that offer some advantages locating wildlife. Aerial nest location methods have been demonstrated using still camera imagery (RGB) from a camera-mounted Unmanned Aerial Vehicle (UAV) to survey gentoo penguins (Ratcliffe et al. 2015), as well as Adélie penguins (Rümmler et al. 2016). However, these species nest in the open so additional technology is required for detecting yellow-eyed penguin nests obscured by vegetation. VHF telemetry is a widely used tool for tracking wildlife, typically involving hand-held VHF receivers and antennas used by ground-based teams (Kenward 2001, Mech and Barber 2002). However, while useful, it can still be time-consuming and inefficient. Thick scrub in the subantarctic reduces detection range and limits how far ground teams can travel, reducing the number of birds which can be VHF-tracked from the ground each day. Tracking of VHF transmitters from the air can increase the size of the search area covered, and reduce difficulties created by terrain or vegetation for ground-based search teams. While the use of aircraft is difficult in the subantarctic, UAVs can offer a number of advantages. The development of additional technology could assist with the location of cryptic penguin nests in vegetated areas, and therefore also with population monitoring.

1.5.4 Yellow-eyed penguin population monitoring

Monitoring of the northern population is usually carried out by conducting nest checks, particularly at mainland breeding sites. Once nests are located, all breeding adults in the population are usually marked for long-term study, formerly with flipper bands, now with subcutaneous microchips (Department of Conservation 2012). Nests are regularly checked throughout the breeding season to monitor breeding success, and individuals are followed throughout their breeding life.

Accurate population monitoring is difficult to achieve for yellow-eyed penguins in the subantarctic, and accessibility is difficult due to terrain, thick vegetation, and inclement weather. Logistics are complicated, and team size often restricted due to the difficulty and expense of travelling to these isolated islands. The cryptic nests cannot easily be located or counted from the air as is done for many other penguin and seabird species (Ratcliffe et al. 2015, Baker et al. 2020), and the difficult terrain reduces the ability of field teams. Large distances are involved, with Auckland Island over 40 km long, and thick vegetation forms dense thickets in many areas (Godley 1965, Taylor 1971, Peat et al. 2006), making ground searching prohibitively time-consuming. Isolation and difficult access make long-term studies logistically challenging, meaning demographic data such as survivorship of different age classes are difficult to obtain, and long-term studies of known individuals are not common. As a result, most research on the southern yellow-eyed penguin population consists of count data of transiting adults, with some breeding productivity studies (since these can be completed in a single breeding season). Key studies are summarised below.

1.5.5 Previous southern population research

Morning counts have been conducted for yellow-eyed penguins, typically for 1–2 days per location, at various landing sites around the Auckland Islands (Moore 1990, Moore 1992a), and also at Campbell Island (Moore and Moffat 1991, Moore 1992b, Moore et al. 2001). This method was adopted for the species since they breed non-colonially in coastal scrub, making it difficult to count breeders and monitor breeding success. Instead, adults are counted during their peak morning commute from 0500–0900 as they head to or from the sea.

Some limitations were identified relating to the areas surveyed, and more detailed studies of population dynamics and breeding success were recommended (Moore 1990). In particular, while corrections were estimated for non-breeding birds, multi-day schedules, and other variability, there was no validation with actual nest numbers. However, a minimum population estimate for the whole Auckland Islands group (including unsurveyed areas) was estimated at approximately 520–680 breeding pairs (Moore 1990, Moore 1992a).

Although morning counts have since been repeated, there has been no comprehensive population survey for the Auckland Islands since Moore's work in 1989. Estimates of Enderby Island penguin numbers in 1989, 2009 and 2012 were all based on morning beach counts, and estimates of Auckland Islands penguin numbers are usually based on a single beach count at historically identified landing sites. For logistical reasons, counts at each location are usually conducted on sequential days as the team moves around the archipelago.

Young (2009) conducted morning counts on Enderby Island as well as recording transit times in an effort to categorise disturbance. Alert behaviours were found to be significantly higher in the presence of humans, and sea lions, with some birds delaying their transit by up to an hour when exposed to a disturbance. Beach counts were also carried out on Enderby Island for the 2001–2012 breeding seasons by Chilvers (2014) and found variation in count numbers between years. Beer (2010) conducted morning counts around the Auckland Islands. A total of 100 landing sites along the North coast/Port Ross and outlying islands were confirmed in 2009, a number comparable to the original survey 20 years earlier. However, searches for landing sites alone proved to be somewhat unreliable (Beer 2010). A coastline search conducted by teams of experienced observers during the incubation period in November 2009 found 22 penguin landing sites, however, only 15 of these (68%) were seen actually being used by penguins during subsequent beach counts. Thus, not every landing site that showed clear sign of recent penguin use was frequented on a daily basis. In addition, beach counts in the same area revealed that penguins departed from a further 27 sites that had not been identified as landing sites during the survey. Hence, more than half of actual landing sites may have been missed by that survey. While beach counts can give a representative indication of numbers and major population trends between years, the numbers may be subject to daily variation due to weather and other effects on foraging schedule timings. Only a portion of the population will be commuting to the sea on a given morning, and this can vary due to unknown factors. Morning counts also include both non-breeding adults and juveniles so cannot be relied on as an accurate representation of the breeding population. While beach count data are easier to collect, in the absence of any calibration data they can provide only an indication of possible population trends over time, rather than an accurate population count.

Annual morning count surveys were carried out around the Auckland Islands for 6 breeding seasons from 2012–2017 by the Department of Conservation, based on methods from Moore (1990). However, prior to this study these data had not been analysed.

1.5.6 Requirements for an accurate population estimate in the subantarctic

From these prior studies, indications are that yellow-eyed penguin numbers may be increasing at Sandy Bay on Enderby Island after a drop in 2002. Numbers at Sandy Bay appear to have significantly declined since the 1990s, and likely across the whole Auckland Islands with a 34% decline in Enderby Island penguin numbers compared to 1989 (Ellenberg 2013).

The main limitation of count data is that the number of birds sighted may fluctuate over the season, especially as nesting birds move from the incubation to guard phase, however, as yet there have been no conclusive data to correlate morning count numbers with the actual number of nesting birds, or to correct for possible daily variations in the number of birds leaving for foraging trips due to weather or other effects while the survey is underway.

Validation of morning count data was attempted in 2012 on Enderby Island by Houston and Thomson (2013) by determining a relationship between nest numbers and the number of birds sighted during counts. Their study also attempted to use remote cameras (still and video) to carry out morning counts over a period of time, and to look for any daily variation in numbers. However, their very short field trip (7 days) provided limited confidence that all nests were located, meaning nest numbers were likely an underestimate. The authors also documented the limited success of the cameras used to attempt remote monitoring. Battery life and problems detecting penguins were an issue, especially at night, and results identified that more comprehensive research is required, including improved technology.

As yet, there is still a lack of comprehensive data to document how penguin numbers using a landing site may vary from day to day, particularly during the incubation stage in November when landing patterns may be less predictable. In addition, preliminary indications are that individual birds may use different access points to get to the sea over the course of the breeding season (pers. obs.), which is likely to complicate attempts to match nests found in the forest to access points where morning counts were carried out. There is also a lack of data on the number of breeding birds, the proportion of breeding birds (with implications for interpreting morning count data), and the success of breeding attempts.

Furthermore, accurate population estimates require accurate data on nesting success, which in turn require efficient nest location and regular monitoring. "Apparent nest success" is the number of successful nests divided by the total number found. This is a simple measure to obtain with minimal effort, however, it invariably overestimates nest success because any nests that fail after laying are underrepresented in the sample, and failure can occur at any point in the season. This problem was first identified in the 1950s (Snow 1955, Hammond and Forward 1956). Apparent nest success rates have been shown to be extremely biased for populations with less intensive monitoring over the course of the breeding season, and bias is also introduced by changes in survival probabilities during the season and/or stage of the nesting cycle (Armstrong et al. 2002). Therefore, regular monitoring for nest failures is needed during the season to estimate survival probabilities at each stage of the breeding cycle (Stanley 2000). It is hoped that accurately identifying the relationship between morning counts and breeding numbers will be an important first step in estimating the breeding population for the wider Auckland Islands, and perhaps even the whole subantarctic. However, it should be noted that breeding success may not be homogenous across all sites. In particular, the presence of introduced mammalian predators (pigs, cats, and mice) on the main Auckland Island may result in a lower breeding success there, particularly later in the season after morning counts have already been carried out. A study which accurately represents population trends across the entire subantarctic would therefore require a comprehensive survey which repeats these methods at each major breeding area. The only “complete” yellow-eyed penguin population estimate in the subantarctic to date was at the Auckland Islands by Moore over two and a half decades ago in 1989 (Moore 1990), followed by Campbell Island (using breeding proportion data from the Auckland Islands survey) (Moore 1992b, Amey and Moore 1995, Moore et al. 2001). The recent decline in some northern breeding populations and suspected population decline on Enderby Island lends urgency to the need for a comprehensive census of the yellow-eyed penguin population on the Auckland Islands. Since Enderby Island is considered a breeding stronghold, this is an important first step and the techniques developed there will assist with the planning of this challenging task on the more rugged and isolated main Auckland Island, and will therefore improve the final population estimate.

1.6 Foraging biology

1.6.1 Penguin foraging behaviour

The distribution of nutrients and therefore primary production at sea depends mainly on oceanographic parameters such as currents, temperature and mixing (Miller and Sydeman 2004). The result is a patchy distribution of productivity and prey biomass, with implications for predator search strategies and foraging methods. As well as affecting what prey items are encountered during a trip, the time spent foraging can affect breeding success. The distance travelled during foraging has been shown to negatively affect reproductive success in many species including Magellanic penguins (Boersma and Rebstock 2009), travelling further uses more energy, and increased digestion time reduces the amount of food that can be provided to chicks (Weimerskirch et al. 1994, Ropert-Coudert et al. 2004). Adult yellow-eyed penguins generally travel further during the incubation phase, and forage closer to shore and for shorter periods during the guard phase when chicks are under 30 days old (Moore 1999). Birds travelling further on average tend to have a lower probability of fledging success, although longer foraging trips can allow them to make use of highly productive waters, as these may be more difficult to reach during the guard phase when time away from the nest is limited to short trips (Wilson et al. 1995, Phillips 2004).

Variation in the life history of different penguin species can be linked to their foraging strategy. For example, offshore foraging species migrate away from breeding colonies in the winter (Croxall and Davis 1999, Davis and Renner 2003), and generally make longer trips during the breeding season than do sedentary species (Davis and Renner 2003), and when not breeding they travel much greater distances, making extended migratory trips to the open ocean (Croxall and Davis 1999, Pütz et al. 2006b). Offshore foraging strategies are more common among *Eudyptes* penguins breeding at more southern latitudes. Conversely, sedentary fixed-place foraging species remain near their breeding area year-round and utilise prey found closer to shore. These include gentoo, African, little (*Eudyptula minor*), Galapagos and yellow-eyed penguins which tend to be larger-bodied, but breed at a younger age and with a lower divorce rate than migratory species such as most *Eudyptes* penguins. Inshore foragers do not migrate and remain near their breeding area all year round (Croxall and Davis 1999, Saraux et al. 2011) which is thought to be related to reduced oceanic productivity at southern latitudes over winter, and a reduced continental shelf area that might support inshore foraging (Croxall and Davis 1999). Despite their range overlapping with many *Eudyptes* penguins in the New Zealand subantarctic, yellow-eyed penguins are inshore foragers and do not migrate in the non-breeding season (Moore et al. 1995, Croxall and Davis 1999, Moore 1999). Inshore foragers may be affected by localised prey depletion (Ashmole 1963, Saraux et al. 2011), making it important for conservation managers to understand the areas used for foraging, and also prey distribution within those areas.

1.6.2 Measuring penguin foraging behaviour

As well as being an important indicator and driver of breeding and population success, penguin foraging behaviour is also considered a useful indicator of wider marine ecosystem health and productivity since breeding adults rely on the availability of prey close to their nests (Croxall and Davis 1999). Foraging behaviour is commonly studied using electronic positioning devices such as GPS loggers or satellite transmitters attached to animals as a means of tracking their foraging activities (Mattern et al. 2007, Chilvers et al. 2011, Chilvers et al. 2014). These data provide valuable insights on foraging location and behaviour, as well as habitat type and other features of the environment (Wilson et al. 2002). However, care needs to be taken to ensure attached devices do not affect the behaviour of animals. For diving species this requires ensuring the device is as small and low-profile as possible to minimise drag, and attached as far back as possible on the animal to maintain hydrodynamic streamlining (Bannasch et al. 1994, Ballard et al. 2001, Ropert-Coudert et al. 2007, Agnew et al. 2013).

Home range analysis involves the delineation of the area in which an animal conducts its "normal" activities (Worton 1989, Seaman and Powell 1996, Rodgers and Kie 2011). Methods for analysis include minimum convex polygons, bivariate normal models (Jennrich-Turner estimator, weighted bivariate normal estimator, multiple ellipses, Dunn estimator), nonparametric models (grid cell counts, Fourier series smoothing, harmonic mean), and contouring models (peeled polygons, kernel methods, hierarchical incremental cluster analysis) (Rodgers and Kie 2011). Penguin foraging behaviour is typically interpreted using a kernel density analysis (KDA), which is a nonparametric statistical method for estimating probability densities from a set of points of position data collected during foraging trips. Kernel methods have been used for home range analysis since the 1990s (Worton 1989). When calculating home range analysis, KDA uses a bivariate probability density function with a nominal unit volume (the "kernel") centred over each point. A regular grid is superimposed over the data and a probability density estimate is calculated at each grid intersection by summing the overlapping volumes of the kernels. A bivariate kernel probability density estimator, or "utilisation distribution" can be calculated over the entire grid using the probability density estimates at each grid intersection (Rodgers and Kie 2011).

The resulting kernel probability density estimator will have larger values in areas with more observations and lower values in areas with fewer observations, which can be interpreted as the probability of finding an animal in any one place. Home range estimates are derived by drawing contour lines (isopleths) based on the summed volumes of the kernels at grid intersections. These isopleths define home range polygons at different probability levels, (Rodgers and Kie 2011), allowing for analysis of foraging area use.

1.6.3 Foraging plasticity

Foraging plasticity describes a consumer adapting their foraging strategy to continue provisioning both themselves and their offspring, particularly when food supply changes within their usual foraging range (Ballard et al. 2010). As central-place foragers, breeding seabirds have a limited foraging area available to them (Costa 1991), therefore, being able to vary their foraging strategy will make best use of limited resources, particularly in times of change (Ashmole 1963). This can include changing their foraging method, for example, from benthic to pelagic diving, or changing their foraging location to move further offshore or to a different habitat. This can expose a predator to different prey assemblages and increase their foraging flexibility (Miller et al. 2009, Saraux et al. 2011).

In order to maximise lifetime reproductive success, seabirds must make a trade-off between the benefits and costs of raising chicks (Stearns 1989). While long-lived species are expected to prioritise their own survival at the expense of a current breeding attempt (Stearns 1989, Mauck and Grubb 1995), many species will forego a breeding attempt if resources are low, or their own body condition is poor in the lead-up to a breeding season (Cubaynes et al. 2011, Baron et al. 2013).

In some species, parents may vary their foraging strategy between provisioning their offspring and maintaining their own body condition. Foraging for chicks is often associated with short coastal trips to minimise the amount of digestion before regurgitation and may include targeting smaller species more suitable for chicks to eat. Conversely, when foraging for themselves adults may make longer trips to more distant areas and may preferentially target larger prey species (Weimerskirch et al. 1994, Weimerskirch et al. 1997, Weimerskirch et al. 1999, Saraux et al. 2011).

Foraging plasticity is therefore an important factor contributing to reproductive success, as well as the long-term survival of individuals, and consequently, the population as a whole. In the context of an endangered species, foraging plasticity (or its absence) can therefore affect the response of a population to current or emerging threats, and is an important consideration for assessing long-term population stability.

1.6.4 Penguin diving behaviour

Diving behaviour is an important component of foraging, and in diving animals such as pinnipeds, penguins, and other seabirds it is commonly studied using miniaturised pressure sensors attached to animals as a means of measuring their underwater foraging activities (Bost et al. 1997, Cherel et al. 1999, Chiaradia et al. 2005, Ropert-Coudert et al. 2007, Boersma and Rebstock 2009). Dive behaviour has been studied in a wide range of seabirds, including comparisons demonstrating that for some specialised diving seabirds such as penguins, swimming to foraging areas has become more energy efficient than flying (Baudinette and Gill 1985, Elliott et al. 2013).

Benthic diving is to the sea floor, whereas pelagic foraging occurs in the water column (Tremblay and Cherel 2000). Since prey on the seabed may be camouflaged or concealed by the substrate, predators need time to locate and capture benthic or demersal species. Typically, this results in a “U” shaped benthic dive profile with the bottom section of the dive constrained by the bathymetry of the seafloor (Wilson 1995, Tremblay and Cherel 2000, Pütz and Cherel 2005, Bost et al. 2007). Conversely, pelagic prey can be encountered anywhere in the water column, and dives are not constrained by depth. Finding prey may require searching over a much larger area to locate, typically resulting in “V” shaped exploratory dives, or “W” shaped dives while pursuing prey (Wilson 1995, Ropert-Coudert et al. 2000, Pütz and Cherel 2005). Diving to pursue and capture benthic prey can be more energetically expensive than targeting pelagic prey, as it frequently requires diving to deeper depths to reach the seabed (Costa et al. 2004, Chilvers and Wilkinson 2009). However, one benefit of utilising benthic prey species is that they tend to be a predictable, evenly distributed prey source, albeit occurring at low densities within a habitat (Costa et al. 2004, Chilvers and Wilkinson 2009). Benthic prey are also less influenced by oceanographic perturbations such as ENSO than are pelagic prey (Costa et al. 2004). A benthic foraging strategy may also allow animals to utilise seabed features to assist with underwater navigation (Mattern et al. 2007), although benthic foragers may be negatively affected by disturbance to the benthos caused by fisheries or other human activities (Browne et al. 2011).

Pelagic feeding dives are more common amongst penguins, with most species catching their prey in the water column (Ratcliffe and Trathan 2011). This is particularly true of migratory species such as *Eudyptes* penguins, which forage further offshore and consequently may not be able to reach the seafloor due to water depth (Croxall and Davis 1999, Davis and Renner 2003). Some species such as the southern rockhopper penguin have a mixed strategy including both pelagic and benthic diving (Tremblay and Cherel 2000). Benthic foraging has been reported in some penguin species, including non-migratory gentoo penguins, but a predominantly benthic diving strategy is uncommon (Tremblay and Cherel 2000). Yellow-eyed penguins were thought to be an exception to this trend, with predominantly benthic dives reported in diving studies (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014). However, previous data were all based on northern breeding populations which may be constrained by local conditions including bathymetry, and prey availability. Therefore, an investigation into yellow-eyed penguin diving behaviour in their subantarctic range is needed.

1.6.5 Penguin diet

Diet quality describes the suitability of prey as an energy source, with optimal diet quality maximising net energy gain per unit of time (Emlen 1966, MacArthur and Pianka 1966). Diet quality also includes the quantity and nutritional quality of different prey species, as well as their abundance in the environment, and ease of capture and consumption. A high-quality diet consists of prey that are energy rich, contain essential components for growth and reproduction, are readily available, and relatively easy to capture, eat, and digest (Emlen 1966, MacArthur and Pianka 1966, Jodice et al. 2006). Conversely, a reduction in prey number, availability, or ease of capture can result in decreasing predator diet quality, foraging success, health, and survival, and ultimately lead to reproductive and population decline.

Diet quality can decline as a result of factors affecting the biomass and distribution of prey species and is likely to decrease in the future as marine ecosystems continue to be heavily modified by climate change and fisheries (Worm et al. 2006, Cury et al. 2011). The potential negative effects of decreases in diet quality are particularly significant for penguins which feed on a variety of zooplankton (especially macrozooplanktonic crustaceans like krill), as well as cephalopods, and fish (Cherel et al. 2010, Masello et al. 2010). These represent species that are increasingly targeted by commercial fisheries (Pauly et al. 1998, Alonzo et al. 2003). Being central-place foragers, penguin foraging ability is therefore limited by travel range, meaning breeding penguins are particularly vulnerable to localised prey depletion (Birt et al. 1987, Pelletier et al. 2014), a situation which is exacerbated because of the generally smaller foraging range for swimming versus flying seabirds (Elliott and Gaston 2009).

Penguins undergo a “catastrophic” total moult during which they cannot swim, requiring sufficient energy reserves for extended periods of fasting during breeding and moulting (Green et al. 2007). Consequently, the body masses of individual penguins are positively correlated with adult reproductive success, chick survival to fledging, and post-fledging survival of juveniles (Olsson 1997, Moreno et al. 1999, McClung et al. 2004, Crawford et al. 2008). Adult survival is also linked to body condition, with birds in poorer condition less able to survive in challenging or changing environmental conditions, as demonstrated by a mass starvation event of adult *Sphenisciform* penguins at the Falkland Islands in 1986 (Keymer et al. 2001).

Diet quality is an important factor in foraging success, as high quality prey can improve the return per unit effort expended in obtaining food. As prey, fish generally have a higher lipid and energy density than zooplankton or cephalopods (Clarke and Prince 1980, Cherel and Ridoux 1992, Meynier et al. 2008), and additionally are more rapidly digested by seabirds, including southern rockhopper penguins (Jackson 1992), than are crustaceans or cephalopods (Wilson et al. 1985, Jackson et al. 1987). Fish are therefore expected to represent higher quality prey, and penguins feeding on a higher proportion of fish expected to be in better body condition. The body condition of Magellanic penguin (*Spheniscus magellanicus*) chicks has been shown to be positively correlated with the proportion of fish in their diet (Forero et al. 2002).

1.6.6 Measuring diet

The importance of diet in seabird ecology and conservation means a comprehensive understanding of diet and foraging ecology is essential for studying population dynamics, and identifying causes of decline. Diet studies can be conducted using a variety of methods, each with their own advantages and disadvantages.

Scat (faecal) samples can be used as a simple and non-invasive method to determine diet based on prey remains in faecal matter. However, faecal samples can be difficult to collect as any samples at sea are likely to be lost, and samples can be difficult to associate with individuals unless defecation was observed (Barrett et al. 2007). Additionally, faecal remains can be biased towards hard parts of prey such as otoliths and bones, meaning species containing proportionally more soft tissue (such as cephalopods) may be more digested and therefore under-represented (Ratcliffe and Trathan 2011). Bird faecal matter tends to be more liquid than in mammals, which can make it more difficult to find and collect samples of hard remains (pers. obs.). DNA analysis can be conducted on scat samples, however, this is still subject to the same biases resulting from differences in prey digestibility (Deagle et al. 2010), and it can provide data on the proportion of species present in a sample, but not the actual number or mass of prey items eaten (Ratcliffe and Trathan 2011).

Stomach contents can be obtained from deceased or euthanised individuals (Furness et al. 1984), or through stomach flushing (Clarke et al. 1998, Berrow and Croxall 1999). Stomach contents analysis has previously been the primary method for establishing diet in penguins (Adams and Brown 1989, Ridoux 1994, Hindell et al. 1995). The majority of seabirds are sampled during the breeding season when they return to shore, however, many species may disperse from their breeding areas in the off-season, meaning diet can be difficult to establish at other times of the year (Cherel et al. 2007). Since most diet studies are carried out during the breeding season when adults are bringing food for their chicks, stomach contents analysis can have difficulty distinguishing what adults are eating themselves versus what they are feeding to chicks (Tierney et al. 2008). Another limitation of stomach contents analysis is that the sample represents a single meal, so may not be representative of diet as a whole, and with increasing digestion time the sample can also be biased towards the more indigestible parts of the diet (Duffy and Jackson 1986, van Heezik and Seddon 1989). Stomach flushing is also a relatively invasive technique with potential handling stress and nutritional implications for the adult and chicks affected, and due to the handling time required, the sample size is likely to be limited compared to other methods of diet analysis.

Stable isotope analysis (SIA) is a common method used in dietary studies of marine predators which can show diet composition derived from prey items which have been incorporated into body tissues, so it does not have the bias towards prey tissue type or digestibility seen in other sampling methods (Bodey et al. 2011). Since SIA can be analysed using easily-obtainable tissues such as feathers and blood (Bearhop et al. 2002), it can be a less invasive method than stomach flushing. SIA relies on the analysis of chemical elements having more than one isotopic form of differing molecular mass, and differing ratios can be used to distinguish between different sources of nutrition. The ratio of different isotopes can identify an animal's foraging location, including differences between marine and terrestrial sources. Marine signatures are enriched with ^{13}C compared to terrestrial sources (Fry 2006), and different types of marine habitats can also be inferred since the isotopic ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in the tissues of a consumer reflect those of its dietary components (DeNiro and Epstein 1978, DeNiro and Epstein 1981, Hobson and Clark 1992a, Hobson and Clark 1992b). Consumers preferentially excrete the lighter isotopes and retain heavier ones, so their tissues become 'enriched' compared with their diet (Owens 1988).

The nitrogen isotope ratio of ^{15}N to ^{14}N (expressed as $\delta^{15}N$) can vary spatially but is more useful as an indicator of the trophic level at which an animal is feeding, with the heavier nitrogen isotope (^{15}N) enriched at increasing trophic levels (DeNiro and Epstein 1981, Bodey et al. 2011). Nitrogen-15 ($\delta^{15}N$) concentrations in the tissues of marine consumers typically increase by 2 to 5‰ per trophic level which can be used to estimate trophic position (Owens 1988, Hobson and Welch 1992), with fish and cephalopod prey producing a higher ^{15}N:^{14}N ratio (i.e. higher $\delta^{15}N$ value) than zooplankton (Owens 1988, Hobson et al. 1994). Diet determined from SIA has been shown to mirror that of stomach contents at the taxonomic level (Tierney et al. 2008). In contrast, ^{13}C shows little enrichment with increasing trophic level (DeNiro and Epstein 1978), with Carbon-13 ($\delta^{13}C$) concentrations increasing by only around

0.8 to 2‰ per trophic level (DeNiro and Epstein 1978, Hobson and Welch 1992, McCutchan et al. 2003). However, carbon isotopes can provide useful insights into dietary sources as they reflect the source of carbon at the base of their food chain (Kelly 2000). Examination of isotopes of carbon determine that the ratio of ^{13}C to ^{12}C (expressed as δ^{13}C) and can be used to discriminate between different sources of primary production, such as differing prey habitats (Bodey et al. 2011). Benthic and inshore plankton at the base of the food chain are enriched in ^{13}C relative to pelagic and offshore plankton, resulting in a higher ^{13}C:^{12}C ratio (i.e. higher δ^{13}C value), and providing information on predator foraging habitat (Hobson et al. 1994). The δ^{13}C values in consumer tissues can therefore be used to infer foraging location, including differentiating between inshore versus offshore, and benthic versus pelagic feeding (Kelly 2000, Cherel et al. 2007). Values of δ^{15}N and particularly δ^{13}C also decrease at higher latitudes (Jaeger et al. 2010), providing additional insight into likely foraging areas.

Additionally, SIA can be used to indicate predator diet over time, as different tissues uptake proteins at different rates as they grow (Hobson and Clark 1993) due to the differing rates of isotopic turnover in different animal tissues (Hobson and Clark 1992a, Cherel et al. 2005), likely linked to the rate of protein turnover (Carleton and del Rio 2005). In the case of birds, whole blood indicates diet for 3–4 weeks prior to sampling (Hobson and Clark 1992a, Haramis et al. 2001, Bearhop et al. 2002, Pearson et al. 2003), and feathers reflect the diet during the feather synthesis. Since feathers are biologically inert after growth, this record is preserved for the life of the feather (Mizutani et al. 1991, Hobson and Clark 1992a, Bearhop et al. 2002). In the case of penguins, which undergo a complete moult annually (Darby et al. 1990), SIA analysis of feathers will provide dietary information from the foraging period leading up the previous moult, with the isotope signature remaining static until feathers are replaced at the next moult.

SIA is therefore a useful method for measuring diet, particularly changes over time. It avoids some of the disadvantages of other methods, although it provides a more general overview with prey composition identified to trophic level rather than individual species.

1.6.7 Yellow-eyed penguin foraging behaviour

There has been limited past research on yellow-eyed penguin foraging behaviour and data are focused on northern populations, although only a subset of these studies recorded foraging areas or distance from shore (see Seddon and van Heezik 1990, Moore et al. 1995, Moore 1999, Mattern 2006, Mattern et al. 2007, Ellenberg and Mattern 2012, Chilvers et al. 2014).

Moore (1999) used VHF telemetry to determine that yellow-eyed penguins in the Otago area concentrated their foraging within 16 km of their breeding sites. Individual penguins also utilised similar areas and foraging patterns on different trips, although some could change their behaviour to forage closer or further from shore (Moore 1999), or to utilise different areas (Moore et al. 1995, Moore 1999). Mattern et al. (2007) used GPS loggers to determine that yellow-eyed penguins foraged in areas of high benthic biodiversity and that these foraging areas were used consistently from year to year. Foraging off the Otago coast was within 12–20 km from shore and predominantly benthic (with consecutive flat-bottomed dives to the same depth and spending a large proportion of each dive at the benthos). A number of studies inferred foraging location from bathymetry data, matched with the dive depth recorded using capillary depth recorders (Seddon and van Heezik 1990), or electronic depth loggers (Chilvers et al. 2014). In all data published for northern yellow-eyed penguins, foraging occurred or was estimated within 20 km from shore (Seddon and van Heezik 1990, Moore 1999, Mattern 2006, Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014).

Chilvers et al. (2014) described variability in yellow-eyed penguin foraging behaviour within New Zealand depending on bathymetry and anthropogenic impacts, mainly affecting dive depth parameters. Penguins breeding at Port Pegasus, Stewart Island had similar foraging patterns to those studied off the Otago coast, despite the proximity of more diverse bathymetry including the option of travelling to deeper water within range of breeding areas. Other studies investigating the foraging behaviour of yellow-eyed penguins in the northwestern areas of Stewart Island and adjacent Codfish Island found that although these areas are geographically close, yellow-eyed penguins displayed very different foraging behaviours, with Codfish Island birds making longer trips and diving deeper during the post-guard breeding phase (Mattern 2006, Elley et al. 2022). This difference in behaviour may be a result of several factors, including breeding phase, and the availability of suitable benthic habitat (Mattern 2006), as well as habitat modification caused by dredging in Foveaux Straight for Bluff oysters (*Tiostrea chilensis*) that may have resulted in altered chick survival and therefore placing greater pressure on parental foraging (Browne et al. 2011). Research using cameras attached to yellow-eyed penguins has shown that prey species were associated with certain types of benthos (Mattern et al. 2018a), which may affect foraging success depending on the availability of suitable foraging habitat.

Foraging data from the southern yellow-eyed penguin population are needed. However, this is more difficult to carry out than on mainland New Zealand due to logistical constraints, including difficulty of access and shorter research seasons in the subantarctic due to the islands' isolation, and more difficult field conditions that can hinder animal capture and logger deployment and recovery. This required fieldwork methods be improved for maximum efficiency in the subantarctic.

1.6.8 Yellow-eyed penguin diving behaviour

Most penguin species generally employ an exclusively pelagic foraging strategy, although yellow-eyed penguins have been described as predominantly benthic foragers, based on results from northern population dive studies (Mattern et al. 2007). However, there is some evidence of pelagic foraging occurring in the northern population from diet and other studies (van Heezik 1990a, Moore et al. 1995, Mattern et al. 2018a), although this is not common.

Research on northern yellow-eyed penguins shows they forage on the continental shelf at mean depths of around 40–80 m. Diving behaviour for breeding birds from the northern population is predominantly benthic, and close to nesting areas (within 12–20 km) (Seddon and van Heezik 1990, Moore 1999, Mattern et al. 2007). Dives at Port Pegasus, Stewart Island were deeper with a mean depth of 61 m, and a maximum depth up to 116 m, although dive depths were affected by variable bathymetry in different areas (Chilvers et al. 2014). Some recent data from northern studies suggest yellow-eyed penguins may dive deeper and travel further outside the breeding season (M. J. Young, unpubl. data).

Differences in bathymetry and underwater habitat have shown the potential for significant variability in yellow-eyed penguin foraging behaviour in different areas. In the northeast of the Auckland Islands, bathymetry is dominated by relatively shallow water depths (under 200 m) that would allow benthic foraging. Further south, water depths drop to depths over 200 m relatively close to the coast (Mitchell et al. 2016). Due to the almost exclusive benthic foraging strategy of yellow-eyed penguins in the northern population, and the assumption that the same holds true for the southern population, researchers have proposed the local bathymetry as a reason for the importance of Enderby Island as a breeding stronghold for yellow-eyed penguins on the Auckland Islands (Ellenberg and Mattern 2012). Adams Island to the south may represent suboptimal foraging conditions due to deeper water closer to the coast, yet due to its importance as a breeding area yellow-eyed penguins breeding there may employ different foraging strategies.

Studies on another marine predator in the subantarctic have shown female New Zealand sea lions exhibit different diving and foraging strategies in different areas, with longer foraging trips, deeper dives, and some mesopelagic foraging dives at the Auckland Islands, as well as individual preference in dive type (Chilvers and Wilkinson 2009, Chilvers et al. 2011). Similar to penguins, northern animals conducted predominantly benthic dives much closer to the coast (Augé et al. 2012, Augé et al. 2015), and the difference in foraging behaviour between the mainland and the subantarctic is believed to be due to differences in prey assemblages and benthic topography in different areas.

A purely benthic foraging strategy may result in reduced behavioural flexibility for penguins, thereby increasing vulnerability to changes in the marine environment (Mattern et al. 2007). If prey sources become less available in time or space, or if seafloor ecosystems are disrupted by commercial fisheries this could result in poor foraging success, and therefore reduced population success (Browne et al. 2011, Mattern et al. 2013).

Prior to this study there have been no dive data published for any southern yellow-eyed penguin populations. However, there is anecdotal evidence to suggest that some pelagic foraging may be occurring at the Auckland Islands, in addition to benthic foraging (B. L. Chilvers, pers. comm.), and two depth loggers deployed on Campbell Island indicated a likely benthic foraging strategy there (P. J. Moore, pers. comm.). Understanding yellow-eyed penguin dive behaviours in the southern population will help to elucidate foraging behaviours, and therefore assist with conservation and management of this endangered species.

1.6.9 Yellow-eyed penguin diet

Diet is an important factor affecting foraging success, and therefore also breeding success, and can be influenced by prey availability. In the lower South Island, seven species of fish are thought to make up 95% of yellow-eyed penguin diet: sprat (*Sprattus antipodum*), red cod (*Pseudophycis bachus*), silverside (*Argentina elongata*), blue cod (*Parapercis colias*), ahuru (*Auchenoceros punctatus*), opalfish (*Hemerocoetes monopterygius*) and squid (*Nototodarus* spp.) (van Heezik 1990c, van Heezik 1990b, Moore and Wakelin 1997, Browne et al. 2011). At northwestern Stewart Island, blue cod and tarakihi (*Nemadactylus macropterus*) were found to be the only two species in the diet (Browne et al. 2011). Yellow-eyed penguins prey on the juveniles of these species and are not thought to be in direct resource conflict with commercial fisheries (Moore and Wakelin 1997). However, it is known that a proportion of adult and juvenile yellow-eyed penguin mortality results from fisheries bycatch in these areas (Darby and Dawson 2000). Knowledge of prey species can therefore highlight any overlap with, and competitive pressure from, commercial fisheries.

Yellow-eyed penguin diet has not been studied in the southern population, and prey species are unknown. Fish species assemblages differ from those around the mainland, and the subantarctic has a low diversity of reef fishes compared to other New Zealand ecosystems (Francis 1996), which would reduce the number of benthic species available to penguins. Knowledge of yellow-eyed penguin prey species, and their distribution in time and space is therefore an important predictor of foraging, and breeding success, and is needed for the management of this endangered species.

1.7 Summary

1.7.1 Summary of previous yellow-eyed penguin research in the Auckland Islands

Little prior research has been carried out on yellow-eyed penguins on the southern yellow-eyed penguin population. The only previous population estimate for the Auckland Islands dates back to 1989 (Moore 1990), and up-to-date data are needed. Moore also carried out beach counts and population estimates on Campbell Island in 1988 and 1992 (Moore 1992b, Amey and Moore 1995, Moore et al. 2001), which are also out of date.

As part of the Auckland Islands population estimate, Moore identified 115 sites used by yellow-eyed penguins as access points to the sea which are therefore indicative of breeding area locations (Moore 1990). Additional landing area surveys were conducted by Hiscock (2009) and Beer (2010), and transit counts were also made for some areas in the Auckland Islands, including Sandy Bay on Enderby Island in 2008–2009 (Young 2009), and 2001–2012 (Chilvers 2014)). However, apart from Moore (1990), these studies used uncorrected count data, and in some cases different methods, so are not suitable for comparison with other studies, or for generating population estimates.

Several brief nest searches have been made for a reference population on Enderby Island (Darby and Seddon 1986, Houston and Thomson 2013, King and Houston 2013), in attempts to estimate nest numbers. However, search times were around a week on average so it is unlikely all nests in the area were located in the available time. Houston and Thomson (2013) also attempted to determine a relationship between transit counts and nesting numbers, including the use of cameras for remote monitoring, however, due to difficulties with the technology and the likelihood not all nests were found, the results should be considered a preliminary estimate only.

During the 2008 breeding season, 40 chicks on Enderby Island were monitored to measure breeding success (survival to fledging) (Argilla et al. 2013). The survival rate was 45%, and while a higher prevalence of the parasite *Leucocytozoon* spp. was detected compared to mainland or Campbell Island populations, no link was found between this and the deaths of either chicks or adults (Argilla et al. 2013). Unlike for the northern population, there have been no documented disease outbreaks or mass-mortality events of adults or chicks in the subantarctic, although it is possible this may be due to much lower levels of monitoring.

To date there has been no research quantifying juvenile survival, or recruitment into the Auckland Islands breeding population. Prior to this study no published data exist documenting foraging location, diving behaviour, or diet for yellow-eyed penguins in the southern population. Moore collected dive logs from two birds at Campbell Island (P. J. Moore, pers.

comm.), however, no other research has been conducted on yellow-eyed penguin foraging behaviour in the southern population.

1.7.2 Research aims of this thesis

Knowledge of population trends, and key contributing factors such as foraging behaviour, and foraging success (inferred from breeding success), are important for endangered species management. This includes not only documenting the population status (e.g., to update the IUCN Red List status), but also identifying what factors may contribute to breeding success – an important consideration when determining what management or intervention may be needed to protect the species in the future. Previous yellow-eyed penguin research has focused primarily on the more accessible northern population, with a large data deficiency in the subantarctic. An up-to-date population estimate for the Auckland Islands was therefore urgently required, along with information on the population trend. Additional data on diving, foraging behaviour, and diet were also needed to highlight possible drivers of population trends, both in the present and future. Filling these knowledge gaps was the key aim of my thesis.

My first field season in 2015 was dominated by the need to prioritise nest searches, using traditional ground searching, plus a small amount of ground-based VHF tracking as a methods trial. The introduction of new technology in subsequent field seasons, including a VHF-tracking drone which greatly improved the efficiency of nest-finding, and allowed more time to be spent on answering my primary research questions. This is reflected in improved nest monitoring and the greater amount of dive data collected in 2016 and 2017. The inclusion of GPS loggers in 2016 and 2017 also provided additional detail on foraging location.

1.7.3 Research chapters

This thesis is structured with the research chapters (Chapters 2 to 6) written as stand-alone scientific journal articles, all of which have been published. Consequently, the chapters contain a degree of repetition, particularly in their Introduction and Methods sections. Cross referencing between chapters is used occasionally to minimise repetition. Since the research chapters are all published in different journals, they may contain some minor differences in formatting and layout.

Each research chapter represents the state of knowledge at the time the research was carried out, and each discussion is up-to-date at the time they were published. Any recent developments post-publication are discussed in the General Discussion section.

The five research chapters had the following aims:

2. To improve nest-location efficiency and document the effectiveness of aerial VHF tracking for monitoring wildlife, in this case developing a multi-channel receiver as a primary method for locating cryptic yellow-eyed penguin nests.
3. To estimate the total yellow-eyed penguin population for the Auckland Islands, and estimate the number of breeders on Enderby Island and the Auckland Islands.
4. To document yellow-eyed penguin diving behaviour in the subantarctic, and investigate the effects of individual preference and sex on diving behaviour, as well as changes between years.
5. To determine the size and location of foraging areas used by yellow-eyed penguins breeding at Enderby Island, as well as any differences in the foraging area size and distance from shore between birds of different sex, diving behaviour, or between different years.
6. To investigate yellow-eyed penguin diet and foraging in the subantarctic, by identifying any variability in diet between sexes, birds utilising different foraging behaviours, or between different years.

This thesis also includes a General Introduction (Chapter 1), and a General Discussion (Chapter 7).

2. Chapter Two – Nest Finding

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GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the candidate and the candidate's Primary Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of candidate:	Chris Muller
Name/title of Primary Supervisor:	Louise Chilvers

In which chapter is the manuscript /published work: 2

Please select one of the following three options:

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Muller, C. G., Chilvers, B. L., Barker, Z., Barnsdale, K. P., Battley, P. F., French, R. K., McCullough, J. and Samandari, F. (2019) Aerial VHF tracking of wildlife using an unmanned aerial vehicle (UAV): comparing efficiency of yellow-eyed penguin (Megadyptes antipodes) nest location methods. Wildlife Research, 46 (2):145-153.

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Chris Muller conceived and designed the experiments, carried out the fieldwork, analysed the data, and wrote the paper.

○ It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Candidate's Signature:	Chris Muller Digitally signed by Chris Muller DN: cn=Chris Muller, o, ou, email=cmuller@technologist.com, c=NZ Date: 2022.06.14 10:57:11 +12'00'
Date:	14-Jun-2022
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Aerial VHF tracking of wildlife using an Unmanned Aerial Vehicle (UAV): Comparing efficiency of yellow-eyed penguin (*Megadyptes antipodes*) nest location

Muller, C. G., Chilvers, B. L., Barker, Z., Barnsdale, K. P., Battley, P. F., French, R. K., McCullough, J., and Samandari, F. (2019) Aerial VHF tracking of wildlife using an unmanned aerial vehicle (UAV): comparing efficiency of yellow-eyed penguin (*Megadyptes antipodes*) nest location methods. Wildlife Research, 46(2):145–153.

2.1 Abstract

Locating cryptic animals is an important aspect of many wildlife management programmes and research studies. However, this process can be inefficient, time-consuming and expensive. Unmanned Aerial Vehicles (UAVs), Unmanned Aircraft Systems (UASs), or drones fitted with a camera are increasingly being used for counting and monitoring wildlife; however, these are often not suitable for cryptic species. Very High Frequency (VHF) radio-tracking is commonplace; however, single-channel VHF receivers mean animals must be tracked individually, or scanning receivers must be used; but this raises the possibility of signals being missed. We aimed to test the effectiveness of aerial VHF tracking using a multi-channel receiver for locating wildlife. We tracked wildlife fitted with VHF transmitters operating on individual frequencies, by means of a UAV with a multi-channel VHF receiver to simultaneously monitor all frequencies. This offered distinct advantages over traditional single-channel scanning receivers. To test and compare this novel method, yellow-eyed penguins (*Megadyptes antipodes*) were located on nests hidden under vegetation on Enderby Island in the New Zealand subantarctic using manual ground searching, unassisted ground VHF

tracking, as well as using location flights by the UAV Drone Ranger system. The UAV system allowed for faster nest location than all other methods, with a higher cumulative success (number of nests found each day) and lower search effort required (person hours per nest). Aerial VHF tracking can greatly extend the search range and minimise search effort compared with ground VHF tracking or manual searching. This technology has applications for locating and tracking a wide range of wildlife, particularly cryptic species that may be difficult to find using other methods.

2.2 Introduction

Tracking wildlife is important for monitoring behaviour, home range, and resource use (Kenward 2001). For example, locating animals is required for accurate long-term monitoring of a breeding population, so as to determine population trends and the effectiveness of ongoing management measures, particularly for intensively managed or cryptic species where finding animals or nesting sites requires intensive effort (Cagnacci et al. 2010). Wild animals can be difficult to track as they are often elusive, wide-ranging, sensitive to human disturbance, dangerous to approach, or live in a challenging environment. Locating animals can, therefore, be time-consuming and inefficient, which can limit the quality of work and collection of data. As a result, the development of technologies that can locate and track animals more efficiently is important.

We studied yellow-eyed penguins (*Megadyptes antipodes*) breeding on subantarctic Enderby Island (50°29′45″S 166°17′44″E), ~500 km south of mainland New Zealand, and home to ~17% of the total breeding population (Couch-Lewis et al. 2016). The endangered yellow-eyed penguin is endemic to New Zealand, and is restricted to the south-east of the South Island, and subantarctic islands (Robertson et al. 2017, BirdLife International 2020). Unlike colonial breeding penguin species, yellow-eyed penguins make solitary nests up to 1 km inland, hidden within coastal forest and scrub, making nests difficult and time-consuming to find (Darby et al. 1990). Yellow-eyed penguins nest an average of 12–32 m and up to 78 m from other nests on mainland New Zealand (Seddon and Davis 1989), and seldom use the same nest bowl between years, with 55% of females moving their nest site more than 20 m away (Setiawan et al. 2005). Location of nests is critical for accurate population assessment of yellow-eyed penguins, and facilitating other research such as monitoring breeding success. Ground searching for penguin nests is labour-intensive, and success is dependent on searcher experience. Ground search teams have been shown to locate a maximum of 88% of nests; therefore, two independent teams are recommended for maximum efficacy (Hegg et al. 2012). This method cannot be adequately used at remote field sites such as Enderby Island where team size is limited to two people who cannot conduct independent searches for safety reasons. Nest searching is also more time-consuming in the subantarctic than on the mainland because of difficult terrain, inclement weather, and thick vegetation.

Unmanned Aerial Vehicles (UAVs or drones) have been predicted to revolutionise ecology (Anderson and Gaston 2013, Chabot and Bird 2015) and have been increasingly employed in wildlife studies, commonly utilising still imagery to perform counts or surveys (Goebel et al. 2015, Chrétien et al. 2016). Methods for counting colonially-nesting penguins with a camera-mounted UAV have been proven using still imagery for gentoo *Pygoscelis papua* (Ratcliffe et al. 2015), and Adélie penguins *P. adeliae* (Rümmler et al. 2016). However, trials on Enderby Island indicated that visual and thermal imagery were unsuitable for detecting nesting yellow-eyed penguins screened by vegetation cover (C. G. Muller, unpubl. data). Additional technology is, therefore, required for detecting penguins nesting in vegetated areas.

Very High Frequency (VHF) radio transmissions are widely used for tracking wildlife, typically consisting of a transmitter attached to an animal, and hand-held VHF receivers and antennas used by ground-based teams (Kenward 2001). However, although useful, VHF tracking can be time-consuming and inefficient, and detection range can be affected by vegetation and topography, particularly for ground-based tracking (Mech and Barber 2002). UAVs can offer a versatile and cost-effective platform for aerial VHF tracking, and systems described as suitable for tracking wildlife have utilised single-channel (Körner et al. 2010) and multi-channel receivers (Dos Santos et al. 2014, Webber et al. 2017), including one system designed to rotate and calculate a bearing to the strongest signal (VonEhr et al. 2016). Some single-channel VHF systems have been trialled for tracking wildlife and rotated to perform direction-finding for a single frequency at a time (Cliff et al. 2015); however, single-channel receivers are less efficient than are multi-channel receivers if there is a need to track many transmitters. Other systems have tracked multiple birds using coded tags operating on the same frequency, each with a unique ID (Tremblay et al. 2017); however, coded transmitters require a specialised receiver to decode signals, and so, are less practical if manual tracking is also required. We are not aware of any studies comparing the efficiency of a multi-channel receiver to locate wildlife.

In the present study, we describe a system capable of performing simultaneous aerial tracking and location of multiple VHF ‘beeper’ (non-coded) transmitters operating on different frequencies for tracking wildlife. We evaluate the efficiency of nest-finding by using transmitters attached to yellow-eyed penguins and compare this method with previously-used ground VHF and manual search methods.

2.3 Methods

2.3.1 Fieldwork

Ground-based fieldwork was conducted on Enderby Island in the Auckland Islands group in the New Zealand subantarctic (Figure 2.1) for three breeding seasons: 2015 (November 2015 to February 2016), 2016 (November 2016 to February 2017), and 2017 (November 2017 to January 2018). Nest location was primarily during incubation (November) each year.

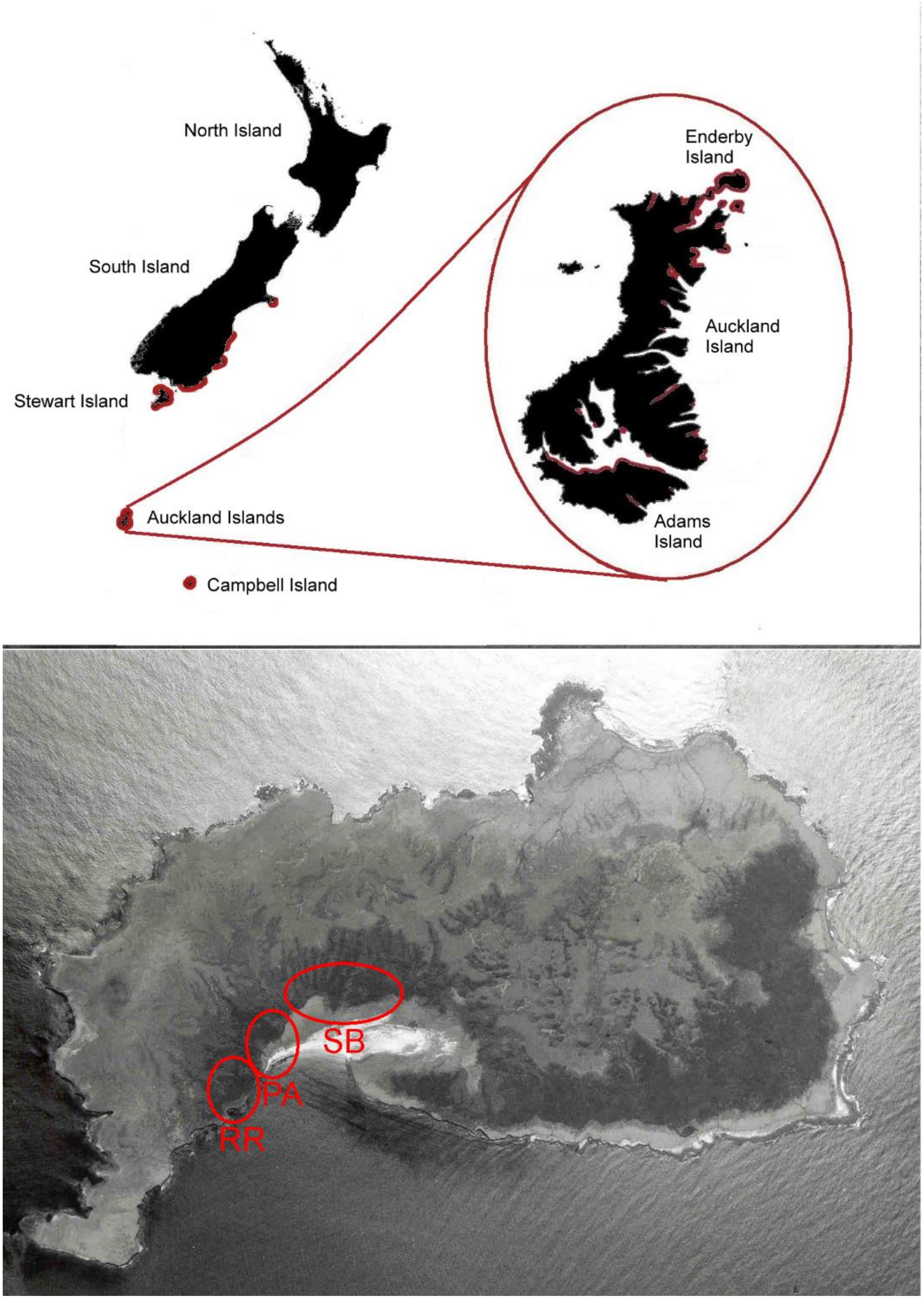


Figure 2.1 Map of yellow-eyed penguin breeding areas (red) showing New Zealand mainland, subantarctic Auckland Islands with Enderby Island to the north-east, and study colonies inset, showing Rocky Ramp (RR), Penguin Alley (PA), and Sandy Bay (SB).

Data for the study were gathered in the context of wider field research into population dynamics; therefore, different search methods were tested as the opportunity arose. It was not practicable, given the overall study aims, to independently locate the same nest using multiple search methods, so adjacent sub-areas of contiguous habitat, namely Rocky Ramp, Penguin Alley, and Sandy Bay (Figure 2.1) were searched using different methods, as follows:

1) Manual ground searches were conducted at Rocky Ramp in 2015. A repeat manual search was conducted in 2016, utilising nest location data from the previous breeding season, but was not independent because knowing past nest locations can assist manual searching. Manual nest searches were conducted by a team of two people searching for nest sign as described in Hegg et al. (2012).
2) Unassisted ground VHF tracking was conducted at Rocky Ramp during the second part of the 2015 season, and early season at Penguin Alley in 2016 and 2017 using an Ultra VHF receiver and directional Yagi antenna (Sirtrack, Havelock North, New Zealand).
3) UAV-based positioning was conducted at Penguin Alley and Sandy Bay in 2016 and 2017. Initial flights (position-only location) were followed by ground location of the nest (UAV-assisted searches). Visiting nests allowed quick recovery of transmitters and immediate verification whether birds were on an active nest or not. This would be more time-consuming to determine from the air as thick vegetation cover prevents visual identification of a nest, meaning that monitoring over several days would be required to determine whether the penguin was returning to the same place after every foraging trip.

VHF-tracked adult penguins were captured by hand as they returned to the shore in the evening following a foraging trip at sea, and transmitters were attached using TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany). Birds were selected on the basis of the presence of a large brood patch, indicating they were likely incubating eggs at the time. Transmitters were taped to the upper back on the mid-line to maintain streamlining, and to ensure electronics would drop off within 1–2 weeks if penguins could not be recaptured. Two different VHF transmitter types were tested: two-stage transmitters (V2G154B with 250 mm whip antenna, weight 18 g) had a greater power output and, therefore, detection range than the smaller single-stage transmitters (V1G118A with 150 mm or 220 mm whip antenna, weight 4.5–5 g) which kept total attachment weight down if other electronics were also fitted (both from Sirtrack, Havelock North, New Zealand). Frequencies were in the 160 MHz band, and pulse rates were either 30 or 40 pulses per minute (ppm). VHF transmitters used for nest location were retrieved for re-use before penguins departed for their next foraging trip to avoid unnecessary impact on foraging ability.

2.3.2 UAV

A proprietary system was developed for this research ("The Drone Ranger") consisting of a Qu4D quadcopter UAV (SteadiDrone) fitted with a custom-built VHF receiver and a dual 2-element directional yagi antenna (payload weight 465 g, Figure 2.2).

Figure 2.2 The Drone Ranger aerial very high frequency (VHF) tracking system in flight.

The multi-channel receiver has a 1 MHz bandwidth capable of tracking 50 VHF frequencies (with 20 KHz separation). Signals from multiple specified frequencies are processed simultaneously by an onboard processor and individually recorded to a data file, along with position information from a GPS receiver.

2.3.3 Flights

The UAV can follow flight plans created using commercially-available autopilot software. The standard search pattern utilised a 30, 40, or 50 m altitude (height above take-off point), with a 30 m separation between flight lines. Dynamic searches followed a 'lawnmower' search pattern with passes in alternate directions, which typically results in less disturbance than other flight patterns (Mulero-Pázmány et al. 2017). The number of VHF transmitters deployed on penguins was limited to five per day, to ensure it was possible to visit all the nests in person the following day (n = 13 flights). Some calibration flights were also conducted to track transmitters placed in the field at known locations to measure VHF detection range and other factors. These flights used a higher number of transmitters than normal search flights (12–24 transmitters per flight), providing a useful measure of detection ability in a higher-density transmitter environment (n = 8 flights).

2.3.4 Data analysis

Data were analysed using Python 3.5.2 (Python Software Foundation, Beaverton USA, www.python.org), Excel 2013 (Microsoft, Redmond, Washington, USA), and ArcGIS 10.2.2 (ESRI). Statistical analyses were performed in R 3.2.2 (R Core Team, Vienna, Austria). Basic position analyses were conducted in the field using a custom-designed Python script to identify the strongest signal strength and the nearest corresponding GPS position for each transmitter frequency. This allowed the field team to begin searching for a nest immediately if required. More detailed analyses could be conducted back at the field base. Because GPS fixes were recorded at a different sample rate than for signal strengths, an additional Python script was used to interpolate position data (assuming a constant speed and heading between fixes). To assist with navigation, spatial data were plotted in ArcGIS with graduated symbology showing signal strength (Figure 2.4).

Effort data (search time and distance travelled) for ground searching were collected using handheld GPS receivers carried by searchers (Map 60Cx, and Etrex Vista HCx; Garmin International, Olathe, Kansas, USA). Search effort was expressed as average number of person hours per nest. Effort data for unassisted ground VHF searching was the time taken for a researcher to find the location by using a handheld VHF receiver. UAV effort was classed as ‘UAV position-only’ and ‘UAV-assisted ground VHF’, depending on whether the nest was visited in person or just located from the air. For position-only UAV searches, effort data for aerial VHF searching were calculated from the average time required to fit transmitters to penguins, setup time for the Drone Ranger system, and flight time. For UAV-assisted ground VHF searches, the time required for a ground team to navigate to the location indicated by the Drone Ranger system (using a handheld VHF receiver if needed) was also included. Cumulative success data (number of nests found per day for each method) were also collected.

2.4 Results

2.4.1 Search time and efficiency

The UAV system was highly effective at locating nests and reducing manual search times. Position-only flights took just 3% of the search effort (person hours per nest) required for manual ground searching in a new area, and 18.1% of the effort for unassisted ground VHF searching (Table 2.1). UAV-assisted nest location (including nest visits) took 14.4% of manual ground search effort, and 87.0% of the effort for unassisted ground VHF searching (Table 2.1).

Table 2.1 Effort data (search time) for nest location using a very high frequency (VHF)-equipped unmanned aerial vehicle (UAV) including: average handling time (penguin capture and VHF transmitter attachment; n = 60); UAV setup time (including pre-takeoff assembly and re-packing for transport; n = 15); UAV flight time (n = 15); Nest visit time (time to locate nests in person using aerial search data and handheld GPS and VHF receivers; n = 34) (shown in grey highlights). Effort for manual nest searches (new area and repeat search) are included for comparison (n = 12 and 63, respectively), and unassisted VHF ground search (n = 24). Times are given as h:min:s.

Search method	**Manual search, new**	**Manual search, repeat**	**VHF ground search**	**UAV search, (VHF aerial) position-only**	**UAV search (VHF aerial) + nest visits**
Number of nests found	12	63	24	54	35
Number of searchers	2	2	1	1	1
Average handling time / penguin	n/a	n/a	00:05:30	00:05:30	00:05:30
Average UAV setup time / nest	n/a	n/a	n/a	00:15:00	00:15:00
Average UAV flight time / nest	n/a	n/a	n/a	00:07:42	00:07:42
Average time to visit / nest	3:06:44	2:31:45	1:01:59	n/a	00:53:55
Total nest visit time	37:20:48	159:19:48	24:47:24	n/a	23:45:00
Total flight time	n/a	n/a	n/a	1:55:03	1:14:34
Total setup time	n/a	n/a	2:12:00	8:12:00	6:27:30
Total search time	**37:20:48**	**159:19:48**	**26:59:24**	**10:07:03**	**31:27:04**
Total search hours (h)	37.38	159.33	24.79	10.12	31.45
Total search effort (person h)	74.76	318.67	24.79	10.12	31.45
Search effort per nest (person h)	**6.23**	**5.06**	**1.03**	**0.19**	**0.90**
Search effort per nest (person min)	**373.80**	**303.49**	**61.98**	**11.24**	**53.92**

Both types of UAV searching were significantly quicker than was manual ground searching (ANOVA, $F_{2,81} = 41.75$, $P < 0.001$), and the time taken for a ground VHF team to locate tagged birds on the nest was significantly quicker following a UAV flight (giving the general location of the nest) compared to normal VHF ground tracking (with no prior knowledge of the transmitter location; $t = -2.47$, $P < 0.05$). For UAV tracking, position-only aerial location took 20.8% of the effort than when nest visits were also conducted, which was significantly quicker ($t = -5.99$, $P < 0.001$).

During position-only UAV calibration flights, the search effort per transmitter in a high-density situation (12 or more transmitters in the search area) was significantly reduced compared to searching in a low-density situation (up to 5 transmitters; taking 20.3% of the search effort; $t = -4.55$, $P < 0.001$). The search times were similar to cover the same area, but more transmitters were located, providing a greater return per effort.

The average search time per nest for manual ground searches took longer in 2015 when the area was searched for the first time. A repeat search in 2016 when searchers were assisted by nest position data from the previous season was quicker (taking 81.2% of the time, although the difference was not significant; $t = -1.29$, $P > 0.1$; Table 2.1).

Aerial VHF tracking significantly increased the rate of finding nests (Figure 2.3), and, in-the-field evaluation of different methods allowed the project to be refined to utilise the most efficient methods, with manual searching replaced by ground VHF, then aerial VHF tracking.

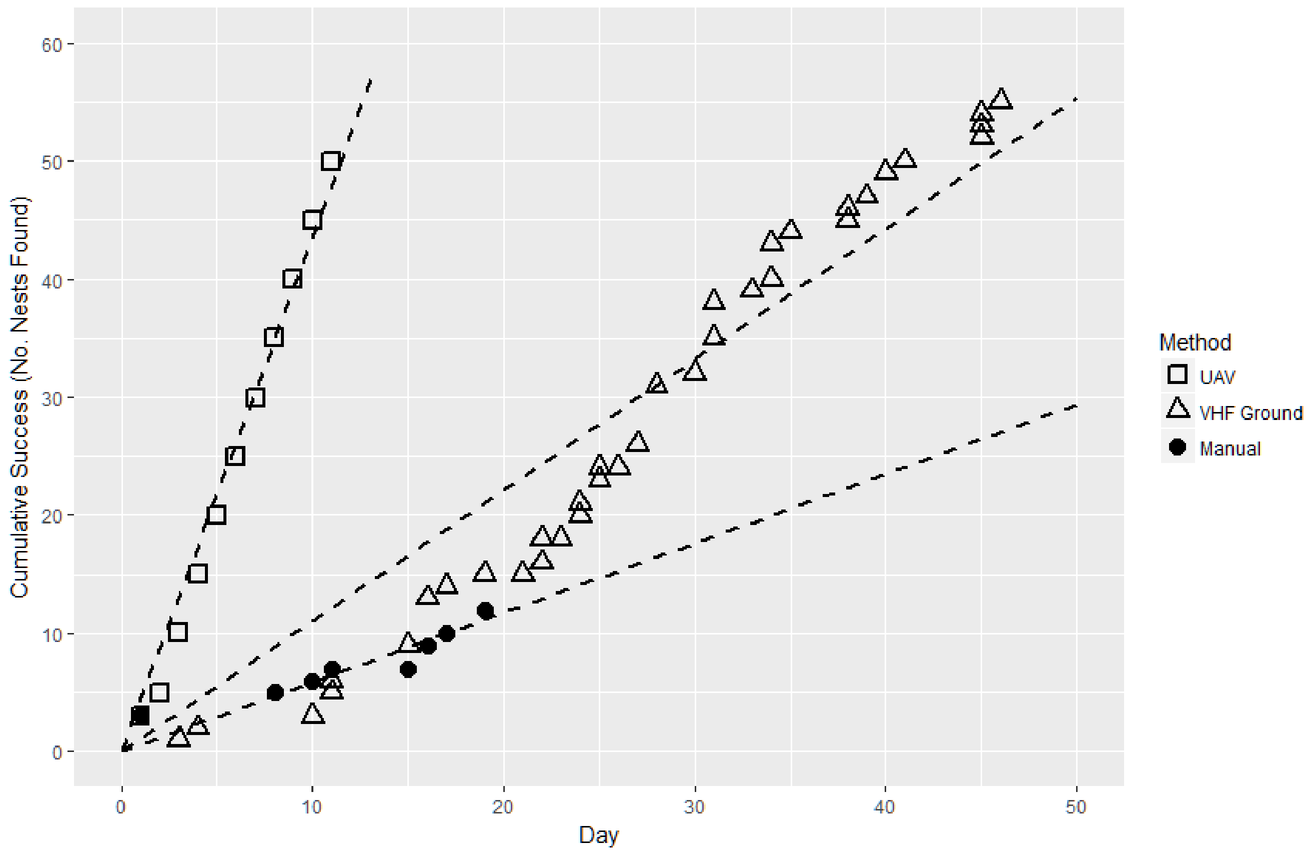


Figure 2.3 Cumulative success (number of nests found per day) by search method, as follows: manual ground search in a new area (circles), unassisted very high frequency (VHF) ground search in a new area (triangles), and UAV-assisted VHF searching (squares), with simple linear regression lines.

No reaction to the drone was observed in the target species, in other birds, or in the only mammal present, the New Zealand sea lion (C. G. Muller, unpubl. data).

2.4.2 Accuracy

Basic positioning provided by the Drone Ranger system depended on the placement of flight lines, and the separation between them. A 30 m separation gave a mean accuracy of 13.6 ± 8.0 m between the UAV position and the actual nest location in the search area. After GPS interpolation this reduced to 10.9 ± 7.0 m, although this improvement was not significant (t = 1.18, *P* > 0.1).

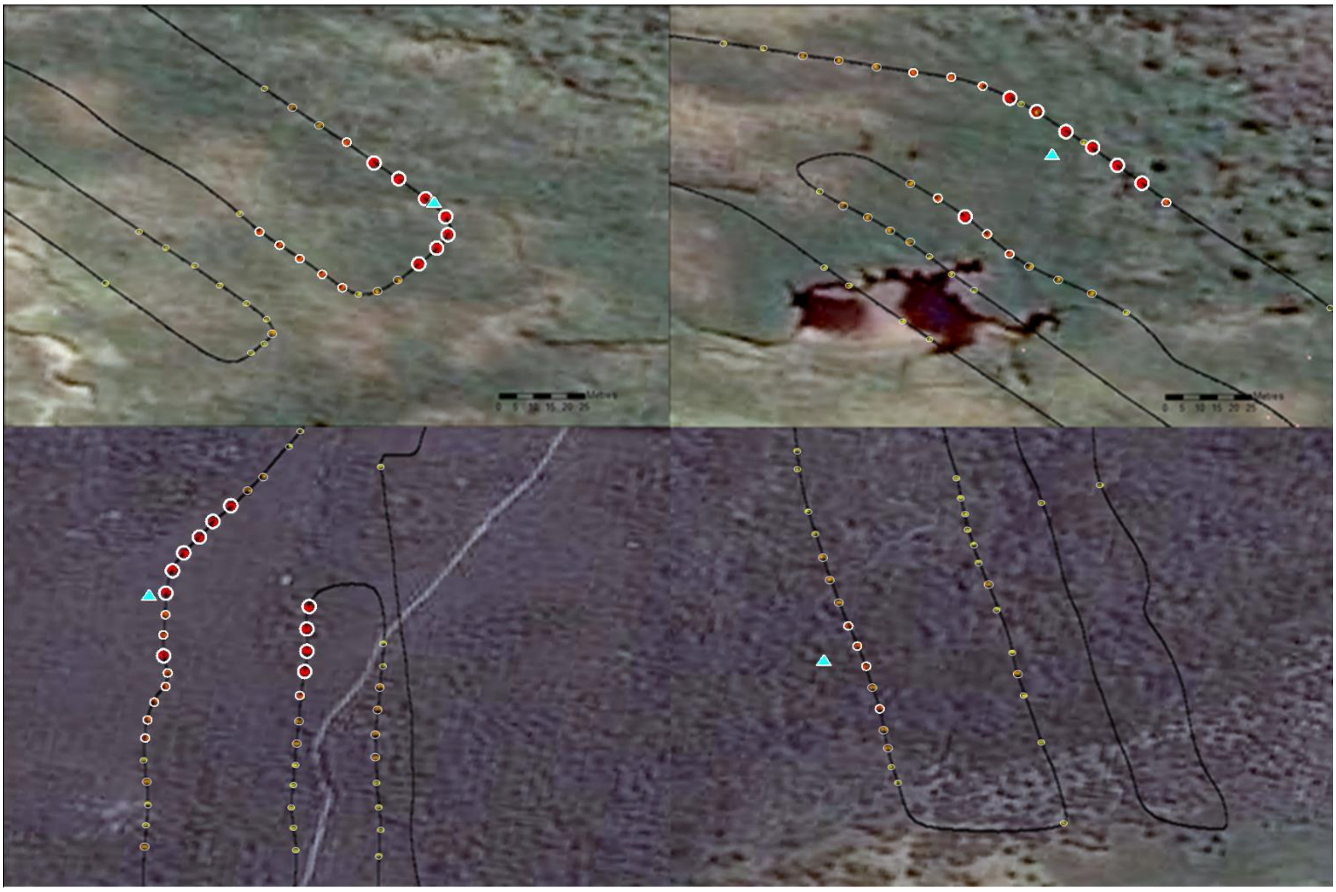


Figure 2.4 Images from GIS showing actual nest locations (blue triangles), unmanned aerial vehicle (UAV) flight paths (black lines), and increasing VHF signal strength indicated by yellow, orange, and red circles of increasing size. Separation between flight lines is initially 30 m, decreasing to 15 m for later passes, as an example of closer spacing used to increase coverage in selected areas.

2.4.3 Attrition rate

Effects of terrain and vegetation on VHF ground tracking were evident with the different transmitter types. During ground searching, only 38 of 43 lower-power single-stage VHF transmitters were successfully recovered (five VHF transmitters were never detected, and another four were eventually recovered with missing antennas that had substantially reduced their detection range). During aerial searching all transmitters were located and recovered.

2.5 Discussion

The Drone Ranger system allowed for significantly more efficient nest location than manual searching and unassisted VHF ground searching. Cumulative success (number of nests found each day) was higher, and the effort required (person hours per nest) was lower. Manual searching is labour-intensive, with additional time required to search difficult or more distant areas (Seddon and Maloney 2004). Over 200 person hours were spent ground searching in 2015, significantly more time than was required to conduct aerial VHF searches. Extrapolating the rate of finding nests using manual ground searching predicted that this method would not be sufficient to find all nests in a breeding colony before the end of the breeding season in late February (Figure 2.3), highlighting the need for alternative methods. Unassisted ground VHF searching was more effective than manual searching; however, the short detection range of single-stage transmitters (~50–100 m) and difficulty of travel in thick vegetation made locating signals difficult, and contributed to the number of lost transmitters. In contrast, UAV searching allowed significantly faster nest location (even when visiting nests in person), and all transmitters were located. Navigating to a supplied waypoint allowed field crews to travel to the location by the best route, without having to locate or follow a signal. The Supplementary Material available to this paper (Appendix 2) describes comparisons between different types of transmitter, and other factors affecting signal strength.

Ideally, all nest-finding methods would be compared concurrently; however, it was not possible for the same team to independently locate the same nest by using different methods without biasing subsequent searches. As in many field studies, decisions needed to be made in real time to improve the methods. Comparing nest-finding methods between sub-sites and breeding seasons could be influenced by changes in the accessibility of nests, weather conditions and experience or prior knowledge over the three-year study. However, these factors do not create practical differences in the ability to detect a VHF signal. In addition, the habitat is contiguous between sub-areas and is not expected to change between subsequent years; only the exact location of nests differs from year to year. Manual search teams gained a small advantage when they had knowledge of nest locations from the previous year, since at least 45% of females nest within 20 m of their previous nest location (Setiawan et al. 2005). This advantage was small and not statistically significant, but was noticeable; so, only the new manual search from 2015 was directly compared with the other search methods. Despite the possibility of confounding factors caused by trialling methods between areas and years, any effect on results was expected to be minimal. Therefore, evaluating methods between sub-areas and years offered a practical method of comparison, as well as minimising researcher disturbance.

The Drone Ranger system can track over 50 transmitters simultaneously; so, deploying additional transmitters in the search area would improve the efficiency over the results presented here, as demonstrated in the high-density transmitter trials. This multi-channel system also has advantages over other single-channel aerial VHF tracking systems (Körner et al. 2010, Dos Santos et al. 2014, Webber et al. 2017) that require either a separate flight per transmitter frequency, or a scanning receiver to listen for each frequency sequentially. Wildlife transmitters commonly beep at 30 or 40 pulses per minute. For a single-channel receiver conducting a scan, ideally each frequency should be monitored for 2–3 cycles (4–6 sec) to maximise the chances of detecting a weak signal (Kenward 2001). Therefore, a scan of 50 frequencies could take 5 minutes to complete. If the receiver does not remain stationary during this time, it introduces the possibility of signals being missed depending on the number of frequencies to scan, the time spent listening for each, and the speed of travel. Scanning 50 transmitter frequencies using a single-channel receiver means each frequency is monitored only ~2% of the time. Hence, the multi-channel receiver used in the study offers a considerable advantage because dynamic searching is possible, and each frequency is monitored 100% of the time.

Recording signal strength 'heat maps' of the area avoids the need for a UAV to deviate from its flight path to triangulate, perform direction-finding, or follow individual signals, meaning the search speed can be much quicker. This ability to conduct quick and efficient search flights allows for regular monitoring of search areas, and collecting data files of signal strength allow analysis of position data in different times and locations, and comparisons between different surveys. With penguins, ongoing daily surveys could, therefore, provide data on foraging trip duration and nest attendance, without needing to visit nests in person.

Location accuracy provided by the Drone Ranger system is dependent on the separation between flight lines. A 30 m separation provided an average position accuracy of 11 m from the actual location. This accuracy was sufficient for a ground team to locate the nest (with assistance from a hand-held VHF receiver if needed). Yellow-eyed penguins are known to defend an area up to 20 m around their nest (Marchant and Higgins 1990); therefore, this accuracy provided an acceptable measure defining the location of each breeding territory. Position accuracy can be improved if the UAV flight line is closer to the nest location, so judicious placement of flight lines over likely habitat could improve position accuracy. Flying a search pattern with a smaller separation between flight lines would also improve position accuracy, with the trade-off of reducing the size of the area that can be covered per flight. If a purely aerial solution was desired, position information could be determined solely by aerial tracking and examination of the data in a GIS, saving time and effort by eliminating ground searching all together. Additional post-processing techniques may improve accuracy further (Appendix 2). A 'coarse acquisition' flight could also be conducted first using flight lines up to 1000 m apart (see Appendix 2), followed by a more accurate flight (e.g., using a 5 m separation) to map, in more detail, those areas identified by the first flight.

The current drone platform provides around ~10–15 min flight time, and a range of ~2–3 km per flight. This was sufficient for monitoring each ~150,000 m^2 penguin breeding area, and with multiple batteries, several neighbouring areas could be searched at a time. The use of different drone platforms would convey different advantages. For example, a small multi-copter was selected for this project because it is cost-effective, compact and light enough to be carried in a backpack, can be operated by one person, and its quick assembly and vertical take-off and landing proved useful operating from forests and other areas where access is difficult. Using a larger drone platform (multi-rotor or fixed-wing) would provide greater range and flight time, and would also offer increased payload capacity for additional sensors (such as a camera) with less effect on flight performance. For example, large fixed-wing UAVs are capable of conducting missions over 900 km and nearly 9 h flight time (Goetzendorf-Grabowski and Rodzewicz 2016).

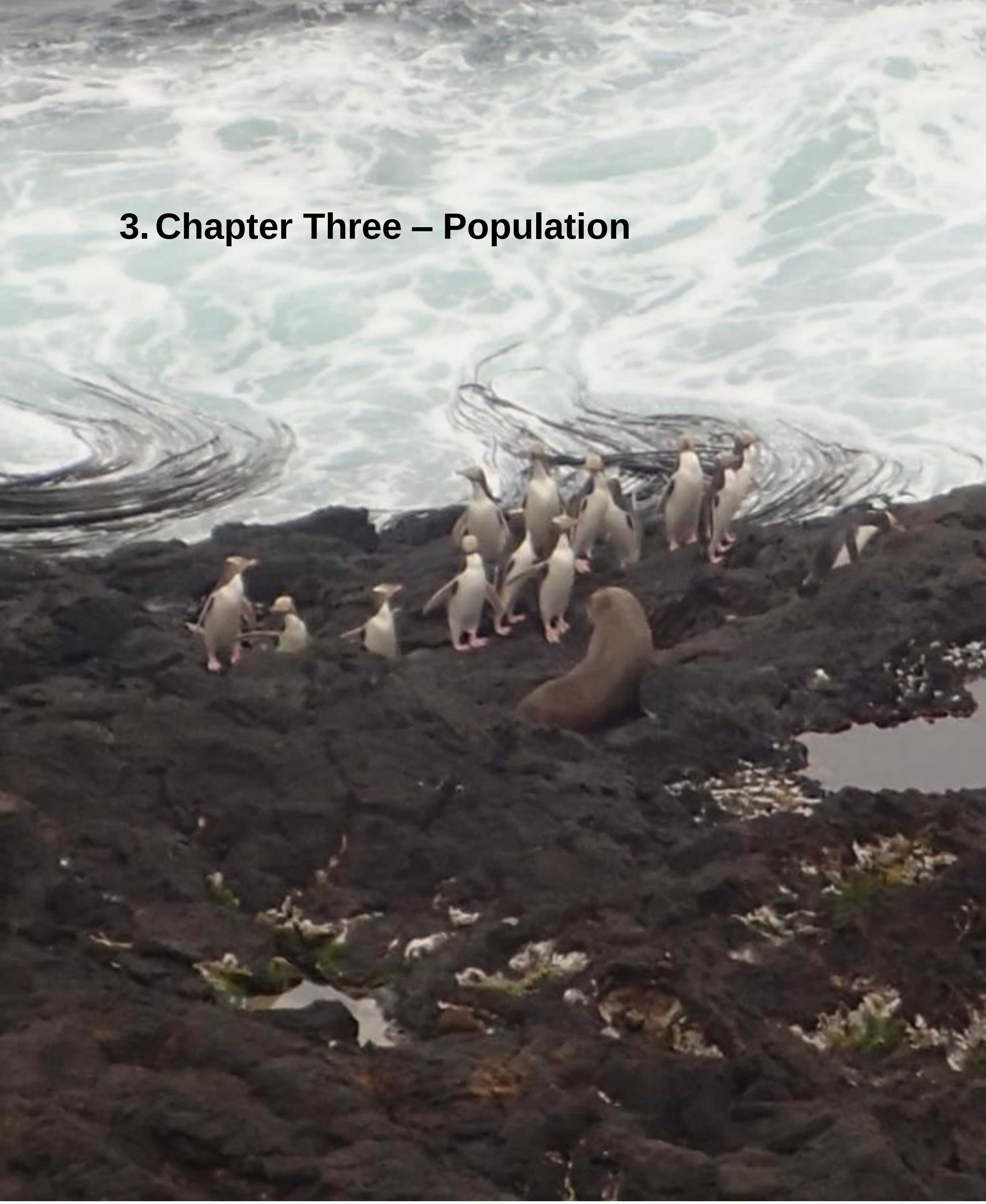
One possible drawback of UAVs is the potential to disturb wildlife. Disturbance effects have been shown to vary depending on the species and technology involved, as well as the type of approach (Hodgson and Koh 2016, Mulero-Pázmány et al. 2017). The use of UAVs to survey wildlife may actually reduce disturbance for some species (Borrelle and Fletcher 2017), although this should be investigated for each experimental situation. Higher altitude flights could increase the coverage area on the ground but will also increase exposure to greater wind strength, whereas lower altitudes could increase the risk of disturbing wildlife. Studies have shown increasing levels of disturbance on breeding Adélie penguins (nesting in the open) from a large octocoptor UAV flying at altitudes below 30 m (Rümmler et al. 2016). Our smaller drone screened by canopy and flying at altitudes above 30 m generated minimal disturbance to nesting yellow-eyed penguins (C. G. Muller, unpubl. data), providing a useful option if regular monitoring was needed, particularly because yellow-eyed penguins are sensitive to human approach (French et al. 2019). Increasing the flight spacing would increase the average horizontal distance between the UAV and target animal, which would further reduce disturbance. Depending on the species and its reaction to human disturbance, a UAV flight over the study area may generate much less investigator disturbance than either an aircraft, or a close approach by a ground team. For cryptic species, which can be difficult to see, visual location by a ground team may result in significant disturbance to the animal (Chabot and Bird 2015), and long-term exposure to such stressors can increase stress responses and reduce individual condition and reproductive output. The Drone Ranger allowed nests to be pinpointed quickly and with minimal disturbance to habitat or other nesting birds, although study animals first needed to be caught to have a transmitter attached. Because penguins were caught at access points to the sea, tracking data also allowed a nest to be immediately linked with an access point, data that were unavailable if a nest was found by manual searching (where further investigation was required to determine which access point was used by birds from that nest).

2.5.1 Applications

One common difficulty with VHF tracking is animals that may travel further than the detection range of their transmitter. The usual solution is to drive or fly large search patterns using a helicopter or fixed-wing aircraft, to attempt to detect the signal (Mech and Barber 2002). However, the cost of using aircraft can be prohibitively expensive, and may not be practical given the habitat. Cost has been cited as the main reason why aerial tracking is not as frequently used as ground tracking (Seddon and Maloney 2004). The Drone Ranger system offers a lower-cost alternative for aerial tracking. It also offers a useful alternative to GPS or satellite tracking (see Appendix 2).

Over 60% of the yellow-eyed penguin population are found in the subantarctic where conditions make research difficult (Couch-Lewis et al. 2016), and because of these difficulties, no comprehensive population survey has been conducted in the Auckland Islands since the late 1980s (Moore 1990). Aerial tracking, therefore, offers a useful tool for population counts in difficult terrain. The Drone Ranger would be useful for tracking a wide range of species, particularly where ground VHF tracking is already employed. It is especially advantageous when used over distances or terrain where a ground search would be difficult, as well as for tracking and monitoring cryptic species where visual or thermal imagery is not suitable, in particular, animals that may only be accessible in a part of their range, life cycle, or due to daily or seasonal movements. Uses for the technology can include locating nest or den sites, conducting presence/absence surveys in an area, tracking movement or dispersal, and monitoring study animals remotely.

This technology is not limited to wildlife applications and could be used to locate radio signals in a variety of scenarios, particularly where visual or thermal imagery is blocked by terrain. For example, in New Zealand, some dementia sufferers prone to wandering already carry VHF transmitters and these signals could be tracked from the air. The system could also track cell phone signals to locate trapped persons in a disaster zone.



3. Chapter Three – Population

DRC 16

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STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the candidate and the candidate's Primary Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of candidate:	Chris Muller
Name/title of Primary Supervisor:	Louise Chilvers

In which chapter is the manuscript /published work: 3

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Chris Muller conceived and designed the experiments, carried out the fieldwork, analysed the data, and wrote the paper.

○ It is intended that the manuscript will be published, but it has not yet been submitted to a journal

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Date:	14-Jun-2022
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DRC 19/09/10

Note that the values presented in this chapter for the proportion of breeders (Table 3.6, last column) and estimated number of breeders (Table 3.4, last column) are slightly modified from the published paper, with the inclusion of an individual camera correction factor for the trail camera data. The graphs are unchanged.

Population estimate for yellow-eyed penguins (*Megadyptes antipodes*) in the subantarctic Auckland Islands, New Zealand

Muller, C. G., Chilvers, B. L., French, R. K., Hiscock, J. A., and Battley, P. F. (2020) Population estimate for yellow-eyed penguins (*Megadyptes antipodes*) in the subantarctic Auckland Islands, New Zealand. Notornis, 67(1):299–319.

3.1 Abstract

Accurate long-term monitoring of a threatened species' population size and trend is important for conservation management. The endangered yellow-eyed penguin (*Megadyptes antipodes*) is a non-colonial breeder. Population monitoring of the southern population has focused on beach counts rather than nesting birds. Here, we combined intensive nest-searching and counts of transiting penguins on Enderby Island, Auckland Islands, over 3 years to establish the relationship between count numbers and breeding birds. Morning beach counts of transiting penguins were extrapolated to estimate breeding population for the entire Auckland Island group from 2012 to 2017. Breeding numbers varied considerably between years, but overall did not appear to be declining in the short term. Breeding birds at the Auckland Islands averaged 577 pairs annually over the three ground-truthed breeding seasons, similar to the lower estimate of 520–680 pairs from the last survey in 1989, but less than the higher estimate of 650–1,009 pairs generated from that survey. Direct comparison of beach counts indicated a large decline, but these may be more prone to uncertainty. Large variations between years indicated variable breeding effort. The Auckland Islands (particularly Enderby Island) represent 37–49% of the total breeding population for yellow-eyed penguins, indicating the importance of the southern population for the species. We recommend ongoing monitoring,

including mark-recapture methods, for future population estimates. At least 50% of the individuals in an area should be marked to reduce confidence intervals of estimates.

3.2 Introduction

Accurate long-term monitoring of a breeding population is important to determine population trends and the effectiveness of conservation-management measures. Monitoring population numbers can reveal a species' resilience to threats (such as predation, mortality, disease, response to climate change, and effects on food supply), determine likelihood of decline, and help inform and measure management decisions (Purvis et al. 2000, Witmer 2005, Lindenmayer and Likens 2009). Population estimates for colonial-breeding seabird species are typically achieved using colony counts (Hutchinson 1980, Trathan 2004, Baker et al. 2017). These methods are used to survey colonial-breeding penguin species (Woehler and Croxall 1997), including western rockhopper (*Eudyptes chrysocome*) in the Falkland Islands (Baylis et al. 2013), and erect-crested penguins (*E. sclateri*) and eastern rockhopper penguins (*E. filholi*) in the New Zealand subantarctic (Hiscock and Chilvers 2014). The endangered yellow-eyed penguin (hoiho, *Megadyptes antipodes*, Figure 3.1) is endemic to New Zealand (Gill et al. 2010).

Figure 3.1 Adult yellow-eyed penguin on a nest in rātā and *Dracophyllum* forest on Enderby Island. *Image: Chris Muller*

It is highly restricted in distribution, found only in the south-east of the South Island/Te Waipounamu, Stewart Island/Rakiura and adjacent islands, and the subantarctic Auckland Islands/Motu Maha and Campbell Island/Motu Ihupuku (Figure 3.2A).

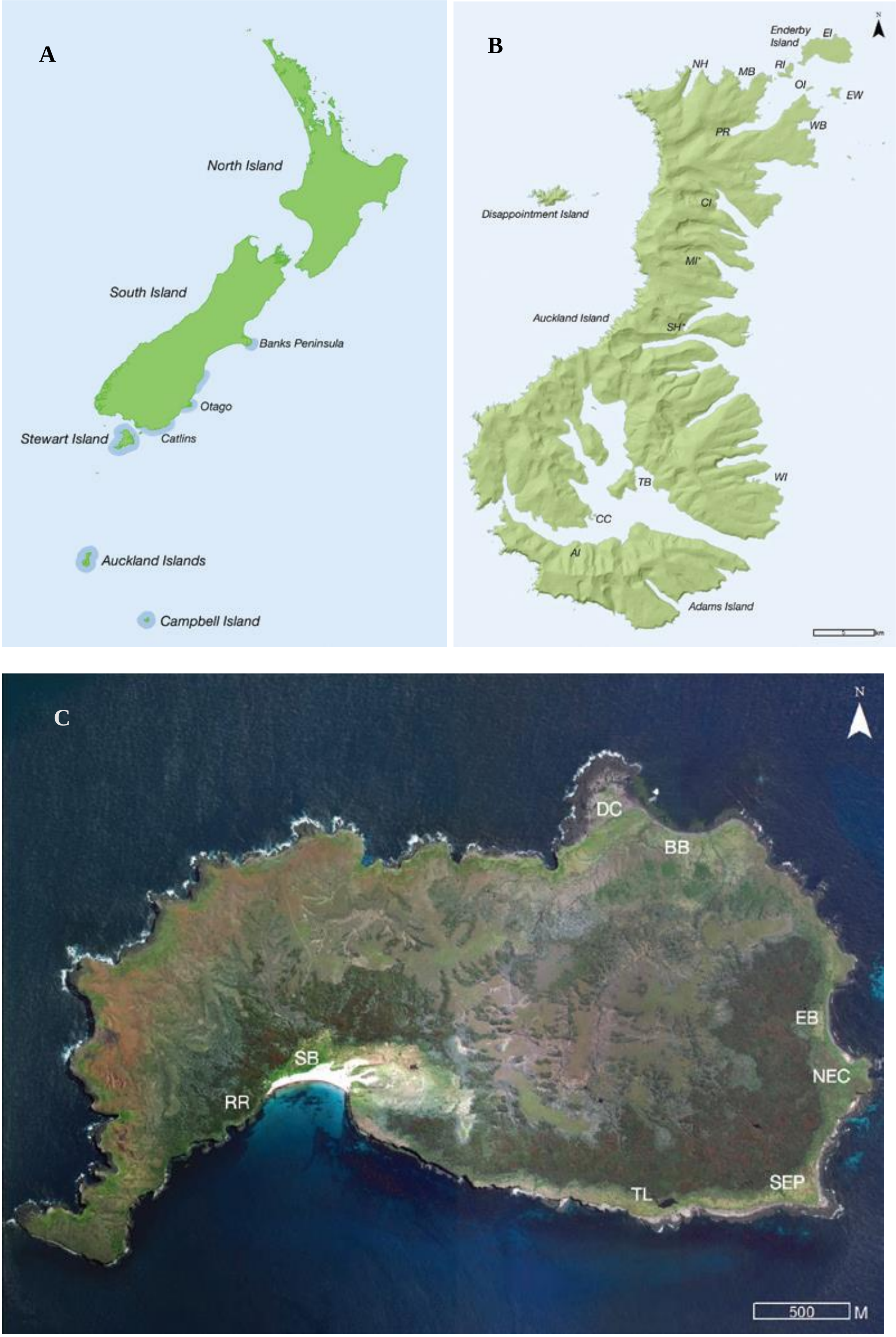

A
North Island
South Island
Banks Peninsula
Otago
Stewart Island
Catlins
Auckland Islands
Campbell Island
B
Enderby Island
EI
NH
MB
RI
OI
EW
PR
WB
Disappointment Island
CI
MI
Auckland Island
SH
TB
WI
CC
AI
Adams Island
C
N
DC
BB
EB
SB
RR
NEC
TL
SEP
500 M

Figure 3.2 A). Location of yellow-eyed penguin breeding areas, including mainland New Zealand (primarily Otago and Catlins coast), Stewart Island (and outlying islands), and the subantarctic Campbell and Auckland Islands. **B)**. Enlargement of the Auckland Islands archipelago, with observation sites listed from north to south: EI Enderby Island, RI Rose Island, MB Matheson Bay, NH North Harbour, OI Ocean Is, EW Ewing Island, PR Port Ross, WB Webling Bay, CI Chambres Inlet, MI Musgrave Inlet*, SH Smith Harbour*, WI Waterfall Inlet, TB Tagua Bay, CC Camp Cove, AI Adams Island. Sites marked with an asterisk (*) have been reported as possible sites of penguin activity (Beer 2010) but were not included in this survey. **C)**. Enlargement of Enderby Island, with observation sites listed clockwise from the south-west: RR Rocky Ramp, DC Derry Castle, BB Bones Bay, EB East Bay, NEC North-east Cape, SEP South-east Point, TL Teal Lake, SB Sandy Bay

Extant yellow-eyed penguins recolonised mainland New Zealand from the subantarctic after the mainland species (*M. waitaha*) became extinct (Boessenkool et al. 2009a, Collins et al. 2014), and there is currently less than 2% migration between the northern and southern populations, meaning that these areas are identified as separate populations (Boessenkool et al. 2009b). The subantarctic breeding areas are an important stronghold, previously representing over 60% of the total population (Ellenberg and Mattern 2012). Despite this importance, the last population estimate for the Auckland Islands was in 1989 (Moore 1990). There is therefore a vital need to collect accurate and up-to-date population information for this area (Ellenberg and Mattern 2012). Concurrently, the Otago (Figure 3.2A) portion of the mainland New Zealand yellow-eyed penguin population is undergoing a serious decline due to successive poor breeding seasons and ongoing high adult mortality (Couch-Lewis et al. 2016), making the need for a survey of the southern population even more important.

Yellow-eyed penguins breed in the austral spring and summer, laying one or two eggs in late-Sep. Chicks hatch in the subantarctic in late-November and fledge in March (Moore 1992a). Yellow-eyed penguins do not form colonies but nest in loose aggregations within coastal forest and scrub, with each breeding area associated with one or more access points to the sea. They prefer to nest out of sight of neighbouring birds, and nests are an average of 12–32 m and up to 78 m apart (Seddon and Davis 1989). The nests furthest from the sea may be up to 1 km inland, making them difficult to find (Darby et al. 1990). Direct colony counts are not possible for yellow-eyed penguins, and nesting birds must be individually located. Ground searching is the main method of nest location around mainland New Zealand (Hegg et al. 2012), often requiring multiple search teams (but with a mean of 16 or fewer nests per breeding area) (Seddon and Davis 1989).

The Auckland Islands (50°44’S, 166°05’E, Figure 3.2B) are located 465 km south of New Zealand’s South Island. The main Auckland Island (45,889 ha) has three non-native mammalian predators: mice (*Mus musculus*), cats (*Felis catus*), and pigs (*Sus scrofa*) – with the latter two suspected of depredating yellow-eyed penguins and nests (Challies 1975, Moore 1990). Isolation and distance make the islands difficult and expensive to access, and large search teams are impractical. In the Auckland Islands, yellow-eyed penguins usually nest in thick coastal vegetation. This may include rātā forests, *Veronica elliptica* bushes, and *Myrsine* divaricating shrubs, which can form almost impenetrable thickets (Godley 1965, Taylor 1971, Peat et al. 2006). The large area, combined with poor weather and terrain, make the New Zealand subantarctic islands a difficult environment in which to survey yellow-eyed penguins, and they can be reliably observed only when they are transiting from the forest to the sea, or vice versa.

Due to the difficulties of surveying in this environment, the manual ground-search method used for locating yellow-eyed penguin nests on mainland New Zealand is less practical in the subantarctic (see Chapter 1). Previous population surveys in the subantarctic have primarily utilised morning and evening beach counts of transiting penguins (Moore 1990, Moore 1992a, Moore 1992b), and more recent count data have been collected at selected locations around the Auckland Islands (Beer 2010) and Enderby Island (Young 2009, Houston and Thomson 2013, Chilvers 2014). Houston and Thomson (2013) attempted validation of morning count data using remote cameras (still and video) combined with nest searches in a representative breeding area on Enderby Island (Rocky Ramp). However, this study was limited by a very short field season (7 days) to search for nests, resulting in only 25 active nests being found, and providing limited confidence that all nests were located. The authors also documented the limited success of the cameras, with battery life and detection issues a problem, especially at night. Results of this study identified that more comprehensive research is required, including improved technology.

There have been no comprehensive population surveys encompassing the wider Auckland Islands area since 1989, nor an accurate measure of the relationship between recent morning counts and breeding numbers. Moore carried out beach counts and population surveys on Campbell Island (Moore and Moffat 1991, Moore 1992b, Moore 1992a, Moore et al. 2001), including determining the number of banded nesting birds sighted during beach counts, a relationship that was used as part of an Auckland Islands population estimate. Moore (1990) carried out count surveys from October–December, when breeding adults were incubating eggs or brooding young chicks, and so had a regular and predictable foraging schedule. Since each site around the Auckland Islands was counted on a different day, there was the possibility that daily variability in penguin numbers heading to sea may have been influenced by weather, sea conditions, and other factors, although this has not been measured. In addition, beach count data represent an unknown proportion of the total population, and since most yellow-eyed penguins remain in the same area year-round (Richdale 1957, Darby et al. 1990), the beach counts will also include an unknown proportion of non-breeding adults. Therefore, this method does not give a reliable breeding population estimate and can provide only an approximate indication of population trends (Chilvers 2014). To generate a reliable breeding population estimate, the survey must include direct counts of nests in at least one site (hereafter referred to as ground-truthing). The previous Auckland Islands survey by Moore (1990) used morning and evening counts with a correction factor from a previous ground-truthing survey on Campbell Island. This derived a relationship between morning count numbers and a known number of banded individuals to determine the proportion of the population sighted during counts (Moore 1992b), and also the relationship to nest numbers (Moore 1992a). From this, and an assumption that 60–70% of the population were breeders, 520–680 breeding pairs were estimated in the Auckland Islands in 1989, with the majority of these (260–360 pairs) estimated on Enderby Island (Moore 1990, Moore 1992b); (Figure 3.2A, B). However, this probably underestimated breeding numbers, since the Campbell Island estimate of 490–600 pairs in 1988 (Moore 1992b) was re-evaluated as 610–890 pairs based on mark recapture analysis (Moore *et al*. 2001).

The aims of this research were to: (1) determine relationships between the proportion of the yellow-eyed penguin population sighted in morning beach counts and the number of breeding adults; (2) estimate the number of breeders on Enderby Island and the total breeding population for the Auckland Islands; and (3) determine the ratio of breeders to non-breeders on Enderby Island, and estimate the total population for the Auckland Islands.

3.3 Methods

We surveyed the population of yellow-eyed penguins at the Auckland Islands (Figure 3.2A) by using morning beach counts of penguins transiting to the sea at sites around the archipelago identified in previous publications (Table S3.1). A population estimate was generated from the count data by using the proportion of the total population likely to have been seen in these counts. This proportion was estimated by conducting a detailed population study of one representative population, including a complete census of breeding birds at that site.

3.3.1 Beach counts

Morning beach counts on Enderby Island (50°30’S, 166°17’E, Figure 3.2A, B) were conducted in November during three breeding seasons (2015–17) in conjunction with ground-truthing to identify breeding parameters, as well as three prior seasons with no ground-truthing (2012–14), as per Moore (1990, 1992b). To allow for comparisons between years, survey sites included major sites identified by Moore (1990) (Table 3.1, Figure 3.2B, C). Estimates were made for sites not visited for logistical reasons (e.g., Ewing Island, Ocean Island, and Matheson Bay) (Table 3.1). It would have been ideal to repeat counts at all previously identified sites; however, for sites that were not surveyed in a given year, an estimate was made based on the average proportion of the total count found there in previous years (Table 3.1). Additional sites were identified as access points to the sea by Beer (2010), but with low numbers of birds recorded these were not surveyed for logistical reasons (e.g., Musgrave Inlet and Smith Harbour). Counts for these sites could not be estimated.

Table 3.1 Results from yellow-eyed penguin morning beach counts conducted around the Auckland Islands, listed from north to south. Sites that were not counted in a particular year (shaded and italics) were adjusted for location based on the mean proportion of birds counted at these sites (shown at right), and applied to the total count from sites that were surveyed in that year. Counts from 2012 to 2017 were adjusted for survey time by incorporating a 12% increase to estimate the total morning commute, and to allow comparison with the 1989 survey. Surveyed sites include major sites identified by Moore (1990). Some additional sites identified as access points to the sea by Beer (2010) but with low numbers of birds recorded were not included for logistical reasons. Where no previous counts had been done, counts could not be estimated.

Location	**1989**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**Average**	**Proportion**
Enderby Island (total)	593	361	221	325	246	330	194	324	49.9%
Rose Island	41	28	27	33	34	114	26	43	6.7%
Matheson Bay	43	*34*	*21*	*27*	*25*	*37*	*21*	43	6.6%
North Harbour	88	50	*31*	*40*	54	*55*	*31*	64	9.9%
Ocean Island	2	*2*	*1*	*1*	*1*	*2*	*1*	2	0.3%
Ewing Island	61	*48*	*30*	*38*	*35*	*53*	*29*	61	9.4%
Terror/Erebus Cove (Port Ross)	13	*5*	*3*	*4*	3	*5*	3	6	1.0%
Webling Bay	26	*10*	*6*	*8*	5	16	4	13	2.0%
Chambres Inlet	*48*	*26*	*16*	*21*	4	67	29	33	5.1%
Waterfall Inlet	*34*	50	15	6	15	21	35	24	3.6%
Tagua Bay (Carnley Harbour)	3	*2*	*1*	*2*	*2*	*3*	*1*	3	0.5%
Camp Cove (Carnley Harbour)	*0*	*0*	*0*	*0*	0	*0*	1	0	0.0%
Adams Island	64	23	54	42	13	13	18	32	5.0%
Total – Raw counts	**934**	**512**	**317**	**406**	**374**	**561**	**310**	**649**	**100%**
Total – Adjusted for location	**1016**	**639**	**427**	**547**	**437**	**716**	**393**		
Total – Adjusted for survey time	1016	716	478	613	489	802	440		

Moore (1990) found that the main peak of morning penguin departures in early- to mid-November occurred during 0500–0800 h NZST, but local sunrise was earlier and the peak of morning transit activity shifted to 0430–0700 h in late-November, and to 0400–0700 h in December. It would have been ideal to repeat this methodology to ensure that count data were directly comparable between studies; however, during the 6 years of data collection for this study, morning counts sometimes commenced at different times at some sites, due to weather and other factors. To ensure that the counts were comparable between different sites and years within this study, the count data were analysed over a standardised time period using the latest recorded start time (0530–0900 h). However, this means that morning count numbers will be an underestimate of the total morning activity peak, and should not be directly compared with counts collected using a different time period – an inherent issue with beach count data. Transit data from an automated microchip reader (see section on electronic monitoring below for details) indicated that a survey covering the 0530–0900 h time period would include around 89% of the peak morning transit numbers in the incubation phase. Count numbers were therefore increased by a 12% correction factor to make them comparable with counts from Moore (1990), which started at first light. However, due to the inherent issues with using beach counts as reliable indicators of population trends, comparison of population estimates is expected to be more accurate.

During 2015–17, morning count data from the Rocky Ramp (Enderby Island) reference population were collected every day for the duration of the survey undertaken elsewhere on the Auckland Islands, in order to measure daily variation in transiting penguin numbers (Figure 3.3).

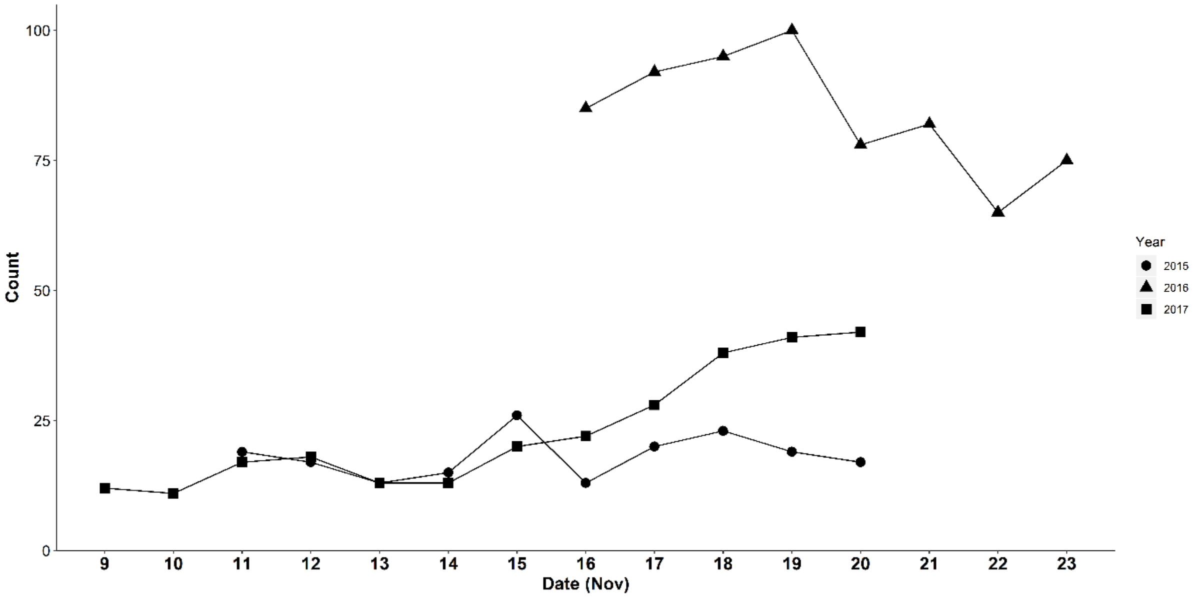


Figure 3.3 Number of adult yellow-eyed penguins counted during morning counts at Rocky Ramp (RR), 9–23 November, over three seasons (2015–17). The x-axis shows the date (in November) each year when counts were made.

3.3.2 Reference population and ground-truthing

Ground-truthing field work was carried out on Enderby Island (Figure 3.2B) for three breeding seasons: 2015 (November 2015–February 2016), 2016 (November 2016– February 2017), and 2017 (November 2017–January 2018). A detailed population study of a reference population of breeding penguins was conducted at Rocky Ramp (Figure 3.2C), including locating nests and identifying breeding and juvenile birds. These data were used to determine the proportion of the reference population seen during each morning count, as well as the proportion of breeders sighted. This correction factor for the morning counts was used to extrapolate a population estimate for the entire Auckland Islands archipelago.

3.3.3 Marking of birds

During 2015–17, all adult penguins using the landing site, nesting, or loafing in forest inland of Rocky Ramp were fitted with a 23 mm, TIRIS compatible, ISO standard Passive Integrated Transponder (PIT) microchip, (Allflex, Palmerston North, New Zealand). Penguins were captured by hand as they returned to the island in the evening following a foraging trip at sea. Microchips were injected subcutaneously at the back of the neck, as per Department of Conservation (DOC) protocol (Department of Conservation 2012). Microchipped penguins were also given a temporary individual mark on the chest using a Tag Pen stock marking pen (Allflex, Palmerston North, New Zealand) to allow visual recognition.

3.3.4 Nest searches

Nest searches were carried out over a 2-month period (November–January) to locate all the nests in the reference population at Rocky Ramp. This approximately 15 ha area was defined by the edge of the habitat (vegetation suitable for nesting) on its western and northern boundaries. The eastern boundary transitioned into the neighbouring breeding area (Sandy Bay), and there was some overlap of nests. The access point to the sea used by each breeding bird (and therefore the Rocky Ramp breeding population) was confirmed by electronic monitoring at the Rocky Ramp access point. Nest searches utilised a variety of methods, including ground-searching (Hegg et al. 2012), and very high frequency (VHF) radio-tracking using transmitters attached to penguins, which significantly improved search efficiency. VHF tracking was carried out on foot and using a VHF-equipped drone, methods as per Muller et al. (2019); see Chapter 2. Ground-search teams used a handheld GPS (Garmin, USA) to record nest locations. GPS trail data of searchers' movements were analysed using mapping software (Garmin Mapsource and ESRI ArcGIS) to ensure that all likely breeding habitat in the reference population area was checked. Based on coverage of the area, and since both the cumulative number of nests located and the number of identified breeding birds reached an asymptote by the end of the season, we were confident that all nests in the area were located.

3.3.5 Electronic monitoring

Access to the sea from the Rocky Ramp area is via a narrow path down a cliff, allowing electronic monitoring of microchipped penguins and visual monitoring of all birds travelling to and from the landing site. A custom-built automatic PIT microchip reader (the ‘autologger’) was constructed from an ASR700 high-power reader (Agrident, Barsinghausen, Germany) and a modified radio frequency identification (RFID) logger (DOC Electronics, Wellington), and was used to record the identities of microchipped penguins passing by. The circular antenna, with a diameter of approximately 1.5 m, was oriented horizontally and spanned the path so that all transiting penguins would walk over it. Using the autologger, a continuous record of all transiting penguins was collected at the Rocky Ramp access point to the sea, from November 2016 to February 2017 (n = 94 days). To determine daily movement patterns, transit times were analysed (using a Python 3.5.2 script, www.python.org) by dividing the time of day into 10-min intervals, then determining the mean number of microchipped birds passing by during each time interval for each of the three main breeding phases:

- Incubation phase was defined from 17 November (the start of electronic monitoring) until 27 November (the mean hatch date for the reference area, determined by nest checks) (n = 11 days).
- Guard phase was defined from 28 November (the day after mean hatch date for the reference area) until 31 December (the estimated date when half the nests in the reference area showed evidence of non-continuous parental attendance, determined by nest visits) (n = 34 days).

- Post-guard phase was defined from 1 January 2017 (the day after mean non-continuous parental attendance) until 18 February (the end date of monitoring) (n = 49 days).

A Panoramic 150i or 180i game trail camera (Moultrie, USA) was set up with a field of view covering a section of the penguin trail adjacent to the autologger, to record a panoramic photo of transiting birds. The camera had three independent infrared movement sensors; movement detected by any one of these as a penguin walked past would trigger a panoramic photograph, increasing the reliability of detections. Panoramic photos also allowed a single camera to record the chest area (where temporary marks were applied) of both arriving and departing birds. The camera and autologger were both powered from a 12 V battery and solar panel, and so could run continuously during the study.

A trial of morning beach count methods was conducted simultaneously at Rocky Ramp using a human observer, plus counts generated from the trail camera and autologger, to compare accuracy between the methods. Trials were conducted at the beginning of each season in 2015 (n = 8 counts), 2016, and 2017 (n = 3 counts each). Comparison data were analysed as part of the population estimate.

3.3.6 Population estimate

A population estimate was determined for the Rocky Ramp reference population using a mark-recapture method. This was conducted on a single day between 19 and 22 November each year, so that results would be comparable with the November counts elsewhere on the Auckland Islands. During the week prior to the survey date, birds were caught and marked with a microchip. The sample size increased each year, as birds marked the previous year that had returned to the area were included in the marked sample the following year. Marked birds were ‘resighted’ using the automatic PIT microchip reader (autologger). Counts used for the mark-recapture were independent of the morning beach count surveys, and so were taken at 0500–

0900 h, when the majority of birds were heading to sea (Figure 3.4; and Moore (1990)), and to minimise the likelihood of double-counting birds if they returned later the same day.

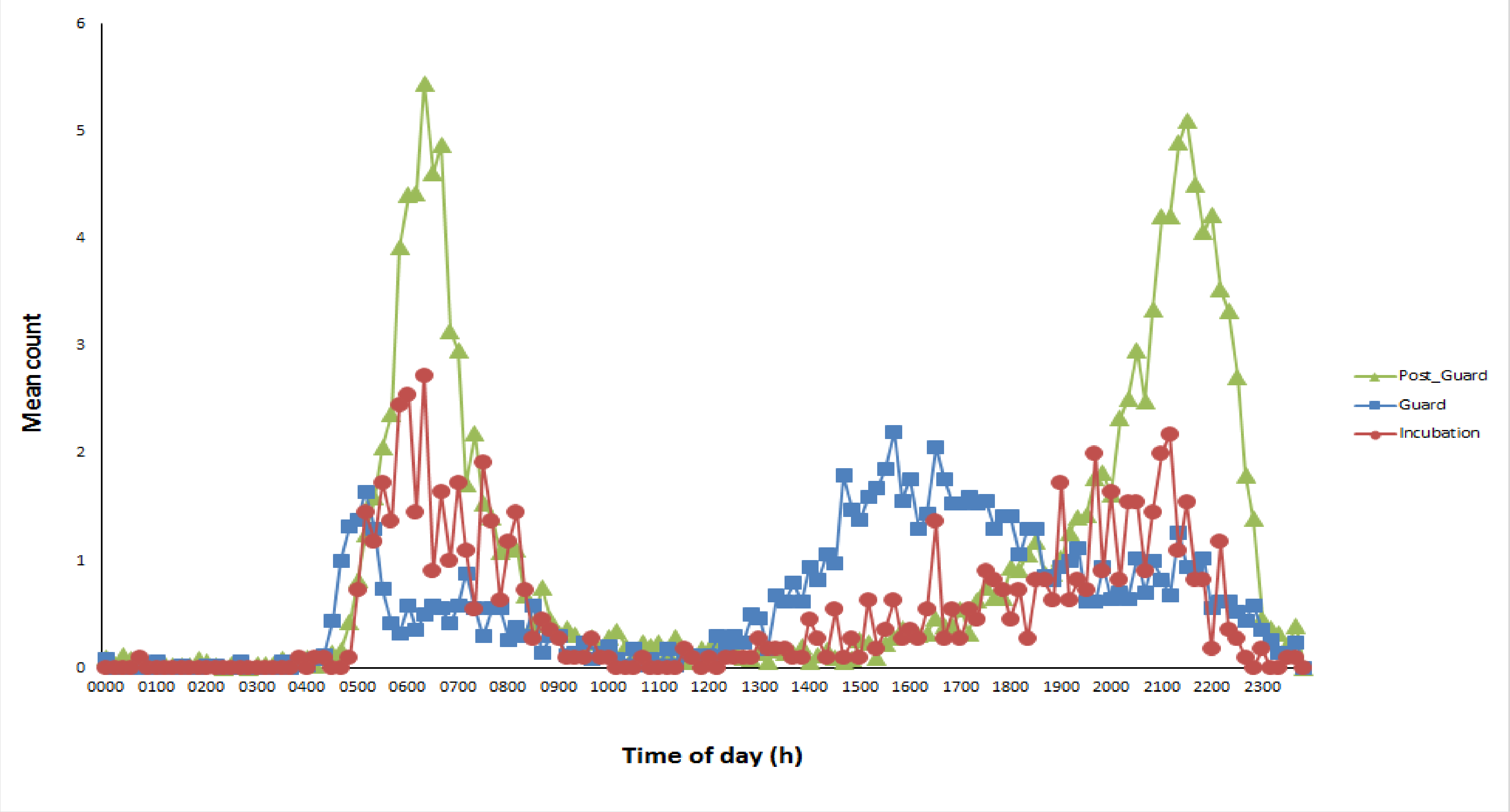


Figure 3.4 Daily activity patterns of nesting yellow-eyed penguins (2016-17 season) transiting to and from the sea during each breeding phase: Incubation (red circles), Guard (blue squares), and Post-guard (green triangles). Data were collected as microchipped birds passed by an automated reader, and represent the mean number of transits counted during each 10-min time block throughout the day, averaged per phase; Incubation (n = 11 days), Guard (n = 34 days), and Post-guard (n = 49 days).

For the same time period, the total number of birds (marked and unmarked) was counted using photographs from the trail camera located adjacent to the autologger. Occasionally the species could not be identified from a photograph (particularly at night), and in some cases penguins did not always trigger the camera, although cameras with multiple sensors gave better results. Comparison with counts made by a human observer for a trial period at the beginning of each season demonstrated that detection rates for camera counts were 71% (with 150i single-sensor camera) in 2015, and 95% and 96% (both with 180i triple-sensor camera), respectively, in 2016 and 2017. A correction factor for the trail camera counts was determined from these data.

A Lincoln-Peterson index using the Chapman equation was used to estimate the total number of birds ($\widehat{N}$) in the Rocky Ramp reference population by using the equation:

$$\widehat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

Where n_1 = number of microchipped birds when the mark-recapture was undertaken, m_2 = number of microchipped birds recorded on the autologger, and n_2 = total number of birds counted on the trail camera. The Chapman equation was used since it is less biased at lower samples sizes than other methods (such as the Lincoln-Peterson; Chapman (1951)). The variance and confidence interval were also calculated using methods described by Chapman (1951).

The population estimate for the reference population was then extrapolated to generate a population estimate for the Auckland Islands. This was determined by using the ratio of birds seen during morning counts (on the same day as the mark-recapture estimate) compared with the total population estimate for the reference population, and applying the same ratio to the total number of birds seen during morning counts around the Auckland Islands. Minimum and maximum estimates were derived using the corresponding values for the reference population from the mark-recapture study.

Morning count data during 2012–14 could not be extrapolated using the same method, since no ground-truth data were collected during these years. Therefore, the average ratio of morning counts to total population estimates was determined for 2015–17 and applied to the 2012–14 count data. The confidence interval for these years was estimated using the largest error (from 2015) to reflect the presumed much larger uncertainty associated with this method. A retrospective population estimate was not possible for counts collected in 2009 by Beer (2010), as methods and sites differed from those of our survey.

3.3.7 Proportion of breeders

For conservation management purposes, it is important to know the number of breeders, as they represent the ability of a population to reproduce and produce future generations (Baasch et al. 2015). All birds caught at the Rocky Ramp reference population were microchipped, and when a nest was located it was revisited until both partners were scanned on the nest and thereby identified as breeders. All microchipped birds located loafing in the forest and/or never found on a nest during nest searches were assumed to be non-breeders. The Rocky Ramp breeding population was confirmed using electronic monitoring, as described in the section on nest searches, above.

Mean daily detection rates for breeding birds recorded on the autologger were determined by averaging the number of detections per day for all known breeding birds from the Rocky Ramp reference population. The proportion of breeders was calculated based on the average number of breeders detected by the autologger, compared with the total number of birds detected by the trail camera per day during the same period. The estimated proportion of breeders was then applied to data from other surveyed sites around the Auckland Islands to determine the total breeding population (assuming that the proportion of breeders was similar across all sites).

3.4 Results

3.4.1 Electronic monitoring

Analysis of the mean number of microchip detections recorded by the autologger during 10-minute intervals throughout the day identified morning and evening peaks in transiting activity during the incubation phase (Figure 3.4). During the guard phase the morning activity peak was smaller and occurred earlier in the morning, whereas during the post-guard phase both morning and evening activity peaks were much larger.

Analysis of the number of microchip detections during the incubation phase indicated that a count period of 0530–0900 h included 89% of the transits recorded during a count period of 0430–0900 h.

3.4.2 Morning counts

A generalised linear model showed that counts at Rocky Ramp in 2016 were significantly higher than the other two years (Figure 3.3, Z = 18.30 and 18.15, $P < 0.01$). There was a smaller difference in counts between 2015 and 2017, but this was still significant (Z = –2.41, $P < 0.02$). The variability between days was more pronounced in 2016 and 2017, as shown by the standard deviations (Table 3.2).

Table 3.2 Mean and standard deviation (sd) of the number of adult yellow-eyed penguins counted during morning counts at the reference site on Enderby Island (Rocky Ramp) over three field seasons. Counts were initially conducted from 0500–0900 h for successive days in 2015 (n = 10 days), 2016 (n = 8 days) and 2017 (n = 12 days). The data shown were re-sampled from 0530–0900 h for comparison with morning beach counts collected around the remainder of the Auckland Islands (Table 3.4).

Year	**Mean**	***SD***
2015	18	3.9
2016	84	10.8
2017	23	11.1

Enderby Island was the largest population centre, accounting for an average of 50% of the total Auckland Islands counts (Table 3.1). Morning count numbers from around the Auckland Islands also varied between years and showed an increase in 2016, similar to that observed on Enderby Island in the same year (Table 3.1). As not all sites were surveyed each year, corrected results incorporate estimates for unsurveyed areas (Figure 3.5).

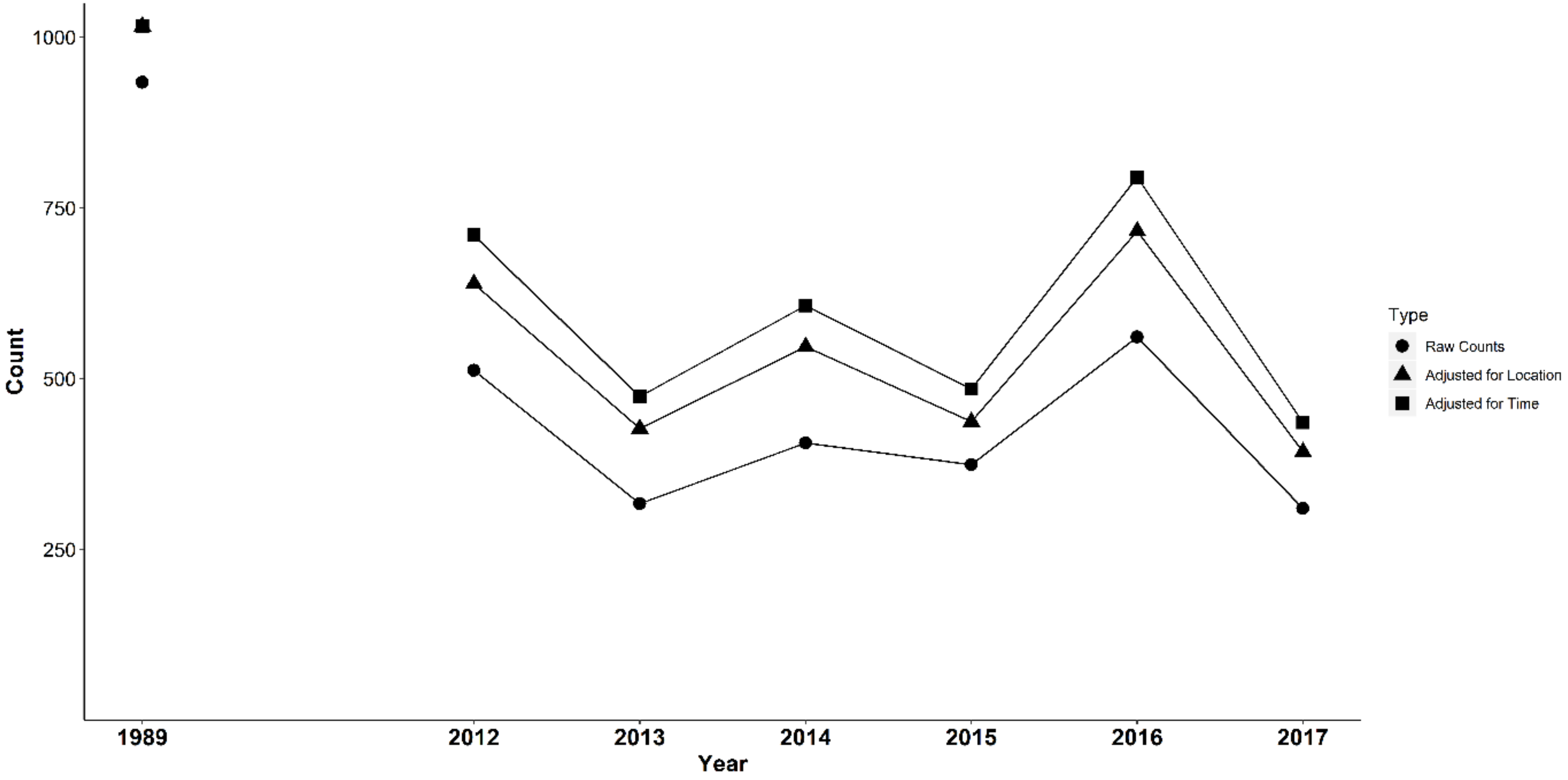


Figure 3.5 Morning count data for yellow-eyed penguins at the Auckland Islands, including total raw counts (circles) that omitted some sites in some years, and adjusted counts including estimates for areas that were missed in a particular year, as per Table 3.1 (triangles), as well as a 12% increase to account for a shorter time period for counts (0530–0900 h) (squares). Totals from Moore's survey in 1989 are shown for reference (Moore 1990). The 1989 counts were made from first light (0430–0900 h) and so should be comparable to the time-adjusted counts, but any direct comparisons between beach counts should be made with caution.

3.4.3 Population and breeding estimates

Population estimates for the reference area (Table 3.3) and the Auckland Islands (Table 3.4) showed a similar trend to the number of nests found in the reference area (Table 3.5).

Table 3.3 Population estimates of yellow-eyed penguins for the reference area on Enderby Island determined using mark-recapture studies. n_1 = number of microchipped birds when the mark-recapture was undertaken (after the first week), m_2 = total number of microchipped birds recorded on the autologger, n_2 = total number of birds counted on the trail camera. The confidence intervals (CIs) are also shown.

Date	Total number chipped (n_1)	Number chipped in count (m_2)	Total counted (n_2)	Reference population estimate	CI
19 Nov 2015	21	4	20	91.4	56.7
22 Nov 2016	101	27	59	217.6	49.5
19 Nov 2017	120	33	39	141.4	15.5

Table 3.4 Population estimates of yellow-eyed penguins for the Auckland Islands determined from the ratio of count to population estimate in the Enderby Island reference area applied to the total count from the Auckland Islands. 'Breeders estimate' was generated using the proportion of breeders from Table 3.6.

Resight date	Reference area count (0530–0900 h)	Reference area est. total	Auckland Is count (adjusted for location) (0530–0900 h)	Akl Is population estimate	Akl Is breeders estimate
19 Nov 2015	19	91	437	2093	963
22 Nov 2016	55	218	716	2838	1504
19 Nov 2017	29	141	393	1911	994

Table 3.5 Number of nests in the reference area (Rocky Ramp). 'Nests identified' values represent the number of active nests during the incubation period when the survey was undertaken. Successful nests included one or more fledged chicks.

Year	Nests identified	Nests successful	Breeding success
2015	51	42	82.4%
2016	69	60	87.0%
2017	51	30	58.8%

Table 3.6 Calculation of the estimated proportion of breeding yellow-eyed penguins in count data during the incubation phase. Total bird numbers were counted using the trail camera, and microchipped breeders were counted using the autologger. 'Daily rate' is the mean number of detections per day for microchipped breeders. (This includes the morning and evening peak commutes to and from the sea. Some birds may have returned on the same day – hence why mean daily detection rates are greater than 1 at certain times, especially in the post-guard breeding phase). The proportion of confirmed breeders out of the number of birds transiting was determined during the post-guard phase (when the maximum number of birds had been microchipped), and used to estimate the proportion of breeders during the incubation phase when morning counts were conducted (but before the majority of breeders had been microchipped).

Year	Daily rate (post guard)	Total breeders (post-guard)	Total birds (post-guard)	Daily rate (incubation)	Total birds (incubation)	Est. proportion of breeders (incubation)
2015-16	0.8	61	74	0.25	29	0.46
2016-17	1.19	132	176	0.73	146	0.53
2017-18	1.49	140	271	0.43	76	0.52

Population estimates varied between years and included a large uncertainty. This uncertainty was more pronounced for counts extrapolated from 2012–14 that were not ground-truthed, and for 2015 where the number of marked birds was lower than subsequent years (Figure 3.6).

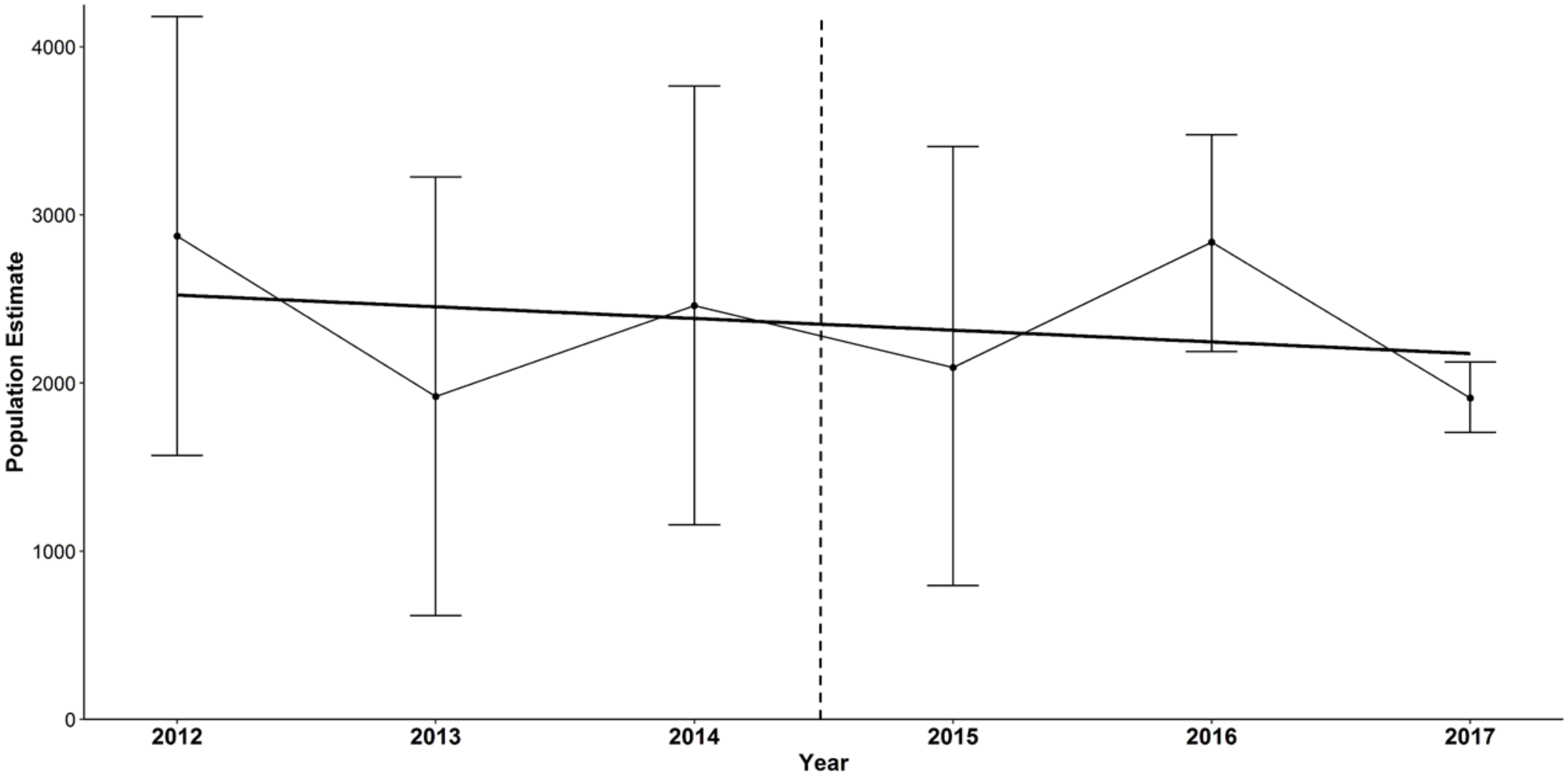


Figure 3.6 Population estimates for yellow-eyed penguins in the Auckland Islands, including error bars and linear regression model. Ground-truthed years (2015–17) are right of the dotted line – estimated from the ratio of birds seen during morning counts of the population in a reference area determined from a mark-recapture study. Also shown are population estimates (2012–14) left of the dotted line – extrapolated from birds seen using data from the ground-truthed years.

The proportion of breeders was estimated for the incubation phase (when morning counts were conducted), based on data collected during the post-guard phase (after microchipping was completed; Table 3.6). The proportion of non-breeders ranged from 0.34 to 0.46 at Enderby Island across the 3 years, averaging 0.42 (sd = 0.06). A lower proportion of breeders was evident in 2015 compared with subsequent years, although numbers of breeders also appeared to fluctuate about a mean (Figure 3.7).

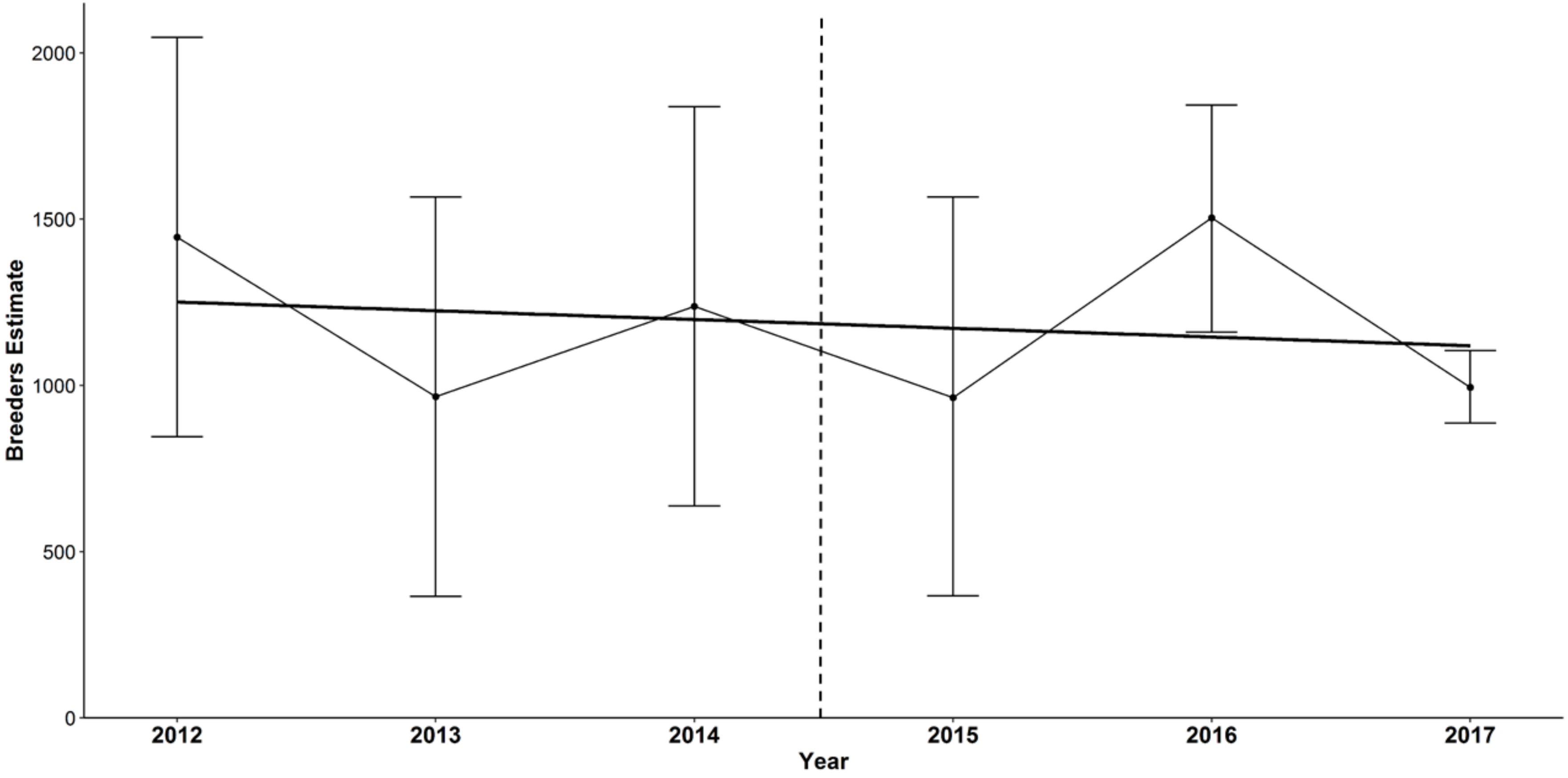


Figure 3.7 Estimate of the number of breeding yellow-eyed penguins in the Auckland Islands, including error bars (as per Table 4) and linear regression model, for ground-truthed years (2015–17), right of the dotted line, and extrapolated estimations (2012–14), left of the dotted line.

Linear regressions of the estimated population (Figure 3.6) and number of breeders (Figure 3.7) both show no significant trend during 2012–17, indicating that on average the population also appeared to be fluctuating around a mean during this time. The most recent season (2017), which had the smallest confidence interval, had an estimated total of 887–1,105 breeders, or 444–553 pairs, for the Auckland Islands, although the estimate for the previous season (2016) was much higher at 580–922 pairs.

3.5 Discussion

Our results showed that despite large annual fluctuations, the overall population trajectory of yellow-eyed penguins at the Auckland Islands appears to have been relatively steady during 2012–17 (Figure 3.6). Similarly, the estimated number of breeders varied considerably between years, but overall the trajectory was stable (Figure 3.7). The number of breeding yellow-eyed penguins in the Auckland Islands averaged 1,154 individuals (or 577 pairs) over the three ground-truthed breeding seasons. The actual population would be expected to be higher than this, since not all known breeding areas were surveyed. However, the population may have declined since 1989, when comparable areas were surveyed.

3.5.1 Population estimate

Our estimate of 577 pairs (range 444–922) in the Auckland Islands is similar to the 520–680 pairs estimated for the entire archipelago in 1989 (Moore 1990). However, Moore’s estimate of breeding pairs on the Auckland Islands may have been an under-estimate (Moore 1990, Moore 1992b) since some breeding areas were not surveyed (e.g., Chambres Inlet and Waterfall Inlet). In addition, the population estimate was based on ground-truthing from Campbell Island survey data, which were adjusted to a total population size based on the proportion of banded breeders known to be alive at a study site, the proportion of banded birds in the beach counts at the study site, and an assumption that 60–70% of the total population were breeders. When count data were re-analysed using mark-recapture analysis, while still assuming that 60–70% of birds were breeders, then the total estimate for Campbell Island went from 490–600 pairs to 610–890 pairs (Moore et al. 2001), an increase of 25–48%. When applied to the Auckland Islands count data, a similar method could give an upper estimate of 650–1,009 pairs for 1989.

Based on the comparison between population estimates in 1989 and 2012–17, there may have been a population decrease, since counts of individual sites also decreased in most cases (Table 3.1). Moore et al. (2001) also found substantial annual variation on Campbell Island, with a 41% population decrease and a 19% decrease in the number of landing sites between 1988 and 1992. Index counts over the next 6 years showed that the population partially recovered during 1994–98, but the recovery was markedly different between areas (Moore et al. 2001).

Extrapolation of the 2012–14 data suggests that the number of breeders on the Auckland Islands also varied annually for successive years. The percentage of breeders present in each season suggests that the number of birds attempting to breed in 2017 was similar to 2015. Breeding success on Enderby Island was poor in 2017, with substantial egg failure early in incubation (C. G. Muller, unpubl. data; see Chapter 7). The 2016 season included larger numbers of breeders, although the proportion of breeders did not increase as much due to a larger increase in the number of non-breeders. The margin of error for population estimates reduced during the 3 years of ground-truthing (2015–17), primarily due to an increasing proportion of microchipped birds (up to c. 85% of the estimated total population in the reference area in 2017), which provided a better sample size for the mark-recapture estimate. Considering the two most recent seasons where the confidence intervals were more accurate, the 2017 estimate of 444–553 pairs for the Auckland Islands is less than the original estimate of 520–680 pairs for 1989 (Moore 1990), but is considerably less than the revised estimate of 650–1,009 pairs. However, the 2016 estimate of 580–922 pairs is more similar, making it difficult to determine trend over the longer time period.

The proportion of yellow-eyed penguins in the southern population (Auckland and Campbell Islands) was previously estimated at around 60% of the population (Ellenberg and Mattern 2012). However, subsequent population surveys on the mainland have shown a significant decline in the number of pairs breeding there in recent years (Mattern and Wilson 2018, Department of Conservation 2019), including Stewart and Codfish Islands (Seddon et al. 2013). The most recent Campbell Island estimate from 1992 (Moore et al. 2001) also indicates a population decline, but likely needs updating. Using these estimates, the mainland updated numbers, and taking our possible range of 444–922 pairs for the Auckland Islands, this gives a revised estimate of 68–79% of the population breeding in the subantarctic, with 38–50% of the total population breeding at the Auckland Islands. The Auckland Islands (particularly Enderby Island) therefore represent a significant proportion of the total breeding population, indicating the importance of the southern population for the species.

Yellow-eyed penguins begin to breed around 2–3 years old for females, and 2–5 years old for males (Marchant and Higgins 1990). It can therefore be surmised that a large proportion of non-breeders are young birds that are yet to breed. An increase in the proportion of non-breeders in some years, as occurred in 2016 on Enderby Island (Table 3.4, Table 3.6), may therefore be due to the presence of cohorts from previous highly successful breeding seasons, and/or higher than usual juvenile survival rates. Non-breeding birds from nearby areas may also visit Enderby Island, affecting counts. Overall, the average proportion of non-breeders across the 3-year study of 0.42 on Enderby Island is consistent with the range of 0.34–0.47 reported on mainland New Zealand (Richdale 1957, McKinlay 2001).

Variable breeding success has been documented in mainland yellow-eyed penguins, and could indicate that both populations are affected by similar processes, such as the effects of climate change and food availability (van Heezik 1990b, Moore and Wakelin 1997, Moore 1999, Mattern et al. 2017). However, some population crashes observed on mainland New Zealand are thought to be the result of mass adult mortality events, possibly due to disease (Seddon et al. 2013, Couch-Lewis et al. 2016). Such die-offs have not been observed in the subantarctic, although this may reflect infrequent monitoring. Avian malaria is present in the yellow-eyed penguin population (Graczyk and Cockrem 1995), and birds carry ticks that could transmit viruses and blood parasites. Tourism has been implicated in declines in nesting success, fledging condition, and juvenile survival for some mainland yellow-eyed penguin areas (McClung et al. 2004, Ellenberg et al. 2007). While human disturbance has been shown to affect yellow-eyed penguin behaviour in the subantarctic (Young 2009, French et al. 2019), tourism is not believed to be a factor affecting breeding success on Enderby Island (French 2018). Banding of penguins has been implicated in poor breeding success in some studies (e.g., Culik et al. (1993)); however, this is not currently a factor the southern yellow-eyed penguin population since no banding is allowed by DOC.

A biennial breeding cycle could result in a pattern of alternating variability in individual breeding success, as occurs in southern royal albatross (*Diomedea epomophora*) and Gibson's wandering albatross (*D. antipodensis gibsoni*), which also breed in the Auckland Islands (Robertson 1972, Walker and Elliott 2001, Childerhouse et al. 2003). However, while individuals of these species breed in alternate years, this does not result in a variable breeding rate between years for the population, as a similar proportion of adults still breed each year (Walker and Elliott 2001, Childerhouse et al. 2003). Furthermore, a breeding 'sabbatical' is not likely for yellow-eyed penguins in the subantarctic. The species has an annual breeding cycle on the mainland (Richdale 1949, Darby et al. 1990), and failure to breed annually is more likely due to partner loss (Setiawan et al. 2005). Known birds were observed breeding in successive years on Enderby Island (C. G. Muller, unpubl. data), and so a biennial breeding cycle is unlikely to be the reason for the high counts in 2016. Deferred breeding after years of poor breeding success and/or abnormal feeding conditions might occur occasionally. Moore et al. (2001) found evidence for deferred breeding on Campbell Island – after poor adult survival and breeding success in 1991-92, only 68% of surviving breeders at the study site bred the following year. Counts (and by assumption breeding attempts) on Adams Island have decreased over the past three years (Table 3.1). Being a large, predator-free island, it would be expected that Adams Island would be an important breeding location. It is possible that birds previously seen there may have moved to new, unmonitored locations, although due to high nest-site fidelity in yellow-eyed penguins this is unlikely (Darby et al. 1990, Seddon et al. 2013). Factors such as climatic effects on food supply or disease outbreaks would result in wider-scale declines, but a localised decline could occur if penguins from different breeding areas were foraging in different locations and subject to localised effects.

Fisheries by-catch and indirect competition have been shown to cause declines in some mainland populations (Ellenberg and Mattern 2012), and therefore it would be useful to know where Adams Island breeders concentrate their foraging effort. Conversely, over the past two years morning count numbers appear to have increased at Chambres Inlet on Auckland Island (Table 3.1), where predators such as pigs, cats, and mice are present). However, there is some evidence that cliffs may limit ground access by large predators to most of the nesting area at this site (C. G. Muller, pers. obs.), which may explain why this area appears more successful than other locations on Auckland Island. Terrestrial predation has been shown to be a significant cause of population decline for mainland yellow-eyed penguin populations (Couch-Lewis et al. 2016). It would therefore be expected that control of mammalian predators on Auckland Island would provide more suitable breeding locations for yellow-eyed penguins. Predation by New Zealand sea lions was implicated in at least localised population declines of yellow-eyed penguins on Campbell Island (Moore and Moffat 1992, Moore et al. 2001). Evidence of predation was observed on Enderby Island during the 1990s (Moore et al. 2001) and in 2015–17 (C. G. Muller, unpubl. data), which indicates that predation by sea lions may also be a factor. Variability in the number of breeders observed each year is cause for concern, as is an apparent decline since 1989. While the population appears stable over recent years, a further decline could occur if the factors contributing to a sub-optimal breeding season intensified, or continued for successive years. Our results show that there are some differences in the ratio between breeders and the total population estimates between years. This suggests that while some factors may be influencing the population as a whole, in some years the proportion of breeders altered. This may indicate greater or lesser pressure on different cohorts within the population. Variability in the proportion of non-breeders could indicate variability in the numbers of juvenile birds returning to their natal areas, and therefore to recruitment of breeders. Recruitment is an important factor affecting long-term population survival; however, little is known about juvenile yellow-eyed penguin movements and survival in the southern population. Moore (1992a) reported that 15% of chicks banded on Campbell Island were subsequently resighted as juveniles or adults. It has been determined that disturbance (McClung et al. 2004) and lower-quality diet (van Heezik and Davis 1990) can contribute to poorer survival for juveniles, but there is no corresponding research for the subantarctic. In addition, loss of a partner may result in the surviving partner not breeding in subsequent years (Richdale 1957, Setiawan et al. 2005), which could also affect breeding proportions.

Changes in climate and ocean environment have been shown to affect the proportion of breeders and breeding success in emperor penguins (*Aptenodytes forsteri*), and are thought to be contributing to declines in chinstrap penguins (*Pygoscelis antarctica*) and Adélie penguins (*P. adeliae*) (Jenouvrier et al. 2009a, Trivelpiece et al. 2011). Decreases in adult survival can have a large impact on population growth rate, which has led to a population crash in emperor penguins and other Antarctic seabirds (Barbraud and Weimerskirch 2001, Jenouvrier et al. 2005). Changes in breeding success may also contribute to population fluctuations, especially if breeding success is more variable than adult survival (Jenouvrier et al. 2005).

As in other penguin species, yellow-eyed penguins are central-place foragers, and on the mainland their breeding success is dependent on foraging within 20 km of the breeding site (Moore 1999, Mattern et al. 2007). The density and distribution of prey species can be affected by warming water, which can reduce the available food or move it further away, making it energetically inefficient for provisioning chicks. El Niño conditions have been associated with declines in breeding success in Galapagos penguins (*Spheniscus mendiculus*) (Boersma 1998, Vargas et al. 2006) and Humboldt penguins (*S. humboldti*) (Hays 1986). Warmer water coincided with declines in rockhopper penguins on subantarctic Campbell Island (Cunningham and Moors 1994), and in yellow-eyed penguins on the mainland (Peacock et al. 2000). The 2015 breeding season was one of the strongest El Niño years reported, associated with warmer conditions in the Pacific (Jacox et al. 2016, Null 2019). In contrast, the 2016 and 2017 seasons were mild La Niña years with cooler conditions. The 2015 El Niño corresponded with a lower breeding population of yellow-eyed penguins on Enderby Island, although similar breeding results in 2017 corresponded with La Niña conditions, indicating a more complex relationship with climate. A link between population decline and El Niño oscillations has not been demonstrated for mainland yellow-eyed penguins, where longer-term climate changes may be more relevant (Peacock et al. 2000).

3.5.2 Limitations of morning counts

Conducting morning counts in mid-November during the incubation phase was supported by the timing of peak morning transits evident in the autologger data (Figure 3.4). These data also showed that during the guard phase fewer transits were detected per day, as adults spent more time on the nest brooding young chicks, and activity began much earlier in the day. While there were more transits recorded during the post-guard phase in January and February, many birds were conducting daily foraging trips. While this would increase the proportion of transiting birds from the population available to be counted each day, both partners may have gone to sea at the same time, making it more difficult to determine the proportion of breeders, and birds returning on the same day would appear in both morning and evening counts, requiring unique identifiers to avoid double-counting. Additionally, any beach counts conducted later in the season would be biased towards successful nests, as a proportion of nests fail during each breeding phase.

Morning count data for the Auckland Islands during 2012–17 show that total numbers of birds counted (Table 3.1) were less than the 934 counted in 1989 (Moore 1990). However, count totals depended on which areas were surveyed, and so required a correction factor. In addition, counts for the present study were analysed from 0530 h to 0900 h, which was a shorter time period than Moore's, and so our raw counts would be expected to be lower. Increasing morning counts by 12% to approximate a longer data collection period from first light (0430–0900 h) would still result in lower counts than in 1989, which would imply a decline in the population. However, beach counts are difficult to compare unless all of the same areas were surveyed under identical conditions, which is difficult to achieve due to weather and other effects. Large daily variation in beach counts has also been demonstrated (Figure 3.3). It is therefore more accurate to compare population estimates derived from beach counts using an appropriate ground-truthing method. Morning counts may be useful as an interim monitoring method between population surveys (Moore 1992a), but ideally should not be used as a sole means of comparison.

In addition, morning count data collected over multiple days on Enderby Island showed daily variation in counts and a progressive change over time, indicating that using a single daily count at other locations could introduce a margin of error (Figure 3.3). The Auckland Islands are around 50 km long, with the potential for weather systems to affect different areas at different times. Enderby Island is in the north-east and has a more benign climate, with greater sunshine hours and less rainfall than other areas in the archipelago (Higham 1991), and so trends there may not be representative of other locations. Nevertheless, since only a single count was taken at each site around the Auckland Islands, it was considered to be more appropriate to adjust counts using Enderby Island count data from the same day, when conditions were relatively similar, rather than use weekly averages of Enderby Island data, which might introduce more variability. A more accurate population estimate could be achieved with multiple counts at each site, as well as conducting a mark-recapture study at each site (or at selected sites across the region), although this would be logistically difficult.

Using a mark-recapture estimate provided a more reliable population estimate than a simple ratio between beach counts and nest numbers, which does not take into account the proportion of breeders counted. Mark-recapture theory utilises the ratio of marked to unmarked individuals so that the whole population does not need to be counted. However, mark-recapture models assume that all members of the population have an equal chance of being resighted, which is not necessarily true for transiting penguins. Only one bird from each nest will commence a foraging trip on a given morning during incubation, and if partners do not swap every day then an even smaller proportion of breeders will be transiting. This effectively reduces the proportion of marked birds available to be resighted in the sample. If birds are marked when returning to their nests following a foraging trip, then the re-sighting survey should be conducted after a suitable time period to prevent bias towards their potentially unmarked partners. Our results showed that the confidence interval surrounding population estimates reduced markedly between years as progressively more of the population was marked.

3.6 Conclusion and recommendations

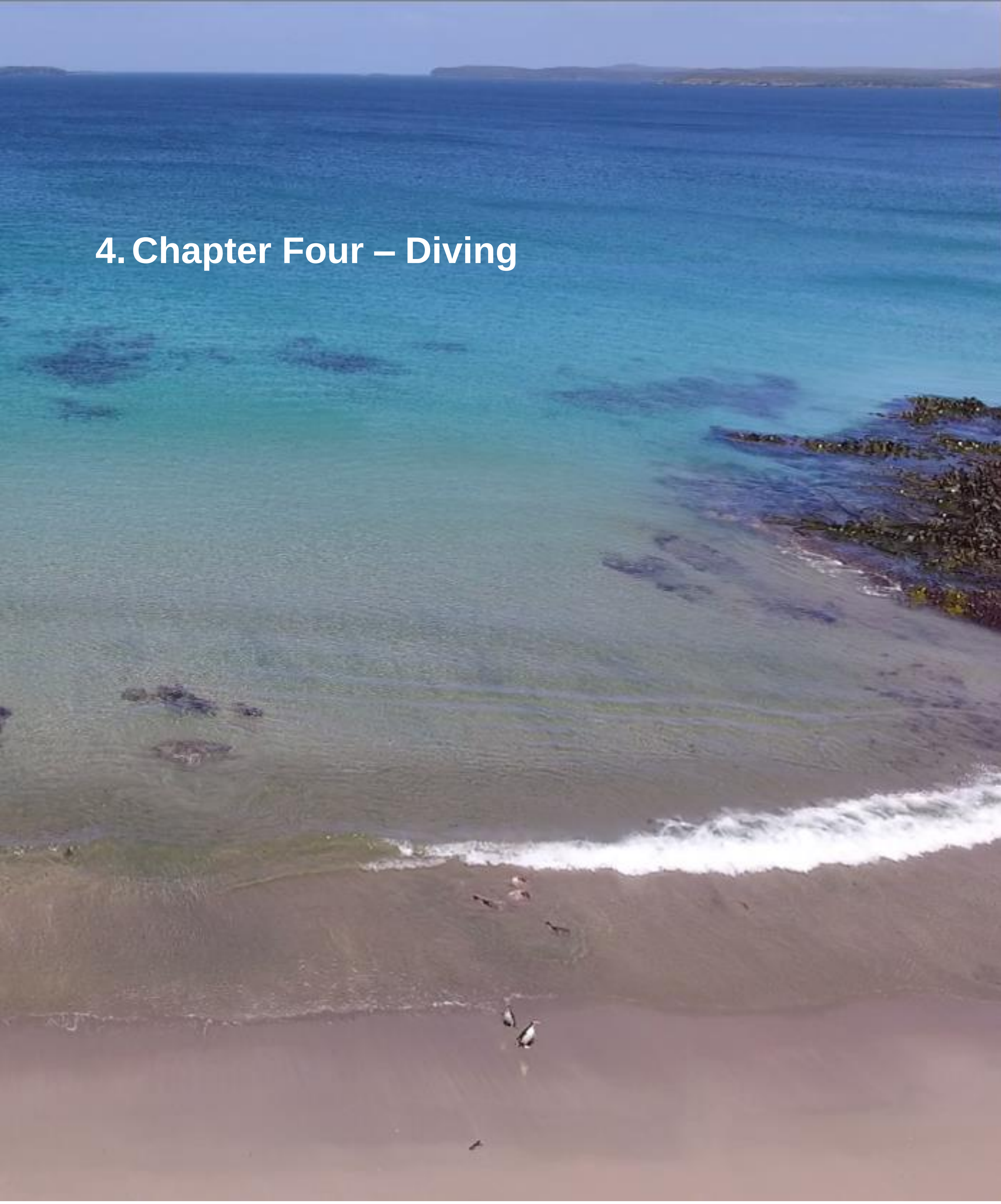
Based on the reduction in confidence interval we observed between ground-truthed years (2015–2017) as more of the population became marked (Figure 3.6, Figure 3.7), the recommended method for future population estimates would be a mark-recapture study at as many of the sites as possible, where at least 50% and preferably over 75% of the expected population in that area is marked – although a compromise with logistics may be needed due to the difficult terrain and weather conditions that can affect research in the subantarctic. Beach counts in all areas would also be needed to derive a total population estimate and determine population trends.

Our estimate of the total number of breeding birds for the Auckland Islands assumed that the proportion of breeders was similar across all sites, which is an untested assumption. The proportion of breeders is similar at most mainland colonies (Richdale 1957, McKinlay 2001), but this could vary in small colonies, or if predation and other factors influence breeders and non-breeders unequally. A more detailed population census at selected sites around the Auckland Islands would determine the variation in the proportion of breeders, which would improve the accuracy of the resulting population estimate. Some breeding sites surveyed by Moore were not included in this survey due to time constraints, or difficult or dangerous access (including Matheson Bay, Ewing Island, and Tagua Bay in Carnley Harbour). In addition, other possible breeding areas (including Musgrave Inlet and Smith Harbour; Figure 3.2B) were identified by Beer (2010) but were not included in this survey. Breeding numbers in these areas are expected to be low but are largely unknown and so cannot be estimated based on previous data. Therefore, the Auckland Islands population estimates should be regarded as a minimum estimate, and future surveys should ideally also include these additional areas where penguins may be breeding.

It is evident that there is some variability between years, not only in the numbers of birds attempting to breed but also in their ability to successfully incubate and hatch eggs, and raise chicks to fledging (C. G. Muller, unpubl. data; see Chapter 7). Morning beach counts are conducted near the beginning of the breeding season, which does not give any indication of breeding success. It would therefore be valuable to conduct breeding success studies to determine hatch rates, fledging rates, and nest-predation rates. The large main Auckland Island provides potential habitat for breeding to increase, and therefore eradication of mammalian pests would be expected to benefit yellow-eyed penguin population numbers. Detailed population surveys before and after any planned eradication would be useful to measure changes.

We recommend that long-term monitoring of the southern yellow-eyed penguin population continues, including measures of breeding success as well as juvenile survival and recruitment, particularly considering population declines recently observed on the mainland. We have demonstrated that the subantarctic still has a large proportion of the population, and the larger population centres, such as Enderby Island, are likely to become more important for the survival of the species if populations on the mainland continue to decline. Continued monitoring and regulation of threats to subantarctic yellow-eyed penguins is therefore important, including protection of habitat, eliminating introduced predators, and minimising negative interactions with fisheries and tourism. Ongoing monitoring is also needed to determine longer-term effects of changes in climate on food availability, as well as potentially catastrophic natural and unnatural events, including disease epidemics, tsunamis, and oil spills from fishing or tourist vessels.

4. Chapter Four – Diving



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We, the candidate and the candidate's Primary Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of candidate:	Chris Muller
Name/title of Primary Supervisor:	Louise Chilvers

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Diving plasticity in the ancestral range of the yellow-eyed penguin *Megadyptes antipodes*, an endangered marine predator

Muller, C. G., Chilvers, B. L., French, R. K., and Battley, P. F. (2020) Diving plasticity in the ancestral range of the yellow-eyed penguin, *Megadyptes antipodes*, an endangered marine predator. Marine Ecology Progress Series, 648:191–205.

4.1 Abstract

In long-lived marine predators such as penguins, foraging behaviour is related to breeding success. Yellow-eyed penguins *Megadyptes antipodes* are thought to be predominantly benthic foragers around mainland New Zealand, with previous dive studies showing little variation in diving behaviour and minimal change by year or breeding status. This apparent absence of foraging flexibility may be linked to local prey availability and therefore also to foraging success, factors believed to contribute to the current population decline. Here, we undertook the first detailed study of yellow-eyed penguin diving and foraging behaviour in the subantarctic Auckland Islands, part of the original ancestral range of the species that colonised mainland New Zealand. We collected dive logs from 134 foraging trips made by 73 breeders from Enderby Island, Auckland Islands, in the New Zealand subantarctic. Pelagic dives and solely pelagic foraging trips were recorded in the southern population—a foraging strategy not previously published in dive studies on this species. Changes between benthic and pelagic foraging were recorded for individuals within foraging trips, within a breeding season, and between years. Differences in diving behaviour between the southern and northern populations are likely influenced by local bathymetry, environmental conditions, and prey availability. However, the southern population shows a greater use of pelagic foraging not evident in the northern population, even in areas that have a similar depth to some mainland foraging areas. This observed foraging

flexibility may have implications for breeding success and potentially the long-term population trends of these two genetically similar populations.

4.2 Introduction

Foraging behaviour is a key factor affecting breeding success and population viability for long-lived marine predators (Villegas-Amtmann et al. 2008, Chilvers and Wilkinson 2009), including seabirds (Sandvik et al. 2005, Catry et al. 2013). Prey availability and foraging success can be affected by processes such as the El Niño Southern Oscillation (ENSO) and climate change (Grémillet and Boulinier 2009, Agnew et al. 2015). Changes in diving behaviour can be an indicator of complex oceanic processes which can affect the location, distribution, availability, and quality of prey species (Cairns 1988, Miller and Sydeman 2004). Many species, while constrained by morphological and physiological specialisation, also show a degree of plasticity in response to environmental variables (Morrison et al. 1990, Tremblay and Cherel 2003). As a result, foraging plasticity can affect the ability to respond to environmental variability. Knowledge of diving behaviour is therefore important for the conservation and management of diving seabirds.

Benthic diving is to the sea floor and is characterised by repeated dives to a uniform maximum depth limited by seabed depth contours (Tremblay and Cherel 2000). Benthic dives have a small change in maximum depth between subsequent dives (inter-dive depth change) and a ‘U-shaped’ dive profile with a longer bottom time than pelagic dives (Tremblay and Cherel 2000). Conversely, pelagic diving occurs mid-water and, therefore, pelagic dives display a more variable maximum depth between dives, since prey could be encountered anywhere in the water column. Pelagic dive profiles also feature a ‘V-shaped’ dive profile with a shorter bottom time (Tremblay and Cherel 2000). Benthic foraging can be a more energetically expensive foraging behaviour than pelagic strategies, especially in deeper water (Costa et al. 2004); however, benthic prey species tend to be a predictable, evenly distributed prey source, albeit occurring at low densities within a habitat (Costa et al. 2004, Chilvers and Wilkinson 2009). Benthic prey are also less influenced by oceanographic perturbations such as

ENSO than are pelagic prey (Costa et al. 2004), so may be a more reliable food source when prey are less abundant. Benthic foraging may assist penguins with underwater navigation, and in some cases this may also be linked to anthropogenic modification of the environment where navigable landmarks are created on the seafloor (Mattern et al. 2007, Preston et al. 2008, Mattern et al. 2013).

The yellow-eyed penguin (hoiho) *Megadyptes antipodes* is endangered and endemic to New Zealand, with a distribution restricted to the south-east of the South Island, Stewart and Codfish Islands (the northern population), and subantarctic islands (the southern population, Figure 4.1) (Seddon et al. 2013).

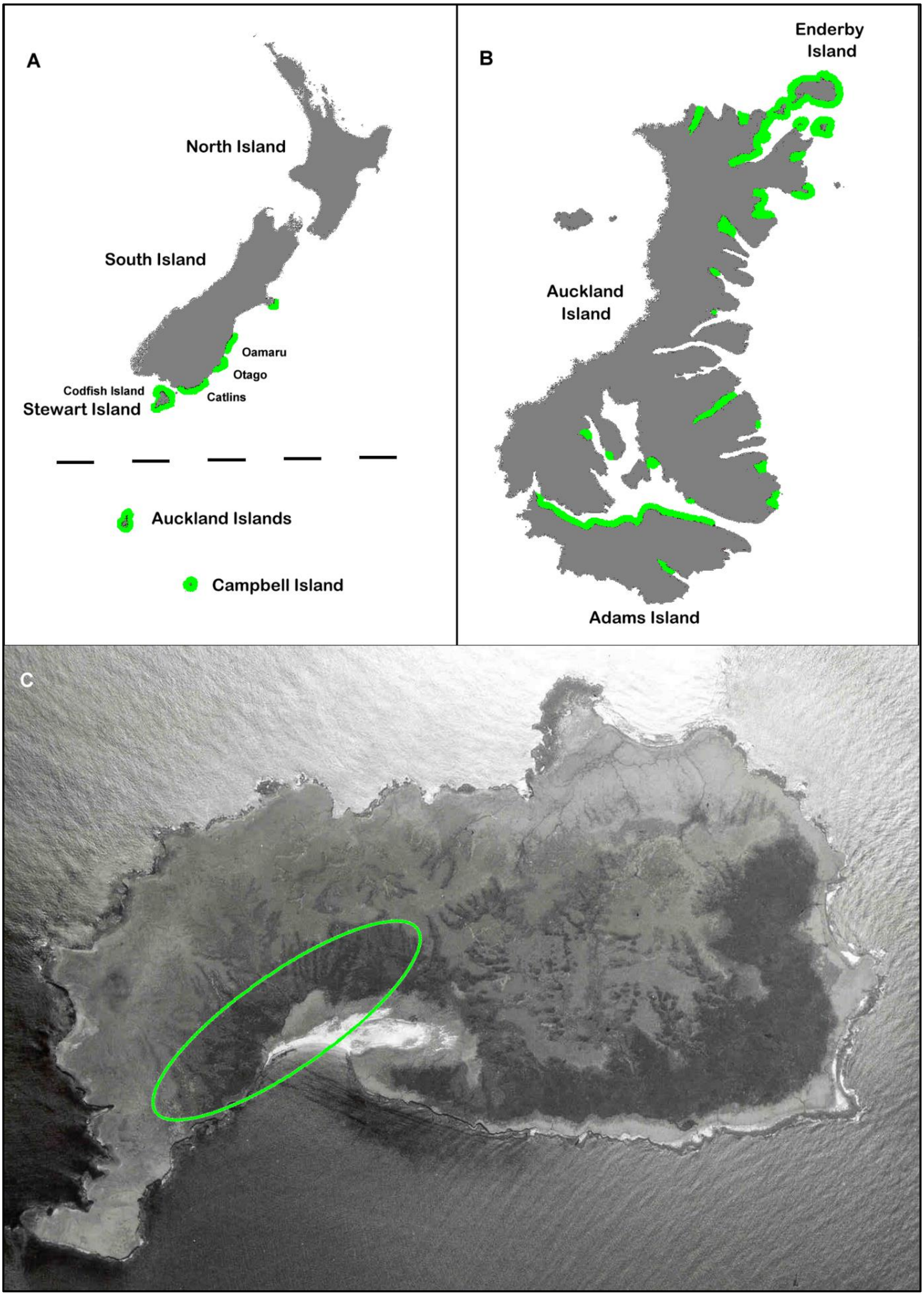


Figure 4.1 A) Yellow-eyed penguin breeding range around New Zealand (green), with the northern population above the dashed line and southern population below. B) Enlarged view of the subantarctic Auckland Islands with Enderby Island to the NE. C) Close-up of Enderby Island showing the area where breeding birds were sampled (green ellipse)

Most populations around mainland New Zealand have been undergoing a serious decline due to successive poor breeding seasons and ongoing high adult mortality (Couch-Lewis et al. 2016, Mattern et al. 2017, Mattern and Wilson 2018). The southern population comprises at least 60% of the total yellow-eyed penguin population (Couch-Lewis et al. 2016, Muller et al. 2020b; see Chapter 3) and is considered an important stronghold for the species. Ancient DNA analysis has shown yellow-eyed penguins originated in the New Zealand subantarctic and populated mainland New Zealand following the extinction of the endemic mainland species *M. waitaha* after Polynesian settlement (Boessenkool et al. 2009a, Collins et al. 2014). However, there is now almost no migration (<2%) between the southern and northern populations, meaning these areas represent separate management units (Boessenkool et al. 2009b).

Yellow-eyed penguins are non-colonial breeders, nesting in vegetation up to 1 km inland from the sea (Seddon and Davis 1989, Darby et al. 1990). Nesting begins in August/September and normally two eggs are laid, with hatching occurring in November/December. Both partners alternate incubating the eggs and caring for the young chicks during the incubation and guard phases (September/October to January). During this time they undertake frequent foraging trips while their partner is at the nest (Seddon 1989). Both parents leave the nest to make foraging trips during the post-guard phase (January to March), returning to the nest intermittently to feed the chicks (Darby et al. 1990). Breeding dates in the subantarctic are approximately 2 weeks later than the mainland, with chicks hatching in late November and fledging in March (Moore 1992a).

Most penguin species rely on pelagic foraging methods, with prey caught within the water column (Ratcliffe and Trathan 2011), although some species such as southern rockhopper penguins *Eudyptes chrysocome filholi* have a mixed strategy incorporating both pelagic and benthic foraging (Tremblay and Cherel 2000). Yellow-eyed penguins are thought to be an exception based on dive studies to date (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014). The northern population are central-place foragers relying on prey close to their breeding area. During the breeding season they forage in shallow coastal waters, travelling up to 25 km from shore, and foraging over mid-shelf areas (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). Foraging is predominantly benthic around mainland New Zealand and Stewart Island, with flat-bottomed feeding dives to the same depth and a large proportion of each dive spent at the benthos (Seddon and van Heezik 1990, Moore et al. 1995, Mattern 2006, Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014, Mattern et al. 2018a). Outside the breeding season, they forage further offshore, but remain over the continental shelf in waters less than 160 m deep (Mattern and Wilson 2018). However, while current evidence suggests predominantly benthic foraging in the northern population, earlier diet studies have shown occasional indications of pelagic foraging (van Heezik 1990c, Moore et al. 1995). This suggests that a switch to predominantly benthic diving may have occurred relatively recently, likely due to changes in prey availability (Mattern and Ellenberg 2018). Mean maximum dive depths ranged from 26 to 77 m during different studies at mainland sites, and 48 to 94 m at Stewart Island (Table 4.1).

Table 4.1 Yellow-eyed penguin diving summary review from mainland New Zealand showing mean maximum dive depths published in the literature, and other details where known. Maximum dive depth values are summarised per trip. Where dive data were reported for different experimental categories, the deeper measurements were used. *Calculated from data obtained from the indicated authors; all other data were obtained from the cited references. Studies are listed by geographic location (north to south), and year. TDR: Time Depth Recorder.

	Maximum depth per trip (m)								
Location	**Min**	**Max**	**Mean**	**Method**	**No. birds**	**No. dives**	**No. trips**	**Authors**	**Year**
Oamaru			26 ± 0.2	Electronic TDR loggers	3			Mattern	2006
Oamaru			41 ± 3	Electronic TDR loggers	3			Mattern et al.	2007
Otago	19	56	34 ± 8	Capillary depth recorders	24		43	Seddon & van Heezik	1990
Otago	6.8	94.8	54 ± 12*	Electronic TDR loggers	8		109	Moore et al.	1995
Otago			77 ± 0.2	Electronic TDR loggers	23			Mattern et al.	2013
Otago	4.8	62.1	54 ± 0	Electronic TDR loggers	1	286		Mattern et al.	2018
Catlins	13.5	127.9	99 ± 24*	Electronic TDR loggers	3		24	Moore et al.	1995
Codfish Is			63 ± 3	Electronic TDR loggers	10			Mattern	2006
Stewart Is			48 ± 7	Electronic TDR loggers	9			Mattern	2006
Stewart Is	53	116	94 ± 20*	Electronic TDR loggers	8	2079	8	Chilvers et al.	2014

Deeper dive depths around Stewart Island were confirmed as benthic dives (Chilvers et al. 2014). Yellow-eyed penguins have been recorded undertaking shallow ‘epipelagic’ dives centred in the upper 10 m of the water column off the Otago coast, although these were thought to be travelling dives rather than foraging (Mattern et al. 2018a). Video cameras attached to birds have recorded some pelagic foraging, in some cases when visibility or foraging conditions were poor at the bottom (Thiebot et al. 2017, Mattern et al. 2018a). No difference in foraging or dive behaviour is evident between sexes (Seddon and van Heezik 1990, Moore 1999, Mattern et al. 2007) with one exception (Chilvers et al. 2014), in which females (n = 5) made deeper dives around Stewart Island and with a greater mean dive depth and shorter bottom time (time at depth) than males (n = 3).

Despite the importance of the southern population to the species, there is little information available on yellow-eyed penguin diving behaviour, foraging, and diet in the subantarctic, and whether this may differ from the northern population.

Foraging data were collected concurrently using GPS loggers attached to some diving birds. The majority of foraging by breeding birds from Enderby Island was concentrated in an area to the south-east of the island, up to 50 km offshore. A smaller number of birds travelled north-west to forage around the top of Auckland Island (Muller et al. 2021; see Chapter 5). These areas are over the continental shelf, with the majority in water with a maximum depth contour of 100 m. A smaller proportion of foraging extended further offshore where water depth was up to 150 m over the shelf (Mitchell et al. 2016). Satellite tracking of two juvenile yellow-eyed penguins from Enderby Island showed they travelled predominantly north-east for at least 205 km and remained at sea for at least 11 days at a time (Muller et al. 2020a, Muller et al. 2021; see Chapters 4 and 5). Foraging in these areas is likely restricted to pelagic dives due to the water depth of 150 to 500 m (Mitchell et al. 2016). Shorter trips by juveniles were also observed to the north-west in pelagic water over 3000 m deep.

The northern population decline is thought to be due in large part to marine issues, including decreased foraging success and threats at sea (Couch-Lewis et al. 2016, Mattern et al. 2017). In contrast, the southern population appears relatively stable in recent years, although there is significant variation, and it may have suffered from previous declines (Muller et al. 2020b; see Chapter 3). While some foraging parameters, such as maximum dive depth, may be constrained by the physical environment, other factors may be a result of changing environmental parameters, or individuals' preference to forage in certain habitats. Therefore, a study of diving parameters was needed to shed more light on the link between foraging efficiency and breeding success, a timely concern for this endangered species. This is particularly relevant with respect to the southern population. These birds may be expected to expend more energy foraging in deeper water and over greater distances, yet appear to be more successful than the northern population. Accordingly, in this study, we aim to: (1) document yellow-eyed penguin diving behaviour in the New Zealand subantarctic; (2) study changes in diving behaviour over three breeding seasons (2015 to 2017); and (3) investigate the effects of individual preference and sex on diving behaviour.

As this work required analysis of large numbers of dives recorded via time−depth recorders (~73,000) we also developed and describe here a model to automatically categorise dive profiles as benthic or pelagic.

Greater knowledge of yellow-eyed penguin foraging in the subantarctic will allow conservation managers to better understand the relationship between productivity and access to marine resources. In addition, this research will aid in management of the species by helping to highlight differences in foraging and breeding success between the northern and southern populations, and whether there are any unique concerns for yellow-eyed penguins in the isolated subantarctic areas.

4.3 Methods

4.3.1 Fieldwork and equipment

Fieldwork was carried out on Enderby Island, Auckland Islands (50° 29’ 45” S, 166° 17’ 44” E), in the New Zealand subantarctic (Figure 4.1) for three breeding seasons: 2015 (November 2015–February 2016), 2016 (November 2016–February 2017), and 2017 (November 2017–January 2018).

Adult yellow-eyed penguins were captured by hand as they returned to their nest following a foraging trip at sea. Each penguin was placed in a capture bag for processing and collection of morphometric data. Birds were weighed using a spring balance, and measurements taken of the head and beak, and left foot (excluding claw). Sex was determined using the relationship between head plus beak length and foot length (Setiawan et al. 2004), or the relative sizes between breeding partners with males assumed to be the larger (Setiawan et al. 2004). A microchip was inserted subcutaneously at the back of the neck for permanent individual identification (Muller et al. 2020b; see Chapter 3). Nests were located by manual ground searching, and electronic tracking of birds equipped with a Very High Frequency (VHF) radio transmitter. This included ground-based VHF tracking, and aerial tracking using an Unmanned Aerial Vehicle (UAV) equipped with a VHF receiver (Muller et al. 2019; see Chapter 2).

Electronics were deployed on nesting yellow-eyed penguins over three breeding seasons from 2015 to 2017, during the guard phase in December and the first week of January (Table 4.2). Electronics were attached using TESA® tape (Beiersdorf). Use of this attachment method preserved the integrity of the plumage and minimised handling time (Wilson et al. 1997), also ensuring tags would drop off within one to two weeks if penguins were not recaptured. Electronics were taped to the back on the midline to maintain streamlining and were not fitted within one week after hatching of eggs, to minimise disturbance. Time Depth Recorder (TDR) tags were LAT 1400 loggers with 128 kB of memory, 11 × 35 mm, weight 5 g (Lotek). These were programmed to log pressure every 5 s when wet, to allow sufficient data storage for long trips. VHF transmitters, V1G118A with 150 or 220 mm whip antenna, 20 × 13 × 6 mm, weight 4.5 to 5 g (Sirtrack) were attached to the dive loggers to monitor when penguins were ashore and assist with recovery of electronics. GPS loggers were customised CatTraQ™ GPS loggers, 14 × 35 × 70 mm, weight ~30 g (Catnip Technologies) modified for underwater use (Pelletier et al. 2014). After programming, each unit was waterproofed with heat-shrink tubing (TE Connectivity) before deployment.

Dive loggers were deployed on a total of 73 individual birds; 10 birds in 2015, 51 in 2016, and 66 in 2017, of which 55 were single-year, 16 were 2-year, and two were 3-year study animals (Appendix 4, Table S4.2). A grand total of 134 foraging trips were monitored (Table 4.2).

Table 4.2 Electronics deployments on breeding yellow-eyed penguins from Enderby Island, showing the number of loggers of each type deployed in each year of the study. In 2015, only TDRs were deployed, and in 2016 all birds received both types of logger. In 2017, a subset of 31 birds received 2 electronics deployments on separate occasions (one with GPS + TDR, one with TDR only) with the order randomised. Additional single deployments of GPS + TDR electronics were also made on 8 other individuals. Where multiple foraging trips were recorded in one deployment, the data were divided into separate trips.

Year	TDR only	GPS + TDR	Total
2015	13	0	**13**
2016	0	51	**51**
2017	31	39	**70**
Total	**44**	**90**	**134**

Of the total deployments in 2017, a subset of 31 birds received two electronics deployments with the deployment type randomised (Table S4.1); 18 birds received a TDR logger only on the first deployment and a GPS and TDR logger on the second, and 13 birds received the reverse. Dive data from the pairs of trips were examined to determine whether the type of electronics fitted had any effect on diving behaviour (deployment type). Additional trips in the same year were also examined for differences in dive behaviour within a breeding season.

4.3.2 Data analysis

Time−depth logs were only recorded while the loggers were wet. Where penguins undertook more than one foraging trip before electronics were recovered, the data were split into separate trips. Dive data were analysed in R Studio version 1.1.456 running R version 3.5.1 (R. Core Team 2017), and using the DiveMove package (Luque 2007). Summary statistics were generated for each dive including the mean and maximum dive depth and dive duration, as well as identifying the descent, bottom, and ascent phases of the dive. From these, we determined the mean and maximum bottom time (time at depth), bottom depth (depth at the bottom [horizontal] phase of the dive), descent and ascent rates, and surface interval between dives. Sensor calibration for each foraging trip was automated in R and only dives >2 m were analysed. This cut-off depth was used as the TDRs had an error of ±1 m, and to avoid non-feeding dives near the surface. Other studies have used a cut-off depth of 3 m as this was the error of margin of their loggers (Mattern et al. 2007, Chilvers et al. 2014). However, we used a smaller sensitivity margin to ensure any exploratory dives during transits to and from feeding grounds were also logged.

As over 70,000 dives were collected, it was not feasible to manually categorise whether individual dives were benthic or pelagic. Instead, dive types were categorised manually for 10 representative sample foraging trips by identifying instances or bouts of benthic and pelagic dives based on the shape of the dive profile (total = 3979 dives in these 10 trips). Benthic dives were identified by their consistent maximum depth and ‘U-shaped’ dive profile, and pelagic dives by their inconsistent maximum depth and ‘V-shaped’ profile (Tremblay and Cherel 2000). Using Bayesian modelling, different predictor variables were tested for their ability to categorise dives accurately by using manually identified dive types to generate likelihood functions and a log-likelihood ratio criterion for each model (dotted lines in Figure S4.1). These indicated the cut-off values separating the tested dive types, and were used for categorising dive types. Variables including dive depth, bottom time, and percentage time at the bottom of the dive were also tested, but when compared against the manually identified dives, these factors proved less suitable for accurately categorising dive types (Table S4.2). Surface interval time was not used as there was no consistent time gap between dive bouts. A combined model using inter-dive depth change (change in maximum dive depth between subsequent dives) had the highest accuracy of all models tested (it agreed with the manual categorisation for 96% of the sample dives). This model was used to categorise all dives as follows:

(1) Benthic dives were identified with an inter-dive depth change of less than 2.9% (Figure S4.1) from the previous AND following dive. Percentage depth change was determined by dividing the absolute depth change by the smaller depth value to avoid negatives, and so deeper and shallower dives were weighted equally

(2) Transition dives were a new class of dive type we identified with a depth change greater than 45 m from a previous OR following dive (Figure S4.1)

(3) The remainder of dives excluded by these criteria were classified as pelagic. The model assumed no fixed relationship between dive type and the dive depth, or bottom time, which was useful in situations where dives could not be differentiated using these parameters (Table S4.2). Bayesian modelling was also used to qualify each foraging trip based on the percentage of benthic diving (Figure S4.2). A subset of 67 foraging trips was categorised manually by identifying whether trips contained bouts of benthic diving or solely pelagic diving behaviour. Using the model, the log-likelihood ratio criterion identified benthic foraging trips as those where 3.63% or more of the dives were benthic (Figure S4.2), and this characteristic was used to categorise all foraging trips. This method ensured that those foraging trips categorised as

pelagic contained no substantial bouts of benthic diving. Statistical analyses were performed using the lme4 package (Bates et al. 2015). Year, sex, and deployment type (as fixed variables) were analysed using linear mixed-effects (LME) models to determine the effect on the proportion of each dive type in a foraging trip. Dive type, year, sex, and deployment type (as fixed variables) were also analysed using LME models to determine the effect on maximum dive depth, dive time, and bottom time. ANOVA tests were used to determine the significance of these effects in each model. Model assumptions (normally distributed residuals and homoscedasticity) were confirmed visually using the function plot_model from the R package sjplot (Lüdecke and Schwemmer 2017).

Bird ID (a unique identifier assigned to each bird) was used in all models as a random effect with a random intercept to avoid pseudo-replication. A separate ANOVA test of models with and without bird ID was used to test whether bird ID significantly improved the model fit, based on the resulting corrected Akaike’s information criterion (AICc) values. This hypothesis-driven test was used to investigate whether any individual preferences in diving behaviour existed. The alpha value for all statistical tests was 0.05. Graphs were generated in R, including the ggplot2 package (Wickham 2016). Day and night times were determined from sunrise and sunset tables for the Auckland Islands (TimeAndDate.com 2019) for comparison. The time of day (day or night) of every dive was compared with dive type (benthic or pelagic), total dive time, and surface interval.

4.4 Results

Over three breeding seasons, we collected a total of 72,993 valid dives, representing 134 foraging trips by 73 individual nesting birds, including 30 males, 42 females, and one of unknown sex (Table S4.1). The deepest recorded dive was 134 m and the longest dive duration was 3.9 min (Table 4.3), with 55% of that time spent in the bottom portion of the dive.

Table 4.3 Dive statistics for breeding yellow-eyed penguins on Enderby Island during 2015 to 2017, showing summary values for benthic and pelagic dives (as categorised in Section 2). Not shown are transition dives (n = 3,056 dives), which were associated with bouts of benthic diving. Max. depth: greatest depth reached per dive; Max. dive time: total dive time; Max. bottom time: time spent in the bottom portion of the dive (at max. depth). All values are calculated per trip. Min., max., mean and SE values are shown per column, by dive type.

Dive Type	Parameter	Max Depth (m)	Max Dive Time (s)	Max Bottom Time (s)
Benthic	**Min**	35.8	120.0	65.0
n=6,853 dives	**Max**	134.3	235.0	130.0
58 trips, 43 birds	**Mean (±SE)**	92.7 (2.8)	179.4 (3.0)	93.1 (1.9)
Pelagic	**Min**	29.0	110.0	55.0
n=62,957 dives	**Max**	114.8	215.0	115.0
76 trips, 43 birds	**Mean (±SE)**	67.0 (2.4)	146.9 (2.5)	82.9 (1.5)

ANOVA analysis of all dives showed there was no significant difference in maximum dive depth between sexes (Table S4.3). Dives by females did have significantly shorter dive time and bottom time, although these differences were in the order of a few seconds so were unlikely to be biologically significant (Table S4.3). Similarly, maximum dive depth and bottom time were significantly affected by deployment type, although the differences in the estimate values were also unlikely to be biologically significant (Table S4.3).

Analysis of dive profiles identified distinct diving behaviours. Benthic dives were characterised by a smaller and more uniform depth change between subsequent dives, and pelagic dives were defined by a greater depth variation between subsequent dives (Figure 4.2). ANOVA results showed that benthic dives were deeper, longer overall, and with longer bottom time than pelagic dives (Table S4.3). The maximum dive depth range was 36 to 134 m for benthic dives, and 29 to 115 m for pelagic dives (Figure 4.3, Table 4.3), indicating a large overlap in the depth ranges between dive types. Maximum dive time and bottom time (time at depth) ranges also overlapped between benthic and pelagic dives (Figure 4.3, Table 4.3) making these factors unsuitable for identifying dive type. When considering all dives, 86.4% were classified as pelagic, and 9.4% were benthic (Table 4.3). This indicated that even within benthic foraging trips, there was a high proportion of pelagic dives (likely also including travelling dives to and from the foraging area). Transition dives made up only 4.2% of all dives.

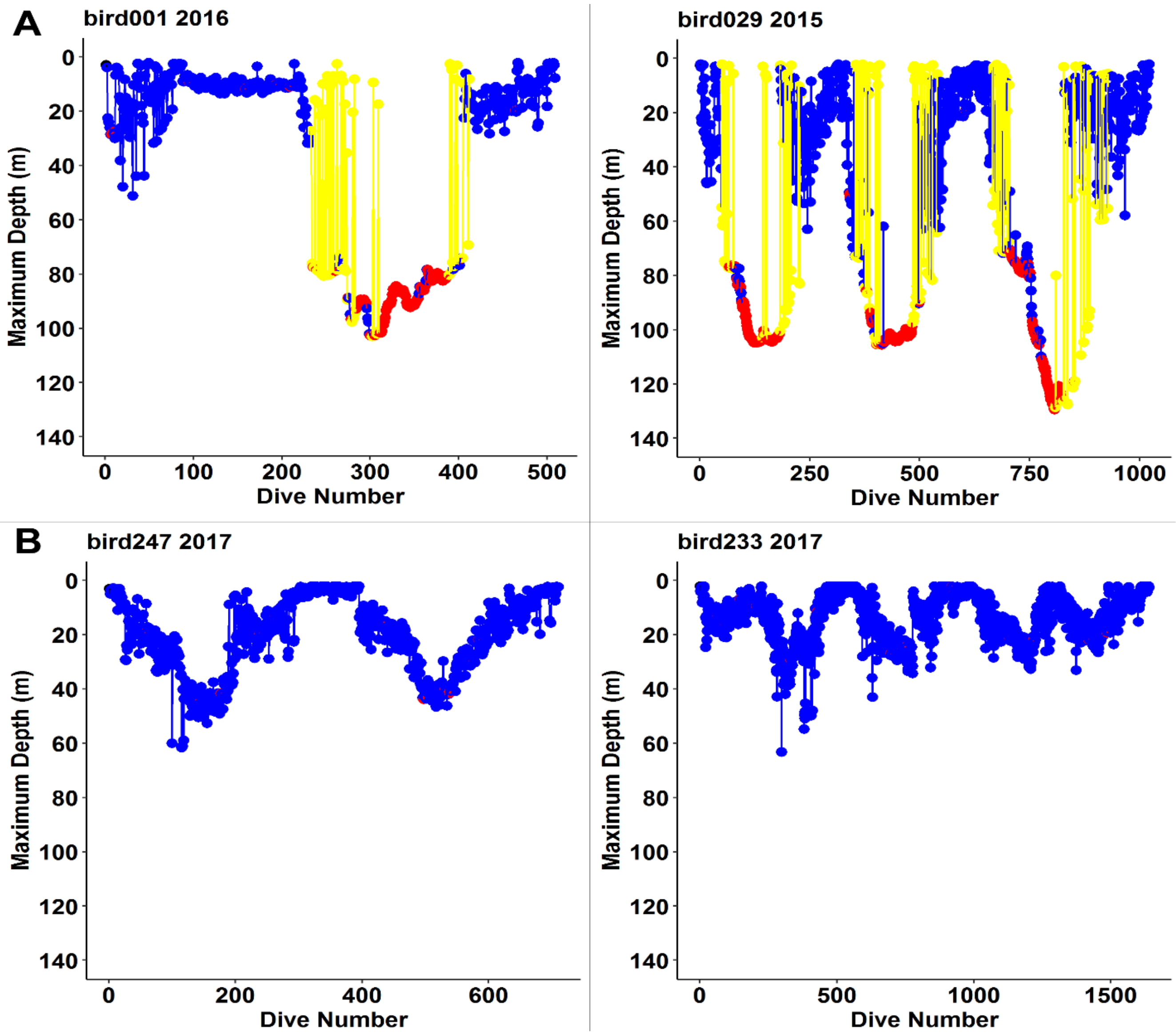


Figure 4.2 Maximum depth vs. dive number (numbered sequentially from the first dive in a foraging trip) demonstrating example dive profiles: A) benthic foraging and B) pelagic foraging. Dive type was classified for individual dives using a Bayesian model. Benthic dives (red) had an inter-dive depth change of <2.9% from the previous AND following dives. Transition dives (yellow) had an inter-dive depth change of >45 m from a previous

OR following dive. The remainder of dives were classed as pelagic (blue). The first dive in each foraging trip (black) could not be categorised as they had no preceding dives. The x-axis scales vary depending on the length of each trip.

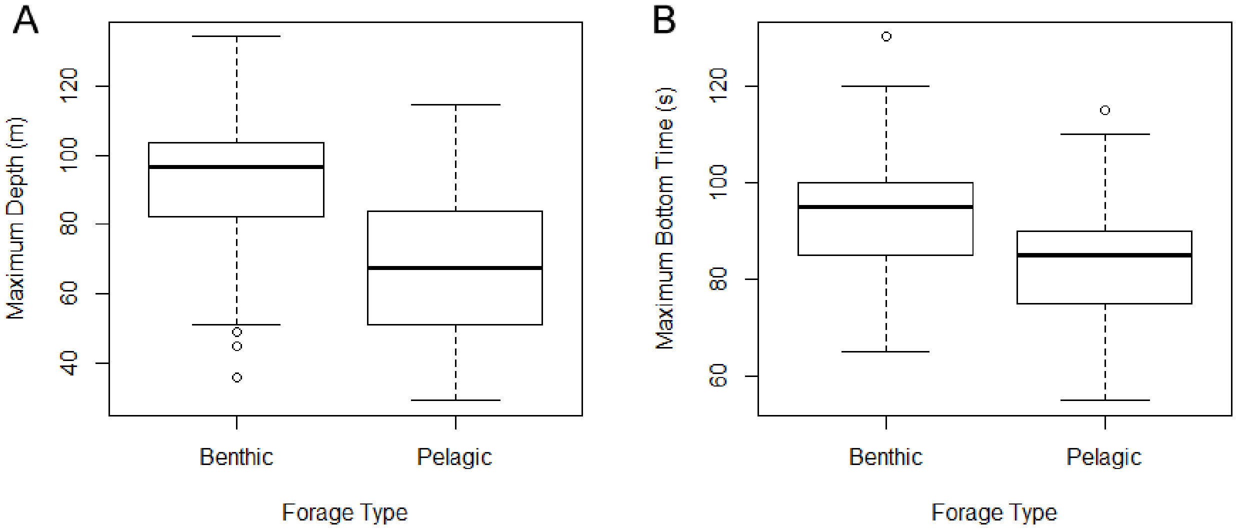


Figure 4.3 Comparison between A) maximum depth and B) maximum bottom time (time at depth) for benthic and pelagic dive types. There was some overlap between dive types, and categorising dive types by inter-dive depth change produced a better model than using depth or bottom time (Table S4.2). Boxes represent the median (bold line) and 25th to 75th percentiles, whiskers the range to 1.5× the interquartile range, and circles are outliers beyond that range.

ANOVA tests showed that the mean proportion of benthic dives (out of all three dive types) within foraging trips significantly decreased from 2015 to 2017 (Figure 4.4), (χ^2 = 110.31, p < 0.0001), and pelagic dives significantly increased (χ^2 = 123.47, p < 0.0001). The major dive behaviour represented in foraging trips varied over the three-year study, with the percentage of pelagic foraging trips increasing from none in 2015 to 79% in 2017 (Figure 4.5). Individual bird ID (as a random effect) did not significantly improve the LME model fit for pelagic dives (χ^2 = 1.96, p = 0.16) or transition dives (χ^2 = 2.23, p = 0.14). Bird ID also did not significantly improve the model fit for benthic dives (χ^2 = 3.40, p = 0.065), except when the ‘Sex’ variable was removed (χ^2 = 6.27, p = 0.012). However, when comparing the effect of sex on the proportion of benthic dives in a foraging trip (including bird ID as a random factor) there was no significant effect of sex (χ^2 = 2.58, p = 0.11), indicating that males (n = 32) and females (n = 43) did not have a different proportion of benthic (or pelagic) dives in their foraging trips.

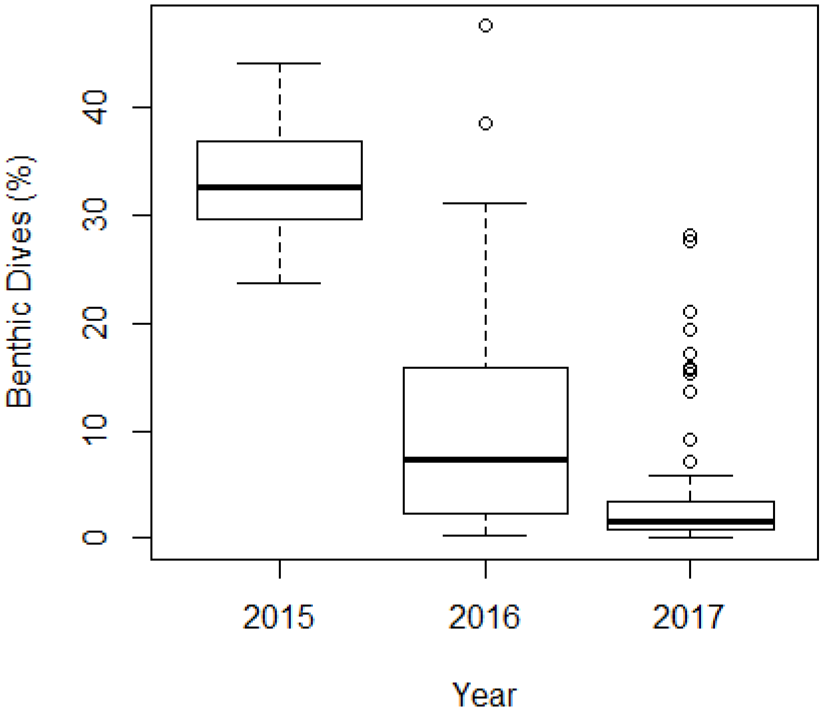


Figure 4.4 Mean percentage of benthic dives per foraging trip in each year; 2015 (n = 13 trips), 2016 (n = 51 trips), 2017 (n = 70 trips). Circles show outliers. The remaining proportion of dives was taken up with other dive profile types including transition and pelagic dives, and travelling (i.e. non-feeding) dives. Box conventions are as per Figure 4.3.

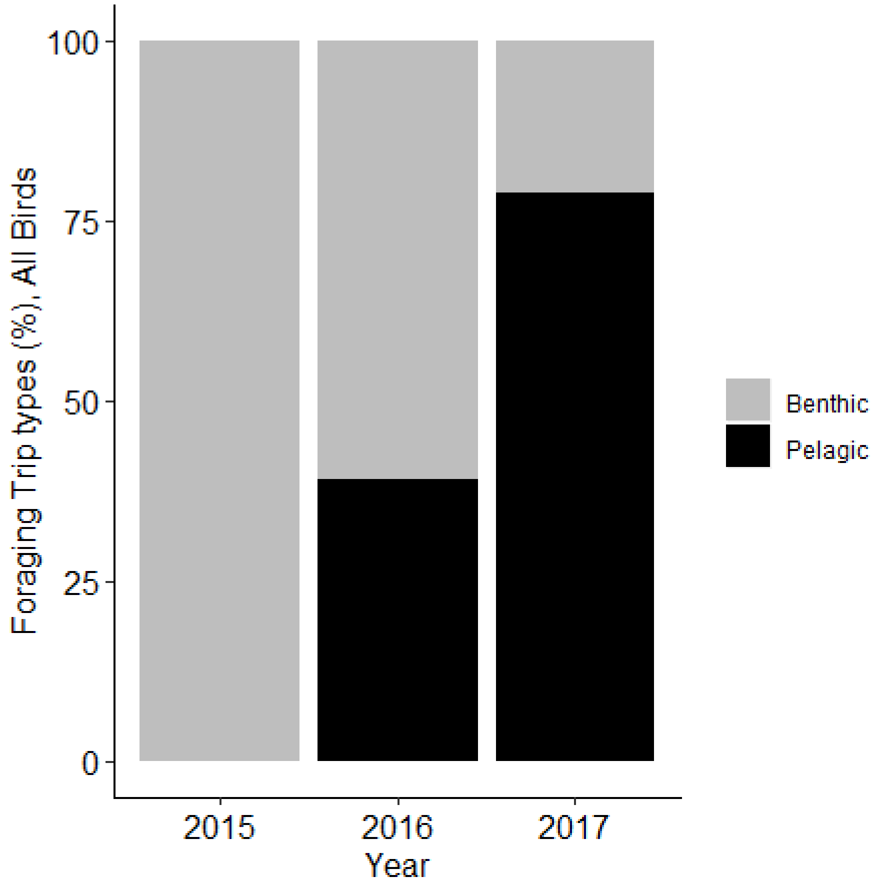


Figure 4.5 Foraging trip classification showing the percentage of primarily benthic, and primarily pelagic foraging behaviour. Foraging trip types were classified using a Bayesian model where pelagic foraging trips had <3.6% benthic dives within a trip, and benthic foraging trips had ≥3.6% benthic dives within a trip. Percentages are calculated from the proportion of all dives within each foraging trip recorded for each bird in each year; 2015 (n = 13 trips), 2016 (n = 51 trips), 2017 (n = 70 trips).

Of the birds with electronics fitted for more than one foraging trip in the same season, 29 had valid dive data for trip comparisons. Of these, eight (28%) changed their foraging trip type on a subsequent trip, and of the 18 birds monitored for two or more years, 10 (56%) changed their behaviour between seasons (Table S4.1). Deployment type did not have a significant effect on the percentage of benthic dives ($\chi^2 = 0.51$, p = 0.78), pelagic dives ($\chi^2 = 0.31$, p = 0.86), or transition dives ($\chi^2 = 0.50$, p = 0.78), indicating that the presence of both a TDR and GPS logger or a TDR logger only had no effect on diving behaviour, nor was the order in which the electronics were deployed significant.

Only 9.6% of dives took place at night, indicating that diving at night was not common. While some night dives may have represented late commutes back home, some occurred while penguins were at sea during multi-day trips, so foraging at night was possible. There were insufficient data to determine whether foraging in darkness was an important factor influencing dive type, depth, or other parameters. The mean number of days per foraging trip was 1.8 ± 0.1 (mean ± SE), with 71.6% multi-day trips and 28.4% single-day trips. The mean trip duration was 44.7 ± 2.4 h. Trip duration varied significantly by year ($\chi^2 = 14.59$, $p = 0.00068$), with trips in 2017 shorter than trips in 2015 and 2016. Bird ID did not significantly improve this model fit ($\chi^2 = 2.89$, $p = 0.09$). Sex had no significant effect on trip duration ($\chi^2 = 0.73$, $p = 0.39$).

4.5 Discussion

In this study, we demonstrate diving plasticity in southern yellow-eyed penguins breeding at subantarctic Enderby Island, including variation between years, and within the same breeding season. Results represent the most comprehensive dive data published on yellow-eyed penguins to date. The data also confirm that southern birds dive on average much deeper than do birds of the northern population, and provide evidence for birds adopting both benthic and pelagic diving strategies.

4.5.1 Dive behaviour and modelling

There were three dive types identified in our data: benthic, pelagic, and a small number of transitional dives. Maximum recorded dive depths were 115 m for pelagic diving and 134 m for benthic dive types (Table 4.1, Table 4.3). We developed an algorithm to qualify dive types automatically (Figure S4.1, Table S4.2), which was invaluable for analysing and accurately categorising large numbers of dives. Parameters relating to individual dive depths or times were not used to categorise dive type to ensure the determination of dive type was independent of water depth. This allowed the identification of different dive types, including both benthic and pelagic diving in water of varying depths. This method was useful as our bathymetry information was accurate to 50 m depth increments only, and there was a large overlap in the depth ranges for different dive types (Table 4.3), meaning dive depth alone was not sufficient for categorising dive type. This may have been due to the presence of transition dives, which did not fit the usual criteria defining either benthic or pelagic dives. The depth change between subsequent dives proved a better measure for categorising benthic and pelagic dive types than using dive depth, bottom depth, bottom time, or percentage of time at the bottom, indicating that dive profiles were independent of the water depth in some situations. Both benthic and pelagic diving occurred in shallower coastal waters close to land where the maximum depth is around 35 m, as well as further offshore over the continental shelf where water depths can reach 150 m (Mitchell et al. 2016, Muller et al. 2021; see Chapter 5). Additionally, dive bouts containing dives of similar types could not be defined using surface time intervals as there was no consistent time gap between dive bouts, unlike in other dive research (Chilvers and Wilkinson 2009), including studies on diving yellow-eyed penguins around mainland New Zealand (Mattern et al. 2007, Chilvers et al. 2014).

4.5.2 Diving plasticity

Sex did not have a significant effect on yellow-eyed penguin dive behaviour in the southern population, and males and females conducted similar proportions of benthic and pelagic dives. This is consistent with research from the northern population which found no difference in dive behaviour between sexes (Seddon and van Heezik 1990, Moore 1999, Mattern et al. 2007).

However, bird ID significantly improved the benthic dive model fit when the sex variable was excluded, suggesting that some individual birds of each sex may consistently utilise benthic foraging. Bird ID did not improve the model fit for pelagic and transitional dives (whether sex was included or not) implying there was no link between sex and these dive types, and sex did not significantly affect the proportion of pelagic and transitional diving. Most birds also displayed some pelagic or epipelagic diving bouts, regardless of their foraging preference. During predominantly benthic foraging trips, these pelagic bouts were commonly at the beginning and end of a foraging trip, so some may represent exploratory or travelling dives rather than foraging dives (Figure 4.2, upper left). Additionally, while there may be some evidence for an individual preference or learned behaviour in some individuals, the mean incidence of benthic foraging declined over the three years of monitoring. Some individual birds were observed displaying different behaviour between breeding seasons (Table S4.1), and over a quarter changed their foraging method during the same season (although multiple trips were measured only in 2017). This suggests that foraging behaviour may be flexible and is likely influenced by current prey availability and location as the season progresses. Flexible diving and foraging strategies have been recorded between different colonies of Magellanic penguins *Spheniscus magellanicus* (Sala et al. 2014), implying local-scale differences may be a factor. Like many other penguin species, rockhopper penguins *Eudyptes chrysocome* spp. employ a primarily pelagic foraging strategy, but may switch to benthic feeding if this offers improved foraging success (Tremblay and Cherel 2000). Therefore, it is likely that similar factors may be present for yellow-eyed penguins in the southern population, with some plasticity in the adoption of a benthic or pelagic foraging strategy. Individuals may utilise either, or both strategies, likely influenced by local bathymetry as well as prey availability, which is in turn likely influenced by factors such as water temperature.

Yellow-eyed penguins around mainland New Zealand have been shown to utilise the same foraging areas consistently over different years (Mattern et al. 2007) and this was true in the subantarctic too, with a core foraging area to the east-southeast of Enderby Island used by breeding birds in all surveyed years (Muller et al. 2021; see Chapter 5). The predominantly benthic foraging behaviour observed in the northern population may be influenced by a number of factors including local bathymetry, prey availability and distribution, which can in turn be influenced by warmer water temperature, as well as the possible effect of commercial fisheries in the area. These factors may affect pelagic and benthic prey differently.

Mattern (2006) found that birds from neighbouring Codfish and Stewart Islands exhibited different foraging behaviours from each other, with Codfish Island birds making longer trips and diving deeper during the post-guard breeding phase. This suggests that yellow-eyed penguins may vary their foraging strategy depending on local conditions, and that more energy may be put into diving during the post-guard phase of breeding. While there is currently less evidence for pelagic diving occurring in the northern population, this may have been more common in the past. In addition to diet studies in the 1990s (van Heezik 1990c), some shallower dives were recorded around Otago, and also deep dives that were interspersed with mid-water dives (Moore et al. 1995), which may have been an indication of pelagic foraging. Moore also noted that although individuals tended to be either inshore or offshore foragers, some could switch strategies (Moore 1999), and foraging areas shifted between years and with different breeding phases (Moore et al. 1995, Moore 1999).

While benthic dives are constrained by seafloor depth, the range of dive profiles evident around the Auckland Islands suggests that the influences of factors other than bathymetry were governing dive behaviour in this area. At times when both types of foraging behaviour were evident in areas with similar bathymetry, the difference seems to be driven in some part by individuals' foraging decisions and presumably prey assemblages. Given that there is considerable overlap in dive depth between pelagic and benthic diving in the southern population (Figure 4.3), it may be expected that pelagic diving could also occur at similar depths in other locations. The small sample of TDRs deployed on Campbell Island indicated a bottom feeding strategy there (P. J. Moore, pers. comm.); however, this does not preclude the possibility of pelagic diving also occurring. The much lower incidence of pelagic foraging reported around the mainland may indicate that other factors such as prey availability could be influencing diving behaviour and foraging strategy in the northern population, as it seems unlikely that this genetically similar population would be unable to display similar diving plasticity where similar circumstances occur. Our data included only dives during the guard phase, so there may be more or less plasticity in dive behaviour or foraging location in the southern population during other breeding phases. Birds from the northern population tend to make shorter trips and feed closer to shore during the guard stage when chicks need to be fed often, whereas during incubation and post-guard stages, birds range more widely from the breeding area (Moore 1999). Other studies into penguin diving have shown differences in behaviour, including foraging area utilisation, in little penguins between different breeding phases (Sánchez et al. 2018). Little penguins from different habitats around mainland New Zealand also display a large variation in foraging strategy and breeding success (Chilvers 2017a, Chilvers 2019).

Yellow-eyed penguins use vision to navigate underwater and locate prey (Mattern et al. 2007), which is consistent with the majority of dives taking place during daylight. However, a small number of feeding dives occurred at night. Studies with other visual predators have shown that feeding at night is possible, particularly with pelagic foraging strategies, when using illumination from moonlight or phosphorescence in the water (Muller 1998). Visibility will also affect the ability of a visual predator to locate prey, and factors affecting water turbidity may therefore also influence dive behaviour. As visual predators, any reduction in water clarity could affect penguins’ ability to navigate and undertake benthic foraging, and consequently may favour pelagic over benthic diving strategies.

4.5.3 Different foraging strategies between populations

Yellow-eyed penguins currently inhabiting mainland New Zealand and offshore islands originated from the subantarctic, dispersing north after the original mainland species (*Megadyptes waitaha*) was eliminated soon after Polynesian settlement (Boessenkool et al. 2009a). Therefore, any differences in diving and foraging behaviour between locations are more likely due to local environmental factors than genetic predisposition.

Benthic diving occurs in the shallower water around mainland New Zealand, with U-shaped dive profiles and maximum depths consistent with the local bathymetry (Mattern et al. 2007, Mattern et al. 2013). Benthic dive depths will be dictated by the water depth, and benthic dives were around 40–60 m (max. 66 m) at Otago Peninsula and 80–110 m at the Catlins, in areas where the continental shelf is 40–80 and 80–120 m deep, respectively (Moore et al. 1995, Moore 1999). The depth range for foraging around mainland New Zealand is much shallower in some areas than our recorded maximum depths for pelagic and benthic diving (Table 4.1, Table 4.3), and with the inclusion of greater amounts of pelagic foraging in the subantarctic, this suggests that the southern population are making use of a greater vertical area for foraging. In comparison, yellow-eyed penguins have a much larger area of relatively shallower water to forage in off the mainland coast, which may favour a more benthic foraging strategy. Some deeper dives have been reported to 128 m (Moore et al. 1995) and 156 m (Young 2018) at the Catlins where the continental shelf is deeper, implying that benthic diving depths are adaptable depending on local bathymetry. There was some overlap in maximum depth ranges for benthic and pelagic dives in the southern population (Figure 4.3), implying both dive types occurred at a range of depths in the core foraging area. Deeper dives have been recorded at Campbell Island in the New Zealand subantarctic (Figure 4.1), with depths up to 158 m recorded during benthic dive bouts of birds in the post-guard breeding phase (determined from two TDRs; P. J. Moore, pers. comm.). This is consistent with benthic foraging on the continental shelf, which is around 130 to 200 m deep at that location (Mitchell et al. 2016). The Enderby birds were diving over a similar shelf depth of around 100 to 150 m, suggesting that Campbell birds may also have the opportunity to utilise a mixed foraging strategy incorporating pelagic diving. As dive loggers have been deployed on only two birds at Campbell Island, further dive research there would be valuable for management of the species.

Deeper diving around the subantarctic Auckland Islands, and likely also Campbell Island, reflects the deeper water depth over the continental shelf in these locations (Mitchell et al. 2016). Both benthic and pelagic dives occurred in the same general location at the Auckland Islands, suggesting that factors other than bathymetry were influencing foraging behaviour there. Deeper water may restrict benthic diving due to the physiological demands associated with diving to the benthos (Costa et al. 2004). However, the deeper water may also introduce new opportunities for pelagic foraging which may not be as common around mainland New Zealand. Yellow-eyed penguins from Otago have been recorded undertaking shallow travelling epipelagic dives centred in the upper 10 m of the water column (with a range of 0.5 to 32 m depth) (Mattern et al. 2018a). Using animal-borne cameras, these dives were confirmed to be principally travelling dives to and from the core foraging area (Mattern et al. 2018a).

Dive time will have a physiological limit, meaning the bottom time will be reduced during deeper dives. This will reduce the time available to find and capture prey, and may mean it is not profitable to dive benthically if the substrate at the bottom is not a reliable predictor of prey availability and ease of capture. Benthic diving by yellow-eyed penguins foraging around mainland New Zealand occurs over a range of substrates including sand flats, shingle, cobbles, and inshore reefs (Andrews 1973, Mattern et al. 2007). The bottom phase of the dive includes a mix of searching for camouflaged prey, followed by high-speed prey pursuit (Mattern et al. 2018a). Many unsuccessful predation attempts result from the prey species finding refuge on the sea floor (Mattern et al. 2018a), which would be much less likely during mid-water foraging. Some larger benthic species, such as blue cod *Parapercis colias*, require a greater energy expenditure to locate and capture (Mattern et al. 2018a), a skill which may therefore be improved with age and experience, as has been shown for a range of survival skills (Forslund and Pärt 1995). Such difficulties may limit juveniles to foraging on more accessible mid-water prey, which is consistent with recorded foraging tracks in areas with a maximum water depth of 150 to 3000 m (C. G. Muller, unpubl. data; see Chapter 5).

We identified a small number of transition dives which were characterised by a large variation in maximum dive depth between two subsequent dives. These had similar profiles to pelagic dives, but with a much greater variation in depth. However, the majority were associated with benthic diving (before and after, as well as interspersed in the middle of benthic diving bouts). These dives may therefore represent a transition between benthic and pelagic diving behaviour, exploratory dives while searching for prey, or dives where prey was encountered in mid-water on the way down, or for some other reason where a dive to the benthos was aborted. Recent studies where cameras were deployed on foraging yellow-eyed penguins illustrated instances where birds took some time to swallow larger prey items. On some occasions, birds released the prey during the ascent and returned to the surface to breathe, then reacquired the prey in mid-water to continue the encounter (T. Mattern, pers. comm.). This correlates with the large depth variability observed between transition dives and could explain why many instances were associated with bouts of benthic diving. These transition dives may also represent periods of rest where penguins were making shallower dives following a series of deeper dives, or possibly the physiological limits when an individual was unable to continue making deeper dives straight away. Swimming underwater has been shown to use less energy than swimming at the surface for penguins; however, deeper diving uses more energy and requires a longer recovery time (Baudinette and Gill 1985). Benthic foraging is more energetically demanding, and benthic-diving mammals have a greater probability of exceeding their physiological aerobic dive limit than for pelagic diving (Costa et al. 2004, Chilvers and Wilkinson 2009).

4.5.4 Implications for breeding success

Both 2015 and 2017 had poorer breeding outcomes for yellow-eyed penguins on Enderby Island compared to 2016. There were similar numbers of nesting attempts on Enderby Island during these years, but both were significantly lower than during 2016 (Muller et al. 2020b; see Chapter 3). However, overall fledging success on Enderby Island was significantly lower in 2017 (Muller et al. 2020b), due to a large egg mortality that year (C. G. Muller, unpubl. data; see Chapter 7). The number of breeders and breeding attempts in a population is likely to be dependent on longer-term factors affecting adult foraging and body condition prior to the breeding season (Forslund and Pärt 1995), whereas nest failures during a breeding season are more likely due to more immediate factors. These could include prey availability and the ability of parents to provision chicks (Forslund and Pärt 1995), as well as sudden weather events (Grémillet and Boulinier 2009).

The distribution and availability of prey species, particularly mid-water prey utilised by pelagic foragers can be affected by Sea Surface Temperature (SST) (Grémillet and Boulinier 2009, Agnew et al. 2015). Therefore, processes such as the ENSO and climate change which can affect SST (Grémillet and Boulinier 2009) are likely also to affect the foraging success of yellow-eyed penguins. Warmer water has been shown to negatively influence mainland yellow-eyed penguin foraging (Young 2014, Mattern and Ellenberg 2018). As a result, the degree of foraging plasticity demonstrated by a population can affect its ability to respond to environmental variability.

Yellow-eyed penguin population declines have previously been associated with El Niño conditions (Peacock et al. 2000, Darby 2003). However, the situation is now believed to be more complex, with breeding outcomes more variable in El Niño conditions and affected also by large changes in ENSO conditions (Young 2014). La Niña conditions in the New Zealand region are associated with warm water events on the Pacific coast, and more stochastic weather and wind patterns, which have been shown to negatively affect yellow-eyed penguin breeding success more strongly than El Niño conditions (Young 2014). Little is known about the effects of ENSO on southern yellow-eyed penguins, and whether this may vary from the northern population. The 2015 season was the strongest ENSO recorded since monitoring began in 1950 (Null 2019), and corresponded with 100% benthic foraging for the monitored yellow-eyed penguins on Enderby Island (Figure 4.5). Conversely, 2016 and 2017 were both weak La Niña years (Null 2019), which corresponded with greater amounts of pelagic foraging (Figure 4.5). The 2015 season also coincided with poor breeding in the northern population, where there was a 20% decline in the number of breeding pairs around mainland New Zealand compared with the previous year (Department of Conservation 2019).

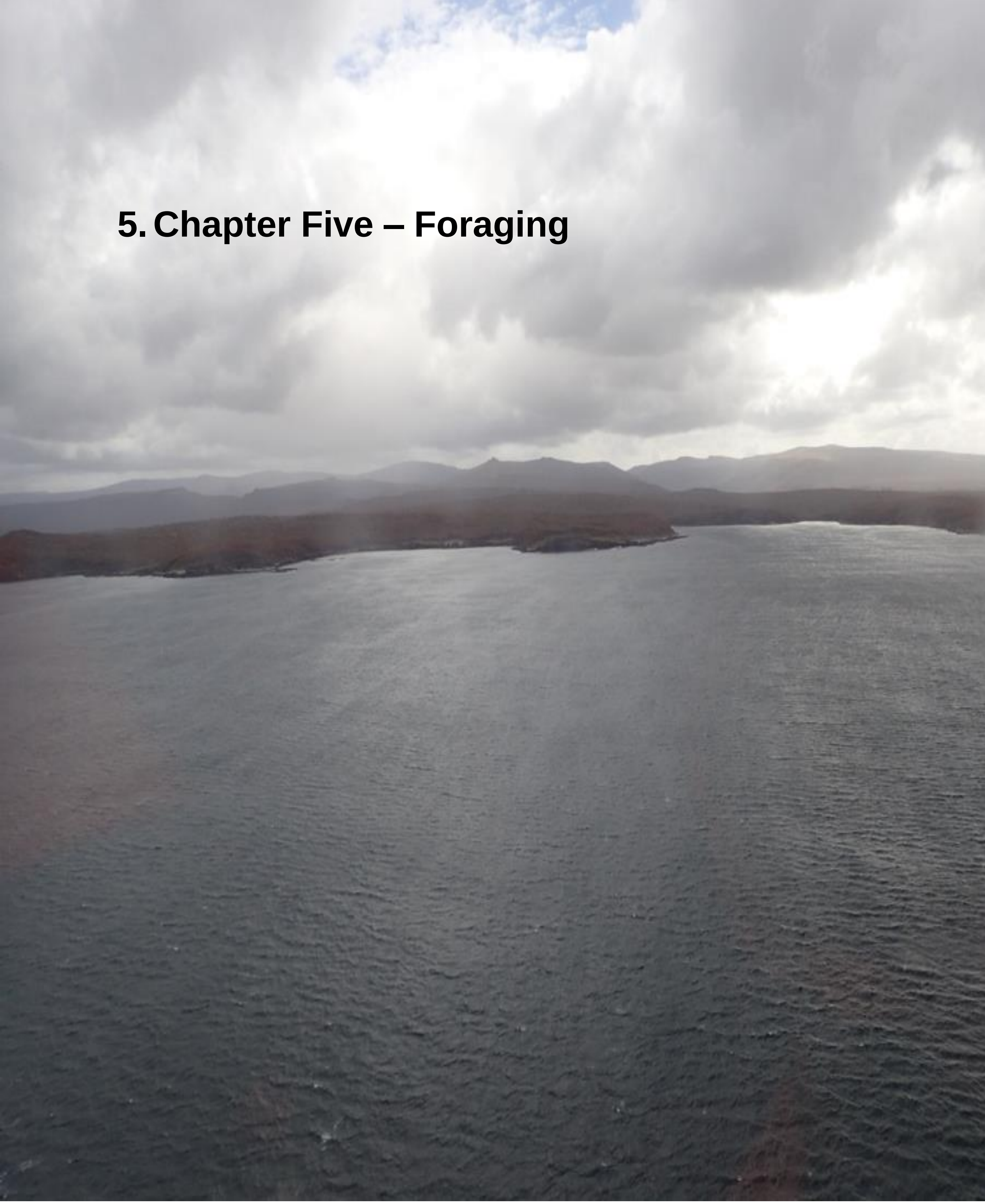
Foraging trips in 2017 were significantly shorter than in 2015 or 2016 which is consistent with the greater proportion of pelagic foraging in 2017 (Figure 4.4, Figure 4.5). There was no evidence this effect was due to individual preference (bird ID, random effect), implying an overall shift in diving behaviour by a proportion of the population. Foraging variation between years did result in an increase in the proportion of pelagic dives (Figure 4.4) and pelagic foraging trips (Figure 4.5) during La Niña conditions. During 2016, around 33% of foraging trips included pelagic foraging, rising to 79% in 2017 (Figure 4.5).

Benthic prey species often represent a predictable, evenly distributed prey source, although typically occurring at low densities (Costa et al. 2004). Benthic prey are also less influenced by oceanographic perturbations such as ENSO than are pelagic prey (Costa et al. 2004), and benthic foraging has been shown to be a predictable and reliable food source for subantarctic New Zealand sea lions *Phocarctos hookeri*, even during particularly strong El Niño years (Chilvers and Wilkinson 2009). In contrast, pelagic prey tend to occur in unpredictable, higher density aggregations, such as schools and bait balls, providing a richer food source once located (Chilvers and Wilkinson 2009). Benthic foraging around the Auckland Islands was most prevalent in the 2015 El Niño season and corresponded with a lower number of nesting attempts. The 2016 La Niña season had an increasing proportion of pelagic diving and a higher number of nesting attempts. However, the 2017 La Niña season had the greatest proportion of pelagic diving, but a lower number of nesting attempts than 2016 (comparable to 2015), indicating that factors in addition to the current ENSO state may also be affecting foraging behaviour and breeding success. These data demonstrate it is likely that yellow-eyed penguins are able to take advantage of more mobile pelagic resources when available, and when the cost–benefit ratio outweighs a benthic foraging strategy. This correlates to some extent with improved outcomes for breeding.

4.6 Conclusions

Pelagic foraging is common amongst penguin species, and we have demonstrated for the first time that this is also true for yellow-eyed penguins foraging in the Auckland Islands. This is in contrast to previous research on yellow-eyed penguins around mainland New Zealand, where they have been described as predominantly benthic foragers. Southern yellow-eyed penguins are genetically similar to the northern population and are the source population for migrants which have colonised the mainland, so it is likely that greater foraging plasticity in this subantarctic population represents better foraging conditions there. Our data from the Auckland Islands show that yellow-eyed penguins demonstrate diving plasticity with a range of different diving and foraging behaviours evident, and are able to switch strategies to take advantage of local conditions and prey availability. An observed reliance on a benthic foraging strategy around the mainland may therefore be a relatively new adaptation to local bathymetry or prey distribution. While the northern population may be near the limit of their biological range, they may also have some capacity for pelagic diving, and therefore the possibility of diving plasticity given suitable prey availability. However, factors affecting prey species' abundance and distribution, such as warmer water temperature and impacts of commercial fisheries, may become more significant in the future, particularly for pelagic foraging where prey availability can be more variable in time and space. Benthic foraging may provide an alternative stable food supply for both populations when pelagic prey is unavailable. However, a reliance on benthic foraging by subantarctic penguins in some years (such as occurred in 2015) may disadvantage these populations where the deeper benthos requires greater energy expenditure to reach. Despite demonstrating greater diving plasticity at the present time, the southern population is likely still vulnerable to changes affecting their food supply, including those due to ENSO fluctuations and climate change. These results may suggest a greater capacity to respond to future environmental change in the subantarctic habitat, although this is by no means certain given that fluctuations and declines have previously been noted in the southern population as well.

5. Chapter Five – Foraging



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STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the candidate and the candidate's Primary Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of candidate:	Chris Muller
Name/title of Primary Supervisor:	Louise Chilvers

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Foraging areas and plasticity of yellow-eyed penguins (*Megadyptes antipodes*) in their subantarctic range

Muller, C. G., Chilvers, B. L., Chiaradia, A., French, R. K., Kato, A., Ropert-Coudert, Y., and Battley, P. F. (2021) Foraging areas and plasticity of yellow-eyed penguins (*Megadyptes antipodes*) in their subantarctic range. Marine Ecology Progress Series, 679:149–162.

5.1 Abstract

Foraging behaviour is crucial to breeding success for marine predators, including seabirds. Yellow-eyed penguins *Megadyptes antipodes* are central-place, predominantly benthic foragers around mainland New Zealand. The northern (mainland) population of this endangered species is declining, with changes in the marine environment a suspected cause, particularly warming water and poorer foraging success. We undertook a detailed foraging study of the data deficient southern (subantarctic) population, which is distinct from the northern population. Over two breeding seasons (2016 and 2017), we collected 91 GPS foraging logs from 69 breeding yellow-eyed penguins from Enderby Island, Auckland Islands, New Zealand. The mean foraging distance was 24 km from shore (max 47 km). Foraging area size was greater for females and for pelagic foragers, although benthic foragers travelled further from shore on average. Diving plasticity was evident both in diving behaviour and foraging area use. Foraging area and distance from shore were greater for all birds in a year of greater breeding effort and fledging success (2016). Foraging occurred over continental shelf waters, similar to the mainland, and in areas up to 150 m deep, so any differences in foraging behaviour compared to those reported for the northern population are likely influenced by local bathymetry, environmental conditions, and individual preference. Despite comparable bathymetry in some areas, the southern population showed greater foraging plasticity, with 62% of foraging trips categorised as

pelagic, implying that subantarctic foraging conditions may differ from the predominantly benthic foraging around mainland New Zealand. Variable foraging conditions may therefore have implications for future breeding success in the southern population.

5.2 Introduction

Many marine predators are central-place foragers, including seabirds and pinnipeds that breed on land but forage at sea, returning ashore to provide for their young (Boyd et al. 1994, Boersma and Rebstock 2009, Jones et al. 2020). Finding food is essential for breeding success and population viability for long-lived marine predators (Villegas-Amtmann et al. 2008, Chilvers and Wilkinson 2009), including seabirds (Sandvik et al. 2005, Catry et al. 2013). Seabird foraging success can vary between years, as oceanic conditions, reflected in indices such as the El Niño Southern Oscillation (ENSO), can change and may affect prey abundance and distribution (Boyd et al. 1994, Miller and Sydeman 2004, Grémillet and Boulinier 2009, Ropert-Coudert et al. 2009, Catry et al. 2013, Agnew et al. 2015, Ropert-Coudert et al. 2015, Poupart et al. 2017).

Foraging plasticity describes the adaptability of an organism to changes in its environment with respect to foraging behaviour. While this can include changes in the type of foraging method used (e.g., benthic vs. mid-water or pelagic diving), plasticity can also include other changes related to foraging location. Foraging over a greater area may increase the time and effort required, while foraging closer to or further from shore may also correspond to changes in water depth, and all foraging changes can expose a predator to different prey assemblages. Benthic prey are less influenced by oceanographic perturbations such as ENSO and they may be a more reliable food source than pelagic prey over time (Costa et al. 2004). However, changes to the benthos can affect benthic penguin foraging (Browne et al. 2011). One approach to classify benthic and pelagic dives is by determining dive shape and depth. Benthic dives to the seafloor are characterised by a U- or square-shaped dive profile with a uniform maximum depth limited by bathymetry (Wilson 1995, Tremblay and Cherel 2000, Pütz and Cherel 2005, Bost et al. 2007). Conversely, pelagic dives occur in mid-water and display a V- or W-shaped dive profile with a more variable maximum depth between dives, with the former sometimes considered exploratory behaviour, and the latter linked with prey-pursuit activity (Wilson 1995, Ropert-Coudert et al. 2000, Pütz and Cherel 2005). Pelagic dives tend to have a shorter bottom time and maximum depth, given that prey could be encountered anywhere in the water column (Wilson 1995, Tremblay and Cherel 2000, Pütz and Cherel 2005, Bost et al. 2007). When foraging, most penguin species rely on pelagic feeding dives, catching prey within the water column (Ratcliffe and Trathan 2011), although some species such as southern rockhopper penguins *Eudyptes chrysocome filholi* have a mixed strategy incorporating both pelagic and benthic diving (Tremblay and Cherel 2000).

Yellow-eyed penguins (hoiho, *Megadyptes antipodes*) are Endangered (Couch-Lewis et al. 2016, BirdLife International 2020, Department of Conservation 2020a), and endemic to New Zealand. Their distribution is restricted to the south-east of the South Island, Stewart and Codfish Islands (the northern population), and subantarctic Auckland and Campbell Islands (the southern population; Figure 5.1) (Seddon et al. 2013).

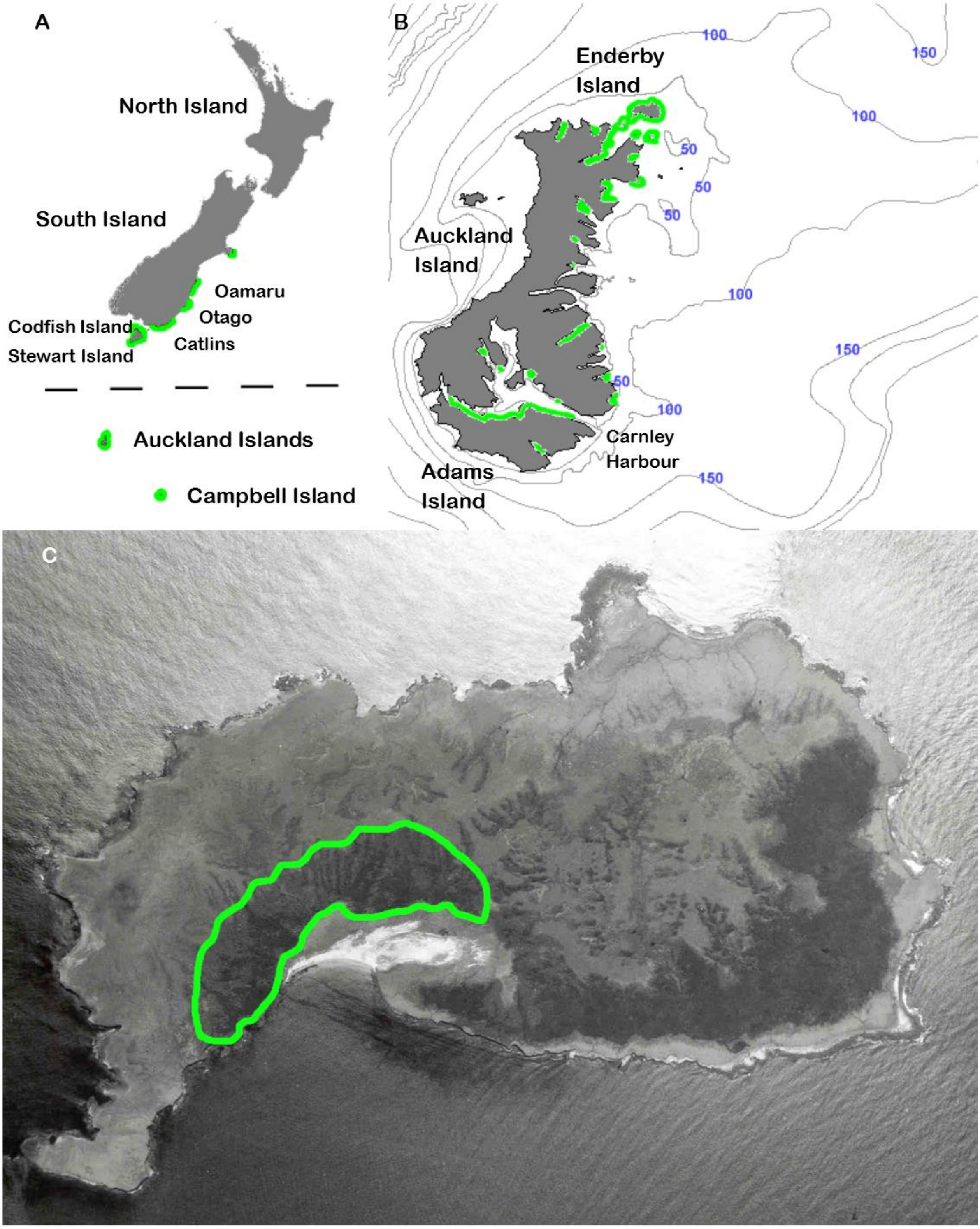


Figure 5.1 A) Breeding range of yellow-eyed penguins (green highlights) around the New Zealand mainland (northern population; above the dashed line) and in the subantarctic (southern population; below the dashed line). B) Auckland Islands archipelago, with Enderby Island to the northeast (ca. 4.5 km wide, 50° 29’ 45’’ S, 166° 17’ 44’’ E). Selected depth contours are labelled in blue, from Mitchell et al. (2016). C) Close-up of Enderby Island, showing the area where breeding birds were sampled (green). Modified from Figure 4.1 in Chapter 4, Muller et al. (2020a).

The northern population is undergoing a severe decline due to successive poor breeding seasons and high adult mortality, thought to be primarily a result of threats at sea including poor foraging success, fisheries interactions, pollution, and human disturbance (Couch-Lewis et al. 2016, Mattern et al. 2017, Mattern and Wilson 2018, Department of Conservation 2020a). At least 60−79% of the total yellow-eyed penguin population is estimated to breed in the subantarctic (Couch-Lewis et al. 2016, Department of Conservation 2020a, Muller et al. 2020b; see Chapter 3), which is considered the stronghold for the species. The southern population appears stable at present, but with evidence of wide fluctuations and a possible decline at the Auckland Islands since the 1980s (Moore 1992b, Muller et al. 2020b). The Campbell Island population also fluctuated from 1987 to 1998 (Moore et al. 2001), but no recent data are available. Analysis of ancient DNA has shown that the original endemic mainland species *M. waitaha* went extinct soon after Polynesian settlement of New Zealand ca. 1280 CE (Boessenkool et al. 2009a, Collins et al. 2014). Yellow-eyed penguins from the subantarctic expanded their range into this vacant niche and colonised the mainland in the last few hundred years, prior to the increase of European settlers in the late 1800s (Boessenkool et al. 2009a). However, there is currently very little migration (<2%) between the mainland and subantarctic, meaning these areas represent separate populations and management units (Boessenkool et al. 2009b). Basic population ecology information is required for the southern population, which is data deficient (Muller et al. 2020b).

During breeding, yellow-eyed penguins are central-place foragers, and the northern population feeds in shallow coastal waters adjacent to their breeding area, and over mid-shelf areas further from shore where they have access to a large shelf area (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). Around mainland New Zealand, foraging trips are typically up to 25 km from shore and over mid-shelf areas, as confirmed by very high frequency (VHF) radio and GPS tracking studies (Moore 1999, Mattern et al. 2013), although the mean foraging distance can be as short as 6.2 km from shore at some locations (Mattern et al. 2007). Birds from Codfish Island may forage further from shore and over a wider area than birds from neighbouring Stewart Island (Mattern 2006). Many published studies on the northern population involved small numbers of birds, from different locations, in different years, and in some cases during different breeding phases (see Table 5.3). Consequently, while some studies give a relatively good picture of what was happening during a particular time period and location, they may not represent the full range of foraging behaviour of the entire northern population. While diet studies in the 1990s showed occasional indications of pelagic foraging (van Heezik 1990a, Moore et al. 1995), more recent dive data demonstrated a predominantly benthic foraging strategy for the mainland population (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014). In contrast, birds in the southern population use a mixed strategy incorporating varying amounts of pelagic foraging at the subantarctic Auckland Islands, including solely pelagic foraging trips (Muller et al. 2020a; see Chapter 4). Moreover, yellow-eyed penguins in the southern population forage at greater depths than in many northern areas, with a maximum recorded depth of 134 m for benthic dive bouts, and 115 m for pelagic dives for Enderby Island birds (Muller et al. 2020a).

The ENSO is a weather phenomenon which influences rainfall, sea surface temperature (SST), and wind patterns in the Pacific Ocean (Null 2019). The 2015 austral summer was a very strong El Niño (≥2.0°C SST anomaly), and the 2016 and 2017 summers were both weak La Niña events (−0.5 to −0.9°C SST anomaly) (Null 2019). Yellow-eyed penguin foraging is negatively influenced by warmer water in the northern population (Young 2014, Mattern and Ellenberg 2018). Strong La Niña conditions result in warmer water and more stochastic weather and wind patterns in the New Zealand region, with an adverse effect on yellow-eyed penguin breeding success in the northern population (Young 2014). Increasing SST, which can result from La Niña conditions, may cause declines in the northern population in some years (Darby 2003, Mattern et al. 2017). SST and rainfall have the greatest effect on breeding parameters, including some lag effects in subsequent years (Peacock et al. 2000), although more research is needed to determine how variation in prey productivity is related to climate. There is no information about the effects of ENSO and climate variability on foraging and breeding success in the southern yellow-eyed penguin population, and whether this may vary from the northern population.

The southern population displays widely variable breeding success, which is likely linked to foraging success (Moore 1992b, Muller et al. 2020b; see Chapter 3). Foraging parameters are a product of the physical environment, changing environmental parameters, or individual preference to target specific prey in particular habitats. The southern populations forage in deeper water and over greater distances than many northern birds do (Muller et al. 2020a; see Chapter 4) and may be expected to expend more energy foraging. Therefore, the aims of this study were to determine the size and location of foraging areas used by yellow-eyed penguins breeding at Enderby Island in the New Zealand subantarctic (Figure 5.1), as well as any differences in foraging area size and distance from shore between birds of different sex, diving behaviour, or between different years. We compared foraging habits to published data for the northern population. Given the importance of the southern population to the species, greater knowledge of foraging behaviour by southern yellow-eyed penguins is vital to inform research on diving behaviour and breeding success in the area. This information will also assist with future conservation management of the species and marine-based threats in these isolated subantarctic areas.

5.3 Methods

5.3.1 Fieldwork and equipment

Fieldwork was carried out on Enderby Island, Auckland Islands, in the New Zealand subantarctic (50° 29’ 45” S, 166° 17’ 44” E, Figure 5.1). GPS data were collected for two breeding seasons, 2016 (November 2016−February 2017) and 2017 (November 2017−January 2018), while dive and breeding success data were collected for the 2015−2017 seasons in parallel studies (Muller et al. 2020a, Muller et al. 2020b; see Chapters 3 and 4). Nests were located using manual ground searches, ground-based VHF telemetry, and an unmanned aerial vehicle equipped with a VHF radio receiver (Muller et al. 2019; see Chapter 2). Adult yellow-eyed penguins were captured by hand as they returned from sea and placed in a capture bag for processing and collection of morphometric data using a spring balance and callipers. Birds were marked with a microchip (Allflex) for permanent identification (Muller et al. 2020b), and sex was determined using the relationship between head length (including beak) and foot length (Setiawan et al. 2004), or the relative sizes between breeding partners with males assumed to be the larger individual (Setiawan et al. 2004).

Data loggers were deployed during late November and December, corresponding to the guard phase of breeding. GPS loggers were attached using waterproof tape (TESA) to the lower back to optimise streamlining (Bannasch et al. 1994) and orientation to the sky during the typical posture adopted during swimming or brooding (Muller et al. 2020a). For consistency, time−depth recorder (TDR) loggers were always taped to the centre of the back, below the shoulder blades (Figure 5.2) even when no other electronics were attached.

Figure 5.2 Nesting yellow-eyed penguin with a time‒depth recorder and very high frequency transmitter attached to the centre of the back, and a GPS logger attached to the lower back: inset shows close-up view. Enderby Island, Auckland Islands, New Zealand subantarctic. Photo credit: C. G. Muller

GPS loggers were customised Cat-TraQ™ GPS loggers (Catnip Technologies), with time-to-fix of 45 s cold start, 35 s warm start, 1 s hot start. Units were modified for underwater use with the addition of a magnetic on/off switch, and a moulded resin housing (Pelletier et al. 2014), 45 × 30 × 12 mm, weight ~25 g. These GPS loggers have been used in a number of penguin foraging studies (Pelletier et al. 2014, Carpenter-Kling et al. 2017, Sánchez et al. 2018, Phillips et al. 2019). GPS loggers were programmed to record a fix every 3 min, providing a battery life of approximately 4‒5 d. This was necessary, as birds remained on the nest for a period of time before commencing their logged foraging trip; the maximum foraging trip duration of all TDR deployments from 2015‒2017 (n = 134) was up to 113.3 h (4.7 d) (Muller et al. 2020a), and fine-scale position logging was not needed to identify foraging locations. After programming, each GPS logger was waterproofed with heat-shrink tubing, weighing ~5 g (TE Connectivity) before deployment. TDR tags were LAT 1400 loggers with 128 kB of memory, 11 × 35 mm, weight 5 g (Lotek). These were programmed to log pressure every 5 s when wet, to allow sufficient data storage for long trips. VHF transmitters, V1G118A with 150 or 220 mm whip antenna, 20 × 13 × 6 mm, weight 4.5−5 g (Sirtrack) were attached to the dive loggers to monitor when penguins were ashore and assist with recovery of electronics. TDRs and VHF transmitters were attached following a similar protocol (Muller et al. 2020a). Where possible, loggers were retrieved after one foraging trip to minimise attachment time. Additional TDR-only deployments were carried out in 2015 and 2017, and 31 paired deployments in 2017 allowed comparison of dive behaviour with and without the addition of the larger GPS logger (Muller et al. 2020a).

5.3.2 Data Analysis

Total trip duration was determined using the wet/dry switch on the TDR logger, as this was considered more accurate than the GPS log. GPS data files were downloaded and filtered by deleting any duplicate records (those with a distance of 0 m between subsequent positions), and any with implausible changes in distance or speed. Positions were interpolated to account for missed GPS fixes when the unit was underwater during a scheduled fix attempt. Interpolation used a custom-made script in Python 3.5.2 (Python Software Foundation, www. python.org), which added missed positions (at 3 min intervals) assuming a constant heading and velocity between recorded locations. Where multiple foraging trips were recorded in one deployment, the data were considered as separate trips (Muller et al. 2020a; see Chapter 4). Spatial analyses were performed in ArcGIS 10.2.2 (ESRI), with the National Institute of Water and Atmospheric Research (NIWA) New Zealand region bathymetry data at depth contours in 50 m increments overlaid for comparison (Mitchell et al. 2016). Points on land, generated before or after a foraging trip, were deleted using a spatial selection tool in ArcGIS. Data were projected in the New Zealand Transverse Mercator coordinate system, and geodesic distance calculations between points were automated in a Python script using the ‘GeoPy’ library.

The foraging distance (maximum straight-line distance away from the shore, measured from the sea access point) and the total trip distance (cumulative distance travelled between all points in a foraging trip, including the start and end location at the sea access point) were calculated from interpolated data. Summary data were calculated from these distances (mean ± SD). Comparisons with trip data collected independently using the wet-dry switch on the TDR logger (Muller et al. 2020a) indicated that some GPS logs may have been partial trips, and may not accurately represent the furthest distance travelled (see Figure S5.2). Consequently, these values represent minimum estimates of the actual foraging distances. For comparison, foraging distance means were also calculated with some partial trips (≤5% GPS fix success) removed. All GPS fixes were included for all other distance analyses, statistical tests, and when determining area calculations.

Foraging areas were analysed using GME 0.7.3.0 (Spatial Ecology) and ArcGIS functions (Beyer 2012, Locher and Lindenberg 2016). Position data were grouped according to year, dive type, and sex for kernel density estimates (Worton 1989), which were determined with smoothed cross-validation bandwidth, and a cell size of 50 m. Values were calculated using 95% and 50% kernel contours to represent the home range and core foraging areas, respectively (Hamer et al. 2007), and isopleth and polygon features were imported into ArcGIS for further spatial analysis. The intersection between home range kernel density polygons was used to compare the percentage overlap of foraging activity location between groups of interest representing different years, sexes, and dive types (i.e., benthic or pelagic diving).

Dive data were categorised separately using Bayesian analysis (see Muller et al. (2020a)). Individual dives were classified as benthic if they displayed an inter-dive depth change of less than 2.9% from both the previous and following dives. Foraging trips were also classified, with benthic trips having more than 3.6% benthic dives, which ensured that remaining trips classified as pelagic contained almost exclusively pelagic diving bouts (Muller et al. 2020a). Dive analysis included all dives >2 m depth which likely included some travelling dives to and from the foraging area. Polygon areas were calculated in ArcGIS, along with percentage of spatial overlap between different foraging areas. All GPS data were used to determine foraging areas. When commuting, penguins swim quickly and surface only briefly (Mattern et al. 2007). Therefore, due to the time-to-fix and programmed fix rate of the GPS loggers, whenever a GPS fix was collected, the penguin was most likely resting at the surface between dives, rather than commuting.

Statistical analyses were performed in R Studio version 1.1.456 running R version 3.5.1 (R. Core Team 2017), and using the ‘lme4’ package (Bates et al. 2015). All continuous variables were visually assessed to be normally distributed using histograms and Q-Q plots, so dependent variables were not transformed. Linear mixed effects models were used to compare maximum foraging distance and total trip distance with year, dive type, and sex (as fixed variables), and with bird ID as a random effect (since some birds made more than one trip). For each model, the homogeneity of variance was visually confirmed using residuals vs. fitted value plots. ANOVAs were used to determine the significance of effects in each model. For comparison, statistical tests on distance were also repeated with subsequent trips by the same individual excluded from analysis, and separately with suspected partial trips (≤5% GPS fix success) excluded to see if these significantly affected the model results. Trip duration was also compared with foraging distance and total distance using a linear model. Graphs were generated in R, including the ‘ggplot2’ package (Wickham 2016).

5.4 Results

5.4.1 Foraging area

A total of 91 GPS foraging tracks were collected (55 in 2016, and 36 in 2017), from 69 individual birds (Table 5.1; Table S5.1). These data included 51 trips made by 38 females and 39 trips by 30 males, plus one trip by one bird of unknown sex. Seven birds had GPS tracks logged for two or more foraging trips in 2017 and two birds in 2016, and 12 birds were tracked in both years, with three individuals tracked for multiple trips both between years, and during a year.

Table 5.1 Summary of foraging logs collected from breeding yellow-eyed penguins from Enderby Island (n=91), showing the number of logs collected in each category, and the number of individual birds (n=69). Where multiple foraging trips were recorded in one deployment, the data were divided into separate trips. Not all deployments were successful, and in at least one case a logger collected multiple foraging trips before being recovered. More detail on the GPS tracks collected (including analysis by category) is summarised in the Results section, and the full list of foraging trips is shown in Table S5.1. In 2016 all birds received a GPS and TDR logger, and in 2017 a subset of 31 birds carried different data loggers on two separate occasions (one with GPS + TDR, and one with TDR only) with the order randomised. These paired deployments were used to analyse the effect on diving behaviour of carrying the larger GPS loggers (Muller et al. 2020a).

Foraging logs		**Individuals**	
Year	**91**	**Birds**	**69**
2016	55	Males	30
2017	36	Females	38
		Unknown	1
Sex	**90**		
Males	39		
Females	51		
Dive Type	**87**		
Benthic	35		
Pelagic	52		

Yellow-eyed penguins foraged over a continental shelf plateau approximately 30−40 km south-east of Enderby Island (**Figure 5.3**), where the water depth is predominantly 50−100 m, with some spill-over into deeper water up to 150 m deep.

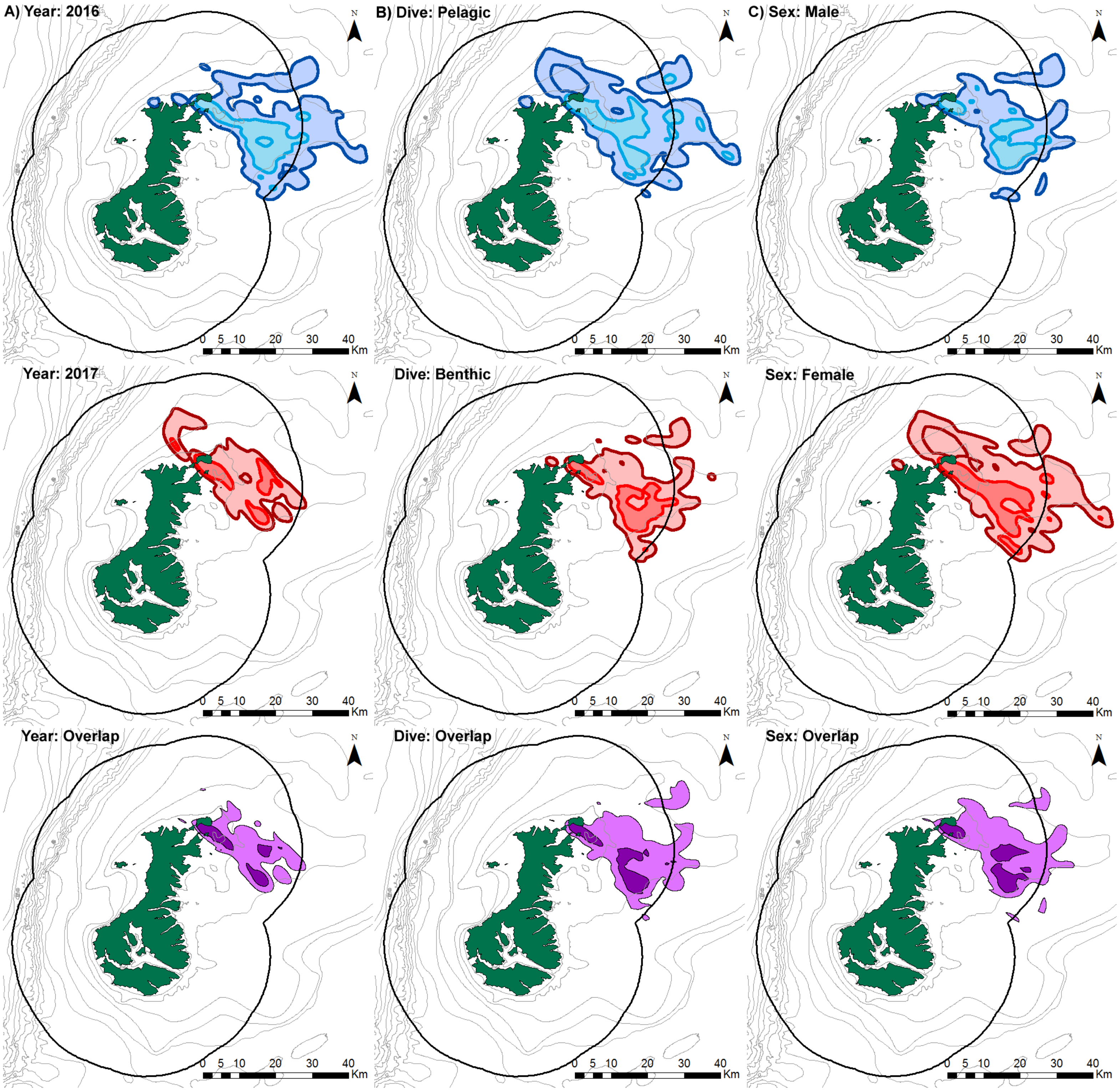

A) Year: 2016
B) Dive: Pelagic
C) Sex: Male
Year: 2017
Dive: Benthic
Sex: Female
Year: Overlap
Dive: Overlap
Sex: Overlap
N
0 5 10 20 30 40
Km

Figure 5.3 Kernel density estimates of yellow-eyed penguin foraging trips to compare different parameters showing comparison by A) year, B) dive type, and C) sex. In all cases, 95% contours (outer polygons) indicate combined home range use, and 50% contours (inner polygons) indicate combined core foraging area use. The spatial intersection of kernel density estimates (lower panels) show the overlap areas common to both parameters (upper and middle panels). The overlap outer 95% contours (violet) indicate shared home range use and inner 50% contours (purple) indicate shared core foraging use. Also shown on all maps are depth contours (light grey), for which selected depth values are labelled in Figure 5.1, and the extent of the marine reserve 12 nautical miles from shore (black line).

Of the 87 GPS tracks where dive type was determined from accompanying TDR data, 35 (40%) corresponded to benthic and 52 (60%) to pelagic foraging trips, with 42% pelagic foraging in 2016 and 81% in 2017 (**Error! Reference source not found.**). Dive type could not be determined for four trips for which there were no corresponding dive records. A small subset of 11 birds (seven in 2016 and four in 2017) travelled to the northwest to forage off the northern coast of Auckland Island (Figure 5.3), with nine of these (82%) conducting pelagic foraging trips.

Table 5.2 Combined foraging area size of breeding yellow-eyed penguins from Enderby Island, comparing different parameters (year, dive type, and sex). Areas were calculated from GPS data with the 95% confidence interval of kernel density estimates representing the combined foraging area used by all birds, and the 50% confidence interval representing the combined core foraging area. For each comparison, the intersect parameter shows the size of the spatial overlap indicating the shared area common to both parameters, and overlap shows the percentage overlap of the shared intersect area for each parameter. Spatial representations of the areas for all parameters are shown on separate maps (Figure 5.3).

		Foraging area (95% CI)		**Core foraging area (50% CI)**	
Comparison	**Parameter**	**Area (km^2)**	**Overlap**	**Area (km^2)**	**Overlap**
Year	2016	801	37%	196	29%
Year	2017	462	65%	91	63%
Year	Intersect	299	100%	57	100%
Dive Type	Benthic	571	91%	134	64%
Dive Type	Pelagic	985	52%	203	42%
Dive Type	Intersect	517	100%	86	100%
Sex	Females	963	52%	191	48%
Sex	Males	585	85%	132	69%
Sex	Intersect	497	100%	91	100%

Birds travelled over a more extensive foraging area in 2016 compared to 2017 (Figure 5.3A), with an estimated total foraging area size of 801 vs. 462 km^2, respectively (Table 5.2). Analysis of the intersection (overlap) between years (Figure 5.3A) showed that only 37% of birds foraged in the overlap area in 2016, compared to 65% of birds in 2017 (Table 5.2). Benthic foraging trips covered a smaller area than pelagic trips (Figure 5.3B), with estimated total foraging areas of 571 vs. 985 km^2, respectively (Table 5.2). Across all years, the benthic foraging area was smaller than the pelagic foraging area. The shared foraging area for dive type had a 91% overlap with the foraging area used by individuals undertaking benthic foraging (Figure 5.3B), compared to only 52% overlap with the area used by pelagic foragers (Table 5.2). Females foraged over a much larger range than males (Figure 5.3C), with foraging areas of 963 vs. 585

km^2, respectively (Table 5.2), and 85% of males foraged in this overlap area (Figure 5.3C), compared to only 52% of females (Table 5.2).

5.4.2 Foraging distances

The largest foraging distance was 46.7 km from shore, and the mean across both years was 19.5 ± 12.6 (SD) km for all trips, or an estimated 23.8 ± 11.2 km with some suspected partial trips (≤5% GPS fix success, Figure S5.2) removed. Foraging distance averaged an estimated 28.1 ± 9.2 km from shore in 2016 (max 46.7 km), and 14.8 ± 9.4 km from shore in 2017 (max 36.1 km) (Table 5.3).

Table 5.3 Foraging distance (maximum distance from shore) and total trip distance (cumulative distance travelled) of breeding yellow-eyed penguins from Enderby Island in different years. The first data series includes all trip data, including partial trips, therefore distances are likely underestimates. The second data series shows estimated means with some suspected partial trips (≤5% GPS fix success) removed for comparison. Also shown are the number of individual birds and foraging trips with valid GPS logs in each data series. Additional data from the northern population are included for comparison.

					Foraging distance (km)			Total distance (km)			No. Birds	No. Trips
Reference	Location	Site	Year	Phase	Mean	SD	Max	Mean	SD	Max		
This study	Subantarctic	Enderby Is	2016 (All)	guard	25.2	11.4	46.7	63.2	30.7	136.7	52	55
	Subantarctic	Enderby Is	2017 (All)	guard	10.8	9.1	36.1	26.7	24.6	95.4	29	36
	Subantarctic	Enderby Is	2016-17 (All)	guard	19.5	12.6	46.7	48.7	33.5	136.7	69	91
	Subantarctic	Enderby Is	2016 (Est)	guard	28.1	9.2	46.7	70.7	25.8	136.7	44	45
	Subantarctic	Enderby Is	2017 (Est)	guard	14.8	9.4	36.1	37.1	26.1	95.4	20	22
	Subantarctic	Enderby Is	2016-17 (Est)	guard	23.8	11.2	46.7	59.7	30.2	136.7	56	67
Mattern (2013)	Mainland	Boulder Beach, Otago	2004	guard	21.1	5.9		54.5	12.0		8	
	Mainland	Boulder Beach, Otago	2005	guard	11.0	3.1		30.5	10.3		4	
	Mainland	Boulder Beach, Otago	2012	guard, post-guard	10.8	6.2		33.6	18.9		11	
Mattern (2007)	Mainland	Bushy Beach, Oamaru	2003	guard, post-guard	6.2	0.8		15.9	1.2		5	
	Mainland	Bushy Beach, Oamaru	2003	guard, post-guard	17.5	2.5		47.5	1.8		5	
	Mainland	Bushy Beach, Oamaru	2004	guard	18.2	1.1		46.0	3.0		4	
Mattern (2006)	Stewart Is	Golden, Rollers beaches	2005	guard	11.4	2.7		29.5	1.0		3	
	Codfish Is	Sealers Bay	2005	guard	24.3	4.8		66.9	9.5		6	
	Stewart Is	Golden, Rollers beaches	2004	post-guard	11.7	4.8		37.0	5.1		3	
	Codfish Is	Sealers Bay	2005	post-guard	55.4	6.2		139.9	26.3		3	
Moore (1999)	Mainland	Boulder Beach, Otago	1990	post-guard	14.4	7.2					6	
	Mainland	Boulder Beach, Otago	1991	incubation	23.3	11.2					13	
	Mainland	Boulder Beach, Otago	1991	guard	13.4	6.1					10	
	Mainland	Boulder Beach, Otago	1991	post-guard	15.5	8.7					10	
	Mainland	Boulder Beach, Otago	1992	incubation	14.0	8.6					14	
	Mainland	Boulder Beach, Otago	1992	guard	14.4	5.8					10	
	Mainland	Boulder Beach, Otago	1992	post-guard	12.4	6.1					10	
	Mainland	Long Point, Catlins	1991	post-guard	11.1	7.2					9	
	Mainland	Long Point, Catlins	1992	post-guard	9.4	5.3					10	

Total trip distance was also greater in 2016, with a maximum of 136.7 km and an estimated mean of 70.7 ± 25.8 km travelled (Table 5.3). Linear mixed-effects model results (Table S5.2) showed that the foraging distance was significantly greater in 2016 than 2017 (ANOVA, χ^2 = 24.63, $p < 0.001$) and was also significantly greater for benthic than for pelagic foragers (ANOVA, χ^2 = 5.45, p = 0.020). Pelagic foragers used a greater geographical area including travelling furthest from shore (Figure 5.3B, Table S5.1). However, they also had a wider variation in foraging distance (Figure S5.1A), and on average the pelagic foraging distance was closer to shore than for benthic foragers (Figure 5.3B), suggesting that a greater number of pelagic birds foraged closer to shore. The total trip distance was also significantly greater in 2016 compared to 2017 (ANOVA, χ^2 = 20.62, $p < 0.001$), and benthic trips had significantly greater total distance than pelagic foraging trips (χ^2 = 6.45, p = 0.011), although they showed a similar trend to foraging distance (Figure S5.1B). Sex was not significant for foraging distance (p = 0.2), but males had a significantly shorter total trip distance (ANOVA, χ^2 = 4.8657, p = 0.0274). There was a significant relationship between trip duration and foraging distance (t = 4.40, $p < 0.001$), and also total distance (t = 5.60, $p < 0.001$), with travelling further taking longer (Figure S5.3). For the statistical tests on distance, the significance was the same when subsequent trips by the same individual were excluded from analysis. Significance was also the same when all trips were included as when some partial trips were excluded, except for foraging type, which was not significant for both foraging distance (p = 0.15) and total distance (p = 0.07) when partial trips were excluded. This suggests the relationship between dive type and distance is not as strong as for other factors.

5.5 Discussion

Foraging by breeding yellow-eyed penguins during the guard phase was concentrated over a continental shelf plateau to the east of Enderby Island and primarily in water 50−100 m deep

(Mitchell et al. 2016), where the substrate is a mixture of coarse sand, broken shells, coral, and pebbles (Tidey and Hulbe 2019, LINZ 2020). Foraging plasticity was evident between years, both for diving behaviour and foraging area use. Foraging distances were greater in 2016 than in 2017, and also greater than many data reported during the guard phase around mainland New Zealand where birds typically forage less than 25 km from shore (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). In 2017, in particular, there was evidence that a subset of birds had shorter foraging distances (<10 km from shore), although there was some uncertainty due to the presence of partial trip records. This finding is comparable with mainland data, where birds foraged closer to shore during the guard phase, and some individuals habitually foraged <5 km from shore (Moore 1999). Together, these data suggest that 2016 may have been an unusual year at the Auckland Islands, with much longer and more widespread foraging trips. The foraging area size and distance from shore are related to the shape and size of the available continental shelf close to the breeding area, although use of this area can vary between breeding phases. In some years, foraging trips at Enderby Island appear to have longer duration during incubation than in other breeding phases (Muller et al. 2020b; see Chapter 3), so may result in a greater foraging area than these data from the guard phase. This is true for the northern population, where birds can be at sea for up to 6 days during incubation (Moore 1999), and where birds had greater foraging distances during incubation than during guard and post-guard breeding phases (Moore 1999). Trip duration was shorter on subantarctic Campbell Island during the guard phase, with some birds making two short foraging trips per day (Moore and Moffat 1990), likely indicating close proximity to foraging areas at that locality. Similarly at Long Point on mainland New Zealand, some individual birds made 2−3 trips per day (Moore 1999).

The total distance travelled per trip by Enderby Island birds was a mean of 48.7 ± 33.5 km (59.7 ± 30.2 km when some partial trips were excluded), and a maximum of 136.7 km, which was greater than at many northern population locations where penguins typically swam a total of 31 ± 10 km per trip with extremes of 55 ± 12 km recorded (Mattern et al. 2013). The northern population is considered to comprise predominantly benthic foragers with only benthic dives published in studies using dive loggers (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014), although there is evidence for some pelagic foraging from diet and other studies (van Heezik 1990a, Moore et al. 1995, Mattern et al. 2018a). In contrast, our data demonstrate that birds in the subantarctic Auckland Islands show a much greater degree of diving plasticity. They have a mixed diving strategy incorporating varying amounts of pelagic foraging between and within seasons, including solely pelagic foraging trips (Muller et al. 2020a; see Chapter 4). Changes in diving behaviour between years also corresponded with changes in foraging behaviour, including home range size and distance travelled. Foraging trip duration in the southern population also changed between years, with trips in 2017 significantly shorter than trips in 2015 and 2016, although there was no difference evident between the sexes (Muller et al. 2020a).

5.5.1 Changes in foraging behaviour

In 2016, birds foraged further from shore, over a larger area, and with a smaller overlap of shared areas than in 2017, when the foraging home range area reduced in size by 340 km2 or 42% (Figure 5.3A). Mean foraging distance was significantly greater for benthic foragers than pelagic foragers in both years. The majority of benthic foraging took place in an area centred approximately 20−25 km from shore (Figure 5.3B), utilising a smaller area than pelagic foraging. However, pelagic foragers also displayed greater variance in foraging distance, with the majority of foraging closer to shore than benthic foragers, but others using a much larger and more variable area, including travelling further from shore than benthic foragers (Figure 5.3B). Benthic diving, especially in deep water, can use more energy than other types of diving

(Costa et al. 2004, Chilvers and Wilkinson 2009), so this may represent a greater energy expenditure by birds conducting benthic foraging. Given that both benthic and pelagic diving occurred together in some locations (the overlap areas), this indicates that dive type was not governed by bathymetry or water depth in these shared areas.

Additional dive logger data showed that the proportion of pelagic foraging trips increased each year with none recorded in 2015 (Muller et al. 2020a; see Chapter 4) and increasing proportions in 2016 and 2017. Since pelagic foraging was associated with a larger foraging area size (Figure 5.3B), it might be expected that the overall foraging area size would be greater in 2017 when the highest proportion of pelagic diving was recorded. However, the foraging area was actually smaller in 2017 than in 2016 (Figure 5.3A), although sample size was also smaller in 2017. Foraging area use is therefore likely influenced by additional complexity related to the type and distribution of prey species available each year, and possibly conditions for all types of foraging were less favourable in 2017. Cameras deployed on mainland birds indicated that pelagic foraging there was generally on poorer quality prey items such as jellyfish and other gelata and was associated with poor visibility at the sea floor which prevented benthic foraging (Mattern and Ellenberg 2018).

During 2017, 28% of birds changed their diving behaviour (from benthic to pelagic, or vice versa) on a subsequent trip in the same year, and 56% changed their behaviour between different years (Muller et al. 2020a). This demonstrates plasticity of dive type for individual birds, and the general change in foraging locations between years also suggests a large degree of plasticity in foraging area use. There is no difference evident in foraging behaviour between male and female birds in the southern population (Muller et al. 2020a), although females may have been foraging over a wider area during the guard phase (Figure 5.3C), with only 51.6% overlap with the shared foraging area, compared to 85.1% overlap for males.

Mean ± SD foraging distances for the northern population ranged from 6.2 ± 0.8 to 23.3 ± 11.2 km (Table 5.3), although these included data collected using different methods, and during different breeding phases and years when birds may have foraged differently (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). Mean and maximum mainland foraging distances were closer to shore than in the southern population; however, statistical comparison between these data sets was not possible. The northern population displays a generally consistent benthic foraging strategy, using the same foraging areas consistently over different years (Mattern et al. 2007). However, while mainland birds tend to forage either close to shore or further from shore, some could switch strategies (Moore 1999) and foraging areas (Moore et al. 1995, Moore 1999), indicating a degree of foraging plasticity in the northern population as well. Since these populations are genetically similar (Boessenkool et al. 2009a), any differences are likely due to the local environment and prey availability (Muller et al. 2020a), rather than any inherent behavioural differences.

This study reports on the foraging area used by breeding penguins during the guard phase when parental attendance at the nest is high (Richdale 1957, Darby et al. 1990). However, many penguin species forage over considerably larger areas during incubation and post-guard phases of the breeding season compared to the guard phase (Jouventin et al. 1994), including an area over 5 times larger for little penguins *Eudyptula minor* (Sánchez et al. 2018). In little penguins, foraging closer to the colony during chick-rearing was also associated with a diet switch to higher trophic level prey (Poupart et al. 2017), and the mean maximum foraging distance in winter was significantly larger (up to eight times greater) than during the breeding season (Hoskins et al. 2008, McCutcheon et al. 2011). Yellow-eyed penguins in the northern population travel further from the breeding area during incubation and post-guard stages (Moore 1999) and in winter (M. J. Young, pers. comm.). Therefore, given that no foraging data are available for other breeding phases in the southern population, the foraging areas and distances described here should be regarded as minima for yellow-eyed penguins from Enderby Island. Our data also tended to show that larger datasets represented larger foraging areas, so collecting additional data may reveal additional areas used by penguins. However, sampling a greater number of birds than in this study is likely impractical due to logistics and ethical considerations for this endangered species.

While the attachment of any device to a diving animal can introduce hydrodynamic drag, this was minimised by using smaller individual loggers, and by attaching the loggers as far back as possible to maintain streamlining (Bannasch et al. 1994). In particular, it is possible that carrying the larger GPS loggers may have influenced behaviour. However, Muller et al. (2020a) showed that the type of loggers deployed (TDR only, or TDR + GPS), or the deployment order did not have a biologically significant effect on diving behaviour (the difference in dive depth was 0.55 m, which was less than the error margin of the loggers).

5.5.2 Foraging and breeding success

The weak La Niña conditions during the 2016 and 2017 seasons corresponded to increasing amounts of pelagic foraging (Muller et al. 2020a; see Chapter 4), as well as to greater breeding effort and success in 2016 (Muller et al. 2020b; see Chapter 3). Strong La Niña conditions can increase SST and have a greater negative effect on northern yellow-eyed penguin breeding success than during El Niño conditions (Young 2014), although effects on breeding success can manifest in subsequent years (Peacock et al. 2000). Therefore, more investigation is needed on the interaction between the strength of ENSO cycles, foraging, diet, and breeding success in the subantarctic. During 2015, the proportion of benthic foraging at Enderby Island (100%) was greater than in subsequent years (Muller et al. 2020a), and since benthic foraging generally took place over a smaller area (Figure 5.3B), it follows that smaller foraging areas would be expected during El Niño conditions. While we do not have GPS data from 2015 to confirm this, trip times in 2015 (mean and maximum duration) were longer than in 2016, which would be consistent with more benthic foraging, although the difference was not significant (Muller et al. 2020a). Yellow-eyed penguin prey species in the subantarctic are unknown, and it is not known whether prey assemblages at the Auckland Islands are consistent in the region during different ENSO conditions. Further research is needed to confirm how ENSO conditions may affect prey species distribution in space and time, and to what extent this affects yellow-eyed penguin foraging and breeding success.

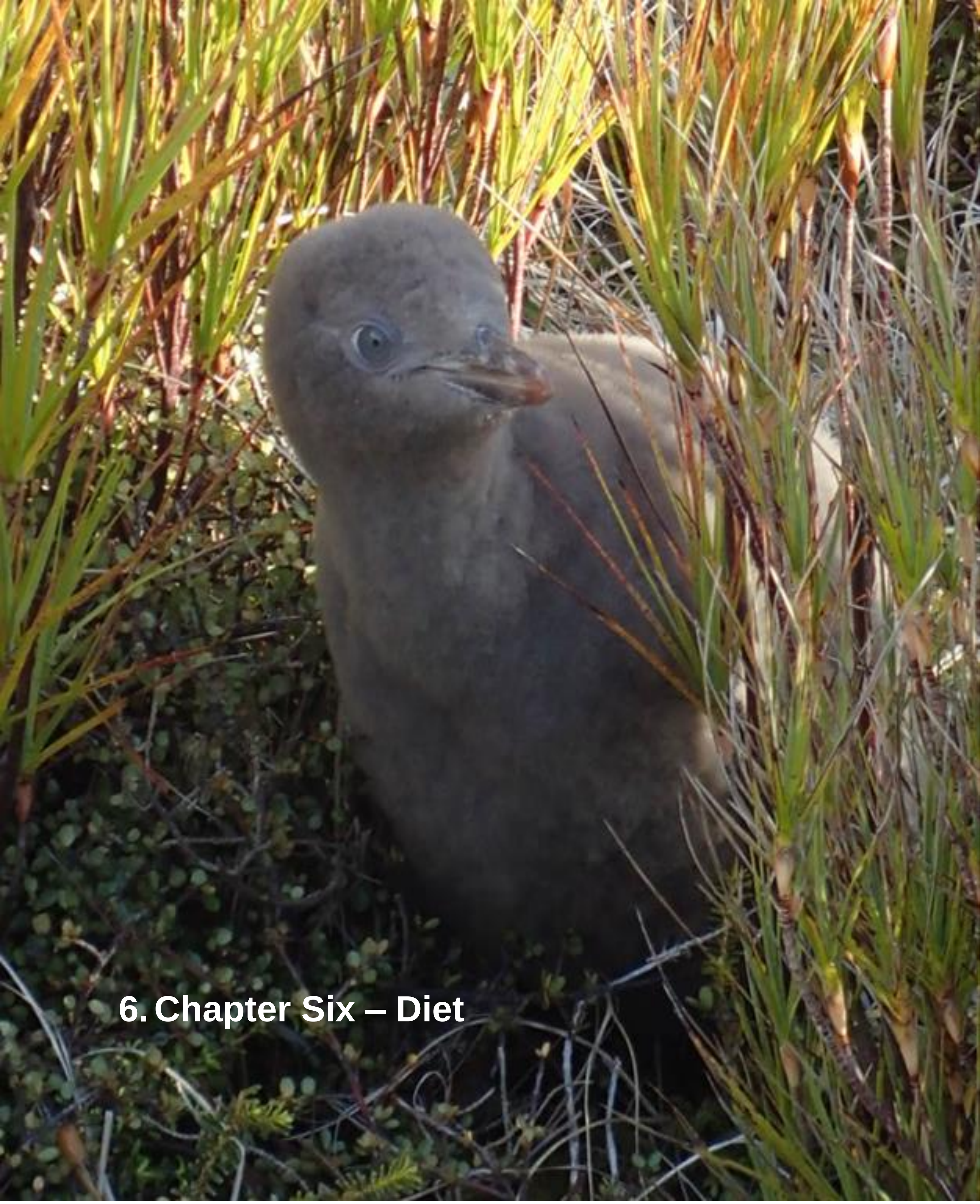
Travelling greater distances resulted in longer times at sea, although this may not always be the case. For southern yellow-eyed penguins, pelagic foraging trips were not significantly different in time duration from benthic trips (Muller et al. 2020a), or in total trip length (Figure S5.1B), although individual trip distances could vary. Trips in 2016 were significantly longer in duration than in 2017 (Muller et al. 2020a), and foraging areas were also larger (Figure 5.3A), although breeding success was better (Muller et al. 2020b). These findings tend to contradict the conclusions of other studies. For example, longer foraging trips in other seabirds including Magellanic *Spheniscus magellanicus*, Adélie *Pygoscelis adeliae*, and little penguins were directly related to lower breeding success (Chiaradia and Nisbet 2006, Boersma and Rebstock 2009). Changes in prey availability, particularly the distance travelled to obtain it, will affect the effort required (Miller and Sydeman 2004). This, in turn, affects both adult energetics and chick provisioning; longer travel or search times by foraging parents can result in less-frequent feeding of chicks, and may result in lower growth rates and fledging weights for chicks (Kitaysky et al. 2000, Davoren and Montevecchi 2003, Pinaud et al. 2005). Longer foraging trips may also result in more food digestion, with less available for transfer to offspring (Weimerskirch et al. 1994, Ropert-Coudert et al. 2004). Increased energy expenditure by foraging adults may lead to a reduction in their body condition (Arnould et al. 1996, Shaffer et al. 2003), as well as breeding success (Inchausti et al. 2003), thereby influencing long-term survival and evolutionary fitness of breeders. However, the larger foraging area in 2016 may have allowed birds to exploit prey which was further from shore, or distributed more widely, but which justified travelling greater distances to obtain it. Nevertheless, any factors affecting the type and distribution of prey which may require travelling greater distances or spending more time at sea could have a negative effect on future yellow-eyed penguin breeding success.

5.5.3 Foraging and conservation management

Enderby Island represents over 50% of the breeding population for the Auckland Islands archipelago and will likely continue to be the main breeding location in the future unless introduced predators are removed from Auckland Island (Muller et al. 2020b; see Chapter 3). Only part of the foraging area used by Enderby Island birds is protected from potential fisheries interactions by the Auckland Islands Motu Maha Marine Reserve, which extends 12 nautical miles (22.22 km) from shore (Figure 5.3). Although no yellow-eyed penguins were reported as bycatch in the trawl fishery around the Auckland Islands during the period of this study (Ministry of Primary Industries 2018b), fisheries activities such as bottom-trawling modify the benthos and may affect penguin foraging (Browne et al. 2011). Indirect competition with fisheries has been linked to declines in some mainland yellow-eyed penguin populations (Ellenberg and Mattern 2012). Therefore, research into the direct and indirect impacts of fishing activities on yellow-eyed penguins in the Auckland Islands area is crucial for their long-term conservation. The core foraging areas (represented by the 50% isopleths) were contained within the marine reserve boundary, and the home range of all penguins we examined (represented by the 95% isopleths) contained 595 km^2 (81%) of foraging area within the marine reserve. However, the areas presented here represent minimum estimates of the habitat used, and therefore a larger area than the current marine reserve would be required to fully protect the yellow-eyed penguin at the Auckland Islands. Further research is needed into foraging area use during other breeding phases, including incubation, post-guard, pre-moult, and winter foraging, as foraging areas may be larger at these times. Additionally, we recommend further research on other breeding populations in the Auckland Islands area, as foraging conditions may differ. For example, birds breeding at Carnley Harbour in the south may have a smaller foraging area available, as the shelf drops off to 150 m deep and beyond benthic diving range within only 11 km of the harbour entrance.

5.6 Conclusions

The yellow-eyed penguin was classified as Endangered in 2000 and numbers have continued to decline, particularly for the northern population (Couch-Lewis et al. 2016, BirdLife International 2020, Department of Conservation 2020a). This study of yellow-eyed penguins at Enderby Island found foraging plasticity between years, including differing foraging behaviour and locations. Some foraging trips during the guard phase covered greater distance and area compared with northern populations, with any differences likely a result of local conditions, rather than any inherent differences between these two genetically similar populations. However, the subantarctic environment may predispose the southern population to more difficult foraging conditions. Ongoing monitoring of foraging and breeding success is needed to ensure timely warnings if poor foraging seasons combine with other factors to initiate or exacerbate population declines in the subantarctic. Management should also include appropriate protection of foraging areas used by yellow-eyed penguins, with the data presented here considered as a minimum estimate.



6. Chapter Six – Diet

DRC 16

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Name of candidate:	Chris Muller
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Diet plasticity and links to foraging behaviour in the conservation of subantarctic yellow-eyed penguins (*Megadyptes antipodes*)

Muller, C. G., Chilvers, B. L., French, R. K., and Battley, P. F. (2022) Diet plasticity and links to foraging behaviour in the conservation of subantarctic yellow-eyed penguins (*Megadyptes antipodes*). Aquatic Conservation: Marine and Freshwater Ecosystems, 32(5):753–765.

6.1 Abstract

Diet is a key factor affecting seabird foraging behaviour, ultimately influencing survival, breeding success and long-term population viability. The density and distribution of prey species in the marine environment are influenced by many factors including climate effects such as El Niño southern oscillation and climate change that alter water temperature. While poor quality diet has been implicated as a contributing factor in the decline of some mainland New Zealand yellow-eyed penguin (*Megadyptes antipodes*) populations, little is known about their diet in the subantarctic where the majority of the species breeds. Blood and feather samples (n = 63) were collected for stable isotope analysis of diet from 25 individual birds breeding on subantarctic Enderby Island, Auckland Islands, New Zealand, from 2015 to 2018. Diet data were analysed by factors such as breeding year, sex and foraging behaviour. Stable isotope analysis demonstrated significant changes in diet during each year of the study, which included both El Niño and La Niña conditions. Diet during El Niño conditions comprised lower trophic level prey, which were more benthic, and found closer to shore than diet during La Niña. Coupled with the reported variable breeding success of yellow-eyed penguins in the subantarctic, variable diet suggests prey availability is likely to be a limiting factor in some years. Prey availability is therefore expected to be a major influence on survival and breeding

success of this endangered species in the future, particularly if the effects of climate change become more pronounced. This research highlights an urgent conservation need to identify prey species utilised by the southern population, along with their distribution in time and space, and therefore also the effect of diet on long-term population stability.

6.2 Introduction

The diet of long-lived marine predators is a key indicator of individual foraging success (Emlen 1966, MacArthur and Pianka 1966), as it affects adult survival (Keymer et al. 2001), chick provisioning (Jodice et al. 2006), and ultimately breeding success and long-term population viability (Emlen 1966, MacArthur and Pianka 1966, Olsson 1997, Moreno et al. 1999, McClung et al. 2004, Jodice et al. 2006, Crawford et al. 2008). Prey availability is determined by the density and distribution of prey species, with horizontal and vertical distribution affecting predators' travel distance and dive depth (Croxall et al. 1999, Inchausti et al. 2003, Boersma and Rebstock 2009). Prey species can be affected by changes in environmental conditions such as water temperature, with diet quality predicted to decrease for many marine species due to climate change (Worm et al. 2006, Cury et al. 2011). Studying broader changes in prey trophic level can shed light on foraging behaviour even where prey species are not directly analysed (Chilvers 2017b, Chilvers 2017a). Changes in the diet of a diving seabird can indicate variability in prey species utilised between years, sexes and age classes (Cherel et al. 2000, Ainley et al. 2003, Tremblay and Cherel 2003), and, therefore, foraging variability. Interpretation of dive data often relies on the assumption that sampling a small number of foraging trips is representative of diving behaviour over a whole breeding season, which may not be the case (Amélineau et al. 2021). However, diet studies can be used to interpret dive results, since significant differences in diet between individuals in the same population can indicate that different foraging behaviours were occurring, and that these were maintained across multiple foraging trips for the period in question.

Stable isotope analysis (SIA) is a method of analysing diet composition by determining the chemical makeup of prey items that have been incorporated into body tissues (Hobson and Clark 1992a, Cherel et al. 2000, Bearhop et al. 2002, Bearhop et al. 2006). Stable isotope analysis offers advantages over other techniques such as stomach contents analysis, which often represent diet from only a single meal, and can be biased by differing prey digestibility (Duffy and Jackson 1986, van Heezik and Seddon 1989, van Heezik 1990a, Pütz 1995). Techniques such as faecal analysis, and particularly faecal DNA analysis, can be used to determine prey species over extended periods and multiple individuals to avoid the single meal constraint, and faecal DNA avoids differential digestion issues (Deagle et al. 2010, Young et al. 2020). However, DNA samples need to be stored at -20°C to prevent degradation (Young et al. 2020), so transport from the subantarctic is logistically difficult. While results are easier to obtain from SIA than DNA analysis (especially from feathers), SIA allows identification of prey to trophic level only (Hobson et al. 1994), making it useful for measuring broad-scale taxonomic-level changes in the diet of marine predators. Stable isotope analysis measures the dietary components of prey species, which are assimilated in the tissues of consumers in a reliable and predictable way (DeNiro and Epstein 1978, DeNiro and Epstein 1981, Hobson and Clark 1992a, Hobson and Clark 1992b). Chemical elements with more than one isotopic form have different molecular mass, and differing ratios of these can distinguish between prey from different sources. The isotopic ratio of nitrogen ($^{15}N/^{14}N$) indicates which trophic level an animal is feeding at (DeNiro and Epstein 1981, Bodey et al. 2011), with fish and cephalopods higher than zooplankton prey (Owens 1988, Hobson et al. 1994). The isotopic ratios of carbon ($^{13}C/^{12}C$) can be used to confirm foraging location, with higher (less negative) values indicating more inshore versus offshore feeding (Hobson et al. 1994, Kelly 2000), and more benthic versus pelagic (Hobson et al. 1994, Cherel et al. 2007). Stable isotopes can be analysed from body samples such as feathers and blood, which represent diet over different time frames (Bearhop et al. 2002). Nitrogen and carbon signatures persist in blood for around 1–5 weeks after prey consumption (Hobson and Clark 1992a, Haramis et al. 2001, Bearhop et al. 2002, Pearson et al. 2003, Cherel et al. 2005), with a half-life of around 2 weeks (Bearhop et al. 2002). Feather samples are logistically simpler and less invasive to obtain than taking blood, or some other methods of determining diet, such as stomach flushing. Isotope signatures in feathers are stable but reflect the diet at the time they were grown (Hobson and Clark 1992a, Haramis et al. 2001, Bearhop et al. 2002, Pearson et al. 2003, Cherel et al. 2005), meaning they represent a portion of the diet of the total breeding season. Unlike other seabirds, most species of penguin generally undergo a single annual feather moult, which often occurs during a period of fasting at the end of the breeding season (Adams and Brown 1990). Since penguins remain on shore and rely on stored energy reserves during the period new feathers are grown (Adams and Brown 1990), the SIA signature in the feathers is therefore homogenous and represents the nutritional content of the diet for a period of around 4–6 weeks during the pre-moult period (Flemming and van Heezik 2014, Chilvers 2017a).

Breeding penguins are central-place foragers that must frequently travel from their nest to their foraging area at sea, and return to feed chicks (Williams 1995, Borboroglu and Boersma 2013). Consequently, breeding penguins and other seabirds are particularly vulnerable to localised prey depletion, as well as to changes affecting the location or depth of prey, which can increase the effort required to find and exploit a food source (Birt et al. 1987). Penguins are diving predators, capturing and consuming live prey underwater. The predominant dive types are benthic diving (to the sea floor), which is characterised by repeated dives to a uniform maximum depth limited by seabed depth (Tremblay and Cherel 2000); and pelagic diving, which occurs midwater with a more variable maximum depth between dives since prey could be encountered anywhere in the water column (Tremblay and Cherel 2000). Deeper dives require more energy expenditure, so benthic foraging can be more energetically expensive than pelagic foraging, especially in deeper water (Costa et al. 2004). However, benthic prey species tend to be a predictable, evenly distributed prey source, although often occurring at low densities within a habitat (Costa et al. 2004, Chilvers and Wilkinson 2009). Conversely, while pelagic foraging is unpredictable and may require birds to travel larger distances to search for prey, pelagic prey are often found in higher density aggregations, such as schools and bait balls, providing a richer food source once located (Chilvers and Wilkinson 2009). Overall, pelagic prey are often more influenced by oceanographic and weather conditions such as El Niño southern oscillation (ENSO) than are benthic prey (Costa et al. 2004), meaning benthic prey may be a more reliable food source when prey are less abundant. Successful foraging must balance the energy expenditure required to catch prey with their nutritional quality. Fish generally have a higher lipid and energy content than do cephalopods or zooplankton and therefore represent higher quality prey (Clarke and Prince 1980, Cherel and Ridoux 1992, Meynier et al. 2008). Penguins feeding on a higher proportion of fish are therefore expected to be in better body condition, and the body condition of penguin chicks is positively correlated with the proportion of fish in their diet (Forero et al. 2002). Factors affecting the makeup of prey species in the diet can therefore affect foraging success, which in turn has implications for both nutrition and chick provisioning.

The yellow-eyed penguin (hoiho, *Megadyptes antipodes*) is classified as Endangered (Couch-Lewis et al. 2016, BirdLife International 2020) and is endemic to New Zealand, with a highly restricted distribution. The northern population includes breeding areas in the south-east of the South Island, and Stewart and Codfish Islands (Figure 6.1A, above dotted line), and the southern population includes the subantarctic Auckland and Campbell Islands (Figure 6.1A, below dotted line) (Seddon et al. 2013), with these areas representing discrete populations for conservation management (Boessenkool et al. 2009b). Most populations around mainland New Zealand are in serious decline due to successive poor breeding seasons and ongoing high adult mortality, believed to be due to threats at sea including poor foraging success, fisheries interactions, pollution and human disturbance (Couch-Lewis et al. 2016, Mattern et al. 2017, Mattern and Wilson 2018). The southern yellow-eyed penguin population comprises at least 60–79% of the total population (Couch-Lewis et al. 2016, Muller et al. 2020b; see Chapter 3), and while apparently not declining in the 2010s, there were large fluctuations in breeding success, and counts have reduced since the 1980s (Moore 1992b, Moore et al. 2001, Muller et al. 2020b). As in most other penguin species, yellow-eyed penguins typically moult after breeding; in late March on mainland New Zealand (Seddon et al. 2013), or during April in the subantarctic (Moore et al. 2001). Warmer water has a detrimental effect on foraging and breeding success in the northern population (Young 2014, Mattern and Ellenberg 2018). The warmer water and more stochastic weather and wind patterns associated with strong La Niña conditions around mainland New Zealand negatively affect yellow-eyed penguin breeding success (Moore and Wakelin 1997, Darby 2003, Young 2014, Mattern et al. 2017). However, there are few data on the effects of ENSO on foraging and breeding success in the southern population, although a greater proportion of pelagic foraging was observed during La Niña conditions (Muller et al. 2021; see Chapter 5). Breeding yellow-eyed penguins typically forage in coastal and mid-shelf waters around mainland New Zealand (Moore 1999, Mattern et al. 2007, Mattern et al. 2013), while, at the subantarctic Auckland Islands, yellow-eyed penguins forage further offshore than many mainland birds do (Muller et al. 2021), and at greater depths (Muller et al. 2020a; see Chapter 4). Dive data from the northern population revealed predominantly benthic foraging behaviour (Seddon and van Heezik 1990, Moore et al. 1995, Mattern 2006, Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014). Earlier diet studies suggested that some pelagic prey species were utilised (van Heezik 1990c); however, more recently, prey were interpreted as being mainly demersal (Moore and Wakelin 1997). A predominantly benthic foraging strategy in the northern population may be influenced by changes in prey availability and environmental conditions, with some pelagic foraging occurring when visibility is poor at the sea bed (Mattern and Ellenberg 2018). In contrast, Enderby Island birds displayed apparently greater diving plasticity, with foraging behaviour switching from solely benthic to almost 80% pelagic in some years, as well as trips consisting almost entirely of pelagic dives (Muller et al. 2020a), a diving behaviour not common in the northern population. It is likely that diving and foraging plasticity is a function of the physical environment and changes in prey availability and location, rather than an inherent characteristic of either population (Muller et al. 2021).

Knowledge of diet diversity is important for ecosystem-based management plans (Shiffman et al. 2012). Understanding diet and foraging behaviour is essential for conservation monitoring because it allows for informed management decisions such as predicting where and how poor diet may affect population viability, and how to address that when it occurs. Poor diet can result in poorer chick condition in yellow-eyed penguins (van Heezik and Davis 1990), leading to decreased post-fledging survival rates (McClung et al. 2004). Poor foraging success has also been linked to reduced adult survival, with negative long-term population outcomes (Couch-Lewis et al. 2016, Mattern and Wilson 2018, Department of Conservation 2020a). Variable breeding success is evident in the southern population, probably linked to changes in foraging success (Muller et al. 2020b, Muller et al. 2021; see Chapters 3 and 5). As yellow-eyed penguin foraging is influenced by climate patterns (Moore and Wakelin 1997, Darby 2003, Young 2014, Mattern et al. 2017, Muller et al. 2021), a comprehensive understanding of diet and foraging ecology across the range of the species is essential for monitoring yellow-eyed penguin breeding and guiding effective conservation management, particularly as the effects of climate change are expected to become more pronounced in the future (Collins et al. 2013, Ramírez et al. 2017). While variable foraging behaviour has been identified in the southern population (Muller et al. 2020a, Muller et al. 2021; see Chapters 4 and 5), little information on diet is available for the southern population. Better knowledge of yellow-eyed penguin diet will also help determine whether food availability or quality might be limiting factors, and as a result, to anticipate any possible impacts on successful breeding for these populations. The aims of this study were therefore to better understand diet and foraging in the southern population, by: 1) identifying changes in diet between years and relating these to population-level changes in foraging, breeding and ENSO state; 2) identifying variability in diet between sexes, or birds utilising different foraging behaviours in order to identify pressure on particular cohorts; and 3) comparing diet trends in the subantarctic with data published for the northern population, to identify specific regional threats to the southern population.

6.3 Methods

6.3.1 Fieldwork

Ground-based fieldwork was carried out on Enderby Island, Auckland Islands, in the New Zealand subantarctic (50°29’45”S 166 °17’44”E, Figure 6.1C) for three breeding seasons 2015 (November 2015–February 2016), 2016 (November 2016–February 2017), and 2017 (November 2017–January 2018).

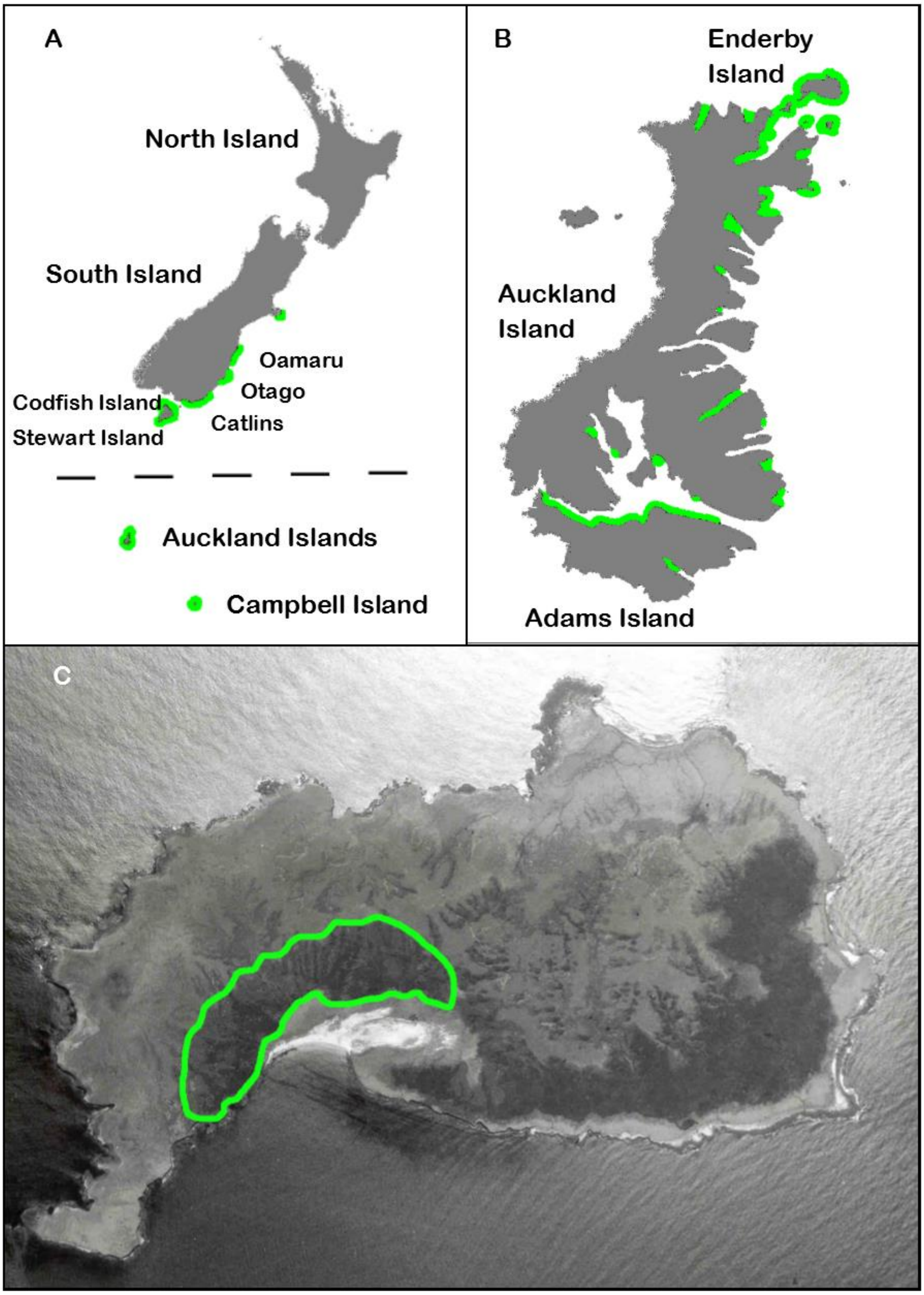


Figure 6.1 A) Map of yellow-eyed penguin breeding range around New Zealand (green), with the northern population above the dotted line, and southern population below the line. Also shown is B) an enlarged view of the subantarctic Auckland Islands with Enderby Island to the north east, and C) a close-up of Enderby Island showing the area where breeding birds were sampled (green ellipse). Modified from Muller et al. (2020a).

GPS foraging data were collected during concurrent research in 2016 and 2017 (Muller et al. 2021; see Chapter 5), and dive and breeding success data were collected in all three years (Muller et al. 2020a, Muller et al. 2020b; see Chapters 3 and 4). Nests were located using manual ground searching, ground-based very high frequency radio tracking, and aerial tracking using an unmanned aerial vehicle equipped with a very high frequency receiver (Muller et al. 2019). Adult penguins were captured by hand as they returned to the shore in the evening following a foraging trip at sea, and transferred to a custom-made holding bag. This held the wings against the body but left the head and feet exposed for processing and collection of morphometric data using a spring balance and callipers. Birds were marked with a microchip for permanent individual identification (Muller et al. 2019, Muller et al. 2020b; see Chapters 2 and 3), and sex was determined using the relationship between head plus beak length and foot length (Setiawan et al. 2004), or the relative sizes between breeding partners with males assumed to be the larger (Setiawan et al. 2004). Blood and feather samples for SIA were taken while birds were restrained.

6.3.2 Sampling and stable isotope analysis

Blood samples were collected in November 2015 only, due to logistical constraints. A 1 ml sample of blood was taken using a 25-gauge needle from either the medial metatarsal vein (inside of the leg) or dorsal digital vein (on top of the foot) while penguins were restrained in the holding bag. Blood samples were transferred to an Eppendorf tube then spun in the field using a centrifuge, and the serum and red blood cell components were transferred into separate tubes and frozen in liquid nitrogen for transfer back to the mainland. Serum samples were then freeze-dried and ground to a fine powder for SIA analysis.

Feather samples were collected in the 2015, 2016 and 2017 breeding seasons (representing diet during pre-moult periods in the 2014, 2015 and 2016 seasons, respectively). Six feathers were cut with scissors from haphazard locations on the central and lower back of each bird. Feathers were cleaned by soaking for 5 min each in distilled water, followed by a 2:1 solution of chloroform and methanol to remove lipids, then rinsed in clean distilled water again for 1 min to remove solvents (Cherel et al. 2007). Feathers were dried using clean paper towels, and placed in clean Ziploc bags for storage.

Stable isotope analysis of blood and feathers was conducted by Waikato Stable Isotope Unit (Department of Biological Sciences, University of Waikato). Blood samples were compared with feather samples from the same bird, representing a similar nutritional period (i.e. feathers collected during the following breeding season in 2016). Feathers and powdered serum were weighed and packed in tin-foil capsules, and carbon and nitrogen isotope ratios were determined by a Dumas elemental analyser (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20–20 Stable Isotope Analyser). Results are presented in the conventional notation relative to a laboratory standard or reference for sucrose (^{13}C) and urea (^{15}N), with urea calibrated relative to atmospheric nitrogen. Quality-control samples were run before and after every 12 samples, and unless otherwise stated, data are presented as means ± SE and results are considered significant at the $P < 0.05$ level.

Statistical analyses were performed in R Studio version 1.1.456 running R version 3.5.1 (R. Core Team 2017) and using the lme4 package (Bates et al. 2015). All continuous variables were visually assessed to be normally distributed using histograms and Q-Q plots, so dependent variables were not transformed. Stable isotope analysis results were analysed using general linear mixed effects models, with bird ID (an individual identifier) as a random effect to avoid pseudoreplication. A separate ANOVA test of models with and without bird ID was used to test whether bird ID significantly improved the model fit, based on the resulting corrected

Akaike's information criterion (AICc) values. This hypothesis-driven test was used to investigate whether any individual preferences in diet existed. Graphs were generated in R including the ggplot2 package (Wickham 2016).

6.3.3 Dive type and foraging distance

Concurrent dive data were collected using Lotek LAT 1400 time depth recorders attached to the middle of the back using waterproof tape, as described in Muller et al. (2020a); see Chapter 4. Dives were categorised as benthic if the depth change between subsequent dives was <2.9%, with the remainder of dives classed as pelagic (Muller et al. 2020a). Foraging trips were also classified using Bayesian analysis, with benthic trips having >3.6% benthic dives, accounting for the large proportion of non-feeding travelling dives and ensuring that the remaining trips classified as pelagic contained no significant instances of benthic diving (Muller et al. 2020a). Foraging data were collected using customised CatTraQ GPS loggers modified for underwater use according to Pelletier et al. (2014), and attached to the lower back (Muller et al. 2021; see Chapter 5). GPS data were interpolated to account for missed fixes, and distance measures were calculated including the foraging distance (maximum straight-line distance away from shore, measured from the sea access point) and the total trip distance (cumulative distance travelled between all points in a foraging trip) (Muller et al. 2021). Where possible, electronics were deployed for only one foraging trip before being recovered to minimise attachment time. However, if penguins undertook more than one foraging trip before electronics were recovered, the data were divided into separate trips. For full methodology refer to (Muller et al. 2021).

6.4 Results

6.4.1 Summary

A total of 63 SIA samples were processed, from 25 individual birds (14 males and 11 females; Table S1). This included 10 blood samples from 10 different birds collected in 2015, and 53 feather samples from 25 birds collected from 2015 to 2017 and representing diet years 2014 (n = 10), 2015 (n = 23) and 2016 (n = 20). Included in the feather samples were seven birds sampled in all three years, 14 birds sampled in two different years, and four birds sampled in a single year only. SIA data were matched with 22 dive logs, including 15 benthic and seven pelagic foraging trips (Muller et al. 2020a; see Chapter 4). A comparison (n = 9 pairs) was also made between blood and feathers representing the 2015 diet year (Figure S6.1). Foraging data were analysed in detail in concurrent studies (Muller et al. 2020a, Muller et al. 2021; see Chapters 4 and 5). Summary data are provided for each individual bird (Table S1).

6.4.2 Blood versus feathers

The nitrogen ($\delta^{15}N$) values for blood and feathers had a range of 1.1 and 1.8‰, respectively, and the carbon ($\delta^{13}C$) values had a range of 0.9 and 1.4‰, respectively (Table 6.1, Table S6.1). Blood SIA values generally followed a similar trend to feather samples from the same diet year, but were offset lower. This was the case for all $\delta^{13}C$ and most $\delta^{15}N$ measures (Figure S6.1). General linear models comparing isotope values confirmed that blood and feather samples were significantly different for both $\delta^{15}N$ ($t = 8.278$, $P = 1.31e\text{-}11$) and $\delta^{13}C$ ($t = 19.62$, $P < 2e\text{-}16$). Therefore, although their trends were similar, SIA results for blood and feathers needed to be considered separately. Since blood was collected only in 2015, feather samples were analysed to compare diet with other factors between multiple years, although feathers were not available for the final breeding year.

Table 6.1 Isotope values (‰) for blood and feather samples from yellow-eyed penguins breeding on Enderby Island.

	Blood		Feathers	
	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
Min	10.28	-20.99	10.98	-19.01
Max	11.40	-20.10	12.75	-17.58
Difference	1.12	0.89	1.77	1.43
Mean	10.69	-20.50	11.78	-18.40
SD	0.40	0.28	0.38	0.32

6.4.3 Isotope analysis

The $\delta^{15}N$ isotope values were lowest in 2015 (Figure 6.2a, Figure 6.3a). General linear models comparing nitrogen isotope values showed that all were significantly different between years; 2016 and 2015 were both significantly different from 2014 ($t = 2.717$, $P = 0.00897$, and $t = -2.521$, $P = 0.01486$ respectively), and 2014 and 2015 were both significantly different from 2016 ($t = -2.717$, $P = 0.00897$, and $t = -6.623$, $P = 2.14e-08$ respectively). A linear mixed effects model with bird ID as a random effect (to account for individual birds' preferences as a potential confounding effect) had the same result, with a significant difference between years ($\chi^2 = 114.73$, $P < 2.2e-16$).

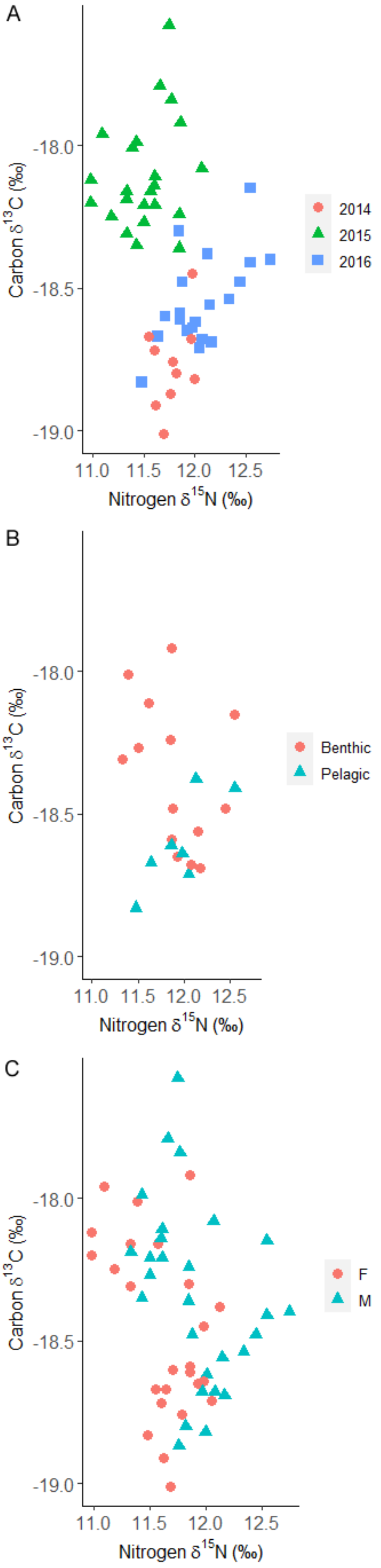


Figure 6.1 Comparison of stable isotope analysis results extracted from feathers for different groups of foraging yellow-eyed penguins, breeding on Enderby Island in the New Zealand subantarctic (n = 54 birds). Results show nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes in ‰ for: A) the diet year when feather samples were formed (during the pre-moult period); B) birds conducting different dive types (benthic or pelagic) as per Muller et al. (2020); and C) for birds of different sex.

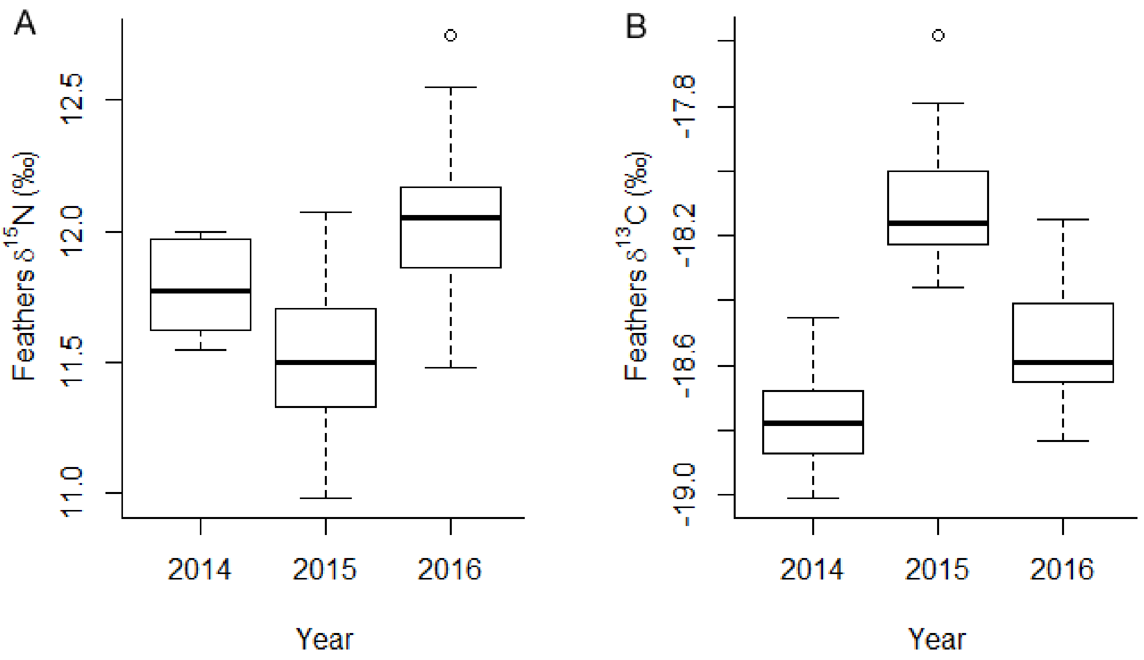


Figure 6.3 Comparison of stable isotope analysis results extracted from feathers for foraging yellow-eyed penguins breeding on Enderby Island in the New Zealand subantarctic (n = 54 birds) in different diet years (when feathers were formed), showing isotopes in ‰ for: A) nitrogen $\delta^{15}N$ (left); and B) carbon $\delta^{13}C$ (right). N and C values in all years were significantly different from each other.

A general linear model comparing $\delta^{15}N$ isotope values with foraging type (Figure 6.2B) was not significant (t = 0.492, *P* = 0.628); however, sex was significant (t = 2.795, *P* = 0.00725), with males tending towards larger $\delta^{15}N$ values (Figure 6.2C). This was not the case when only blood samples were analysed, with no significant difference evident between sexes in this case (t = 1.432, *P* = 0.19), although sample sizes were much smaller (n = 5 males and 5 females for blood sample analysis). While carbon $\delta^{13}C$ isotope values were generally lower for benthic foragers (Figure 6.2B) and some males tended towards smaller (less negative) $\delta^{13}C$ values (Figure 6.2C), these values were not significantly different for either foraging type (t = 2.069, *P* = 0.0517) or sex (t = 1.403, *P* = 0.167). Individual bird ID (as a random effect) significantly improved the linear mixed effects model fit for $\delta^{15}N$ ($\chi^2 = 11.097$, $P = 0.0008647$), and $\delta^{13}C$ ($\chi^2 = 7.9297$, $P = 0.004863$).

General linear models comparing isotope values with foraging distances in 2016 (Table S6.1) showed that foraging distance (maximum distance offshore) had no significant effect on $\delta^{15}N$ ratios ($t = -2.083$, $P = 0.0561$); however, the total foraging distance (cumulative distance travelled) did have a significant effect on $\delta^{15}N$ ($t = -2.162$, $P = 0.0484$). Neither maximum distance nor cumulative distance travelled had a significant effect on $\delta^{13}C$ ($t = -1.031$, $P = 0.32$, $t = -0.48$, $P = 0.638$ respectively). Distance and year could not be tested in the same model since there was only one year where both GPS and SIA data were available (2016).

6.5 Discussion

Significant differences were evident in the isotope ratios of both nitrogen and carbon in different breeding seasons, indicating dietary shifts by foraging yellow-eyed penguins. The models including bird ID were a better fit, implying that individual diet preferences were present for both nitrogen (approximating trophic level) and carbon (approximating foraging location) isotopes.

6.5.1 Blood versus feathers comparison

Isotope values for blood and feathers followed similar trends to each other; however, all $\delta^{13}C$ and most $\delta^{15}N$ blood values were significantly lower than feather samples from the same diet year (Figure S6.1), meaning that they could not be grouped together for analysis. This is consistent with Cherel et al. (2005) who found significantly lower isotope values for blood compared to feathers in all penguin species studied, and is due to fractionation differences, which mean that SIA signatures of feathers are typically enriched relative to blood for many seabird species (Ogden et al. 2004, Quillfeldt et al. 2008, Bond and Jones 2009).

6.5.2 Nitrogen 15 analysis (trophic level)

Isotopic ratios of nitrogen ($^{15}N/^{14}N$) represent the trophic level at which an animal is feeding (DeNiro and Epstein 1981, Bodey et al. 2011), with fish being a higher trophic level to cephalopods to zooplankton prey (Owens 1988, Hobson et al. 1994). The $\delta^{15}N$ isotope levels of prey obtained by breeding yellow-eyed penguins in the southern population were significantly different in each year, indicating that penguins consumed differing proportions of prey from different trophic levels in different breeding seasons. A change of $\delta^{15}N$ isotope levels of around 2.3–3.4‰ is considered to represent a change in trophic level (McCutchan et al. 2003). The $\delta^{15}N$ results had a range of 1.8‰ for feathers, which was lower than this threshold, meaning that the variability in the diet of yellow-eyed penguins probably relates to differing amounts of prey from each trophic level rather than comprehensive switches between trophic levels.

The trophic level inferred from nitrogen isotope levels was not significantly affected by dive type, implying that benthic and pelagic foragers were generally feeding at similar trophic levels. There was also no significant effect from the maximum foraging distance away from the colony, indicating that there was no consistent correlation between distance from the colony and the availability of different trophic level prey. However, the trophic level was affected by the cumulative total foraging distance (length of trip), implying that birds undertaking trips of longer total distance may have been targeting prey at a different trophic level.

Nitrogen isotope levels were also affected by sex, with females having a lower $\delta^{15}N$ value implying feeding at a lower trophic level or consuming greater amounts of lower trophic level prey. However, sex was not significant when only blood samples were analysed. The variances in feather and blood samples were similar (0.14 and 0.16, respectively) so this is unlikely to have influenced this result; however, the sample size for blood was smaller so may not have been representative. There is no evidence for different diving behaviour between sexes in the northern population (Seddon and van Heezik 1990, Moore 1999, Mattern et al. 2007). This is also true for the southern population, although some individual birds of each sex may consistently use benthic foraging in preference to other methods (Muller et al. 2020a; see Chapter 4), and females may use a larger foraging area during the guard phase (Muller et al. 2021; see Chapter 5). These foraging trends suggest that some females in the southern population may target different prey species (or differing amounts of each species) than males.

6.5.3 Carbon 13 analysis (foraging location)

Isotopic ratios of carbon ($^{13}C/^{12}C$) can be used to infer foraging location, differentiating between inshore versus offshore and benthic versus pelagic feeding (Kelly 2000, Cherel et al. 2007). The $\delta^{13}C$ isotope levels of prey obtained by breeding yellow-eyed penguins in the southern population were significantly different in all years, implying that penguins were feeding at different locations or on prey with different carbon inputs in different breeding seasons. While this implies changing foraging locations, carbon inputs in the same physical location may also be influenced by ocean currents bringing varying amounts of nutrients (Cherel and Hobson 2007). The $\delta^{13}C$ isotope levels were highest (less negative) in 2015, indicating that foraging was associated with more inshore and benthic habitats during this severe El Niño season. This is consistent with the higher proportion of benthic foraging trips evident in 2015 (Muller et al. 2020a; see Chapter 4). Carbon isotope levels were not affected by the maximum foraging distance away from the colony, or the cumulative foraging distance (length of trip). There was also no difference evident between sexes or dive types.

6.5.4 Diet plasticity

Dietary partitioning has also been demonstrated in other penguin species using SIA analysis. SIA of blood from breeding Adélie penguins was able to distinguish between prey at a broad taxonomic level (e.g., fish vs. krill), and this was confirmed by stomach contents analysis (Tierney et al. 2008). They also found that diet composition changed during the breeding season. SIA demonstrated broad diet composition (e.g., fish, cephalopod, crustacean) in little blue penguins, with greater accuracy than stomach sampling (Flemming and van Heezik 2014). In that study, blood isotopes had narrower confidence intervals but also mirrored trends for feathers.

Yellow-eyed penguins are predominantly benthic divers in the northern population (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014). The greater variability in diet at Enderby Island was also consistent with greater plasticity in diving and foraging behaviour, with significant proportions of pelagic diving, probably influenced by different foraging conditions affecting prey species availability and their distribution over time (Muller et al. 2020a; see Chapter 4).

In multiple trips recorded for the same individuals, the majority of birds (72%) displayed consistent foraging behaviour during multiple trips within a season (Muller et al. 2020a). This is also consistent with the significant differences evident in dietary stable isotopes when individual bird ID was included as a factor, demonstrating that individual foraging preferences were maintained over the period while feathers were formed.

6.5.5 Yellow-eyed penguin diet

The diet of the northern population consists primarily of demersal fish species. The main prey species in the 1980s by frequency eaten, were sprat (*Sprattus antipodum*), and by proportion of mass eaten, were red cod (*Pseudophycis bachus*) and opalfish (*Hemerocoetes* spp.), with smaller amounts of other fish species, and arrow squid (*Nototodarus sloanii*), other cephalopods and crustaceans (van Heezik 1990a). There were considerable differences in diet between locations and years (van Heezik 1990a). Later studies revealed a dietary shift to less feeding on red cod, and more blue cod (*Parapercis colias*) along with opalfish (Moore and Wakelin 1997, Mattern et al. 2017, Mattern and Ellenberg 2018, Mattern and Wilson 2018). Regional differences in diet composition are evident for the northern population, probably due to differing benthic habitat (Mattern and Ellenberg 2018). Diet can also be influenced in regions exposed to disturbance caused by bottom trawls favouring scavenging species such as blue cod (Mattern et al. 2013), which can be more difficult for penguins to locate and capture (Mattern et al. 2018a), and as a food source such prey may therefore be restricted to individuals with acquired foraging experience (Forslund and Pärt 1995). In the northern population, larval fish, gelata and other mid-water species were targeted during short periods of pelagic foraging but only when poor visibility prevented benthic foraging (Mattern et al. 2017, Mattern and Ellenberg 2018, Mattern et al. 2018a).

Diet composition of the southern population was unknown prior to this study. Consequently, there is no information on subantarctic prey species targeted by yellow-eyed penguins. Furthermore, many of the northern prey species do not occur in the subantarctic. Diet of the northern population includes juveniles of some commercial species (van Heezik 1990c, van Heezik 1990a, Moore and Wakelin 1997, Browne et al. 2011) and this may also be the case in the subantarctic (Table S6.2). Diversity of reef fishes is negatively correlated with latitude, and the subantarctic Auckland and Campbell Islands have a low diversity of reef fishes compared to other New Zealand ecosystems (Francis 1996), which would be expected to reduce the number of benthic fish species available as a food resource for penguins (Table S6.2). Benthic diving occurs at Campbell Island (P. J. Moore, pers. comm.), with pelagic dives possible but not confirmed there, and prey species similarly unknown.

Future SIA work in the subantarctic would benefit from a reference collection of yellow-eyed penguin prey species and determination of their isotopic signatures, enabling the use of mixing models to estimate relative contributions of specific prey types. Faecal DNA analysis can also assist with identifying diet to species level (Young et al. 2020), provided suitable logistics can be arranged for DNA samples to be transported to New Zealand for analysis. In combination with data on foraging area and diving behaviour from GPS/TDR device deployment (Muller et al. 2020a, Muller et al. 2021; see Chapters 4 and 5), this could provide more detailed information on yellow-eyed penguin foraging ecology in the face of climate change.

6.5.6 Breeding success

Adult seabirds may be able to compensate for declining availability of high-energy prey by bringing back a larger volume of prey (Suryan et al. 2000, Litzow et al. 2002). However, declining diet quality has been linked to selective provisioning and poor reproductive success of yellow-eyed penguins on Stewart and Codfish Islands in the northern population (Browne et al. 2011). Stable isotope analysis has shown that poorer chick nutrition was associated with unsuccessful foraging trips by parents, as well as prey species having a lower energetic content, or being unsuitable for chicks to eat (Browne et al. 2011). Larger food items are less suitable for feeding to chicks and can result in poorer nutritional outcomes (Moore and Wakelin 1997, Mattern et al. 2017, Mattern and Ellenberg 2018), and a corresponding reduction in breeding success (Browne et al. 2011, Mattern and Ellenberg 2018). However, there is no evidence that prey size is an issue for chick nutrition in the southern population.

The amount and distribution of many fish species around New Zealand are affected by water temperature, with warmer water leading to lower recruitment and subsequent biomass (Francis 1996, Beentjes and Renwick 2001), and increasing water temperature since the mid-1990s has been implicated in reduced survival rates and population decline for the northern yellow-eyed penguin population (Mattern et al. 2017).

6.5.7 Climate

In New Zealand waters, El Niño corresponds to a cooler and wetter climate, with implications for many marine species including yellow-eyed penguins (see Peacock et al. (2000) for review). In the northern population, colder temperatures (including air and sea surface temperatures) and wetter conditions are generally more favourable for breeding success (Peacock et al. 2000, Darby 2003), and warmer conditions, such as warm water events associated with La Niña, generally result in poorer and more variable breeding success outcomes (Moore and Wakelin 1997, Young 2014, Mattern et al. 2017). High air temperatures around mainland New Zealand can also subject nesting birds to heat stress, which can affect breeding success (Seddon and Davis 1989, Clark et al. 2015). This study suggests that southern populations may differ from the mainland, and El Niño conditions may be less productive or even detrimental to breeding success. However, it may also be the case that any severe climate effects are detrimental, regardless of type.

El Niño conditions were present in 2014 (weak) and 2015 (severe), and both 2016 and 2017 were mild La Niña years (Null 2019). At Enderby Island, the $\delta^{15}N$ isotope levels were lowest in 2015, suggesting that birds were feeding more on lower trophic level prey during this severe El Niño season, and levels were highest in 2016 during mild La Niña conditions. Lower trophic level prey generally have a lower energy content than prey of higher tropic level (Meynier et al. 2008), which indicates poorer-value prey during the El Niño conditions in 2015. Stable isotope analysis of carbon indicated foraging (based on prey species composition) was on average closer to shore and more benthic in 2015 than in 2016 or 2017. This corresponded with a high incidence of benthic foraging recorded for southern yellow-eyed penguins in 2015

(Muller et al. 2020a; see Chapter 4), and a lower breeding population and breeding attempts during El Niño conditions these years (Muller et al. 2020b; see Chapter 3).

Studies on many prey species have shown poorer recruitment and lower biomass related to periods of warmer water, including for red cod (Beentjes and Renwick 2001), an important part of the diet of the northern population, and for southern blue whiting, an important species in subantarctic fisheries (Hanchet and Renwick 1999). Southern blue whiting are also negatively affected by other weather events in the subantarctic (Willis et al. 2007). Our study indicates that diet and foraging for the southern yellow-eyed penguin population are variable, and may also be affected by ENSO index, with implications for breeding success.

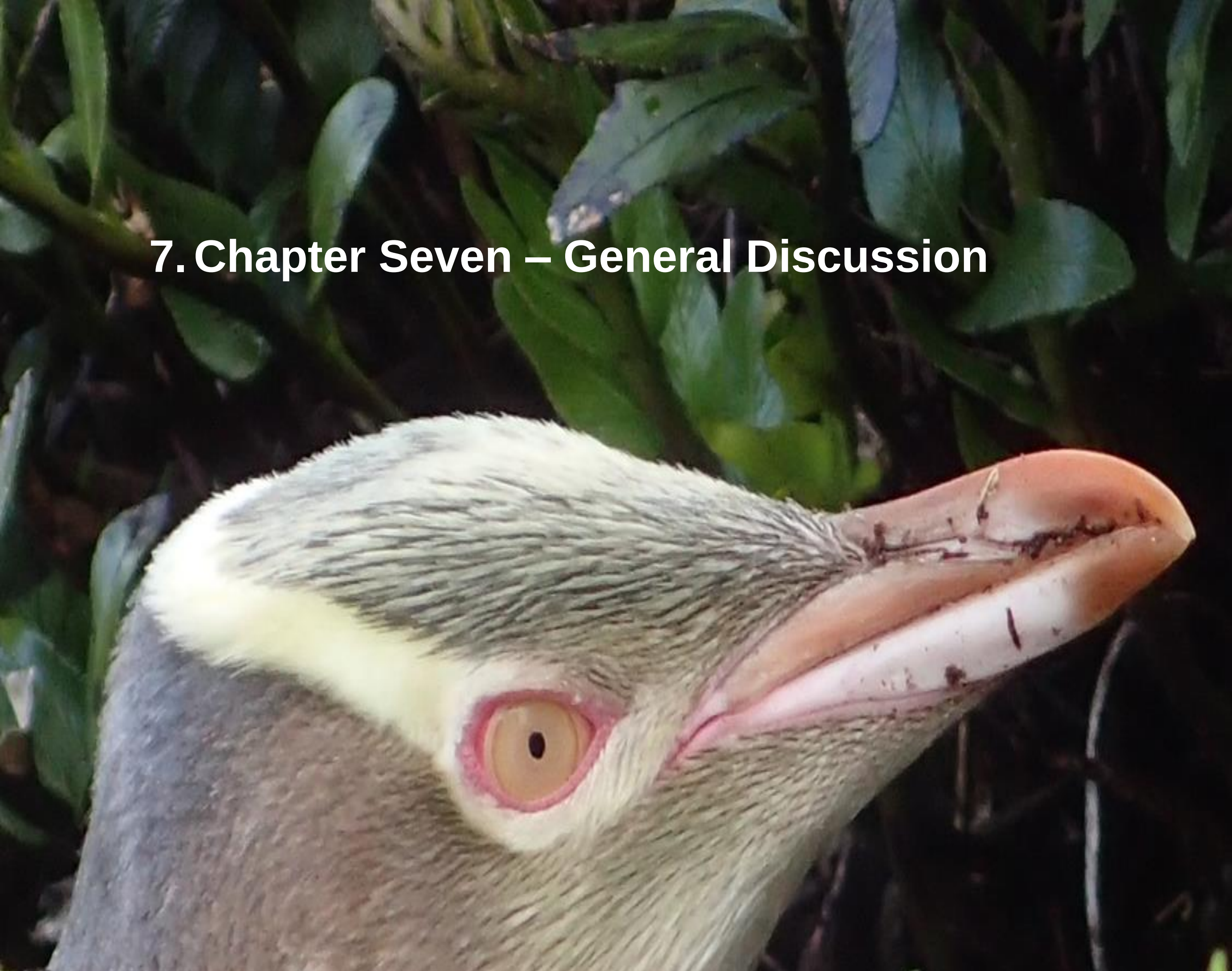
These results corresponded to poorer breeding success during the severe El Niño in 2015, and the weak La Niña in 2017, but positive breeding success during the weak La Niña in 2016 (Muller et al. 2020b). Since weather conditions can be more severe in the subantarctic (Eden 1955, Higham 1991), it may be that individual weather events play a more significant role than ENSO state in the region, although climate changes that lead to an increase in number or severity of severe weather events would be expected to have a detrimental effect on yellow-eyed penguin population stability.

6.5.8 Conservation considerations

In addition to direct impact on individual foraging success, climate effects can also increase the pressure on a population rendering it less able to respond to non-climate related impacts, such as fisheries interactions, habitat degradation, human disturbance, and prey availability, which have all been implicated in declines in the northern yellow-eyed penguin population (Mattern et al. 2017). This study demonstrates that yellow-eyed penguin diet is variable in the southern population, probably influenced by local climatic conditions including ENSO. Diet during El Niño conditions comprised lower trophic level and more benthic prey, and during La

Niña conditions was more pelagic and associated with greater foraging distances. By implication, prey availability is probably also a limiting factor in this region in some years, and therefore a major influencer of future survival and breeding success. This could be exacerbated if the effects of climate change become more pronounced as predicted (Easterling et al. 2000, Ramírez et al. 2017). Therefore, the findings of this study suggest that poor breeding seasons driven by reduced prey availability could become more common in the future. Southern yellow-eyed penguins are also vulnerable to other threats such as nest predation on islands with introduced predators, potential negative interactions with commercial fisheries in the area, including resource competition as well as adult mortality, and to catastrophic events such as oil spills (Muller et al. 2020b; see Chapter 3), all of which could compound the effects of a poor breeding season. Unlike in the northern population, logistical constraints largely prevent direct intervention in the subantarctic to rehabilitate individual adults or chicks in poor condition. As a result, intervention is likely to be only possible at a population level to attempt to mitigate large-scale threats. Therefore, ongoing future monitoring of population and breeding success is needed to identify declines and allow intervention as soon as possible. Any potential threats to yellow-eyed penguin survival and foraging need to be investigated in greater detail, and if necessary, pre-emptive interventions made to ensure they do not become a significant contributor to declines in yellow-eyed penguin foraging efficiency or population. The isotope signatures collected for this study provide a foundation to match with the SIA signatures of individual prey species, and this could be expanded on by the use of DNA diet analysis to identify prey species around the Auckland Islands archipelago. This is a key step to understanding the distribution of prey species in space and time, in order to model and predict future constraints on food availability. Future management of the species will benefit from greater knowledge of all potential threats to foraging success, and therefore also to breeding success and population stability.

7. Chapter Seven – General Discussion



7.1 Outline

This discussion chapter will focus on the following topics:

1. Research overview
2. Foraging plasticity
3. Other factors affecting foraging
4. Foraging and breeding success
5. Foraging and climate
6. Implications for other species
7. Conservation
8. General conclusions

7.2 Research overview

Human impacts on the world's environment have been profound and are accelerating, including deforestation, habitat loss and fragmentation, overpopulation, chemical pollution, invasive species, over-exploitation of natural resources, and burning of fossil fuels leading to climate change (Crutzen 2006, Barnosky et al. 2011). These effects are significant to the extent that a new geological epoch, the Anthropocene, has been proposed for the period following the Industrial Revolution beginning in the 1800s (Crutzen 2006, Steffen et al. 2011, Ruddiman 2013). The period of recent human history is characterised by large-scale extinctions, which together have been suggested to comprise the sixth mass extinction event in the history of life on this planet, defined as over 75% of species going extinct in a geologically short time period (Barnosky et al. 2011). The present increased extinction rate highlights the need for targeted and effective conservation measures to prevent additional extinctions, particularly for species already identified as endangered.

Penguins are considered to be sentinel species due to their reliance on healthy, functioning marine systems, and their vulnerability to human-induced changes (Boersma 2008). The yellow-eyed penguin is one of the rarest penguins in the world, with a conservation status listed as Endangered (BirdLife International 2020). Nest numbers on mainland New Zealand have declined considerably from those documented in the early 20th century (Richdale 1957), and this decline has accelerated in recent years, with a 75% decline in nest numbers on the Otago Peninsula since the 1990s (Mattern et al. 2017). Modelling has predicted that at the current rate of decline, the northern (mainland) yellow-eyed penguin population could be functionally extinct within the next two to four decades (Mattern et al. 2017, Mattern and Wilson 2018). Yellow-eyed penguins are an iconic New Zealand species, and important culturally as well as ecologically as they are considered a taonga (treasure) by Māori (Department of Conservation 2020a), are featured on the New Zealand $5 banknote, and are an important contributor to local eco-tourism (McClung et al. 2004, French et al. 2019), so the loss of this species would be felt nationwide.

While the southern (subantarctic) population is widely assumed to be an “insurance population” for the species (Mattern and Wilson 2018), prior to this study no recent population data or measurement of population trends had been collected. The primary purpose of this research was therefore to fill these knowledge gaps for the southern yellow-eyed penguin population, and to identify key conservation concerns.

The main aims of this thesis were to document the population status of yellow-eyed penguins breeding at the Auckland Islands, as well as investigating population and foraging trends, including factors which may affect breeding success in the subantarctic. Each of the five data chapters examined different aspects of yellow-eyed penguin breeding and foraging success, including how these may differ from the northern population.

7.2.1 Key findings

Chapter 2 developed new methodology including novel UAV-based aerial VHF search technology for finding cryptic penguin nests, which was critical to the success of data collection to answer all other research questions. This technology was able to locate nests in only 3% of the time taken for traditional ground-based nest searches. These gains in efficiency, as well as a general increase in the search area size and speed, also has wider applications for locating and tracking many other cryptic species for wildlife research and conservation management.

Chapter 3 refined the existing methodology to estimate the Auckland Islands population in the difficult subantarctic habitat, including developing new methods for ground-truthing count data. Population estimates fluctuated over a 6–year period from 2012–2017, with alternating years of higher and lower populations, and the proportion of breeders following a similar trend. The estimated number of breeders averaged 577 pairs annually, and the Auckland Islands therefore represent 37–49% of the total breeding population for the species, with Enderby Island one of the largest breeding areas. While raw numbers indicated a possible population decline since the only previous population estimate in 1989, there was no evidence of a continuing decline during the mid-2010s. However, the fluctuation in breeding success remains a cause for concern.

Chapter 4 investigated diving behaviour, including developing new methods for analysing dive profiles which are independent of depth. This led to the discovery of pelagic dives occurring in the same foraging area as benthic dives, and identification of entirely-pelagic foraging trips – a foraging strategy not common in the northern population. Dive depth was a maximum of

134 m for benthic dives, and 115 m for pelagic dives, greater than for many northern birds. Diving behaviour differed between years, with predominantly benthic diving during an El Niño year, and increasing amounts of pelagic diving during subsequent La Niña years. Plasticity between benthic and pelagic diving was recorded for individuals within foraging trips, within a breeding season, and between years.

Chapter 5 investigated foraging area, identifying the main foraging location for Enderby Island birds to the south-east of the island. The foraging distance was up to 47 km from shore, which is greater than for many northern birds. There was a large spatial overlap between benthic and pelagic diving areas, indicating that foraging behaviour was independent of bathymetry in those locations. Pelagic foraging took place over a larger area than benthic foraging, and the size of the foraging area changed between years, with a greater area and distance from shore in a year of greater breeding effort and fledging success. Females also travelled greater distances in this study during the guard phase of breeding.

Chapter 6 investigated the trophic level of prey and demonstrated that diet changed significantly between all years in this study; including more benthic foraging, located closer to shore, and with a greater proportion of lower tropic level prey during an El Niño year. This corresponded with lower breeding success in the same year, suggesting that prey availability is likely a limiting factor in some years, particularly for more-variable pelagic prey. Prey availability is therefore expected to have a major influence on survival and breeding success.

7.2.2 Research limitations

Research, especially field-based, is often restricted by budget, time, or logistics. Logistics are particularly difficult in the New Zealand subantarctic, where personnel and equipment need to be transported to the field site by boat and remain in situ for up to three months during the penguin breeding season. Available vessels usually have limited space for personnel and equipment, and the journey usually takes 24–36 hours in rough seas, with implications for some methods of sample storage and transport. Fieldwork is challenging due to inclement weather and difficult terrain, and costs per person-day in the field are comparatively more expensive than research on the mainland, reducing the amount of funding available for equipment. With these restrictions in mind, research was planned to maximise the gain in information for the expenditure of time, effort, and money. With that said, in many cases additional information could be gained in the future with further effort and investment, and to answer different research questions.

Nest finding was a high priority fieldwork task as all other research depended on it, including monitoring nest numbers and breeding success, and identifying individual breeders to collect data on foraging behaviour. Traditional ground-searching methods were unsuitable due to the thick vegetation, and by extrapolation would not have found all the nests in the reference population before the end of the breeding season (which would have been too late to monitor hatching and breeding success in any case).

VHF radio-tracking was useful for finding nests, and for identifying nesting locations within the breeding area. However, traditional ground-tracking equipment still had drawbacks including limited detection range and difficulty travelling on foot due to the topography and thick vegetation, and a number of transmitters were lost as a result. Aerial VHF tracking using a drone avoided many of these limitations and was an invaluable tool for efficient and timely nest location. The main drawback when trying to locate every nest in an area is that it becomes increasingly time-consuming to capture and track a penguin from every nest, and there may be some redundancy if a partner is tracked to an already-known nest.

A search dog was not trialled as no certified yellow-eyed penguin tracking dog was available at the time, although this method would be useful to compare on a similar-sized breeding area (around 50 nests). It would be expected that while a drone may be quicker at finding nests, a trained search dog may be more efficient at finding all the nests in an area, however, results may be biased towards nests closer to the start point (presumably at the coast) since the dog and handler would still need to travel to every nest location on foot.

An accurate population estimate is necessary to determine the number of individuals and breeders in a species, and trends over time. The methods developed during this study for surveying yellow-eyed penguin populations in the subantarctic offer a much more reliable measure than previous studies which used distribution surveys (which do not account for the number of birds in an area) or raw count data of transiting birds (which can be subject to large daily variation, and do not accurately represent the breeding population) (Muller et al. 2020b; see Chapter 3). Ground-truthing is required to determine correction factors for the proportion of breeders in a population, and the proportion of the population seen during a count. (This changes according to foraging schedule and therefore during different breeding phases, and also on a smaller scale due to weather effects). Estimated uncertainties were lower when more of the population was marked, with implications for future research. While ground-truthing data from this study could be re-used for future population estimates, new data will be required if any of the underlying conditions change. The population estimate methods assume a closed population (Chapman 1951), and we assumed the number of unmarked birds did not change during the calculation. The number of marked breeders remained constant. Ongoing research is recommended to monitor numbers and trends for the population, and the number of breeders. Additionally, measuring breeding success, juvenile recruitment and survival of different age classes would be useful information, although much of this would require long-term studies of known (marked) individuals.

To measure foraging behaviour, this study used separate GPS and dive loggers to monitor foraging location and diving, as opposed to a larger unit with integrated electronics. The methods used offered a number of advantages including animal ethics (two smaller units create less drag than one large one), cost (two simple loggers were considerably cheaper than one integrated unit), sample size (using smaller and cheaper loggers allowed a much larger number of units and therefore more deployments than if more expensive loggers were used), and data recoverability (if a device is lost at sea only one set of data is lost, not everything). The use of separate loggers also allowed comparison of dive behaviour with and without the larger GPS logger, which indicated that diving behaviour did not change significantly as a result.

The GPS loggers in this study utilised standard GPS technology which requires several seconds at the surface to compute a fix. This was suitable for determining foraging areas where fixes are needed at the foraging grounds and are collected while birds are resting at the surface between dives. While the use of integrated loggers with fast-acquisition GPS would be expected to provide greater detail on all parts of a foraging trip (including the travelling phase), their greater cost means fewer units would be available for a smaller number of deployments. However, the aim of this study was to determine the foraging extent of the population, which required as large a sample size as possible. Further research using fast-acquisition GPS may reveal more detail on foraging and diving behaviour. Additionally, it should be noted that with any type of GPS logger, penguins with a longer surface interval may be more likely to have successful GPS data recorded, which may lead to better data collection for deeper diving birds which tend to spend longer at the surface between dives (Mattern 2006).

Stable Isotope Analysis of diet is useful to show trends between different groups, and changes over time, although it cannot differentiate prey to individual species level. As a method, SIA of feathers provided a useful measure for diet comparison between years. It is less invasive than taking blood, and logistically simpler to collect, store and transport samples. However, SIA signatures in feathers relate to diet prior to the previous moult, so it was not possible to collect data for the final field season using this method. Therefore, for future research it may be useful to collect blood samples for the final season when feathers are not available, although it will be more difficult to compare SIA results from blood with feathers due to the significant difference between them (Muller et al. 2022; see Chapter 6), which is due to the SIA signatures of feathers being enriched relative to blood (Ogden et al. 2004, Quillfeldt et al. 2008, Bond and Jones 2009). SIA signatures can also be affected by an individual's growth as well as diet. This study looked at SIA of adults only, however, tissue depletion in $\delta^{15}N$ occurs in both food-restricted and rapidly-growing chicks, implying that factors other than diet may be involved. This phenomenon is evident in red blood cells, but not feathers, due to the greater natural variability in this tissue type (Sears et al. 2009). Therefore, for SIA samples with small variance, disparity due to growth should also be considered when evaluating effects of diet on tissue $\delta^{15}N$ composition for faster-growing individuals such as chicks.

Because SIA results provide only a broad indication of diet trends to trophic level only, and cannot identify individual prey species, it is recommended that future work be done to identify prey species in more detail. Data from this study could serve as a baseline for comparison with prey isotope signatures. Additionally, SIA can be combined with DNA metagenomic analysis of faecal samples taken from a cloacal swab, or latrine samples from nest sites. Metagenomics is an emerging technology capable of sequencing all DNA and RNA present in a faecal or body tissue sample, and can be used to document diet (Srivathsan et al. 2015) and food web pathways (French et al. 2022). Collection of DNA samples requires some additional logistical considerations, as they ideally need to be stored and transported at -20^{o}C (Kim et al. 2012), but this method should allow diet identification to species level, as well as the complete microbiome of the host.

Reviews of home range analysis have found that methods and quality of statistical analysis of spatial data between different studies often varied, which introduced difficulties when comparing home range estimates (Chessel 1992, Tufto and Cavallini 2005, Laver and Kelly 2008). This was compounded by different statistical methods used in reporting results, and the authors therefore recommended standardised methods be adopted to ensure consistency and comparability of results (Elise and Rodgers 1997, Laver and Kelly 2008). Unlike other methods such as Minimum Convex Polygons, which do not indicate how intensively different parts of an animal's range are used, kernel methods allow determination of centres of activity (Worton 1989, Worton 1995, Seaman and Powell 1996). Utilisation distribution can be useful for measuring how much overlap exists between home ranges, such as assessing site fidelity or space-use sharing between individuals (Fieberg et al. 2005, Chilvers et al. 2011). Uniform Distribution Overlap Index (UDOI) is a method of comparing the amount of overlap between two different foraging areas (Fieberg et al. 2005) and has been used to analyse penguin foraging behaviour (Sánchez et al. 2018). UDOI distribution analysis was carried out on the yellow-eyed penguin foraging location data from Enderby Island (by year, dive type, and sex), however, results showed no significant difference for any comparisons. This is likely due to the fact that all penguins foraged in a generally similar geographic area, with a large spatial overlap between groups representing different years, dive types, and sexes. Any spatial partitioning was therefore likely occurring on a micro scale within a foraging area rather than between separate areas, and the type of foraging occurring at a given location was therefore likely influenced primarily by prey availability and individuals' foraging preferences rather than geographical partitioning.

7.3 Foraging plasticity

Foraging plasticity is defined as a consumer adapting their foraging strategy to continue finding food, particularly when food supply changes within their usual foraging range (Ballard et al. 2010). In the case of diving penguins this can include changing their foraging method, for example, from benthic to pelagic diving, or changing their foraging location to move further offshore or to a different habitat. Such changes can expose a predator to different prey assemblages and thereby increase their foraging flexibility (Saraux et al. 2011). Behavioural plasticity may differ from flexibility in that the former is a reaction to an external condition rather than an individual choice (Ducatez et al. 2020). While motivators can be difficult to determine, due to their importance for survival and reproductive success I have assumed that observed foraging behaviour changes arose as a result of external stimuli or pressure.

7.3.1 Southern population plasticity

This study highlights a high degree of foraging plasticity demonstrated by breeding birds from Enderby Island, and by extension, the southern population. Some individuals switched between different dive types in different years, and even within breeding seasons, and there were large changes in the location and size of grouped foraging areas between years. This suggests that yellow-eyed penguins have a wide propensity for foraging plasticity in the subantarctic and can adapt their foraging method depending on local prey availability. General trends in foraging behaviour were identified during different ENSO states, with more benthic diving during El Niño conditions and more pelagic diving during La Niña. Therefore, it is probable that some foraging behaviour changes are a response to changing climatic conditions such as SST, likely due to their flow-on effects on the availability and distribution of prey species. This is expected to be most relevant in the case of pelagic prey species which are more variable in time and space than benthic species (Costa et al. 2004, Chilvers and Wilkinson 2009).

Furthermore, given that there was a large intersection between the benthic and pelagic foraging areas used by penguins, with both types of diving occurring together in these shared overlap areas, this indicates that diving behaviour was not governed by water depth or bathymetry in these locations, but presumably by individual choice (Muller et al. 2021; see Chapter 5). This suggests a wide degree of foraging plasticity is present in the species, giving them the ability to target a variety of prey species in different habitats, provided the opportunity is available.

7.3.2 Northern population plasticity

The northern yellow-eyed penguin populations (including mainland New Zealand and Stewart Island birds) are believed to rely on a predominantly benthic foraging strategy, based on recent dive studies (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014). Benthic foraging dives generally take place over shallow continental shelf waters within 25 km from shore (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). Maximum dive depths vary in different locations depending on local bathymetry, ranging from 26–77 m at mainland sites (Seddon and van Heezik 1990, Moore et al. 1995, Mattern 2006, Mattern et al. 2007, Mattern et al. 2013, Mattern et al. 2018a), and 48–94 m at Stewart Island sites (Chilvers et al. 2014), with a maximum dive depth of 114 m at Port Pegasus (Elley et al. 2022). Birds from Stewart Island show consistent foraging behaviours between different years and breeding areas (Elley et al. 2022), with foraging plasticity generally more pronounced between different Stewart Island breeding populations, with birds from the same area tending to share centres of foraging activity (Elley 2022). Exceptions were also noted, with benthic diving observed in a tidal mudflat area at Stewart Island having a maximum dive depth of only 0.5–3 m, and another instance where a bird foraged over a biogenic reef surrounded by deeper water (Elley et al. 2022), indicating a degree of individual foraging plasticity by the birds involved. There was no clear distinction in foraging range size between breeding, premoult, and winter seasons in the northern population, as foraging ranges differed depending on breeding site (Hickcox 2022).

Additional foraging plasticity is also evident during diet studies in the 1990s where some pelagic species were documented in the diet (van Heezik 1990a, Moore et al. 1995). Together, these data may be evidence of a focus on more demersal species (Moore et al. 1995), or a change in foraging behaviour of the northern population to a predominantly benthic strategy in recent times. However, occasional pelagic dives have recently been recorded using video camera loggers (Mattern et al. 2017, Mattern and Ellenberg 2018, Mattern et al. 2018a), although during these dives penguins targeted lower-quality prey items during short periods of pelagic foraging when poor visibility likely prevented benthic foraging. Nevertheless, this does demonstrate that the northern population is able to perform pelagic foraging, even if this behaviour does not currently appear common. Considerable differences in diet have been reported between different locations and years (van Heezik 1990a, Moore et al. 1995), and birds were also observed to change their foraging strategies and areas (Moore et al. 1995, Moore 1999), providing further evidence of some foraging plasticity occurring in the northern population. For example, the foraging behaviour of yellow-eyed penguins from north-western Stewart Island and neighbouring Codfish Island are significantly different (Mattern 2006, Ellenberg and Mattern 2012), with flow-on effects on chick nutrition (Browne et al. 2011). Both the distribution and ease of capture of some prey species can depend on the substrate type (Mattern et al. 2018a), necessitating different foraging strategies in different locations.

A large variation in foraging behaviour was evident between individuals in this study of the southern population, including foraging methods, locations, and presumably also prey species targeted. Many mainland studies have used smaller numbers of birds, therefore, an apparently lower foraging plasticity for northern birds may be an artefact of smaller sample sizes and may not represent the full range of foraging behaviour in the northern population. It is also possible that pelagic foraging may have been more common in the northern population in the past, and an apparently lower foraging plasticity at the present time may be a result of external factors acting on the population and therefore may not represent their full potential.

Given the shared evolutionary history and genetic similarities between the northern and southern populations (Boessenkool et al. 2009a, Boessenkool et al. 2009b), yellow-eyed penguins would not be expected to display inherently different foraging behaviours. Rather, any differences between these populations are likely due to local conditions such as the physical characteristics of the marine environment, including depth gradients, the size of suitable foraging areas, and their proximity to shore. Foraging differences can also be driven by the type of prey species present, and their availability. This may be particularly relevant in the case of pelagic species which tend to be more variable in time and space. Prey availability can also be affected by external factors such as fisheries pressure, as well as environmental variables including water temperature. Consequently, the apparent reliance on benthic foraging by the northern population may represent an absence of suitable pelagic prey located close to breeding areas, since they could presumably utilise this resource if it was available (and may have done so to a greater degree in the past) (van Heezik 1990c, Moore et al. 1995).

7.3.3 Implications for the future

As foraging plasticity represents the ability of a species to adapt to changing conditions and continue to procure food for themselves and their offspring, greater foraging plasticity is therefore associated with a decreased risk of extinction in birds (Ducatez et al. 2020). The present study demonstrates that yellow-eyed penguins are clearly capable of foraging plasticity and can adapt their foraging method depending on prey availability. However, previous evidence shows more limited foraging plasticity in the northern population than in the subantarctic. If true, this may indicate greater environmental limitations, or increased pressures on prey availability for yellow-eyed penguins around mainland New Zealand, or alternatively, that the northern population is able to achieve foraging success without needing to be as plastic. Breeding birds from Enderby Island generally undertook longer foraging trips than many of their counterparts in the northern population, travelling further offshore, and diving deeper. While this is undoubtedly influenced by local bathymetry and prey availability, it does suggest a greater amount of foraging effort may be expended by the southern population to obtain food. This is likely balanced if suitable prey sources are available in sufficient quantities, and with sufficient nutritional content to outweigh the energy required to obtain them (Croxall et al. 1999). However, any factors affecting prey availability, efficiency of capture, or nutritional quality in the future could have an overall detrimental effect on foraging success, and therefore also on the viability of the southern population.

7.4 Other factors affecting foraging

Factors known to influence foraging activity include adult age and foraging experience (Nisbet and Dann 2009), body mass (Kato et al. 2008), variable environmental conditions within a breeding stage (Chiaradia et al. 2007), food requirement of chicks depending on age (Takahashi et al. 1999), and an interaction of other factors which can vary over time (Zimmer et al. 2011b).

7.4.1 Sex-related differences

This study found no significant difference in maximum dive depth between sexes. Dives by females did have significantly shorter dive time and bottom time, although these time differences were small (a few seconds), and therefore unlikely to be biologically significant. Males and females conducted similar proportions of benthic and pelagic dives, although some individual birds of each sex may consistently utilise benthic foraging behaviour. While females did travel greater distances and use a larger foraging area, this may have been related to breeding phase as only the guard phase was examined. There is also evidence females were consuming greater amounts of lower trophic level prey, which may indicate some resource partitioning, or a possible difficulty finding or capturing some higher trophic level prey such as larger fish.

Males in the northern population had larger home ranges across different breeding phases, however comparisons were complicated by different sized ranges evident in different areas (Hickcox 2022). In contrast, no sex-specific diving differences have been documented in northern yellow-eyed penguins (Seddon and van Heezik 1990, Moore 1999, Mattern et al. 2007), except around Stewart Island, where females dived deeper with a mean depth of 50 ± 5.9 m but shorter bottom time (Chilvers et al. 2014). That study had a small sample size (n = 5 females and 3 males) so may not represent the full range of behaviours of the population. However, the similarity is interesting and it may be the case that smaller females with a smaller lung capacity can spend less time at the bottom when making deeper dives, but any physiological differences may be less significant if birds are making shallower dives. Diving animals face physiological restrictions on dive time, and therefore also dive depth during benthic diving, which may make it harder for juveniles and smaller individuals to forage at deeper depths (Costa et al. 2004). Body size therefore has a direct correlation to maximum dive depth. Larger penguin species generally dive deeper than smaller species, with a maximum dive depth of over 400 m for 25 kg emperor penguins (*Aptenodytes forsteri*) (Wienecke and Robertson 1997), compared to <50 m for 1.2 kg little penguins (Chiaradia et al. 2007).

Intra-species size differences due to sexual dimorphism are less pronounced than many inter-species size differences. Nevertheless, a degree of sexual dimorphism is evident in most penguin species, with males generally larger and heavier, and this size difference is most pronounced in the smaller crested penguins (*Eudyptes* spp.) (Croxall 1995). This also translates to differences in dive behaviour and maximum dive depth between sexes in many penguin species, including emperor penguins where males are able to dive deeper than females (Wienecke and Robertson 1997).

Sex-specific differences in foraging behaviour during breeding have been observed in a number of seabirds (Lewis et al. 2002) and are often related to sexual size dimorphism (González-Solís et al. 2000, Lewis et al. 2005, Weimerskirch et al. 2009). Larger and heavier diving birds can dive to greater depths (Kato et al. 1999, Taylor et al. 2002, Zavalaga et al. 2007, Weimerskirch et al. 2009, Quillfeldt et al. 2011), and diving deeper may allow them to exploit different species or larger prey (Williams 1991, Bearhop et al. 2006, Quillfeldt et al. 2011). Competitive exclusion may result in sexual segregation in foraging areas, with smaller birds (often females and younger individuals) needing to feed further away from the colony (Weimerskirch et al. 1993, González-Solís et al. 2000, Quillfeldt et al. 2011).

Sex-related differences in foraging behaviour can also be due to behavioural responses such as avoiding inter-sexual competition for finite resources, or to males and females undertaking different roles during breeding with varying energy requirements at different times in the breeding cycle. This behaviour has been observed in monomorphic seabirds (Lewis et al. 2002, Welcker et al. 2009), where it is often related to chick provisioning rates (Gray and Hamer 2001, Quillfeldt et al. 2004), and also in sexually dimorphic species, such as southern rockhopper penguins. In that species, both sexes are involved in incubation and chick provisioning, but with a different schedule and different energetic requirements at different times. Consequently, males typically feed at a higher trophic level, particularly if prey availability is limited (Dehnhard et al. 2011, Dehnhard et al. 2013a). Sex-specific differences in foraging behaviour may therefore be a result of different energetic requirements for males and females during different breeding stages, and the same may be true for individuals alternating between foraging for themselves or their offspring (Welcker et al. 2009). Differences can also be caused by prey preferences, energetic needs, or time available for foraging during each breeding phase.

Many penguin species, including little penguins, demonstrate a complex interaction of factors affecting foraging, some of which vary in influence over time (Zimmer et al. 2011b). Significant differences are evident between male and female penguins in dive depth, dive frequency, dive duration, swimming speed, energy expenditure, trip duration, foraging location, or diet, including for little penguins (Bethge et al. 1997, Chiaradia and Nisbet 2006, Hoskins et al. 2008), Adélie penguins (*Pygoscelis adeliae*) (Chappell et al. 1993, Clarke et al.

1998), Humbolt penguins (*Spheniscus humboldti*) (Taylor et al. 2002), king penguins (*Aptenodytes patagonicus*) (Le Vaillant et al. 2013), and emperor penguins (Wienecke and Robertson 1997). Sex-related foraging differences have also been observed in other seabirds, with male shags (*Phalacrocorax* spp.) feeding at a higher trophic level than females (Bearhop et al. 2006). In contrast, no sex-linked foraging differences have been described for gentoo penguins (*Pygoscelis papua*) (Croxall et al. 1988), or royal penguins (Hull 2000), although it is unknown whether such differences may manifest under different environmental conditions.

7.4.2 Age-related differences

My research showed preliminary information that juveniles from the Auckland Islands travel over 200 km offshore where they are likely undertaking pelagic foraging (Muller et al. 2020a; see Chapter 4). They remain at sea for several weeks at a time, demonstrating a non-central place foraging strategy which is more efficient than frequently returning to land. However, more information is needed on what food sources juvenile penguins depend on, and what additional threats they may be exposed to from greater overlap with oceanic predators and commercial fisheries in the Southern Ocean. As the future source of recruitment to the adult breeding population, more information on juvenile foraging and survival is also needed to identify these risks to the southern yellow-eyed penguin population.

Little is known about juvenile foraging behaviour or survival in yellow-eyed penguins, particularly in the southern population, as this usually requires a long-term longitudinal study of known individuals over a number of years. Juveniles from the northern population are believed to travel much more widely and further offshore than adults (M. J. Young, pers. comm.). The median annual survival rate of yellow-eyed penguins in the first year after fledging is only 12.4% on the New Zealand mainland, compared to 87.4% for breeding-age adults (Mattern et al. 2017).

Foraging behaviour and success can vary according to age in many seabird species, with larger, older, and more experienced individuals often more successful hunters, and more likely to take on larger or more difficult prey species (Forslund and Pärt 1995). Older penguins are frequently more efficient foragers (Zimmer et al. 2011a), with emperor (Le Vaillant et al. 2012) and king penguins (Saraux et al. 2012) changing their foraging strategy and dive behaviour with age, and in response to environmental variability. As younger, smaller, and less experienced hunters, juveniles are often less efficient at obtaining food (Forslund and Pärt 1995). The survival of juveniles from fledging until recruitment into the adult breeding population is important in the study of population dynamics, however, is often the least-studied demographic in many seabird populations, primarily due to the long-term studies and sometimes wide dispersal area required to monitor juveniles (Dehnhard et al. 2014). Learning the foraging skills required to survive leads to high mortality of seabirds in their first year, particularly during years of low prey quality or abundance, or those in poor condition at fledging (Morrison et al. 2009). First-year survival is typically lower than the survival of pre-breeders in subsequent years, and survival rates are likely to improve to approximate those of adults by the time of recruitment (Guinard et al. 1998, Dehnhard et al. 2014). Sex- and age-related differences in foraging behaviour may partition resources to prioritise breeders in their prime. However, if resources become scarce or more difficult to obtain, this could result in differential pressure on other age classes within a population, possibly resulting in a destabilising effect on overall population viability.

7.5 Foraging and breeding success

As top consumers, seabirds often mirror changes in the physical parameters of the marine ecosystem (Diamond and Devlin 2003). Seabirds typically have a low reproduction rate, making them vulnerable to any factors which decrease adult survival, or which reduce breeding success or the survival of offspring to recruitment age (Cairns 1988, Ricklefs 1990, Purvis et al. 2000). Breeding success is therefore linked to the individual body condition of parents, and by extension, to their foraging success (Chapman and Reiss 1999). Predators are able to vary their diet and can switch prey to target abundant species and maximise their dietary input (Murdoch 1969), yet this ability is still dependent on the type and volume of prey available, and the ease of obtaining it (Chapman and Reiss 1999). As a result, seabird breeding success can be limited by a combination of environmental factors such as climate and extreme weather events influencing prey availability, as well as the foraging success of individual breeders (Forslund and Pärt 1995, Fowler 1995, Wendeln and Becker 1999, Moreno 2003), which can be less efficient in younger or very old birds (Moreno 2003).

7.5.1 Southern population breeding

Population status and trend data were needed for yellow-eyed penguins at the Auckland Islands. Where it is not possible to easily count all individuals in a population, estimates can be made of the total population and the proportion of breeders. Monitoring over time can then indicate whether numbers are increasing or decreasing (Dowding 2012). Comparison of raw count data indicated a possible decline since the previous population estimate in 1989 (Moore 1990, Moore 1992b), although there is some uncertainty with using count data in this way, and there was no evidence of a continued decline in population estimates during the 2010s. Nevertheless, the estimated population and number of breeders at the Auckland Islands fluctuated considerably between years, with alternating higher and lower breeding attempts and productivity (Muller et al. 2020b; see Chapter 3). While this could be related to behavioural trends such as birds breeding only in alternate years, a two-year breeding cycle has not been documented in the species, and breeding sabbaticals were primarily linked to a prior breeding failure and a subsequent partner change in the northern population (Setiawan et al. 2005).

Nesting attempts in established pairs are likely linked to the individual body condition of breeders in the lead-up to the breeding season, and therefore to their recent foraging success (Cubaynes et al. 2011, Baron et al. 2013). Variable foraging success at the Auckland Islands was documented during this study (Muller et al. 2020a, Muller et al. 2021, Muller et al. 2022; see Chapters 4, 5, and 6), suggesting a likely link to variable breeding success.

In some years the number of nesting attempts at Enderby Island was noticeably lower (Muller et al. 2020b), likely as a result of some birds not achieving sufficient body condition leading up to the breeding season (pers. obs.). This is expected to relate to poorer foraging conditions and success during the previous winter, particularly for inshore foragers that may be affected by localised prey depletion (Ashmole 1963, Saraux et al. 2011), and prior to egg laying which occurs in September in the subantarctic (Moore 1990). In one year (2017), a large number of eggs did not hatch, indicating a large-scale breeding failure during the incubation phase, possibly due to an extreme temperature or weather event (C. G. Muller, unpubl. data). In most years there is also an early peak of chick mortality in the first two weeks after hatching, likely attributable to a combination of disease or climate effects, followed by a later peak of mortality after around two months, due mainly to malnutrition as many deaths were of underweight individuals (C. G. Muller, unpubl. data). There is a complex interrelation between climate, foraging, and breeding success for yellow-eyed penguins, and in fact all penguins, which affects all stages of the breeding process (Croxall et al. 1999, Ballard et al. 2010). This situation provides multiple points of breeding failure if climate conditions were to become less favourable for egg and chick survival, both directly through weather conditions and extreme events, and indirectly by affecting prey distribution and parental foraging success.

As a long-lived, slow-growing species, yellow-eyed penguin populations are strongly affected by adult mortality, and any factors which increase this pressure could have a detrimental effect on overall population viability (Purvis et al. 2000, Boersma et al. 2020). More long-term research is needed to determine average adult lifespan, and to identify rates of adult mortality at the Auckland Islands. This would also assist with identifying unusual or unsustainable threats to the breeding population. Population numbers vary on subantarctic Campbell Island due to adult mortality, with numbers decreasing by 41% between 1988 and 1992, and a partial recovery over the next six years (Moore et al. 2001). This suggests population fluctuations are occurring on Campbell Island, so ongoing population studies are recommended there too.

7.5.2 Northern population breeding

Variable breeding success also occurs in the northern population, with the number of seasons with poor breeding or low adult survival increasing since the 1980s (Moore 1991, Mattern et al. 2018a). The continued decline in the northern population has been linked to successive poor breeding seasons and ongoing high adult mortality (Couch-Lewis et al. 2016), as well as threats at sea (Mattern and Wilson 2018). Yellow-eyed penguins requires a reliable food supply and generally do not cope well with declines in prey availability (van Heezik 1988). This is highlighted by similar declines in the breeding populations on Stewart Island, as well as on neighbouring Codfish Island, a protected and predator-free sanctuary, where terrestrial threats are not considered an issue, therefore suggesting that marine threats are responsible (Mattern and Wilson 2018).

Some foraging differences between Codfish Island and Stewart Island populations are believed to relate to benthic habitat modification from commercial oyster dredging in Foveaux Straight, and likely contributed to different breeding success outcomes, with reduced chick survival where parents foraged in affected areas (Browne et al. 2011). Prey species are associated with certain types of benthos (Mattern et al. 2018a), with implications for foraging success depending on the local availability of suitable foraging habitat.

7.5.3 Other species

Breeding success is linked to foraging success in many other penguin and seabird species. Parental foraging efficiency affected chick provisioning and condition in common murres (*Uria aalge*) (Davoren and Montevecchi 2003) and wandering albatrosses (*Diomedea exulans*) (Shaffer et al. 2003). In many species, chick survival decreases when adult foraging trips are longer and require more energy expenditure to find food, including for Adélie (Ballance et al. 2009), and Magellanic penguins (*Spheniscus magellanicus*) (Boersma and Rebstock 2009). Breeding productivity and chick survival are also positively correlated with food availability in little penguins, and in addition, their foraging plasticity is limited by their short foraging range (Chiaradia and Nisbet 2006). In larger colonies, prey availability is generally reduced nearby, forming a "halo" of depleted prey close to the colony, and foraging penguins are more likely to travel further away to avoid interspecific competition. This phenomenon has been documented in Adélie (Ainley et al. 2004, Ballance et al. 2009), and little penguins (Amélineau et al. 2021), and in other seabirds such as northern gannets (*Morus bassanus*) (Lewis et al. 2001). Localised prey depletion is common in many inshore-foraging seabird species, along with foraging partitioning to avoid competition (Weimerskirch et al. 1986).

As a probable response to localised prey depletion, spatial segregation in foraging areas occurs between neighbouring little penguin colonies (Hoskins et al. 2008), as well as between birds from the same colony (Sánchez et al. 2018). Neighbouring colonies of northern gannets forage in non-overlapping areas, with foraging locations determined by density-dependent competition (Wakefield et al. 2013). Foraging little penguins often alternate between shorter and more frequent trips to provision chicks, and longer trips for self-maintenance (Saraux et al. 2011). Longer trips allow parents to rebuild their reserves by targeting distant and more profitable prey patches (Kato et al. 2008), and also by reducing competition compared to foraging areas closer to the colony (Saraux et al. 2011). Alternate long and short foraging trips have also been documented in other seabirds including common diving petrels (*Pelecanoides urinatrix*), blue petrels (*Halobaena caerulea*), thin-billed prions (*Pachyptilla belcheri*), and albatrosses including yellow-nosed (*Diomedia chlororhynchos*), black-browed (*D. melanophris*), and wandering (*D. exulans*) (Weimerskirch et al. 1994). Diet studies of seabirds have shown that adults may preferentially feed their chicks on fish rather than invertebrates such as krill or squid (Hobson and Clark 1993, Hodum and Hobson 2000, Forero et al. 2002). In some cases, adults may forage separately for their own nutrition, and collect prey intended for their chicks immediately before returning to shore (Forero et al. 2002). This has implications for chick nutrition if their foraging time is extended due to distance travelled, disturbance, or other delays.

In the current study on Enderby Island yellow-eyed penguins, foraging trips were not monitored throughout the season so it was not possible to tell if birds alternated between shorter and longer trips. However, a larger foraging area and distance from shore were observed during 2016 (Muller et al. 2021; see Chapter 5). That year also corresponded to a higher number of nesting birds than other years, which may explain the reason for foraging more widely as a result of intra-specific competition or prey depletion closer to the breeding area. Additional research would be useful to determine if this is a factor affecting foraging and breeding success for the species, in both the southern and northern populations.

7.6 Foraging and climate

7.6.1 Climate effects

The primary driver of seabird productivity is stochasticity or variation in the marine environment, particularly in temperate regions (Chambers et al. 2009). Fluctuating atmospheric pressure can generate greater variability in weather conditions, including unusual regional warming or cooling and an increased prevalence of extreme weather, as frequently occurs during ENSO cycles in New Zealand (Hopkins et al. 2010). Adverse weather events such as intense rainfall, flooding, strong winds, snow or high temperatures can affect seabird productivity. Storms or strong winds at sea can reduce foraging and diving efficiency, or prevent foraging entirely (Finney et al. 1999, Saraux et al. 2016), and these effects can persist for some time after a storm (Barreau et al. 2021). Inclement weather or storms on land can also affect chick-rearing and may prevent some seabirds from breeding altogether (Mallory et al. 2010), and short-term temperature extremes may cause thermal stress for nesting seabirds (Boersma 1976, Williams 1995). Successful incubation and brooding therefore requires consistent temperatures, as extreme conditions may compromise survival of the embryo or chick (Weinrich and Baker 1978), or the resulting stress may cause nest abandonment (Thierry et al. 2013). The survival of chicks is dependent on weather and climate conditions, as well as the amount of incubation and insulation a chick receives from its parents, and adequate provisioning to maintain thermoregulation and growth, including during adverse weather events (Diamond and Devlin 2003).

As a result, any short- or long-term changes to weather patterns or climate can affect sea surface temperatures (SST), and in turn this can have a major impact on marine productivity (Gregg et al. 2003, Lewison et al. 2012). Changes in SST can negatively affect whole food webs (Trenberth and Fasullo 2007), with significant implications for seabird foraging and breeding success (Lewison et al. 2012). Major population declines and breeding failures have occurred in many seabirds as a result of changing environmental conditions (Boersma 2008, Mallory et al. 2009). These include arctic (*Sterna paradisaea*) and common terns (*S. hirundo*) (Diamond and Devlin 2003), thick-billed (*Uria lomvia*) and common murre (Irons et al. 2008), and also many penguins, including little penguins (Mickelson et al. 1992, Perriman et al. 2000), Galapagos (*Spheniscus mendiculus*) (Vargas et al. 2006), eastern rockhopper (*Eudyptes chrysocome filholi*), and other *Eudyptes* penguins (Vargas et al. 2007, Morrison et al. 2015).

Warmer water commonly results in poorer prey conditions for penguins, with consequent feeding at lower trophic levels, and poorer body condition for adults and chicks (Forcada and Trathan 2009). This resulted in population declines for southern (Dehnhard et al. 2013b) and eastern rockhopper penguins (Morrison 2015). As penguins are long-lived species and therefore slow to adapt to fast-changing conditions, contracting or shifting their distribution range is likely their only response to climate change (Forcada and Trathan 2009). However, in the subantarctic this would be limited by the availability of land suitable for breeding, and in the New Zealand subantarctic there are no other islands to the south of Campbell Island outside of the Antarctic Circle.

7.6.2 El Niño Southern Oscillation

In New Zealand and the Western Pacific, El Niño corresponds to a cooler and wetter climate, while La Niña conditions are typically warmer and drier (Gordon 1986, Mullan 1995).

For yellow-eyed penguins in the northern population, breeding success is generally improved during the colder air and sea temperatures of El Niño (Peacock et al. 2000, Darby 2003), and poorer in the warmer conditions associated with La Niña events (Moore and Wakelin 1997, Young 2014, Mattern et al. 2017). However, the present study suggests that southern populations may differ from the mainland, and El Niño conditions (as occurred during the 2015 breeding season) may be less productive or even detrimental to breeding success. Penguins relied on a significantly greater proportion of benthic foraging, which may indicate an unavailability of pelagic prey. Conversely, it may also be that birds were forced to forage over a much wider area searching for pelagic prey during La Niña conditions as a result of insufficient benthic prey closer to the colony. Either way, foraging success is likely subject to complex interactions involving the number and distribution of prey species, and how they are affected in time and space by climate variability.

However, it may also be that any severe climate effects are detrimental, regardless of the type. In the northern population, nesting yellow-eyed penguins often suffer from heat stress during summer, particularly at exposed breeding sites on mainland New Zealand (Seddon and Davis 1989, Clark et al. 2015). Heat stress has not been observed in the southern population, but the effects of colder temperatures and inclement weather events may be more pronounced in the subantarctic. In this study significant egg mortality was observed during the 2017 breeding season (a mild La Niña year) on Enderby Island, where the number of unhatched eggs rose from an annual mean of around 14% to 41%, and subsequently this reduced the mean offspring produced per nest from around 1.5 to 1.0 for that year (C. G. Muller, unpubl. data). The reasons for this are not clear, as it happened early in the season and prior to researchers' arrival on the island. However, over 70% of unhatched eggs had an embryo inside, indicating they were fertile but had stopped growing. Embryos were different sizes, indicating they were different ages, although laying dates can be staggered by up to three weeks in the northern (Richdale 1949) and southern populations (Moore 1992a), including Enderby Island (C. G. Muller, unpubl. data). Therefore, it is possible that this large-scale egg mortality arose as a result of one or more adverse weather events during incubation.

7.6.3 Climate and yellow-eyed penguins

The relationship between climate variations, including ENSO, and effects on yellow-eyed penguin foraging and breeding success are not well understood, particularly for the southern population. While this study has identified likely correlations, these need to be examined in more detail. It would be useful to compare various measures of foraging and breeding success with climate variables, and to investigate any possible statistical significance between them. As part of this study I used the climwin package in R to compare monthly climate variables (SST and ENSO index) for the Auckland Islands with yellow-eyed penguin population variables (population estimate, estimated number of breeders) and breeding success variables, including 1) nests (number of nests, number of eggs laid, mean number of eggs per nest, egg hatching success (proportion), proportion of nests failing at egg stage), 2) chicks (number of chicks hatched, mean number of chicks per nest, chick survival (proportion), proportion of nests failing at chick stage), and 3) fledging data (number of chicks fledged, mean number of fledglings per nest, nesting success (proportion for the whole season), proportion of failed nests (for the whole season)). However, I had only 3 years of breeding success data and the model would not run successfully on a timeframe that short. I had 6 years' data for the population variables which allowed these to be modelled, and a link between SST was close to significant (p=0.07), indicating a possible link with estimated population and the number of breeders. However, these population parameters were based on estimates with large uncertainty values in the earlier years of the study, so it was not possible to draw any concrete conclusions from this analysis.

Nevertheless, climate effects are expected to have a major influence on yellow-eyed penguin foraging, survival and breeding success in the southern population, and these are expected to become more pronounced in the future due to climate change (Collins et al. 2013, Ramírez et al. 2017). Some northern yellow-eyed penguin breeding populations are predicted to be locally extinct by 2043 due to climate changes affecting food supply (Mattern et al. 2017). Therefore, it is important to understand these relationships in more detail in the subantarctic, highlighting an urgent need to collect additional breeding success data from the Enderby Island population. This could be pooled with my existing data (since data points do not have to be continuous for climate analysis) which would allow for climate modelling analysis and comparisons to be made with yellow-eyed penguin population and breeding success. Since yellow-eyed penguins also displayed a high degree of foraging plasticity in the subantarctic, collecting additional foraging success data (such as the proportion of benthic / pelagic diving, foraging distance, foraging area size, etc) would allow comparisons between these factors and SST, ENSO, and climate effects to be modelled as well. Future management of the southern population will benefit from greater knowledge of the potential threat from climate change to breeding success and population stability.

7.7 Implications for other species

The link between climate, prey availability, foraging success, breeding success, and population declines is a common theme for many marine species. This study has demonstrated differing foraging behaviour in the yellow-eyed penguin, including greater average dive depths and foraging distances for the southern population than at many locations in the northern population, as well as a greater proportion of pelagic foraging. These differences are likely influenced by a combination of the physical environment, biological and environmental factors affecting prey availability and distribution, and also individual behaviour choices. Differences in foraging strategy also occur in other species at different locations across their range.

7.7.1 Penguins

The little penguin (kororā in Māori) is the smallest penguin species, and has a wide distribution around New Zealand and southern Australia (Dann 2013). Some populations are stable, but others are declining, and threats come from fisheries and climate change, as well as predation and human activities on land (Mattern and Wilson 2018). Little penguins display a range of diving behaviours across their range. In some colonies, including Penguin Island in Australia, and Oamaru and Motuara Island in New Zealand, penguins have access to a large area of shallow water for foraging (Chiaradia et al. 2007). Conversely, at Phillip Island in Australia, the majority of foraging habitat is deeper than 50 m, and penguins expend more energy diving deeper, with fledging success comparatively lower as a result (Chiaradia et al. 2007). While foraging is constrained by the physical environment in some locations, penguins are able to adopt alternative successful foraging strategies. Even though fledging success is lower at Phillip Island, it is one of the largest breeding colonies with an estimated 32,000 birds (Phillip Island Nature Parks 2022). Individual foraging plasticity is also evident, with changes in prey and foraging location occurring as the breeding season progresses (Amélineau et al. 2021), as well as changes in trip duration (Saraux et al. 2011) and distance from shore (McCutcheon et al. 2011). This adaptability has led to the little penguin being the most widely-distributed penguin in Australia and New Zealand, although it remains to be seen if the species can successfully cope with new threats, particularly climate change.

The Fiordland Crested penguin (tawaki, *Eudyptes pachyrhynchus*) is the only crested penguin species to breed on the New Zealand mainland, nesting individually in forests on the south-west coast of the South Island, and Stewart Island (Mattern 2013). The population is thought to have declined in recent decades, and is listed as Vulnerable, although detailed information is lacking (BirdLife International 2018, Mattern and Wilson 2018). Tawaki are migratory, and spend the winter at sea in subantarctic waters around 1500–2500 km south-east of New Zealand, foraging between the Subtropical and Subantarctic Fronts (Mattern et al. 2018b). During the breeding season they are central-place foragers, with a much shorter foraging distance from their breeding area, and some evidence of foraging plasticity. In Milford Sound, some birds remained in the fjords during foraging trips, while others from the same breeding area travelled to the open sea up to 30 km offshore (Mattern and Ellenberg 2020). It is not clear if this is a result of behavioural specialisation, or if individuals could display both foraging behaviours on alternate trips.

At the Falkland Islands in the South Atlantic Ocean, a number of penguin species breed on New Island. They all feed in nearby waters but foraging behaviour is partitioned, with gentoo penguins foraging very close to the breeding colony (<10 km), Magellanic penguins foraging at intermediate distances (10–90 km), and rockhopper penguins foraging both very close (<10 km) and very far (>100 km) from shore (Boersma et al. 2002). Magellanic penguins breeding at Argentina on mainland South America travelled further offshore than Falkland Islands birds. Those in the northern colonies where marine productivity is lower travelled greater distances (143–242 km), compared to southern colonies (60–110 km) where productivity is higher (Boersma et al. 2009). This suggests a degree of foraging plasticity in the species, likely determined by local prey availability, and probably also inter-specific competition. This different diving and foraging is likely also due to variations in prey species and their availability around different colonies, and is also linked to varying breeding success (Sala et al. 2014). Rockhopper penguins from Staten Island just off the Argentinian coast dived much deeper and utilised a foraging area roughly double the size of birds from the Falkland Islands (Pütz et al. 2006a). This suggests there is foraging plasticity in rockhoppers also, likely influenced by local bathymetry and prey availability.

The gentoo penguin’s distribution is widespread in the Southern Ocean, but it is considered sedentary on subantarctic islands in the South Atlantic, and migratory on the Antarctic peninsula (Bost and Jouventin 1990). Birds display foraging plasticity, in different years alternating between shorter trips with deeper dives targeting benthic fish, and longer trips with shallower dives targeting krill (Miller et al. 2009). This foraging flexibility allows chick provisioning and breeding success to be maintained between years of differing prey availability (Miller et al. 2009). It may also explain the relatively stable gentoo penguin population compared to less-flexible chinstrap (*P. antarctica*) and Adélie penguins which declined in the area over the same time period. The latter two species breed sympatrically with gentoo penguins on the South Shetland Islands (Woehler and Poncet 1993) but demonstrate more consistent pelagic diving behaviour focusing primarily on krill (Miller and Trivelpiece 2008). Adélie and chinstrap penguin populations are decreasing (Lynch et al. 2008), likely due to environmental variation and poorer breeding success in years of reduced prey availability (Hinke et al. 2007).

7.7.2 Other seabirds

Northern gannets forage on shoaling pelagic fish and can utilise public information from other members of their colony. Foraging areas around Great Britain are largely mutually exclusive, with a wide variation in foraging area size between colonies (from <100 to >500 km from shore). Foraging behaviour is consistent within a colony, with foraging area size determined by density-dependent competition within and between colonies, rather than by travel distance (Wakefield et al. 2013).

Sooty shearwaters (*Puffinus griseus*) from breeding colonies in New Zealand and Australia forage widely across the Southern Ocean, although the foraging effort of all species overlaps and is concentrated around the polar front (Raymond et al. 2010). This upwelling zone is associated with increased primary production, illustrating the importance of prey distribution to foraging success. Foraging sooty shearwaters can also alternate between long (mean 1970 km) trips to the Polar Front, and shorter trips (mean 515 km) remaining within warmer neritic waters of the New Zealand shelf (Shaffer et al. 2009). The use of two separate foraging areas provides foraging plasticity to maximise resource acquisition, and minimise competition, particularly in the waters close to the breeding colony. However, sooty shearwaters breeding at the Falkland Islands in the South Atlantic made only shorter foraging trips (~350 km), foraging solely over neritic and shelf-edge zones (Bonnet-Lebrun et al. 2020). This suggests that Atlantic and Pacific populations face different foraging conditions and pressures at sea, and highlights the need to study discrete breeding populations independently.

Short-tailed shearwaters (*P. tenuirostris*) breeding in Victoria, Australia also vary their foraging range and duration to perform short trips in neritic (coastal) waters over the continental shelf, or longer trips to more distant oceanic waters (Raymond et al. 2010). Short trips range from 20–240 km from the colony into Bass Strait, whereas birds undertaking long trips travel 2400–6100 km into subantarctic or Antarctic waters. As in other breeding seabirds, longer trips are important to maintain adult body condition, and being able to travel offshore to productive waters in the Southern Ocean buffers against local prey variability adjacent to the breeding colony (Berlincourt and Arnould 2015).

White-chinned petrels breeding at South Georgia consume more krill and less squid than other breeding populations in the Indian and Pacific Oceans (Berrow and Croxall 1999), suggesting some diet plasticity, and therefore also foraging plasticity across the species' range. Despite the importance of krill at South Georgia, birds display a broad diet including more fish and squid when krill abundance and nutritional return is insufficient. This foraging versatility allows them to maintain foraging and breeding success in a year of poor krill availability, in contrast to black-browed (*Diomedea melanophris*) and grey-headed albatrosses (*D. chrysostoma*), which both feed primarily on krill, and suffered almost total breeding failure during the same season (Berrow and Croxall 1999).

Many species of albatross, including black-browed, grey-headed and yellow-nosed (*D. chlororhynchos*) also display spatial foraging segregation. These species, all breeding sympatrically at the subantarctic Kerguelen Islands, forage in very distinct areas: black-browed over continental shelf and upper slope water, grey-headed in cold Antarctic oceanic waters and yellow-nosed in warm subtropical oceanic waters (Cherel et al. 2002). This spatial and dietary partitioning minimises the likelihood of inter-specific competition, as larger species can exclude smaller ones (Weimerskirch et al. 1986). Additionally, while all of these species can alternate between long and short foraging trips at some locations, black-browed albatross breeding at the Kerguelen Islands conducted short neritic trips only (Weimerskirch et al. 1994), suggesting that additional foraging plasticity was not required by that population.

7.7.3 Pinnipeds

The New Zealand (Hooker's) sea lion is an endangered pinniped, endemic to New Zealand waters, and with a similar distribution to the yellow-eyed penguin. The majority of breeding occurs on the subantarctic Auckland and Campbell Islands, with some additional breeding on Stewart Island and a small population which has re-established on the lower South Island, following previous extirpation from the mainland (Childerhouse and Gales 1998, Maloney et al. 2009, Chilvers 2018). Breeding female sea lions from Otago on the South Island display significantly smaller foraging areas and distances compared to subantarctic populations, likely due to different prey assemblages and physical features of the marine habitat (Augé et al. 2011, Augé et al. 2015). Stewart Island females display foraging behaviours in between those of Otago and the Auckland Islands, foraging closer to shore but having larger foraging areas (Chilvers 2018). Foraging plasticity is evident within the subantarctic population, with some females specialising in benthic foraging, and others in mesopelagic foraging, with each behaviour taking place at specific foraging locations (Chilvers and Wilkinson 2009). In addition, benthic dives in the subantarctic are particularly deep, with many dives close to the physiological limit for the species (Chilvers and Wilkinson 2009) which could decrease foraging success if prey moved deeper or further from the colony. Foraging locations in the subantarctic also overlap significantly with commercial fisheries (Chilvers et al. 2011), This is an additional threat to the species with significant numbers of animals caught as bycatch (Chilvers 2008) and is contributing to the decline of the species (Robertson and Chilvers 2011), highlighting the need for ongoing monitoring.

Australian fur seals (*Arctocephalus pusillus doriferus*) are predominantly benthic foragers in the adjacent Bass Strait (Arnould and Hindell 2001, Arnould and Kirkwood 2007), and the foraging behaviour and diet of breeding females are known to be affected by changes in prey availability and distribution (Kirkwood et al. 2008, Hoskins and Arnould 2014, Speakman et al. 2020). Foraging is most affected by ENSO index, with larger foraging ranges, and greater distances travelled during higher SST and La Niña conditions (Speakman et al. 2021), suggesting that these benthic foragers may also be vulnerable to changes in prey distribution and availability associated with environmental change.

7.7.4 Foraging plasticity and population viability

Marine predators, including seabirds and pinnipeds, face similar problems worldwide in finding food and successfully raising their offspring. They also face similar threats, particularly in the form of direct and indirect pressure from fisheries, as well as changes to prey biomass and availability due to climate change (Croxall et al. 2012, Kovacs et al. 2012). Foraging plasticity can assist a population to respond to environmental changes or emerging threats, and is therefore an important contributor to long-term population stability and reducing the risk of extinction (Ducatez et al. 2020). Many marine predators display varying degrees of foraging plasticity, in some cases shaped by the physical and biological environment, including prey availability (Croxall et al. 2012, Kovacs et al. 2012). Where individuals can change their foraging behaviour as a result of local conditions, this offers a species the best chance of coping with a changing environment. In other cases, where some individuals have specialised in a particular foraging behaviour (Robertson and Chilvers 2011, Ducatez et al. 2020), this may improve survival chances for a portion of the population. This research highlights the need to understand local conditions and their effect on foraging and breeding success, rather than assuming a species displays consistent behaviour throughout its range. Conservation efforts will be more effective when more detailed information is known about individual populations within a species.

7.8 Conservation

As a species, the yellow-eyed penguin faces numerous threats, and while the northern population appears to be at greater risk of immediate decline, the southern population also faces risks which are unique to the area.

7.8.1 The northern population

The northern yellow-eyed penguin population continues to decline, particularly on mainland New Zealand, with ongoing poor breeding seasons and unsustainable adult mortality. While there are significant terrestrial threats due to human interactions (including habitat loss, predation, and disturbance), the primary cause of population decline is believed to be threats at sea (including direct threats, as well as changes to food supply, and the effects of climate change) (Couch-Lewis et al. 2016, Mattern and Wilson 2018, Department of Conservation 2020a). Due to its proximity to the larger coastal fishing industry around mainland New Zealand, the northern population faces a greater threat from negative interactions with fisheries, both commercial and recreational, including direct mortality of adults as bycatch, particularly in set nets, as well as indirect effects such as a reduced biomass of prey species available (Mattern and Wilson 2018). Fisheries can also cause underwater habitat modification with methods such as dredging and bottom trawling, even if targeting different prey species than penguins (Darby and Dawson 2000, Browne et al. 2011). Disease epidemics are also a recurring issue, including several mass-mortality events (Argilla 2015, Alley et al. 2017, Gartrell et al. 2017). As a result of these threats the northern population is under considerable pressure, and many breeding populations could be functionally extinct on the mainland by 2060, or sooner in some areas (Mattern et al. 2017, Mattern and Wilson 2018). The Department of Conservation has instituted a management plan with 5- and 20-year goals to halt the population decline, and to ‘maintain healthy, resilient, and stable populations which maintain geographical distribution and genetic diversity’ (Department of Conservation 2020a).

7.8.2 The southern population

The southern population faces many of the same threats as the northern population, however, the unique habitat in the subantarctic means effects can differ. The subantarctic islands are protected as a World Heritage Area, meaning habitat loss and most interactions with terrestrial human activities are not a major concern. However, introduced mammalian pest species including feral pigs, cats, and mice are present on Auckland Island, and are expected to have an effect on breeding success, likely contributing to lower penguin numbers there (Muller et al. 2020b; see Chapter 3). Although eradication would require a significant effort, their removal should be a priority. Successful mammal eradications have previously been undertaken on other New Zealand subantarctic islands including Enderby, Campbell, and most recently, Antipodes Island (Miskelly and Fraser 2006, Russell and Broome 2016, Horn et al. 2019, French et al. 2020), as well as Macquarie Island in the Australian subantarctic (Springer 2016). As it is for the northern population, the main threat to yellow-eyed penguins in the southern population is likely to be threats at sea; in particular, the reliable presence of suitable food sources located within the travel range of penguins. My research demonstrated that foraging behaviour is extremely variable in time and space, and success is likely to be negatively affected by climate effects and change. Climate change may also heighten the risk of breeding failure by increasing the prevalence or severity of adverse weather events. More research is needed to identify the prey species utilised by southern yellow-eyed penguins, and to model their availability in time and space. In addition, further research is needed to identify the extent of the foraging area used by breeding birds from different breeding locations, and at different times of the year. Ongoing monitoring of prey species and penguin foraging success may help to predict emerging threats to yellow-eyed penguin foraging, and ultimately, breeding success. Yellow-eyed penguins are very susceptible to human disturbance, which can negatively affect breeding success (McClung et al. 2004), and tourism activities did result in disturbance of transiting penguins in the subantarctic (French et al. 2019). There was the potential for breeding success to be affected by tourism disturbance, particularly on Enderby Island where there is a significant overlap of breeding penguins and tourism activities. Therefore, one hypothesis which required testing was whether tourism disturbance affected breeding success on Enderby Island. To this end, two adjacent sub-populations from neighbouring breeding areas were identified: 1) a "disturbed" population used the beach at Sandy Bay as their access point to the sea, which was also used by tourists so had the potential for conflict, and 2) an adjacent "undisturbed" population at Rocky Ramp, which used a cliff path for access to the sea and did not interact with tourists. Birds from these two breeding areas foraged in a similar location (with 48% and 65% overlap with the shared core foraging area, respectively) and there was no significant difference in their dive depth ($t = 0.94$, $df = 129.33$, $P = 0.34$), maximum distance from shore ($t = -0.96$, $df = 82.51$, $P = 0.34$), or diet ($\delta^{15}N$: $t = -0.33$, $df = 5.60$, $P = 0.75$; and $\delta^{13}C$: $t = 0.33$, $df = 4.86$, $P = 0.764$), indicating that their foraging location and success were similar. Therefore, since nest locations were also similar, if any difference was detected in breeding success between these two groups it was likely a result of land-based disturbance on transiting birds. However, no difference in breeding success was evident between these two groups (French 2018), indicating that tourism did not appear to affect breeding success on Enderby Island. Subantarctic tourism has declined since New Zealand's borders closed in March 2020 due to Covid-19, and international economic sanctions following Russia's invasion of Ukraine in March 2022 which prevented Russian vessels from being used by tour companies. Nevertheless, when tourism resumes this should be monitored to ensure it has no ongoing effect on yellow-eyed penguin breeding success.

While no yellow-eyed penguin deaths have been reported in the subantarctic as bycatch by the fishing industry, there remains the potential for direct and indirect interactions, including bycatch, but also competition, and changes to the benthos affecting prey species. This is particularly important for juveniles which may stay at sea for several weeks at a time and can travel over 200 km from the colony (Muller et al. 2020a; see Chapter 4), making them much more likely to overlap with fisheries. Following a precautionary approach, more research is recommended to identify the extent of foraging areas used by penguins, as well as any negative interactions which may require mitigation.

No disease epidemics or mass-mortality events have been reported in the southern yellow-eyed penguin population, although this may be due to a lack of regular monitoring. Several disease-causing organisms have been identified from Enderby Island, including *Leucocytozoon* (Argilla et al. 2013), *Coccidia* (Kay et al. 2022a) and *Plasmodia* (Kay 2021, Kay et al. 2022b), and these have been linked to the deaths of chicks, and in some cases, adults. A number of other diseases are endemic in the mainland population, and more research is needed to determine which disease-causing organisms are present in the subantarctic, and particularly, whether climate change or other factors may cause them to become more prevalent in the future. Metagenomics can be used to sequence the entire microbiome of a sample, identifying all virus and bacterial DNA and RNA present, including both pathogenic and non-pathogenic species (French and Holmes 2020). This wide scope is recommended to investigate the range of viral and bacterial communities present in yellow-eyed penguin populations across the subantarctic, and to identify known or suspected disease-causing agents. Following this, informed decisions can be made on the need for an ongoing disease-monitoring programme.

Although rare, the possibility and effects of an oil spill increase with the size and frequency of ship traffic (Chilvers 2021), and would have a devastating effect on penguin populations, even if rehabilitation of affected birds is possible (Sievwright et al. 2019). Therefore, an oil spill response plan is critical, particularly for the isolated subantarctic region where the logistics of a response would be difficult and costly, and large-scale rehabilitation may not be feasible (Chilvers 2021).

7.9 General conclusions

My research highlights the value of utilising multiple methods of monitoring a population for conservation purposes, including not only population estimates but investigating factors which can affect population trends. These include documenting breeding success, foraging behaviour, foraging success, and diet which can all influence individual survival as well as breeding success, which can in turn contribute to population declines. Additionally, investigation into climatic effects is important for managing future threats to a population.

The New Zealand subantarctic region is a remote and difficult place to work, making fieldwork logistically difficult and expensive. However, this fact should not be a reason to forego management of the southern yellow-eyed penguin population, or indeed any species or environment within the islands. A regular monitoring programme is needed, which should consist of annual population estimates, measurement of breeding success, and ideally further examination of foraging impacts including the effects of climate change. These recommendations are described in more detail in a report prepared for the Department of Conservation (French and Muller 2021). Southern yellow-eyed penguins appear to be in better shape than the northern population (Muller et al. 2020b; see Chapter 3), however, this is not a reason for complacency. Out of sight should not be out of mind, nor a reason not to be concerned. We have a window of opportunity to act before a plethora of worsening threats may combine to cause irreversible declines in this southern population, which would be catastrophic for the species given the size of the southern population relative to the total population, and the threats and declines already seen in the northern population.

8. Appendices

Appendix 1 – Supplementary material for Chapter 1 (General Introduction)

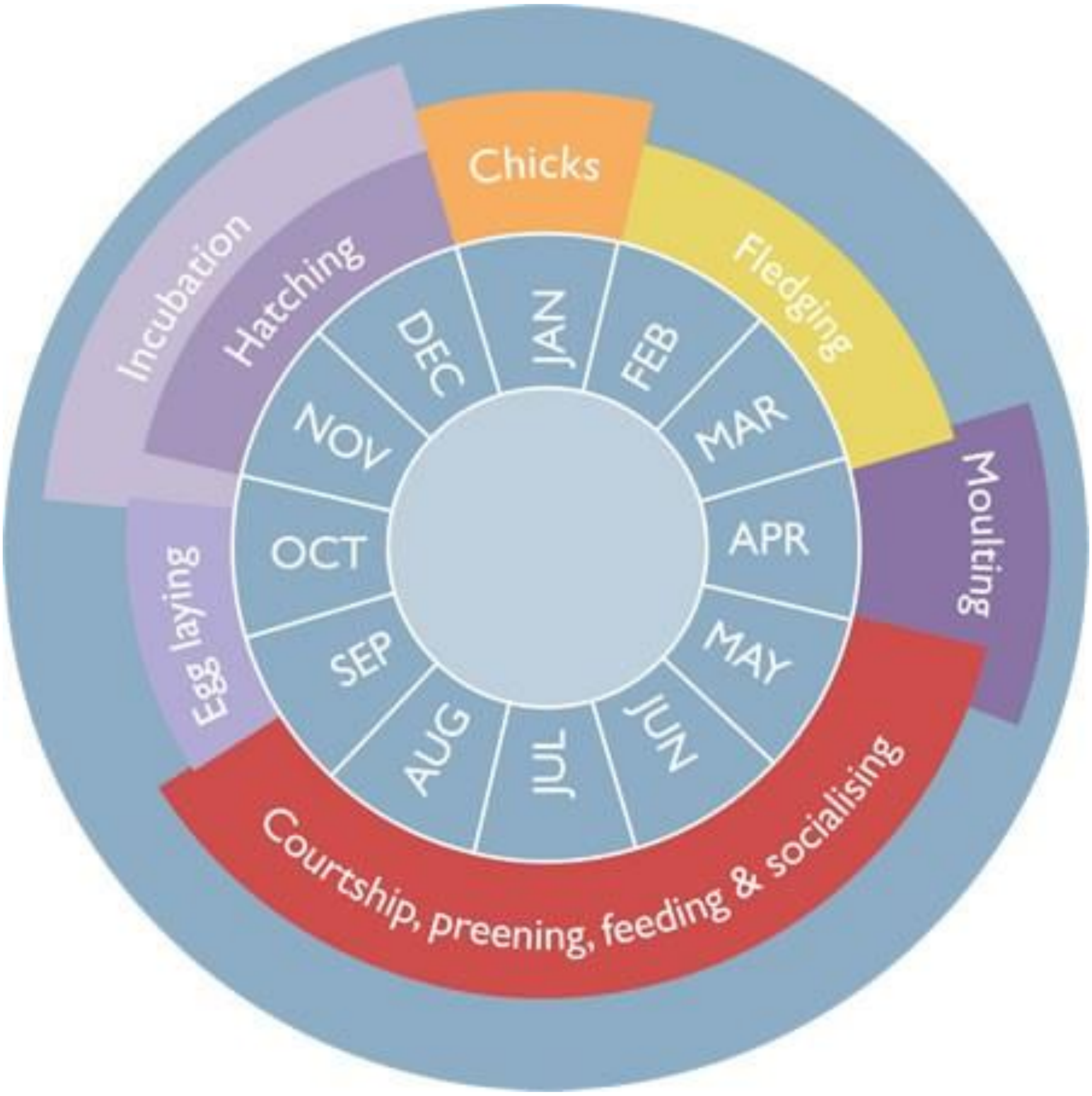


Figure S1.1 Yellow-eyed penguin life cycle (Source: YEP Trust). Dates are up to two weeks later in the subantarctic (Moore 1990).

Appendix 2 – Supplementary material for Chapter 2 (Nest Finding)

8.1.1 Calibration testing

Whereas accuracy is the smallest distance which can be resolved, detection distance is the maximum range where a signal can be detected. Maximum range is more relevant if the main focus is on locating animals (particularly those which may have dispersed widely), as opposed to determining their location as accurately as possible. A wider separation between flight lines can take advantage of detection distance but may reduce accuracy.

UAV calibration flights were conducted to determine detection distance in the experimental environment by measuring signal strength at known distances. Transmitters of different types (single-stage and two-stage) were placed at measured distances perpendicular to the flight path and were taped to a 1.5 kg bottle of water lying on its side to approximate the antenna orientation and transmission characteristics on a nesting penguin.

All transmitters operated on individual frequencies in 160–161 MHz bandwidths, with a separation of >20 KHz between frequencies to avoid interference with other tags.

UAV calibration data were collected at constant altitude (30, 50, or 100 m), with transmitters placed at measured distances perpendicular to the flight path (from 0 m up to 500 m), (Figure S2.1). One transmitter of each type was placed at each distance. The UAV flew along the flight path then turned 180 degrees and returned along the same path, collecting a double peak of signal-strength data from each transmitter, and allowing comparison of signal strength vs range for the different transmitter configurations trialled. (N.B. Depending on the distance between the transmitter line and the turning point, some of the peaks were closer together than others). The UAV's altitude was sometimes changed for the return pass to measure detection ability at two different altitudes during the same flight.

Calibration data showed that signal strength detected at the receiver varied for the different transmitter configurations tested, depending on their output power and antenna type. Two-stage transmitters had the greatest signal strength, and could be reliably detected from 250 m, and in some cases up to 500 m away (the largest distance which was tested) (Figure S2.4).

If the priority of a search was to detect a signal (rather than maximising position accuracy) this would allow a separation distance of up to 1000 m between flight paths when using two-stage transmitters. Lower-power single-stage transmitters could be detected up to 75 m away (Figure S2.2 and Figure S2.3), offering a useful tracking option for smaller animals, or where minimising transmitter size, weight, or hydrodynamic drag is important.

Testing was carried out under real-world conditions at the research site so these calibration data were subject to the effects of topography and vegetation, and therefore provide a measure of detection range using these specific transmitters at this particular site. Consequently, due to the uneven ground and thick scrub these results may be an under-estimate compared to what may be achievable under ideal conditions such as flat open ground, or with better transmission characteristics such as transmitters located higher off the ground and with a vertical transmission antenna orientation.

In addition, changing the detection antenna altitude can alter the “footprint” of coverage seen by the receiver, therefore affecting detection ability. It was evident from testing that at the maximum 500 m range a two-stage signal was detected at the higher altitude of 100 m, but not at the lower altitude of 50 m. This illustrates the complex interaction of factors which can affect detection range. It is therefore advantageous to conduct range testing according to the specific field conditions which will be encountered.

Signal strength affects the detection range of a particular transmitter type in a given set of conditions, with implications for choosing transmitter type, as well as planning flight paths and flight line separation distances. Due to the variability in detected signal strength for different types of transmitters (based on their output power, antenna configuration, as well as different environmental conditions including vegetation and topography), different transmission antenna combinations may be affected in different ways. Calibration tests are also useful when determining an optimum flight path separation and altitude for surveys.

A useable VHF signal strength could be detected by the Drone Ranger system within ± 3 KHz of the peak transmitter frequency. Transmitters can sometimes drift up to 3–5 KHz from their manufactured frequency, highlighting the usefulness of tuning the receiver to scan for peak transmitter signal outputs as well.

8.1.2 Signal detection

Flight path separation and/or height can be modified depending whether the focus is for a larger scale search (eg. locating the signal from a missing transmitter or a widely-dispersing animal), or whether finer scale positioning is required. A wider flight line spacing increases the search area covered thereby increasing the chance of detecting a transmitter during a flight, but decreasing the precision when estimating signal origin.

Successful VHF tracking depends primarily on the signal strength detected by the receiver, which is affected by range. Signal strength decreases with increasing distance from the transmitter according to the inverse-square law, where the signal strength is reduced by 75% when distance from the source is doubled (Kenward 2001).

The most variable factor affecting signal strength and therefore the most likely to affect successful VHF tracking in the field are the effects of terrain and vegetation which can attenuate or reflect the signal, making it difficult to detect and track (Kenward 2001). Ridges, gullies, cliffs, and thick vegetation can all reduce detection range. Additionally, moisture on vegetation can also reduce detection range.

Increasing altitude can overcome the effects of terrain or vegetation on VHF detection. A higher receiving antenna automatically has a wider field of view, and the signal from the transmitter is less likely to be screened by ridges or gullies (Seddon and Maloney 2004). When tracking from the ground a signal may have to travel the entire distance to a ground-based receiver through vegetation, whereas an aerial receiver can fly above the forest canopy (which is a maximum of a few metres high in the subantarctic), thereby reducing effects of terrain and vegetation.

Signal strength can be affected by a number of other factors including the power output of the transmitter and its antenna size, type, and orientation (Kenward 2001). The type of transmission antenna may be influenced by expected animal behaviour. Considerations may include the likelihood of antenna damage, whether tracking underground is needed, or whether there is a chance of it getting entangled in vegetation or other obstacles. Shorter antennas (including internal loop antennas) will generally have a reduced transmission range compared to a longer whip antenna, but may be less prone to damage or becoming entangled. Detection range can also vary due to an animal's posture, or if it moves into different environments.

8.1.3 Search methods

The efficiency of an aerial search method is governed by the area which can be searched at a time (based on the detection range), the total size of the area to be searched, and the speed at which a search can be conducted. UAV-based systems have been described which utilise a single-channel VHF receiver (Cliff et al. 2015). A single-channel receiver determines the approximate location of the transmitter using triangulation. Triangulation of multiple transmitters requires frequencies to be scanned sequentially so becomes progressively less efficient as more transmitters are tracked. Tracking 50 transmitters requires over 5 minutes per scan, and a minimum of three scans is needed to triangulate a bearing to each target location, requiring a total search time of 15 minutes or more. This is approaching the maximum battery life for a small UAV so restricts searching to a single triangulation per flight. However, a single triangulation can only cover a search area equivalent to the detection range. Based on the observed maximum detection range of small single-stage transmitters of 75 m in this environment, a single triangulation would not provide coverage of the whole penguin nesting area. Depending on the location of transmitters within the landscape it could take up to 26 scans to cover each 500 x 300 m breeding area. Based on these efficiency estimates we developed a multi-channel receiver capable of scanning over 50 frequencies simultaneously, while the UAV maintains cruising speed.

A hovering UAV has been shown to generate more disturbance than one passing overhead (Mulero-Pázmány et al. 2017). Therefore, hovering in place for up to 5 minutes at a time as required for triangulation has the potential to create significantly more disturbance than a dynamic search. Yellow-eyed penguin nests are separated by at least 20 m from each other, therefore with a separation of 30 m between flight lines the odds of directly overflying a nest are low. If needed, the separation distance can be increased to reduce the likelihood of disturbance from direct overflights still further. If a dynamic search does happen to directly overfly a nest, the speed the UAV is travelling would limit the exposure to any disturbance to a few seconds.

8.1.4 Comparison with other electronic tracking methods

Aerial VHF tracking has a number of advantages over other common electronic tracking methods. Unlike GPS receivers or satellite transmitters (such as Argos) which require a clear view of the sky, VHF transmitters can be used under forest canopy, underground, or even inside buildings (although the detection range may be reduced).

VHF transmitters are often smaller than GPS tags. At the time of writing, VHF transmitters are available as small as 0.19 g in weight (Biotrack, UK) and can therefore be attached to much smaller animals than is possible with GPS or satellite tags. VHF transmitters are usually cheaper than many other electronic tracking devices designed for use on wildlife, and unlike GPS tags this technology also does not require any separate form of remote download from the tag, or the recovery of the tag in order to retrieve position data. In this situation using VHF tracking is much quicker than using GPS as GPS tags utilising satellite download have an inherent delay, since satellite uploads of position data usually only occur daily (or less frequently where cost or battery life is limiting). Deploying GPS store-onboard tags would also have involved a minimum delay of several days before electronics could be retrieved to download the data.

In addition, GPS and satellite technologies both have higher power requirements which limits battery life and the total number of possible position fixes, and performance is worse in environments where view of the sky is limited. As a result, GPS tags often have a larger battery to compensate, thereby increasing tag size and weight compared to VHF transmitters. To maximise battery life, GPS tags are usually limited to a number of preset GPS fix attempts (pre-programmed at set times of the day based on battery life predictions). However, any failed fixes will use up additional power, so the actual number of fixes that can be recorded will be governed by the terrain and animal behaviour when deployed.

VHF tracking also has a number of advantages over satellite positioning systems (e.g., Argos) since VHF transmitters are smaller, cheaper, and more accurate. Satellite transmitters require a clear view of the sky, and position accuracy can range from +/- 100 m to over a kilometre. Satellite transmitters must transmit continuously, but position data can only be calculated while a satellite passes overhead, restricting the number of positions which can be calculated in a day. To limit data charges and/or battery life, satellite transmitters are often duty-cycled to only transmit during part of the day, meaning no positions can be received outside this time.

Rather than being limited to a finite number of fix attempts, or positions only at certain times of the day, VHF tags transmit continuously while they are on so aerial VHF tracking using the Drone Ranger system could be used to provide positions at any time, or even continuously.

8.1.5 Future uses

We were able to use a GIS to determine the location of nests with a reasonable degree of accuracy, simply by looking at a spatial plot of the signal strength values collected. If a quantitative output and/or greater precision is required an algorithm could be incorporated to calculate a probability surface of the signal strength data, perhaps by using triangulation and/or performing a 'weighted' kernel density analysis. This has the potential to provide greater accuracy than a basic analysis of maximum signal strength since the strongest signal may not necessarily be detected at the closest distance to the target. Doppler shift and/or any slight delays in signal processing could be accounted for to improve accuracy still further.

In addition to locating nests, aerial VHF tracking could also be used to monitor wildlife. Daily flights were useful to determine which penguins were on their nests, and which were away at sea foraging. Comparing location over several flights would also assist with determining whether penguins were on a nest or just loafing in the area, without needing a visit by a ground team. Nesting birds would be expected to be consistently in the same location, whereas loafing birds would be expected to move around over time. Penguin breeding areas were approximately 150,000 m^3, or 300 m x 500 m. With a maximum range of 3 km per battery, an area this size could be searched on one battery with a separation of 50 m between flight lines. With a closer spacing, or in stronger winds this might require two batteries to cover the whole area at once. Depending on project requirements, different UAV platforms could be utilised to increase range, flight time, and payload capacity, and allow operation in a wider range of weather conditions. A camera could also be fitted to assist with monitoring wildlife in the field.

UAVs using a variety of different sensors have proven useful for a wide range of monitoring techniques including estimating body condition (Christiansen et al. 2016) and abundance of animals (Goebel et al. 2015), and for mapping habitat (Koh and Wich 2012). The addition of VHF tracking could improve efficiency and provide comprehensive monitoring techniques for the future.

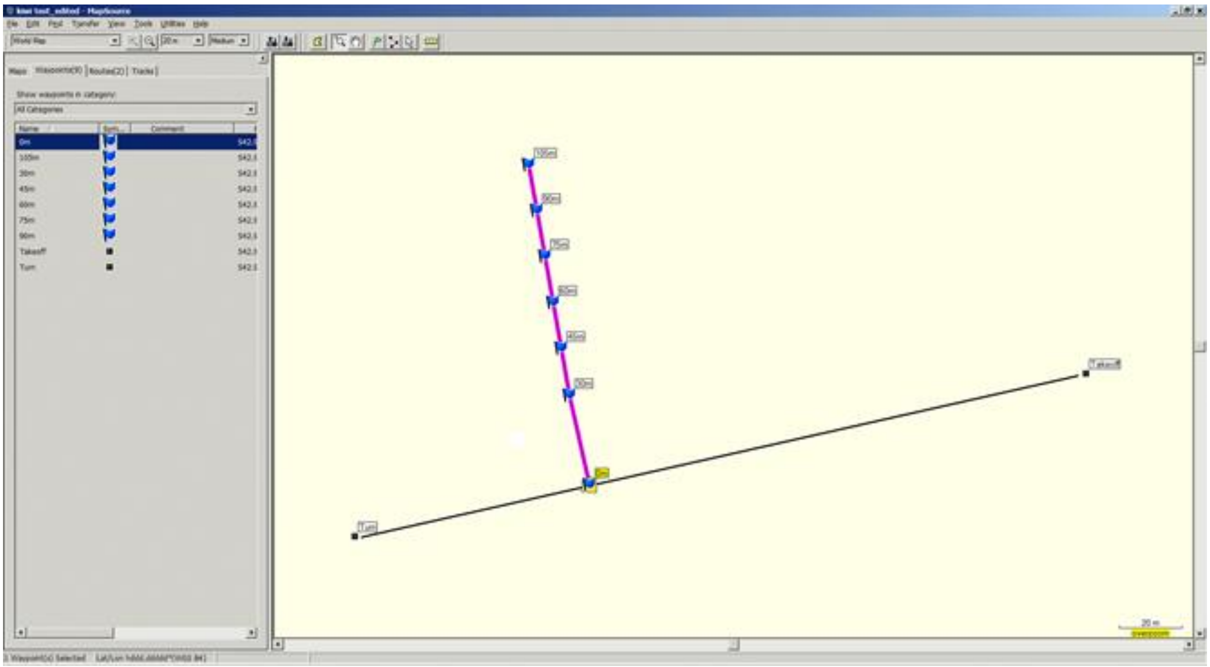


Figure S2.1 Example calibration flight path to map signal strengths (from Takeoff point to Turn point, and return to Takeoff point) showing the placement of transmitters at measured distances, perpendicular to the flight path. This was also used to test high-density transmitter detection.

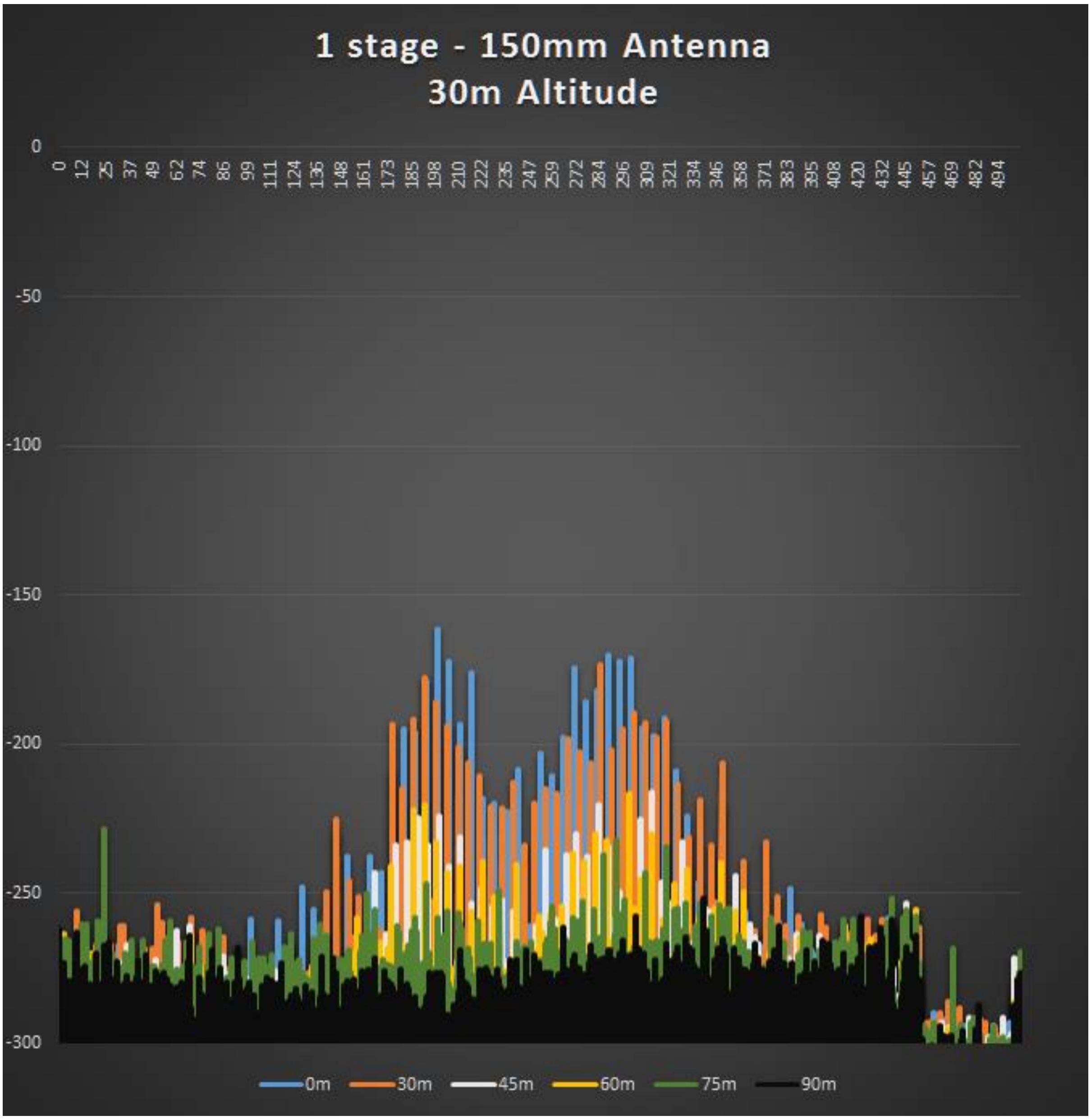


Figure S2.2 Signal strength plot (-dB) vs Time (s): Single-stage transmitter with 150 mm whip antenna at 30 m altitude – signal detected up to 75 m away (green).

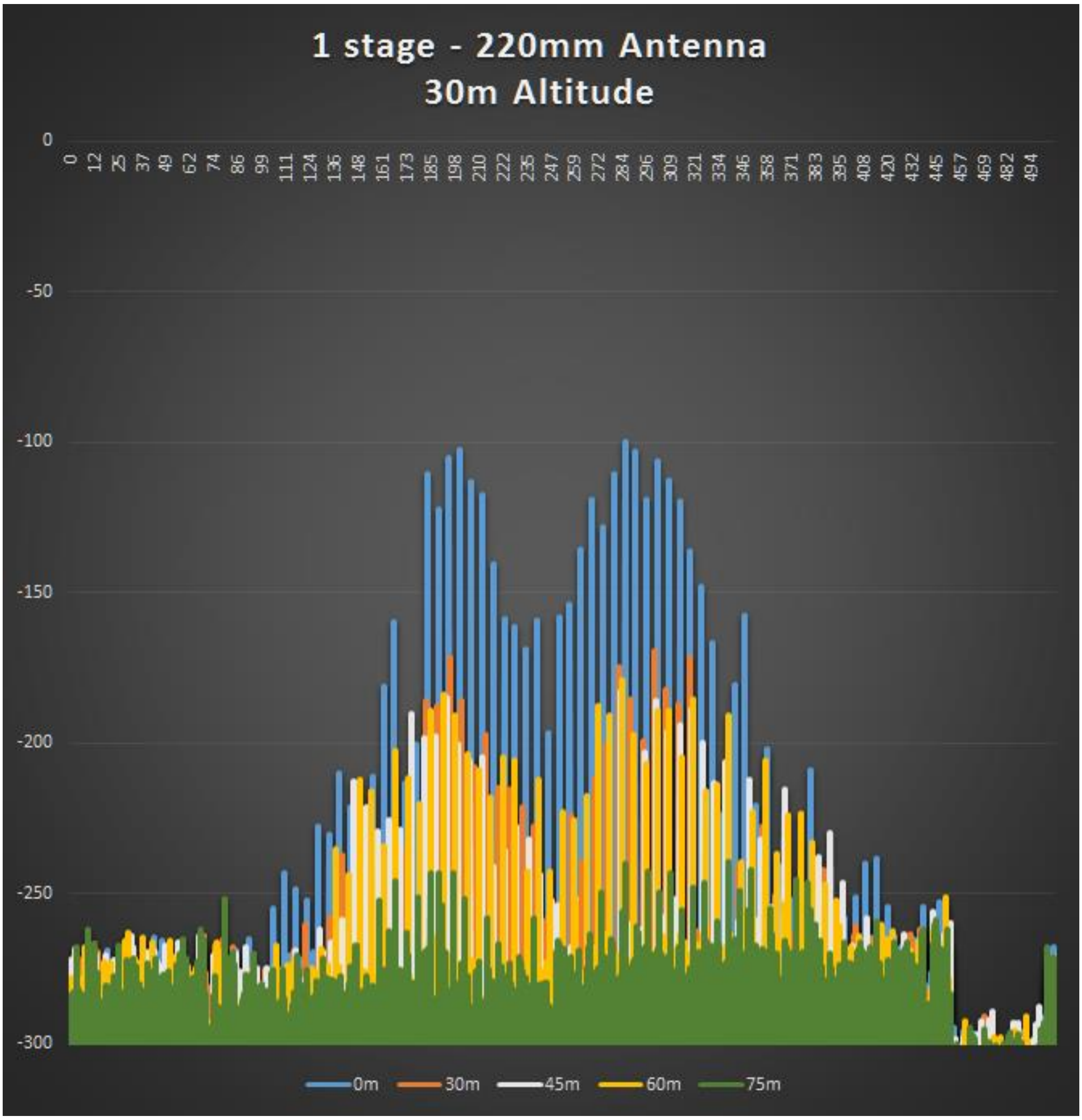


Figure S2.3 Signal strength plot (-dB) vs Time (s): Single-stage transmitter with 220 mm whip antenna at 30 m altitude – signal detected up to 75 m away (green).

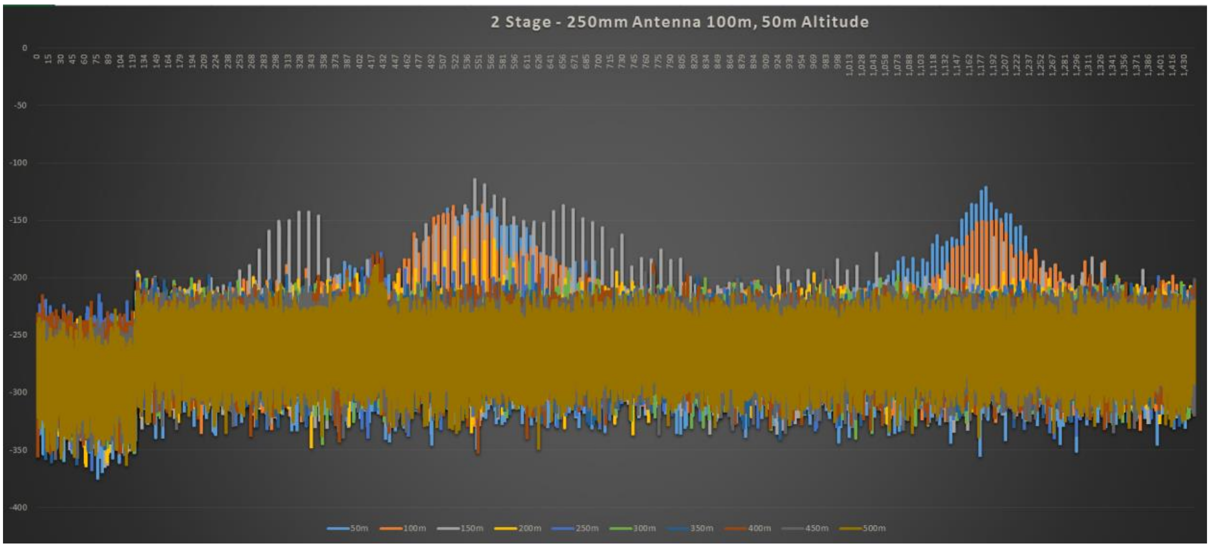


Figure S2.4 Signal strength plot (-dB) vs Time (s): Two-stage transmitter with 250 mm whip antenna at 100 and 50 m altitude (recorded during separate passes in the same flight) – signal detected at least 500 m away at 100 m altitude (olive) only.

Appendix 3 – Supplementary material for Chapter 3 (Population)

Table S3.1 GPS locations of observation points for transit counts and penguin landing points in the Auckland Islands. Data from Department of Conservation trip reports.

Area	Location	Site	Obs Lat	Obs Long	Obs Beach Type	Landing Site Lat	Landing Site Long
Auckland Islands	Adams Island	Adams Island	-50.86395	166.01478	Boulders & Rock		
Auckland Islands	Adams Island	Adams Island	-50.86587	165.99368	Rock	-50.86527	165.99438
Auckland Islands	Adams Island	Adams Island	-50.86555	165.98154	Boulders		
Auckland Islands	Adams Island	Adams Island	-50.86407	166.01382	Boulders	-50.86427	166.01206
Auckland Islands	Adams Island	Adams Island	-50.86388	165.99615	Rock		
Auckland Islands	Adams Island	Adams Island	-50.86407	166.01382	Rock	-50.8643	166.01183
Auckland Islands	Adams Island	Adams Island	-50.8657	165.9815451		1106350	4341607
Auckland Islands	Adams Island	Adams Island	-50.864	166.0136725	Rock	1108590	4342005
Auckland Islands	Adams Island	Adams Island	-50.8641	166.0140553		1108618	4341996
Auckland Islands	Adams Island	Adams Island	-51.0814	166.19639	Boulders & Rock	-50.51.833	165.59.767
Auckland Islands	Adams Island	Harris Bay	-50.85337	165.95738	Rock	-50.8565	165.95611
Auckland Islands	Adams Island	Harris Bay	-50.85337	165.95738	Rock	-50.8564	165.95538
Auckland Islands	Adams Island	Harris Bay	-50.85337	165.95738	Rock	-50.85618	165.95448
Auckland Islands	Adams Island	Harris Bay	-50.85337	165.95738	Rock	-50.85695	165.9568
Auckland Islands	Adams Island	Magnetic Bay	-50.86464	166.01067	Rock	-50.86436	166.00808
Auckland Islands	Adams Island	Magnetic Bay	-50.86464	166.01067	Rock	-50.86456	166.01072
Auckland Islands	Adams Island	Magnetic Bay	-50.86464	166.01067	Rock	-50.86395	166.00769
Auckland Islands	Adams Island	Survey Bay	-50.86559	165.98702	Boulders & Rock	-50.86647	165.98653
Auckland Islands	Adams Island	Survey Bay	-50.86559	165.98702	Boulders & Rock	-50.86649	165.9884
Auckland Islands	Adams Island	Survey Bay	-50.86559	165.98702	Boulders & Rock	-50.86666	165.98703

Auckland Islands	Adams Island	Survey Bay	-50.86559	165.98702	Rock	-50.86569	165.98719
Auckland Islands	Adams Island	Survey Bay	-50.86559	165.98702	Rock	-50.86655	165.98821
Auckland Islands	Adams Island	Survey Bay	-50.86559	165.98702	Rock	-50.86674	165.98721
Auckland Islands	Auckland Island	Chambres Inlet	-50.6157	166.1675666	Boulders & Rock	1116846	4370594
Auckland Islands	Auckland Island	Chambres Inlet	-50.6019	166.1701889	Boulders	1116889	4372148
Auckland Islands	Auckland Island	Chambres Inlet	-50.6163	166.1683079	Rock	1116904	4370538
Auckland Islands	Auckland Island	Chambres Inlet	-51.3903	166.3325	Boulders & Rock	-50.698.65	166.14.357
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81575	166.21121	Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81724	166.20442	Boulders & Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81714	166.20465	Boulders & Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81716	166.20461	Boulders & Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81687	166.21027	Boulders & Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81718	166.20461	Rock	-50.81515	166.20144
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81730	166.20444	Rock	-50.81337	166.21062
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81730	166.20444	Rock	-50.81381	166.2072
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81730	166.20444	Rock	-50.81412	166.20512
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81600	166.21115	Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81704	166.21638	Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.81912	166.21940	Boulders & Rock		
Auckland Islands	Auckland Island	Waterfall Inlet	-50.8162	166.2047318	Boulders & Rock	1121525	4348574
Auckland Islands	Auckland Island	Smiths Harbour	-50.7057	166.1298241		1115111	4360351
Auckland Islands	Auckland Island	Smiths Harbour	-50.7004	166.1341426		1115360	4360975
Auckland Islands	Auckland Island	Smiths Harbour	-51.2692	166.28417		-50.69.429	166.14.183
Auckland Islands	Auckland Island	Smiths Harbour	-51.3897	166.33167		-50.698.63	166.143.54
Auckland Islands	Enderby Island	Bones Bay	-50.48830	166.30832	Boulders & Rock	-50.48843	166.30861
Auckland Islands	Enderby Island	Bones Bay	-50.48830	166.30832	Boulders & Rock	-50.48809	166.31278
Auckland Islands	Enderby Island	Bones Bay	-50.48830	166.30832	Boulders & Rock	-50.48809	166.31277
Auckland Islands	Enderby Island	Butterfield Point	-50.50953	166.26849	Rock	-50.50827	166.2654
Auckland Islands	Enderby Island	Derry Castle	-50.48852	166.30350	Rock	-50.48793	166.30152

Auckland Islands	Enderby Island	Derry Castle	-50.48852	166.30350	Rock	-50.4881	166.30114
Auckland Islands	Enderby Island	Derry Castle	-50.48852	166.30350	Rock	-50.48895	166.30105
Auckland Islands	Enderby Island	East Bay	-50.49619	166.32001	Boulders	-50.49674	166.3202
Auckland Islands	Enderby Island	East Bay	-50.49621	166.32001	Rock	-50.49532	166.32162
Auckland Islands	Enderby Island	Enderby Island	-50.50577	166.31570	Rock	-50.50596	166.31786
Auckland Islands	Enderby Island	Enderby Island	-50.50577	166.31570	Rock	-50.50613	166.31615
Auckland Islands	Enderby Island	Enderby Island	-50.50577	166.31570	Rock		
Auckland Islands	Enderby Island	Enderby Island	-50.50380	166.31954	Boulders	-50.50368	166.31982
Auckland Islands	Enderby Island	Enderby Island	-50.50380	166.31954	Boulders	-50.5039	166.31988
Auckland Islands	Enderby Island	Enderby Island	-50.49862	166.32164	Rock	-50.49682	166.3202
Auckland Islands	Enderby Island	Enderby Island	-50.49862	166.32164	Rock	-50.49814	166.32072
Auckland Islands	Enderby Island	Enderby Island	-50.49862	166.32164	Rock	-50.4974	166.32027
Auckland Islands	Enderby Island	Enderby Island	-50.50091		Sand & Rock	-50.50088	166.32239
Auckland Islands	Enderby Island	Enderby Island	-50.50508	166.29733	Rock	-50.50563	166.29875
Auckland Islands	Enderby Island	Enderby Island	-50.50508	166.29733	Rock	-50.50557	166.29866
Auckland Islands	Enderby Island	Enderby Island	-50.50639	166.30776	Boulders & Rock	-50.50664	166.30891
Auckland Islands	Enderby Island	Enderby Island	-50.50209	166.32084	Rock	-50.50208	166.32263
Auckland Islands	Enderby Island	Enderby Island	-50.50209	166.32084	Rock	-50.50309	166.32183
Auckland Islands	Enderby Island	Enderby Island	-50.50209	166.32084	Rock	-50.50173	166.32319
Auckland Islands	Enderby Island	Enderby Island	-50.50538	166.31909	Rock		
Auckland Islands	Enderby Island	Enderby Island	-50.50320	166.31989	Rock	-50.50347	166.31993
Auckland Islands	Enderby Island	Enderby Island	-50.50592	166.30365	Boulders & Rock	-50.50614	166.30396
Auckland Islands	Enderby Island	Enderby Island	-50.50592	166.30365	Boulders & Rock	-50.50623	166.3057
Auckland Islands	Enderby Island	Enderby Island	-50.50147	166.32129	Rock	-50.50147	166.3213
Auckland Islands	Enderby Island	Enderby Island	-50.50600	166.31250	Boulders & Rock	-50.50644	166.31367
Auckland Islands	Enderby Island	Enderby Island	-50.50600	166.31250	Boulders & Rock	-50.50626	166.31047
Auckland Islands	Enderby Island	Rocky Ramp	-50.50283	166.27603	Rock	-50.50291	166.27631
Auckland Islands	Enderby Island	Rocky Ramp	-50.50278	166.27602	Rock	-50.50291	166.27631
Auckland Islands	Enderby Island	Rocky Ramp	-50.50280	166.27606	Rock	-50.50291	166.27631

Auckland Islands	Enderby Island	Rocky Ramp	-50.50283	166.27603	Rock	-50.50276	166.27639
Auckland Islands	Enderby Island	Rocky Ramp	-50.50283	166.27603	Rock	-50.50317	166.27538
Auckland Islands	Enderby Island	Rocky Ramp	-50.50283	166.27603	Rock	-50.50282	166.27652
Auckland Islands	Enderby Island	Sandy Bay	-50.50024	166.27902	Sand & Rock	-50.5024	166.28614
Auckland Islands	Enderby Island	Sandy Bay	-50.50024	166.27902	Sand & Rock	-50.50053	166.28526
Auckland Islands	Enderby Island	Sandy Bay	-50.50024	166.27902	Sand & Rock	-50.50193	166.28564
Auckland Islands	Enderby Island	Sandy Bay	-50.50025	166.27892	Sand & Rock	-50.50053	166.28526
Auckland Islands	Enderby Island	Sandy Bay	-50.50025	166.27892	Sand & Rock	-50.50193	166.28564
Auckland Islands	Enderby Island	Sandy Bay	-50.50025	166.27892	Sand & Rock	-50.50009	166.28444
Auckland Islands	Enderby Island	Sandy Bay	-50.50025	166.27892	Sand & Rock	-50.50062	166.28517
Auckland Islands	Enderby Island	Sandy Bay	-50.50024	166.27902	Sand	-50.49993	166.28059
Auckland Islands	Enderby Island	Sandy Bay	-50.50025	166.27892	Sand	-50.50019	166.28077
Auckland Islands	Enderby Island	Sandy Bay	-50.50025	166.27892	Sand & Rock	-50.5024	166.28614
Auckland Islands	Rose Island	Rose Island	-50.51198	166.25487	Boulders	-50.51162	166.25575
Auckland Islands	Rose Island	Rose Island	-50.51198	166.25487	Boulders	-50.51223	166.2552
Auckland Islands	Rose Island	Rose Island	-50.51198	166.25487	Boulders	-50.51144	166.25608
Auckland Islands	Rose Island	Rose Island	-50.51198	166.25487	Boulders	-50.51181	166.25559
Auckland Islands	Rose Island	Rose Island	-50.51082	166.25558	Rock	-50.51064	166.2555
Auckland Islands	Rose Island	Rose Island	-50.50921	166.25595	Rock	-50.50792	166.25532
Auckland Islands	Rose Island	Rose Island	-50.50722	166.25390	Rock		
Auckland Islands	Rose Island	Rose Island	-50.51675	166.25264	Boulders	-50.51675	166.25286
Auckland Islands	Rose Island	Rose Island	-50.51721	166.25395	Boulders	-50.51682	166.25358
Auckland Islands	Rose Island	Rose Island	-50.51535	166.25188	Rock		
Auckland Islands	Rose Island	Rose Island	-50.51384	166.25195	Boulders & Rock		
Auckland Islands	Rose Island	Rose Island	-50.51603	166.25195	Boulders & Rock	-50.51572	166.25229
Auckland Islands	Rose Island	Rose Island	-50.51758	166.25388	Rock	-50.51797	166.25394
Auckland Islands	Rose Island	Rose Island	-50.51379	166.25196	Rock		
Auckland Islands	Rose Island	Rose Island	-50.51097	166.25570	Rock		
Auckland Islands	Rose Island	Rose Island	-50.50921	166.25595	Rock	-50.50922	166.25607

Auckland Islands	Rose Island	Rose Island	-50.51082	166.25558	Rock		
Auckland Islands	Rose Island	Rose Island	-50.51758	166.25388	Rock		
Auckland Islands	Rose Island	Rose Island	-50.51379	166.25196	Boulders & Rock	-50.51354	166.25218
Auckland Islands	Rose Island	Rose Island	-50.51721	166.25395	Boulders	-50.51681	166.25356
Auckland Islands	Rose Island	Rose Island	-50.51721	166.25395	Boulders	-50.51681	166.25365
Auckland Islands	Rose Island	Rose Island	-50.50748	166.25392	Rock		
Auckland Islands	Rose Island	Rose Island	-50.5161	166.2519126		1121794	4382205
Auckland Islands	Rose Island	Rose Island	-50.512	166.2548859		1121963	4382679
Auckland Islands	Rose Island	Rose Island	-50.511	166.2556504		1122007	4382795
Auckland Islands	Rose Island	Rose Island	-50.5869	166.2525		-50.32.193	166.13.129

Appendix 4 – Supplementary material for Chapter 4 (Diving)

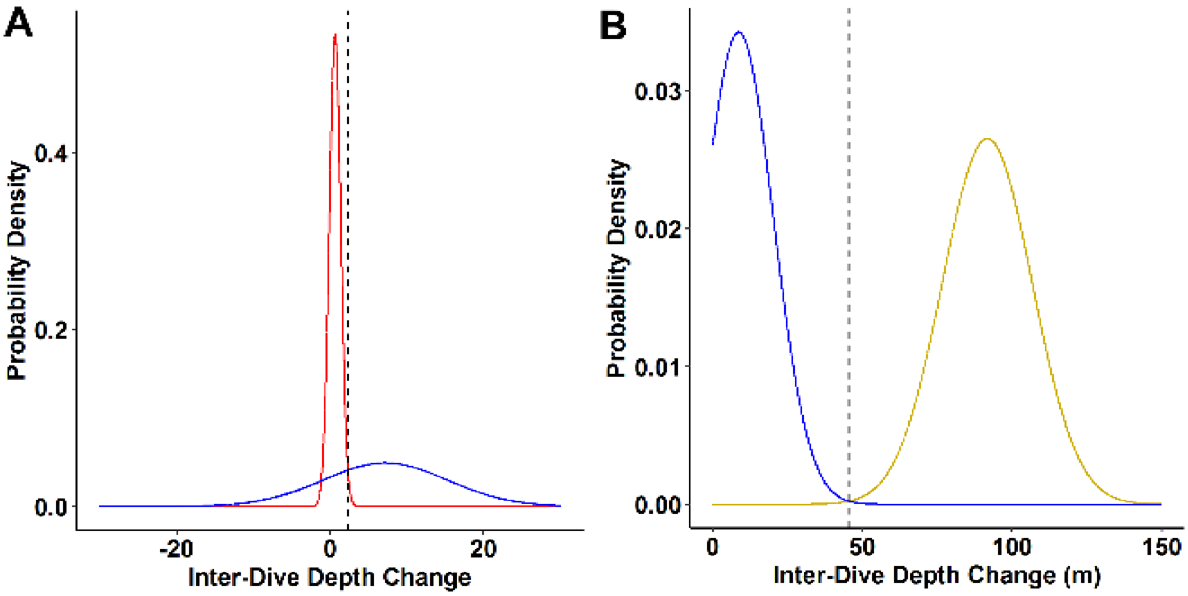


Figure S4.1 Bayesian models used for dive type categorisation. Dive types were defined using the inter-dive depth change (change in maximum depth between subsequent dives) to categorise benthic dives (A, red line) and transition dives (B, yellow line). In both cases the remaining dives (blue lines) were categorised as pelagic. The dotted lines show each log likelihood ratio criterion, which is the cut-off value used to categorise dive types for each model; 2.9% for differentiating between benthic vs pelagic dives (A) and 45 m for differentiating between transition vs pelagic dives (B). A combination of both models was used to automatically categorise all dives.

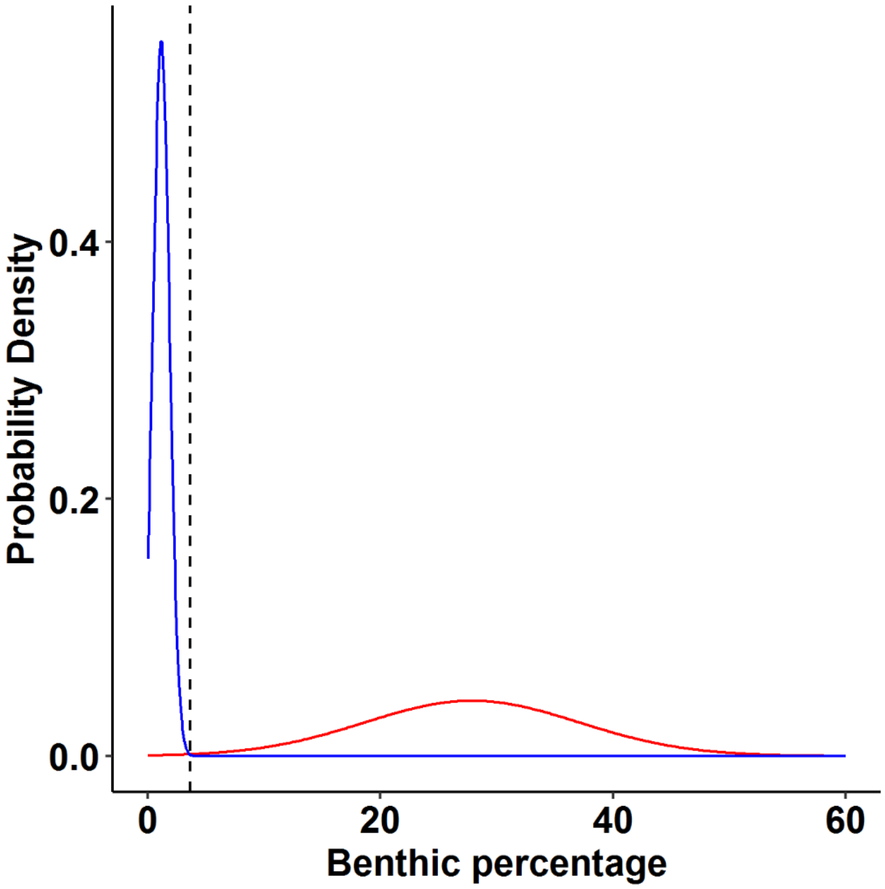


Figure S4.2 Bayesian model used for foraging trip categorisation. Trip types were analysed using the percentage of benthic dives contained in the trip, and were defined as benthic (red line) and pelagic (blue line). The dotted line shows the log likelihood ratio criterion (where 3.63% of the trip were benthic dives), which is the cut-off value used to categorise foraging trips as either a trip containing benthic dives, or solely pelagic dives.

Table S4.1 Success of dive type categorisation using Bayesian modelling with different dive parameters. Success was measured as the percentage of dives agreeing with a sample of manually-categorised dives (n = 3979 dives). The model based on inter-dive depth change (depth change between subsequent dives) gave the best match, and was selected as the model to use for analysing all dives (n = 72,993 dives).

Parameter	Success
Inter-dive depth change	96.4%
Bottom time %	76.5%
Bottom time	83.5%
Dive depth	71.8%

Table S4.2 Dive trips and electronics deployments, ordered by individual bird ID. Where multiple foraging trips were recorded in one deployment the data were separated into individual trips.

Bird ID	Year	Start Date	Start Time	End Date	End Time	Duration (hrs)	Nights	Trip Type	Deploy Type	Forage Type	Sex
bird001	2016	8/12/2016	20:10:04	10/12/2016	08:03:59	35.90	2	Multiday	GPS + TDR	Benthic	M
bird001	2017	13/12/2017	10:10:04	13/12/2017	20:03:59	9.90	0	Daytrip	TDR only	Pelagic	M
bird013	2017	17/12/2017	18:03:04	18/12/2017	22:29:59	28.45	1	Multiday	TDR only	Pelagic	M
bird013	2017	14/12/2017	14:00:04	16/12/2017	23:18:59	57.32	2	Multiday	GPS + TDR	Pelagic	M
bird019	2015	19/12/2015	18:05:04	21/12/2015	22:22:29	52.29	2	Multiday	TDR only	Benthic	M
bird019	2016	10/12/2016	07:05:04	11/12/2016	20:41:59	37.62	1	Multiday	GPS + TDR	Benthic	M
bird022	2016	14/12/2016	18:15:04	18/12/2016	14:25:59	92.18	4	Multiday	GPS + TDR	Pelagic	F
bird022	2017	23/12/2017	06:13:04	25/12/2017	16:03:59	57.85	2	Multiday	TDR only	Pelagic	F
bird022	2017	27/12/2017	05:55:04	27/12/2017	13:16:59	7.37	0	Daytrip	GPS + TDR	Pelagic	F
bird025	2015	27/11/2015	12:40:04	30/11/2015	07:17:39	66.63	3	Multiday	TDR only	Benthic	F
bird025	2017	15/12/2017	19:36:04	19/12/2017	01:16:59	77.68	4	Multiday	TDR only	Pelagic	F
bird025	2017	19/12/2017	16:06:04	20/12/2017	12:46:59	20.68	1	Multiday	GPS + TDR	Pelagic	F
bird029	2015	21/12/2015	20:19:04	25/12/2015	22:00:59	97.70	4	Multiday	TDR only	Benthic	F
bird030	2016	10/12/2016	05:58:04	12/12/2016	16:07:59	58.17	2	Multiday	GPS + TDR	Benthic	M
bird032	2016	26/12/2016	05:21:04	28/12/2016	12:16:59	54.93	2	Multiday	GPS + TDR	Pelagic	F
bird035	2015	3/12/2015	04:58:04	7/12/2015	22:12:59	113.25	4	Multiday	TDR only	Benthic	M
bird035	2017	10/12/2017	17:22:04	13/12/2017	00:19:59	54.97	3	Multiday	TDR only	Benthic	M
bird035	2017	13/12/2017	17:30:04	15/12/2017	18:11:59	48.70	2	Multiday	GPS + TDR	Pelagic	M
bird039	2015	14/12/2015	19:39:04	15/12/2015	08:24:54	12.76	1	Multiday	TDR only	Benthic	F
bird039	2015	23/12/2015	05:54:13	24/12/2015	16:11:13	34.28	1	Multiday	TDR only	Benthic	F
bird040	2015	4/12/2015	19:43:04	7/12/2015	17:39:59	69.95	3	Multiday	TDR only	Benthic	M
bird042	2016	12/12/2016	16:45:04	14/12/2016	14:46:59	46.03	2	Multiday	GPS + TDR	Pelagic	F
bird042	2017	10/12/2017	19:37:04	14/12/2017	15:46:59	92.17	4	Multiday	TDR only	Benthic	F
bird042	2017	15/12/2017	05:33:04	15/12/2017	15:42:59	10.17	0	Daytrip	GPS + TDR	Pelagic	F

bird050	2017	22/12/2017	17:05:04	23/12/2017	22:41:59	29.62	1	Multiday	TDR only	Pelagic	M
bird050	2017	24/12/2017	19:52:04	25/12/2017	16:52:59	21.02	1	Multiday	GPS + TDR	Pelagic	M
bird052	2015	10/12/2015	04:30:04	12/12/2015	19:22:29	62.87	2	Multiday	TDR only	Benthic	F
bird052	2016	9/12/2016	15:03:04	10/12/2016	14:06:59	23.07	1	Multiday	GPS + TDR	Benthic	F
bird052	2017	13/12/2017	18:29:04	14/12/2017	13:01:59	18.55	1	Multiday	TDR only	Benthic	F
bird052	2017	15/12/2017	05:51:04	18/12/2017	13:47:59	79.95	3	Multiday	GPS + TDR	Pelagic	F
bird053	2015	14/12/2015	04:16:04	14/12/2015	23:49:59	19.57	0	Daytrip	TDR only	Benthic	F
bird053	2016	9/12/2016	17:48:04	10/12/2016	19:22:59	25.58	1	Multiday	GPS + TDR	Benthic	F
bird053	2017	11/12/2017	16:46:04	12/12/2017	14:44:59	21.98	1	Multiday	TDR only	Pelagic	F
bird053	2017	13/12/2017	15:39:04	15/12/2017	11:57:59	44.32	2	Multiday	GPS + TDR	Pelagic	F
bird063	2015	13/12/2015	19:03:04	14/12/2015	18:11:59	23.15	1	Multiday	TDR only	Benthic	F
bird063	2015	15/12/2015	20:35:04	16/12/2015	18:43:59	22.15	1	Multiday	TDR only	Benthic	F
bird063	2015	17/12/2015	19:33:04	18/12/2015	13:58:04	18.42	1	Multiday	TDR only	Benthic	F
bird064	2016	26/12/2016	19:37:04	28/12/2016	23:20:59	51.73	2	Multiday	GPS + TDR	Benthic	
bird068	2015	15/12/2015	05:40:04	15/12/2015	21:07:59	15.47	0	Daytrip	TDR only	Benthic	M
bird068	2017	12/12/2017	15:23:04	13/12/2017	15:10:59	23.80	1	Multiday	TDR only	Benthic	M
bird068	2017	10/12/2017	15:37:04	11/12/2017	15:52:59	24.27	1	Multiday	GPS + TDR	Benthic	M
bird086	2016	10/12/2016	05:32:04	10/12/2016	15:01:59	9.50	0	Daytrip	GPS + TDR	Pelagic	M
bird086	2017	14/12/2017	05:13:04	14/12/2017	20:03:59	14.85	0	Daytrip	TDR only	Benthic	M
bird086	2017	17/12/2017	05:49:04	17/12/2017	19:48:59	14.00	0	Daytrip	GPS + TDR	Pelagic	M
bird095	2017	13/12/2017	05:13:04	15/12/2017	13:20:59	56.13	2	Multiday	TDR only	Benthic	F
bird095	2017	11/12/2017	15:55:04	12/12/2017	13:30:59	21.60	1	Multiday	GPS + TDR	Pelagic	F
bird101	2016	16/12/2016	18:19:04	17/12/2016	17:30:59	23.20	1	Multiday	GPS + TDR	Pelagic	F
bird101	2017	21/12/2017	14:49:04	23/12/2017	15:09:59	48.35	2	Multiday	TDR only	Pelagic	F
bird101	2017	24/12/2017	05:46:04	24/12/2017	18:26:59	12.68	0	Daytrip	GPS + TDR	Pelagic	F
bird105	2017	23/12/2017	05:52:04	23/12/2017	17:25:59	11.57	0	Daytrip	TDR only	Pelagic	F
bird105	2017	24/12/2017	13:44:04	24/12/2017	22:53:59	9.17	0	Daytrip	GPS + TDR	Pelagic	F
bird106	2016	12/12/2016	17:59:04	13/12/2016	17:38:59	23.67	1	Multiday	GPS + TDR	Benthic	M
bird106	2017	27/12/2017	12:20:04	27/12/2017	21:36:59	9.28	0	Daytrip	TDR only	Pelagic	M

bird106	2017	21/12/2017	15:47:04	22/12/2017	22:09:59	30.38	1	Multiday	GPS + TDR	Pelagic	M
bird107	2016	13/12/2016	14:47:04	15/12/2016	10:55:59	44.15	2	Multiday	GPS + TDR	Benthic	M
bird107	2017	24/12/2017	17:39:04	24/12/2017	23:18:59	5.67	0	Daytrip	TDR only	Benthic	M
bird107	2017	21/12/2017	14:49:04	22/12/2017	23:05:59	32.28	1	Multiday	GPS + TDR	Pelagic	M
bird111	2016	15/12/2016	05:27:04	16/12/2016	18:52:59	37.43	1	Multiday	GPS + TDR	Pelagic	F
bird117	2016	10/12/2016	15:09:04	11/12/2016	16:44:59	25.60	1	Multiday	GPS + TDR	Benthic	M
bird117	2017	13/12/2017	17:43:04	14/12/2017	14:35:59	20.88	1	Multiday	TDR only	Benthic	M
bird117	2017	10/12/2017	15:16:04	12/12/2017	23:15:59	56.00	2	Multiday	GPS + TDR	Benthic	M
bird120	2016	25/12/2016	17:40:04	28/12/2016	03:57:59	58.30	3	Multiday	GPS + TDR	Benthic	F
bird132	2016	14/12/2016	05:46:04	16/12/2016	00:30:59	42.75	2	Multiday	GPS + TDR	Pelagic	M
bird142	2016	12/12/2016	14:05:04	15/12/2016	19:16:59	77.20	3	Multiday	GPS + TDR	Pelagic	F
bird142	2017	15/12/2017	12:08:04	15/12/2017	21:28:59	9.35	0	Daytrip	TDR only	Pelagic	F
bird142	2017	11/12/2017	05:19:04	13/12/2017	20:52:59	63.57	2	Multiday	GPS + TDR	Pelagic	F
bird143	2016	10/12/2016	07:25:04	11/12/2016	20:29:59	37.08	1	Multiday	GPS + TDR	Benthic	F
bird145	2016	15/12/2016	05:19:04	17/12/2016	16:03:59	58.75	2	Multiday	GPS + TDR	Benthic	F
bird149	2016	25/12/2016	22:04:04	27/12/2016	05:41:59	31.63	2	Multiday	GPS + TDR	Pelagic	F
bird153	2016	9/12/2016	10:18:04	12/12/2016	02:11:49	63.90	3	Multiday	GPS + TDR	Benthic	F
bird154	2016	24/12/2016	17:03:04	25/12/2016	15:03:59	22.02	1	Multiday	GPS + TDR	Benthic	M
bird155	2016	24/12/2016	16:01:04	25/12/2016	16:23:59	24.38	1	Multiday	GPS + TDR	Benthic	M
bird155	2017	31/12/2017	15:46:04	2/01/2018	16:51:59	49.10	2	Multiday	TDR only	Pelagic	M
bird155	2017	16/12/2017	04:49:04	16/12/2017	20:13:59	15.42	0	Daytrip	GPS + TDR	Benthic	M
bird159	2016	24/12/2016	20:00:04	25/12/2016	20:44:59	24.75	1	Multiday	GPS + TDR	Benthic	M
bird160	2016	25/12/2016	18:46:04	27/12/2016	03:36:59	32.85	2	Multiday	GPS + TDR	Benthic	M
bird160	2017	21/12/2017	17:59:04	22/12/2017	12:09:59	18.18	1	Multiday	TDR only	Pelagic	M
bird160	2017	23/12/2017	06:00:04	23/12/2017	16:47:59	10.80	0	Daytrip	GPS + TDR	Pelagic	M
bird160	2017	24/12/2017	13:22:04	24/12/2017	21:59:59	8.63	0	Daytrip	GPS + TDR	Pelagic	M
bird161	2016	24/12/2016	17:36:04	25/12/2016	17:47:59	24.20	1	Multiday	GPS + TDR	Pelagic	F
bird161	2017	27/12/2017	05:00:04	27/12/2017	13:15:59	8.27	0	Daytrip	TDR only	Pelagic	F
bird161	2017	23/12/2017	18:17:04	25/12/2017	16:40:59	46.40	2	Multiday	GPS + TDR	Pelagic	F

bird161	2017	26/12/2017	05:28:04	26/12/2017	11:34:59	6.12	0	Daytrip	GPS + TDR	Pelagic	F
bird162	2016	25/12/2016	22:52:04	27/12/2016	22:21:59	47.50	2	Multiday	GPS + TDR	Pelagic	F
bird164	2016	24/12/2016	13:25:04	26/12/2016	08:00:59	42.60	2	Multiday	GPS + TDR	Pelagic	F
bird170	2016	18/12/2016	06:07:04	18/12/2016	22:00:59	15.90	0	Daytrip	GPS + TDR	Pelagic	F
bird171	2016	17/12/2016	22:48:04	19/12/2016	10:08:59	35.35	2	Multiday	GPS + TDR	Pelagic	M
bird172	2016	17/12/2016	18:17:04	19/12/2016	11:06:59	40.83	2	Multiday	GPS + TDR	Pelagic	M
bird175	2016	13/12/2016	16:35:04	15/12/2016	22:21:59	53.78	2	Multiday	GPS + TDR	Benthic	F
bird183	2016	26/12/2016	18:31:04	27/12/2016	19:18:59	24.80	1	Multiday	GPS + TDR	Pelagic	F
bird185	2016	5/12/2016	18:25:04	7/12/2016	11:30:04	41.08	2	Multiday	GPS + TDR	Benthic	M
bird186	2016	5/12/2016	05:27:04	5/12/2016	20:46:59	15.33	0	Daytrip	GPS + TDR	Benthic	F
bird187	2016	7/12/2016	05:19:04	8/12/2016	11:55:09	30.60	1	Multiday	GPS + TDR	Benthic	F
bird189	2016	14/12/2016	15:01:04	14/12/2016	19:49:59	4.82	0	Daytrip	GPS + TDR	Pelagic	M
bird191	2016	17/12/2016	23:58:04	19/12/2016	20:41:59	44.73	2	Multiday	GPS + TDR	Benthic	M
bird192	2016	17/12/2016	16:41:04	18/12/2016	19:34:59	26.90	1	Multiday	GPS + TDR	Benthic	M
bird205	2016	25/12/2016	16:47:04	27/12/2016	08:48:59	40.03	2	Multiday	GPS + TDR	Pelagic	F
bird206	2016	25/12/2016	17:40:04	26/12/2016	21:07:59	27.47	1	Multiday	GPS + TDR	Benthic	M
bird207	2016	25/12/2016	16:59:04	26/12/2016	17:26:59	24.47	1	Multiday	GPS + TDR	Benthic	F
bird208	2016	25/12/2016	20:40:04	26/12/2016	20:51:59	24.20	1	Multiday	GPS + TDR	Benthic	F
bird209	2016	27/12/2016	05:25:04	28/12/2016	03:54:59	22.50	1	Multiday	GPS + TDR	Benthic	M
bird210	2016	25/12/2016	17:00:04	28/12/2016	07:30:44	62.51	3	Multiday	GPS + TDR	Benthic	F
bird213	2016	30/12/2016	05:17:04	31/12/2016	18:13:59	36.95	1	Multiday	GPS + TDR	Pelagic	F
bird214	2016	30/12/2016	16:00:04	31/12/2016	18:21:59	26.37	1	Multiday	GPS + TDR	Pelagic	F
bird215	2016	30/12/2016	03:47:04	1/01/2017	09:42:59	53.93	2	Multiday	GPS + TDR	Benthic	F
bird216	2016	31/12/2016	18:08:04	1/01/2017	18:09:59	24.03	1	Multiday	GPS + TDR	Benthic	M
bird217	2016	30/12/2016	15:39:04	1/01/2017	13:22:59	45.73	2	Multiday	GPS + TDR	Benthic	M
bird233	2017	4/12/2017	06:01:04	4/12/2017	17:54:59	11.90	0	Daytrip	GPS + TDR	Pelagic	F
bird233	2017	18/12/2017	05:50:04	18/12/2017	17:13:59	11.40	0	Daytrip	GPS + TDR	Pelagic	F
bird233	2017	19/12/2017	05:05:04	19/12/2017	12:53:59	7.82	0	Daytrip	GPS + TDR	Pelagic	F
bird233	2017	20/12/2017	05:23:04	20/12/2017	14:55:59	9.55	0	Daytrip	GPS + TDR	Pelagic	F

bird244	2017	31/12/2017	15:54:04	1/01/2018	12:32:59	20.65	1	Multiday	TDR only	Pelagic	M
bird244	2017	4/12/2017	18:33:04	5/12/2017	18:16:59	23.73	1	Multiday	GPS + TDR	Pelagic	M
bird244	2017	16/12/2017	11:09:04	17/12/2017	00:57:59	13.82	1	Multiday	GPS + TDR	Pelagic	M
bird245	2017	1/01/2018	05:37:04	2/01/2018	16:34:59	34.97	1	Multiday	TDR only	Pelagic	F
bird245	2017	16/12/2017	06:29:04	16/12/2017	20:12:59	13.73	0	Daytrip	GPS + TDR	Pelagic	F
bird247	2017	3/01/2018	06:52:04	3/01/2018	15:38:59	8.78	0	Daytrip	TDR only	Pelagic	F
bird247	2017	4/12/2017	05:44:04	4/12/2017	19:54:59	14.18	0	Daytrip	GPS + TDR	Pelagic	F
bird247	2017	17/12/2017	05:34:04	18/12/2017	16:12:59	34.65	1	Multiday	GPS + TDR	Pelagic	F
bird249	2017	31/12/2017	15:46:04	31/12/2017	21:59:59	6.23	0	Daytrip	TDR only	Pelagic	M
bird249	2017	4/12/2017	01:14:04	5/12/2017	21:37:59	44.40	1	Multiday	GPS + TDR	Benthic	M
bird249	2017	17/12/2017	05:34:04	17/12/2017	20:41:59	15.13	0	Daytrip	GPS + TDR	Benthic	M
bird250	2017	4/12/2017	02:29:04	6/12/2017	23:32:59	69.07	2	Multiday	GPS + TDR	Benthic	F
bird254	2017	1/01/2018	05:37:04	1/01/2018	14:42:59	9.10	0	Daytrip	TDR only	Pelagic	F
bird254	2017	16/12/2017	15:23:04	17/12/2017	10:02:59	18.67	1	Multiday	GPS + TDR	Pelagic	F
bird267	2017	3/01/2018	06:46:04	3/01/2018	14:07:59	7.37	0	Daytrip	TDR only	Pelagic	F
bird267	2017	2/01/2018	07:04:04	2/01/2018	19:18:59	12.25	0	Daytrip	GPS + TDR	Pelagic	F
bird268	2017	31/12/2017	14:22:04	1/01/2018	20:50:59	30.48	1	Multiday	TDR only	Pelagic	M
bird268	2017	2/01/2018	07:57:04	2/01/2018	15:28:59	7.53	0	Daytrip	TDR only	Pelagic	M
bird268	2017	3/01/2018	13:33:04	3/01/2018	21:40:59	8.13	0	Daytrip	GPS + TDR	Pelagic	M
bird269	2017	1/01/2018	14:00:04	2/01/2018	21:14:59	31.25	1	Multiday	TDR only	Pelagic	F
bird269	2017	3/01/2018	14:58:04	4/01/2018	15:03:59	24.10	1	Multiday	GPS + TDR	Pelagic	F
bird270	2017	1/01/2018	06:32:04	1/01/2018	14:51:59	8.33	0	Daytrip	TDR only	Pelagic	F
bird270	2017	2/01/2018	13:03:04	2/01/2018	21:00:59	7.97	0	Daytrip	GPS + TDR	Pelagic	F

Table S4.3 Results for fixed effects from LME models on all dives for selected dive parameters: maximum dive depth, dive time, and bottom time (the time in the bottom portion of the dive, at maximum depth). Independent variables are year (2015, 2016, and 2017); sex (male and female); deployment type (TDR logger only, or GPS and TDR loggers); and dive type (benthic, pelagic, and transition). For each dive parameter the estimates and standard errors show the change in individual variable levels from the intercept value. χ^2 and p-values show the results of ANOVA testing for the variables in each LME model. Asterisks denote significance (***<0.001, **<0.01, *<0.05).

Dive Parameter	Variable	Estimate	Std. Error	χ^2	p-value
Max Depth (m)	(Intercept)	90.49	1.15		
	Year-2016	-16.16	0.49	3698.68	<0.001***
	Year-2017	-23.03	0.41		
	Sex-F	0.16	1.38	0.01	0.91
	Deploy Type-TDR	0.55	0.22	6.43	0.01*
	Dive Type-Pelagic	-50.17	0.26	38478.80	<0.001***
	Dive Type-Transition	-30.54	0.42		
Dive Time (s)	(Intercept)	156.64	1.94		
	Year-2016	-17.21	0.98	1748.14	<0.001***
	Year-2017	-29.48	0.83		
	Sex-F	-5.59	2.24	6.25	0.01*
	Deploy Type-TDR	0.85	0.44	3.74	0.05
	Dive Type-Pelagic	-56.40	0.52	11855.57	<0.001***
	Dive Type-Transition	-39.18	0.84		
Bottom Time (s)	(Intercept)	40.99	1.01		
	Year-2016	4.32	0.50	184.16	<0.001***
	Year-2017	5.44	0.42		
	Sex-F	-4.21	1.17	12.87	<0.001***
	Deploy Type-TDR	1.51	0.22	45.64	<0.001***
	Dive Type-Pelagic	-23.71	0.26	8248.32	<0.001***
	Dive Type-Transition	-22.71	0.43		

Appendix 5 – Supplementary material for Chapter 5 (Foraging)

Table S5.1 Foraging trips by breeding yellow-eyed penguins from Enderby Island. Data were derived from simultaneous GPS and TDR deployments, and are ordered chronologically by bird ID. Trip times shown are from GPS logs, and trip durations are from the TDR log (where available) as these were more complete than the GPS record. GPS fix success was calculated from the theoretical number of possible fixes between the first and last scheduled GPS fix times per trip. Where multiple foraging trips were recorded in one deployment the data were separated into individual trips. Data type shows what data were recorded (all deployments for this study included both a GPS and TDR logger, however, in some cases loggers were lost at sea, or logs were not recorded). Foraging type was determined from dive logs, where available (Muller et al. 2020a).

Bird ID	Sex	Year	Trip No.	Start Date	Start Time	End Date	End Time	Duration (hr)	Fix Success	Foraging Distance (km)	Total Distance (km)	Data Type	Forage Type
bird001	M	2016	1	09/12/2016	04:36:27	09/12/2016	18:41:05	35.90	0.19	31.18	69.66	GPS + TDR	Benthic
bird013	M	2017	1	11/12/2017	17:04:33	13/12/2017	17:27:20	8.20	0.14	22.87	64.02	GPS + TDR	Pelagic
bird013	M	2017	2	16/12/2017	16:20:09	16/12/2017	23:15:17	37.62	0.08	6.38	14.47	GPS + TDR	Benthic
bird019	M	2016	1	10/12/2016	22:46:28	11/12/2016	17:22:16	37.62	0.06	24.89	58.91	GPS + TDR	Pelagic
bird022	F	2016	1	14/12/2016	18:27:15	15/12/2016	15:38:13	21.42	0.08	35.72	73.96	GPS + TDR	Pelagic
bird022	F	2016	2	16/12/2016	06:09:16	16/12/2016	21:34:39	15.65	0.01	5.23	10.69	GPS + TDR	Pelagic
bird022	F	2016	3	17/12/2016	16:56:10	18/12/2016	14:11:15	21.41	0.13	13.29	65.53	GPS + TDR	Pelagic
bird022	F	2017	1	27/12/2017	06:09:49	27/12/2017	13:12:28	7.37	0.06	3.65	7.60	GPS + TDR	Pelagic
bird025	F	2017	1	20/12/2017	04:58:00	20/12/2017	12:39:13	20.68	0.12	5.11	11.36	GPS + TDR	Pelagic
bird030	M	2016	1	11/12/2016	18:30:03	12/12/2016	16:01:28	58.17	0.21	30.67	74.89	GPS + TDR	Benthic
bird032	F	2016	1	26/12/2016	05:42:11	27/12/2016	17:57:34	54.93	0.30	46.73	113.22	GPS + TDR	Pelagic
bird035	M	2017	1	10/12/2017	20:46:21	13/12/2017	00:16:49	48.70	0.02	9.83	28.05	GPS + TDR	Pelagic
bird042	F	2016	1	12/12/2016	16:59:47	13/12/2016	15:12:06	46.03	0.03	2.58	5.57	GPS + TDR	Pelagic

bird042	F	2017	1	15/12/2017	05:47:43	15/12/2017	15:40:46	10.17	0.04	2.39	4.79	GPS + TDR	Pelagic
bird050	M	2017	1	23/12/2017	16:23:09	23/12/2017	22:39:22	21.02	0.09	2.65	5.47	GPS + TDR	Pelagic
bird052	F	2016	1	10/12/2016	04:03:20	10/12/2016	14:02:54	23.07	0.11	32.76	66.40	GPS + TDR	Benthic
bird052	F	2017	1	13/12/2017	20:36:57	14/12/2017	12:56:18	79.95	0.31	23.61	52.75	GPS + TDR	Pelagic
bird053	F	2016	1	10/12/2016	04:03:04	10/12/2016	19:06:15	25.58	0.13	25.72	52.45	GPS + TDR	Benthic
bird053	F	2017	1	14/12/2017	18:18:03	15/12/2017	11:43:14	44.32	0.13	11.62	34.82	GPS + TDR	Pelagic
bird064	?	2016	1	26/12/2016	20:05:23	28/12/2016	23:16:25	51.73	0.11	38.78	100.72	GPS + TDR	Benthic
bird065	F	2016	1	16/12/2016	06:42:48	19/12/2016	19:09:53		0.03	21.02	57.94	GPS	unknown
bird068	M	2017	1	11/12/2017	05:29:52	11/12/2017	15:47:33	24.27	0.04	12.82	25.66	GPS + TDR	Benthic
bird086	M	2016	1	10/12/2016	05:53:06	10/12/2016	14:49:08	9.50	0.08	6.47	13.33	GPS + TDR	Pelagic
bird086	M	2017	1	17/12/2017	06:19:35	17/12/2017	19:43:33	14.00	0.16	8.97	21.50	GPS + TDR	Pelagic
bird095	F	2017	1	11/12/2017	23:14:55	12/12/2017	11:28:45	21.60	0.38	18.36	47.85	GPS + TDR	Pelagic
bird101	F	2016	1	16/12/2016	20:42:16	17/12/2016	15:36:27	23.20	0.11	23.08	62.06	GPS + TDR	Pelagic
bird101	F	2017	1	24/12/2017	06:00:31	24/12/2017	18:23:38	12.68	0.05	5.79	12.68	GPS + TDR	Pelagic
bird106	M	2016	1	12/12/2016	18:19:55	13/12/2016	17:13:01	23.67	0.11	25.01	58.74	GPS + TDR	Benthic
bird106	M	2017	1	22/12/2017	16:48:04	22/12/2017	23:00:28	30.38	0.02	1.65	3.30	GPS + TDR	Pelagic
bird107	M	2016	1	13/12/2016	15:28:57	14/12/2016	16:13:25	44.15	0.06	25.60	55.41	GPS + TDR	Benthic
bird111	F	2016	1	15/12/2016	18:37:30	16/12/2016	18:46:45	37.43	0.09	37.18	91.38	GPS + TDR	Pelagic
bird117	M	2016	1	10/12/2016	22:49:34	11/12/2016	16:41:49	25.60	0.08	26.94	61.61	GPS + TDR	Benthic
bird117	M	2017	1	10/12/2017	22:12:32	12/12/2017	23:12:28	56.00	0.08	27.25	95.44	GPS + TDR	Benthic
bird120	F	2016	1	25/12/2016	22:46:57	27/12/2016	20:44:05	58.30	0.34	33.64	99.97	GPS + TDR	Benthic
bird132	M	2016	1	14/12/2016	06:00:22	14/12/2016	16:13:46	42.75	0.04	3.56	7.33	GPS + TDR	Pelagic
bird142	F	2016	1	12/12/2016	22:52:23	13/12/2016	20:16:25	77.20	0.11	33.36	90.12	GPS + TDR	Pelagic
bird142	F	2017	1	11/12/2017	05:38:09	13/12/2017	20:38:03	63.57	0.02	5.53	15.46	GPS + TDR	Pelagic
bird143	F	2016	1	10/12/2016	07:33:28	11/12/2016	19:29:21	37.08	0.12	34.09	98.38	GPS + TDR	Benthic
bird145	F	2016	1	15/12/2016	05:38:47	17/12/2016	15:42:43	58.75	0.10	27.84	85.85	GPS + TDR	Benthic
bird149	F	2016	1	25/12/2016	22:17:49	26/12/2016	20:53:34	31.63	0.29	33.07	72.30	GPS + TDR	Pelagic
bird154	M	2016	1	24/12/2016	23:03:24	25/12/2016	14:32:33	22.02	0.33	32.30	69.78	GPS + TDR	Benthic
bird155	M	2016	1	24/12/2016	22:44:34	25/12/2016	15:54:01	24.38	0.30	33.92	73.10	GPS + TDR	Benthic

bird155	M	2017	1	16/12/2017	04:57:38	16/12/2017	20:08:54	15.42	0.05	6.19	12.94	GPS + TDR	Benthic
bird159	M	2016	1	24/12/2016	20:21:56	25/12/2016	20:39:20	24.75	0.29	36.57	77.36	GPS + TDR	Benthic
bird160	M	2016	1	25/12/2016	18:55:58	26/12/2016	19:32:04	32.85	0.30	29.32	69.32	GPS + TDR	Benthic
bird160	M	2017	1	23/12/2017	06:25:06	23/12/2017	16:40:38	10.80	0.18	15.49	33.51	GPS + TDR	Pelagic
bird160	M	2017	2	24/12/2017	13:28:56	24/12/2017	21:54:34	8.63	0.09	36.13	9.59	GPS + TDR	Pelagic
bird161	F	2016	1	24/12/2016	22:54:04	25/12/2016	17:41:25	24.20	0.40	35.71	78.91	GPS + TDR	Pelagic
bird161	F	2017	1	23/12/2017	18:35:46	25/12/2017	15:56:48	46.40	0.15	18.08	73.26	GPS + TDR	Pelagic
bird161	F	2017	2	26/12/2017	05:44:29	26/12/2017	11:30:18	6.12	0.04	1.54	3.09	GPS + TDR	Pelagic
bird162	F	2016	1	26/12/2016	06:01:37	27/12/2016	20:40:21	47.50	0.28	34.51	136.70	GPS + TDR	Pelagic
bird164	F	2016	1	24/12/2016	23:06:34	26/12/2016	06:18:39	42.60	0.27	35.71	93.06	GPS + TDR	Pelagic
bird170	F	2016	1	18/12/2016	06:21:46	18/12/2016	21:36:42	15.90	0.03	7.12	17.28	GPS + TDR	Pelagic
bird171	M	2016	1	18/12/2016	06:32:10	18/12/2016	17:45:39	35.35	0.04	7.18	14.67	GPS + TDR	Pelagic
bird172	M	2016	1	17/12/2016	18:29:13	18/12/2016	19:50:51	40.83	0.05	8.66	24.14	GPS + TDR	Pelagic
bird175	F	2016	1	13/12/2016	17:21:15	15/12/2016	22:17:14	53.78	0.10	29.18	74.52	GPS + TDR	Benthic
bird183	F	2016	1	26/12/2016	18:44:47	27/12/2016	19:16:25	24.80	0.25	17.21	39.88	GPS + TDR	Pelagic
bird186	F	2016	1	05/12/2016	05:32:55	05/12/2016	20:25:12	15.33	0.06	6.41	13.12	GPS + TDR	Benthic
bird187	F	2016	1	07/12/2016	05:37:49	07/12/2016	15:16:34	30.60	0.04	1.95	3.94	GPS + TDR	Benthic
bird189	M	2016	1	14/12/2016	15:17:10	14/12/2016	19:34:11	4.82	0.07	1.31	2.66	GPS + TDR	Pelagic
bird191	M	2016	1	18/12/2016	06:32:41	19/12/2016	19:42:54	44.73	0.12	36.41	86.55	GPS + TDR	Benthic
bird192	M	2016	1	17/12/2016	22:33:29	18/12/2016	22:02:33	26.90	0.14	22.03	82.30	GPS + TDR	Benthic
bird193	M	2016	1	18/12/2016	04:03:08	20/12/2016	14:50:08		0.03	30.84	79.75	GPS	unknown
bird204	M	2016	1	25/12/2016	19:27:20	26/12/2016	20:27:47		0.29	23.09	63.54	GPS	unknown
bird205	F	2016	1	25/12/2016	17:28:00	26/12/2016	14:13:36	40.03	0.30	33.23	71.52	GPS + TDR	Pelagic
bird206	M	2016	1	25/12/2016	18:11:25	26/12/2016	19:34:02	27.47	0.43	27.60	68.87	GPS + TDR	Benthic
bird207	F	2016	1	25/12/2016	17:16:01	26/12/2016	16:58:14	24.47	0.45	25.62	65.19	GPS + TDR	Benthic
bird208	F	2016	1	25/12/2016	23:15:57	26/12/2016	20:39:09	24.20	0.29	24.53	56.82	GPS + TDR	Benthic
bird209	M	2016	1	27/12/2016	05:44:23	27/12/2016	22:45:08	22.50	0.23	31.50	67.18	GPS + TDR	Benthic
bird210	F	2016	1	25/12/2016	23:12:41	28/12/2016	06:30:25	62.51	0.22	32.10	118.41	GPS + TDR	Benthic
bird210	F	2016	2	28/12/2016	20:57:06	29/12/2016	07:46:19		0.03	29.49	71.24	GPS	unknown

bird213	F	2016	1	30/12/2016	20:13:52	31/12/2016	12:53:24	36.95	0.45	36.97	83.35	GPS + TDR	Pelagic
bird214	F	2016	1	30/12/2016	16:27:30	30/12/2016	23:47:12	26.37	0.16	8.97	22.10	GPS + TDR	Pelagic
bird215	F	2016	1	30/12/2016	04:02:27	30/12/2016	22:56:40	53.93	0.07	28.14	60.54	GPS + TDR	Benthic
bird216	M	2016	1	31/12/2016	18:43:22	01/01/2017	17:58:22	24.03	0.31	27.13	68.04	GPS + TDR	Benthic
bird217	M	2016	1	29/12/2016	23:01:52	31/12/2016	18:32:44	45.73	0.22	30.32	74.37	GPS + TDR	Benthic
bird233	F	2017	1	04/12/2017	06:23:30	04/12/2017	18:01:53	11.90	0.03	3.33	6.75	GPS + TDR	Pelagic
bird233	F	2017	2	16/12/2017	18:07:58	20/12/2017	06:59:21	11.40	0.09	22.58	68.16	GPS + TDR	Pelagic
bird244	M	2017	1	04/12/2017	19:24:30	05/12/2017	18:07:35	23.73	0.07	6.45	21.99	GPS + TDR	Pelagic
bird244	M	2017	2	16/12/2017	11:23:53	16/12/2017	22:50:21	13.82	0.05	4.16	8.74	GPS + TDR	Pelagic
bird245	F	2017	1	16/12/2017	06:41:48	16/12/2017	18:12:45	13.73	0.02	1.58	3.17	GPS + TDR	Pelagic
bird247	F	2017	1	04/12/2017	05:55:37	04/12/2017	18:52:37	14.18	0.05	4.04	8.29	GPS + TDR	Pelagic
bird247	F	2017	2	17/12/2017	05:47:12	18/12/2017	16:04:55	34.65	0.03	5.59	13.12	GPS + TDR	Pelagic
bird249	M	2017	1	05/12/2017	06:46:44	05/12/2017	21:16:33	44.40	0.03	1.17	2.72	GPS + TDR	Benthic
bird249	M	2017	2	17/12/2017	06:03:05	17/12/2017	20:19:14	15.13	0.01	4.29	8.59	GPS + TDR	Benthic
bird250	F	2017	1	06/12/2017	06:17:51	06/12/2017	22:38:23	69.07	0.23	29.95	68.83	GPS + TDR	Benthic
bird254	F	2017	1	16/12/2017	15:30:56	17/12/2017	09:55:03	18.67	0.26	20.14	58.41	GPS + TDR	Pelagic
bird267	F	2017	1	02/01/2018	07:20:05	02/01/2018	15:56:16	12.25	0.33	12.68	27.60	GPS + TDR	Pelagic
bird268	M	2017	1	03/01/2018	13:44:07	03/01/2018	21:38:23	8.13	0.15	7.51	16.30	GPS + TDR	Pelagic
bird269	F	2017	1	03/01/2018	20:47:34	04/01/2018	14:26:55	24.10	0.49	13.58	52.95	GPS + TDR	Pelagic
bird270	F	2017	1	02/01/2018	13:21:03	02/01/2018	20:49:38	7.97	0.19	7.22	17.76	GPS + TDR	Pelagic

Table S5.2 Results for fixed effects from LME models (lmer(Parameter~(1|BirdID)+Year+DiveType+Sex)) for selected distance parameters: foraging distance (maximum distance from shore), and total distance (cumulative distance travelled during a trip). Independent variables are year (2016, and 2017); dive type (benthic, and pelagic), and sex. For each parameter the estimates and standard errors show the change in individual variable levels from the intercept value. χ^2 and p-values show the results of ANOVA testing for the variables in each LME model. Asterisks denote significance (***<0.001, **<0.01, *<0.05).

Parameter	Variable	Estimate	Std. Error	χ^2	Df	p-value	Sig
Foraging Distance (km)	(Intercept)	28.851	2.242				
	Year_2017	-11.889	2.396	24.631	1	6.94E-07	***
	Dive_Pelagic	-5.925	2.537	5.452	1	0.01955	*
	Sex_Male	-3.065	2.376	1.664	1	0.19707	
Total Distance (km)	(Intercept)	75.539	5.926				
	Year_2017	-29.027	6.392	20.6212	1	5.60E-06	***
	Dive_Pelagic	-17.034	6.705	6.4548	1	0.01107	*
	Sex_Male	-13.715	6.217	4.8657	1	0.0274	*

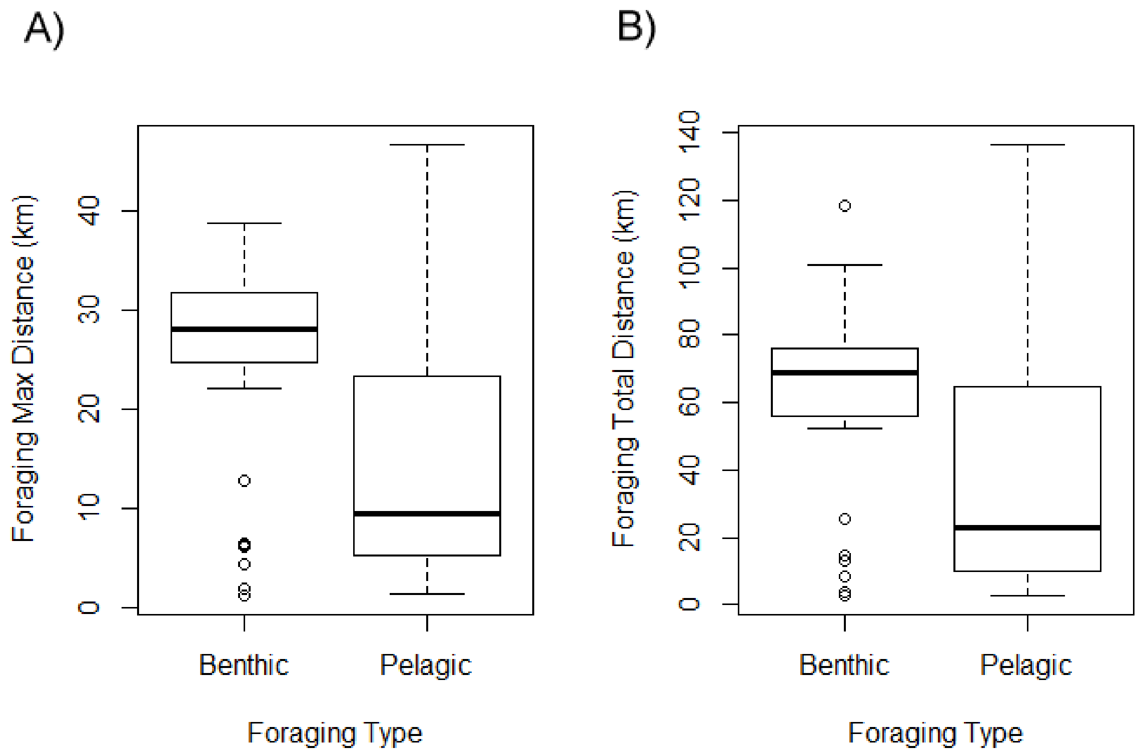


Figure S5.1 A) Foraging distance (maximum distance travelled offshore), and B) Total distance (cumulative distance travelled per foraging trip) by foraging type for breeding yellow-eyed penguins from Enderby Island for both study years (2016 and 2017). Distance was determined from GPS logs and foraging type was determined from analysis of simultaneous dive (TDR) logs (Muller et al. 2020a).

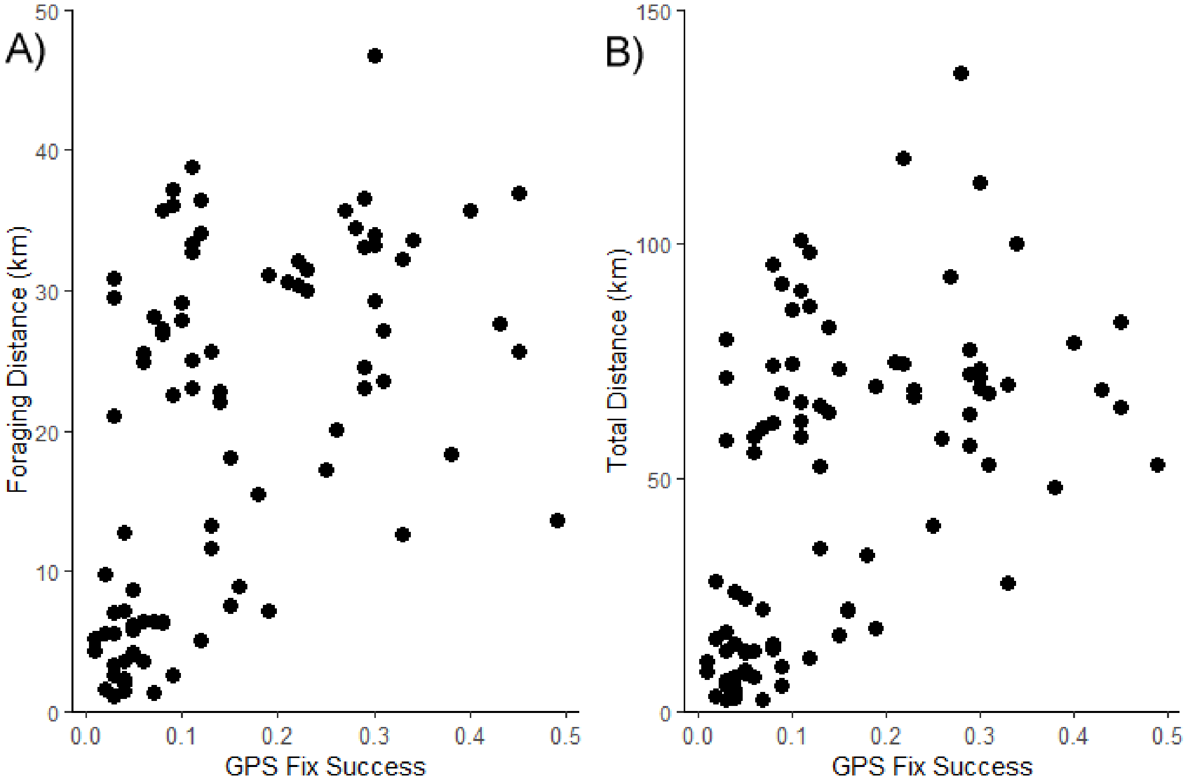


Figure S5.2 GPS fix success (proportion of successful fixes) vs maximum distance recorded per foraging trip for A) Foraging distance (maximum distance travelled offshore), and B) Total distance (cumulative distance travelled per foraging trip) for breeding yellow-eyed penguins from Enderby Island. Distance was determined from GPS positions, and measured from the sea access point. Trip duration was determined independently using TDR loggers (Muller et al. 2020a), and from that, GPS fix success. A GPS fix success value of ≤5% likely represented a partial trip record, therefore, as a comparison these trips were excluded from calculations of mean foraging distances as they may not represent the maximum distance travelled during foraging trips. All GPS data were included for all other calculations.

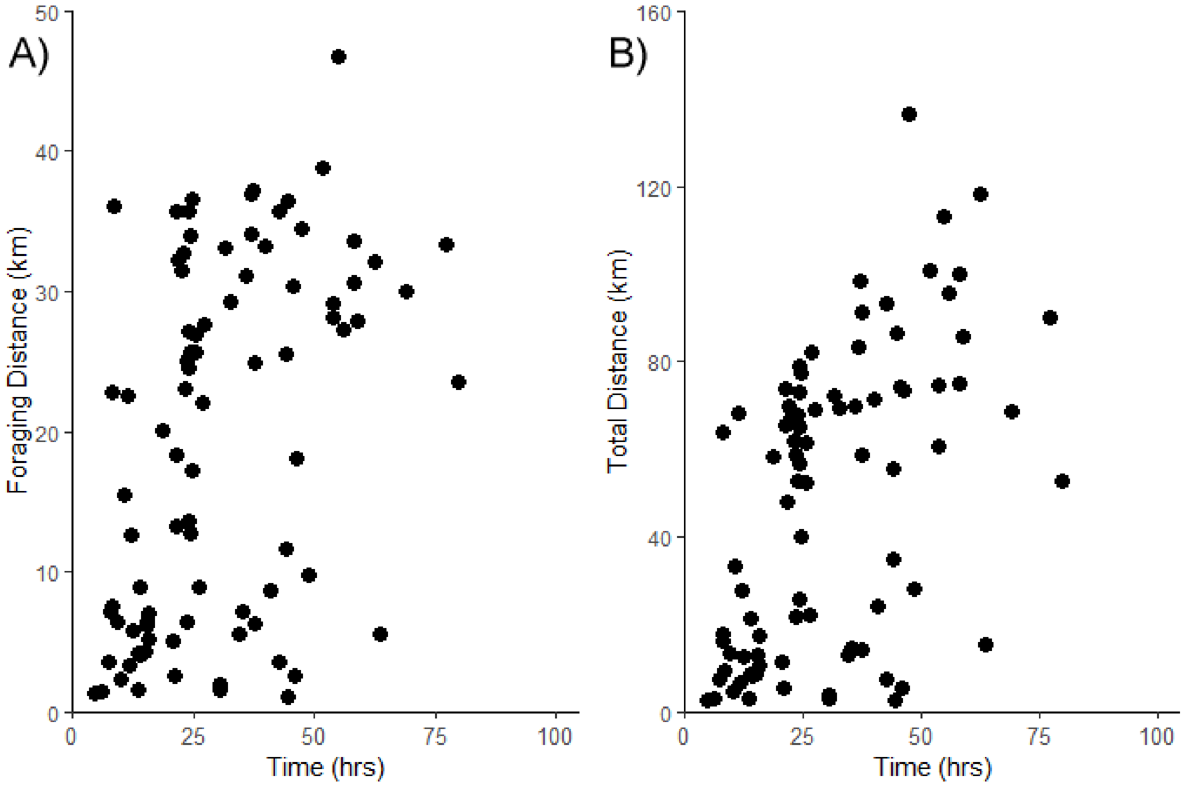


Figure S5.3 Foraging trip duration (hours) vs A) foraging distance (maximum distance travelled offshore), and B) Total distance (cumulative distance travelled per foraging trip) for breeding yellow-eyed penguins from Enderby Island. Distance was determined from GPS positions, and measured from the sea access point. Trip duration was determined independently using TDR loggers (Muller et al. 2020a).

Appendix 6 – Supplementary material for Chapter 6 (Diet)

Table S6.1 Stable Isotope Analysis (SIA) and foraging trip summary results, ordered by sample type and individual bird ID. Where known, forage types were determined from TDR loggers attached to birds (Muller et al. 2020a), and foraging distances were determined from GPS loggers (Muller et al. 2021). SIA samples were collected in the 'year sampled', which reflects the diet during the previous year for feather samples. Dive and GPS data were collected in the 'diet year'. Where multiple foraging trips were recorded in one deployment the data were separated into individual trips.

Bird ID	Sex	Diet Year	Year Sampled	Sample Type	Foraging Range (km)	Total Distance (km)	Forage Type	N	DELTA^{15}N	~C	DELTA^{13}C
bird001	M	2015	2015	Blood				10.56	10.28	43.94	-20.32
bird019	M	2015	2015	Blood			Benthic	10.80	10.37	44.32	-20.25
bird022	F	2015	2015	Blood				10.76	11.40	43.02	-20.10
bird025	F	2015	2015	Blood			Benthic	10.73	10.34	44.02	-20.58
bird030	M	2015	2015	Blood				10.51	10.51	42.46	-20.23
bird032	F	2015	2015	Blood				10.65	11.30	43.39	-20.73
bird035	M	2015	2015	Blood			Benthic	10.61	10.50	43.40	-20.49
bird039	F	2015	2015	Blood			Benthic	10.18	10.56	42.95	-20.80
bird042	F	2015	2015	Blood				10.57	10.70	38.25	-20.99
bird050	M	2015	2015	Blood				10.37	10.94	43.74	-20.53
bird001	M	2014	2015	Feathers				13.28	11.76	45.23	-18.87
bird001	M	2015	2016	Feathers				12.18	11.50	40.92	-18.21
bird001	M	2016	2017	Feathers	31.18	52.21	Benthic	14.27	12.17	47.18	-18.69

bird019	M	2014	2015	Feathers				13.81	11.97	45.73	-18.68
bird019	M	2015	2016	Feathers			Benthic	13.44	11.61	45.02	-18.11
bird022	F	2014	2015	Feathers				14.03	11.55	46.59	-18.67
bird022	F	2015	2016	Feathers				13.14	10.98	43.87	-18.12
bird022	F	2016	2017	Feathers	35.72	143.37	Pelagic	14.21	12.13	47.13	-18.38
bird025	F	2014	2015	Feathers			Benthic	13.88	11.98	45.82	-18.45
bird025	F	2016	2017	Feathers				13.79	11.71	45.78	-18.60
bird030	M	2015	2016	Feathers				14.16	11.43	46.85	-18.35
bird032	F	2015	2016	Feathers				13.63	11.18	45.39	-18.25
bird032	F	2016	2017	Feathers	46.73	110.35	Pelagic	14.31	11.48	47.31	-18.83
bird035	M	2014	2015	Feathers				13.81	12.00	45.67	-18.82
bird035	M	2015	2016	Feathers			Benthic	13.85	11.50	46.40	-18.27
bird035	M	2016	2017	Feathers				14.11	12.01	46.69	-18.62
bird039	F	2014	2015	Feathers				13.76	11.60	45.57	-18.72
bird039	F	2015	2016	Feathers			Benthic	13.47	11.86	46.42	-17.92
bird042	F	2014	2015	Feathers				14.86	11.79	49.19	-18.76
bird042	F	2015	2016	Feathers				13.82	11.57	46.07	-18.16
bird042	F	2016	2017	Feathers	2.58	4.67	Pelagic	14.22	12.05	47.21	-18.71
bird050	M	2015	2016	Feathers				14.11	11.75	46.86	-17.58
bird050	M	2016	2017	Feathers				14.22	12.75	47.19	-18.40
bird052	F	2014	2015	Feathers				12.15	11.62	40.77	-18.91
bird052	F	2015	2016	Feathers			Benthic	14.43	11.39	47.62	-18.01
bird052	F	2016	2017	Feathers	32.76	63.96	Benthic	14.20	11.86	47.07	-18.59
bird053	F	2014	2015	Feathers				14.01	11.69	46.41	-19.01
bird053	F	2015	2016	Feathers			Benthic	14.02	11.33	46.57	-18.31
bird053	F	2016	2017	Feathers	25.72	31.18	Benthic	14.42	11.93	47.52	-18.65
bird068	M	2014	2015	Feathers				12.51	11.82	41.96	-18.80
bird068	M	2015	2016	Feathers			Benthic	13.95	11.85	46.44	-18.24
bird068	M	2016	2017	Feathers				14.38	12.34	47.46	-18.54

bird086	M	2015	2016	Feathers				14.07	11.85	46.61	-18.36
bird086	M	2016	2017	Feathers	6.47	11.57	Pelagic	14.14	12.55	46.96	-18.41
bird101	F	2015	2016	Feathers				14.02	11.09	46.47	-17.96
bird101	F	2016	2017	Feathers	23.08	56.19	Pelagic	14.11	11.86	46.94	-18.61
bird105	F	2016	2017	Feathers				14.49	11.85	47.58	-18.30
bird106	M	2015	2016	Feathers				14.09	11.66	46.82	-17.79
bird106	M	2016	2017	Feathers	25.01	56.79	Benthic	14.29	12.55	47.06	-18.15
bird107	M	2015	2016	Feathers				14.18	11.77	46.93	-17.84
bird107	M	2016	2017	Feathers	25.6	53.4	Benthic	14.16	12.15	46.98	-18.56
bird117	M	2015	2016	Feathers				14.06	11.61	46.74	-18.21
bird117	M	2016	2017	Feathers	26.94	59.63	Benthic	14.05	12.08	46.41	-18.68
bird142	F	2015	2016	Feathers				13.85	11.33	45.75	-18.16
bird142	F	2016	2017	Feathers	33.36	81.02	Pelagic	14.30	11.98	47.34	-18.64
bird155	M	2015	2016	Feathers				13.82	11.60	46.04	-18.14
bird155	M	2016	2017	Feathers	33.92	67.14	Benthic	13.96	12.45	46.05	-18.48
bird160	M	2015	2016	Feathers				13.70	11.33	45.39	-18.19
bird160	M	2016	2017	Feathers	29.32	66.42	Benthic	13.90	11.88	45.78	-18.48
bird161	F	2015	2016	Feathers				13.95	10.98	46.24	-18.20
bird161	F	2016	2017	Feathers	35.71	76.51	Pelagic	14.20	11.64	46.79	-18.67
bird192	M	2015	2016	Feathers				14.01	11.43	46.17	-17.99
bird193	M	2015	2016	Feathers				12.82	12.07	42.81	-18.08

Table S6.1 Possible yellow-eyed penguin prey species in the subantarctic Auckland Islands. Data are listed alphabetically and sorted by trophic level and commercial fishery status. Benthic location includes benthic and demersal species, which would require benthic foraging to exploit. Commercial species (area SQU6T) data from (Ministry of Primary Industries 2018a, McMillan et al. 2019), and non-commercial species data (grey highlight) from (Francis 1996).

Scientific name	**Common name**	**Trophic level**	**Location**	**Commercial**
Nototodarus sloanii	Arrow squid	Cephalopod	Midwater	Y
Metanephrops challengeri	Scampi	Crustacean	Benthic	Y
Argentina elongata	Silverside	Fish	Benthic	Y
Genypterus blacodes	Ling	Fish	Benthic	Y
Hoplostethus atlanticus	Orange roughy	Fish	Benthic	Y
Macruronus novaezelandiae	Hoki	Fish	Benthic	Y
Pseudocyttus maculatus	Smooth oreo dory	Fish	Benthic	Y
Seriolella caerulea	White warehou	Fish	Benthic	Y
Micromesistius australis	Southern blue whiting	Fish	Midwater	Y
Bovichtus psychrolutes		Fish	Benthic	N
Gastrocymba quadriradiata		Fish	Benthic	N
Notothenia microlepidota		Fish	Benthic	N
Paranotothenia magellanica		Fish	Benthic	N

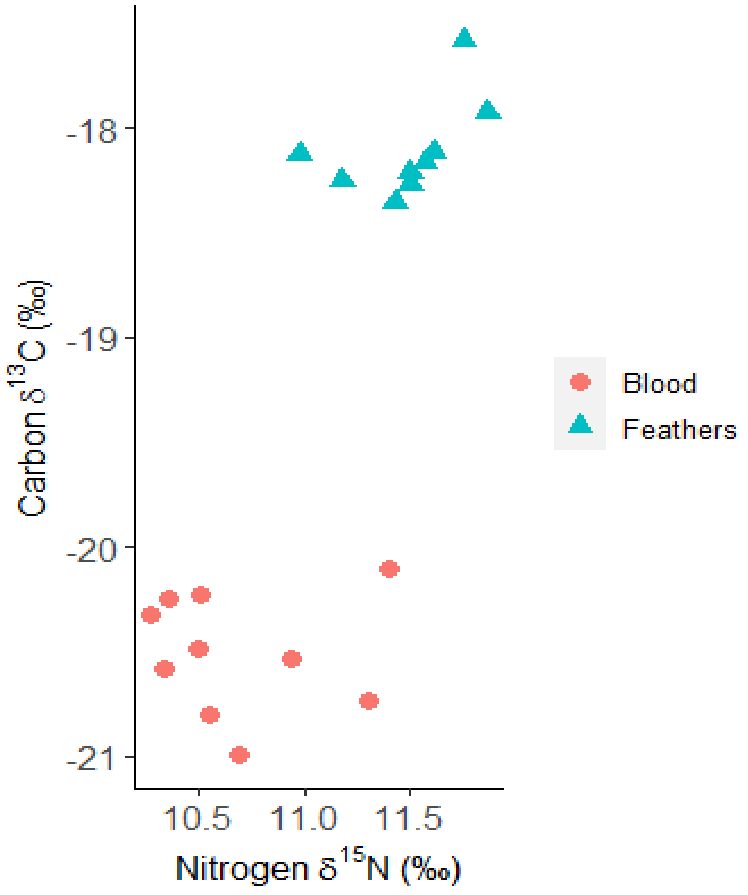


Figure S6.1 Comparison of SIA results between blood and feathers of breeding Yellow eyed-penguins from Enderby Island, in the subantarctic Auckland Islands, New Zealand. Data were compared for nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) in ‰ for selected birds (n = 10 birds). One bird did not have a matching feather sample. Year represents the diet year when samples were formed, which in the case of feathers is annually during moult at the end of the previous breeding season. Blood samples (red) were sampled in the same year they were formed (2015). Feather samples (blue) for the same diet year were collected during the following breeding season (2016). Blood and feather samples were significantly different, meaning results needed to be considered separately.

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