Stable isotope analysis of New Zealand fur seal (*Arctocephalus forsteri*) pup vibrissae used to explore dispersal and isotopic niche widths

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

Master of Science

in

Ecology

at Massey University, Palmerston North, New Zealand

Diana Galbraith

2024

Abstract

The New Zealand fur seal/kekeno (*Arctocephalus forsteri*, NZFS) is a mobile, top predator native to Aotearoa/New Zealand, that was almost extirpated by hunting. Knowledge of life history (demographics), abundance, distribution, and movement patterns is essential to understanding the ecological implications of NZFS dispersal and recolonisation. Intrinsic markers are increasingly being used to identify individuals. Stable isotope analysis (SIA) is used to study diet, trophic level, and movement patterns in many marine mammal species.

Otariid pup vibrissae are metabolically inert, relatively easy to sample, and provide a sequential record of nutrient uptake from gestation onwards. Vibrissae from NZFS pups were collected from seven established breeding colonies around the coast of New Zealand. $\delta^{13}C$ and $\delta^{15}N$ values in the proximal vibrissa were used to calculate isotopic niche widths for each colony. Isotopic separation was not sufficient to identify the colony of origin of pups. Vibrissae from stranded (deceased) NZFS young-of-the-year were collected opportunistically from areas not known to have breeding colonies in Northland and Hawkes Bay, New Zealand. $\delta^{13}C$ and $\delta^{15}N$ values were measured in the proximal vibrissa and in a section two-thirds of the length from the base corresponding to the time that individuals would have been at their natal colony. Values from young-of-the-year overlapped with pups at colonies.

Isotopic niche widths were greater for young-of-the-year than for pups at colonies and greater for samples at the base of the vibrissa than at two-thirds.

Vibrissa growth rates and estimated vibrissa lengths at birth were calculated using linear regression on colony and stranded samples. The mean vibrissa growth rate was 0.21 mm/day for colony samples and 0.24 mm/day for all samples. The estimated vibrissa length at birth was 55 ± 11 mm.

Mean $\delta^{15}N$ decreased by 4.7 ‰ between two-thirds of the vibrissa and the base. The estimated maximum age at weaning was 223 to 247 days; less than any published lactation lengths for the NZFS.

SIA is a practical and economical way to monitor the isotopic niche width of NZFSs, providing indirect information on foraging.

Acknowledgements

Thanks very much to my supervisor, Louise Chilvers, for her enthusiastic support for the project, prompt attention to questions, and endless advice on thesis drafts. This project would not have been possible without her.

I am grateful to the many people who assisted with sample collection, including those who helped hold wriggling pups for sampling. Department of Conservation (DOC) staff in Napier provided samples from stranded individuals, and DOC staff collected vibrissae at the West Coast, South Island colonies. Special thanks to Laura Boren for coordinating sample collection, and collecting many of the vibrissae herself. Thanks to Alasdair Hall for including me in the Kaikōura mark/recapture study. Thanks to Phil Seddon, Yolanda van Heezik, Jo Monks, and the Wildlife Management class of 2023 at Otago University for assistance with collecting vibrissae at Sandymount. Pat Miller provided invaluable information on the locations of stranded fur seals in Northland. Karen Stockin and Odette Howarth generously provided laboratory access.

Staff at GNS Science, Lower Hutt, carried out the stable isotope analysis and provided helpful information.

I am very grateful for funding provided by: Wildbase, Massey University; School of Veterinary Science, Massey University; the Wildlife Society of the New Zealand Veterinary Association; Massey University Master’s Research Scholarship.

This study was carried out under Massey University Animal Ethics Permit AEC 22/60. Iwi consultation was carried out in conjunction with DOC management protocols. Finally, thanks very much to Michael Winch, and Doug and Wendy Galbraith, for their unwavering support.

Table of Contents

Abstract ... i

Acknowledgements ... ii

Tables ... vi

Figures ... viii

Research Objectives ... 1

Chapter 1. Introduction ... 2

1.1 Thesis Rationale ... 2

1.2 New Zealand Fur Seal ... 3

1.2.1 Taxonomy ... 3

1.2.2 Biology/life history ... 3

1.2.3 Threats ... 4

1.2.3.1 Fisheries and Aquaculture ... 4

1.2.3.2 Early Weaning ... 5

1.2.3.3 Climate Change ... 5

1.2.3.4 Highly Pathogenic Avian Influenza (HPAI) ... 6

1.2.4 Annual Cycle and Reproduction ... 6

1.2.5 Distribution ... 7

1.2.6 Population numbers ... 10

1.3 Movement Ecology and Animal Identification ... 12

1.3.1 Population estimates and tracking ... 12

1.3.2 Photo-identification Using Natural Markings ... 12

1.3.3 Identification Using Artificial Marks ... 13

1.3.4 Telemetry ... 14

1.4 DNA ... 15

1.5 Biochemical tracing methods ... 16

1.6 Stable Isotope Analysis ... 17

1.6.1 Explanation of Stable Isotopes ... 18

1.6.2 Examples of SIA Use in Pinnipeds ... 20

1.6.4 Isotopic Niche Widths ... 22

1.6.5 The Use of Pinniped Pups as Proxies ... 22

1.7 Foraging Studies ... 24

1.7.1 Otariid Foraging Studies ... 24

1.7.2 New Zealand Fur Seal Foraging – Time Depth Recorders (TDR) and Satellite Tracking ... 26

1.7.3 Biogeochemical Markers in New Zealand fur seals ... 27

1.7.4 New Zealand Fur Seal Diets ... 28

1.8 Vibrissae – Structure, Function, and Growth Rates 30
1.9 Summary of Stable Isotope Analysis and Foraging Behaviour 31
Thesis Aims and Plan 33
Chapter 2. Stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissae at seven established breeding areas in New Zealand 35
Abstract 35
Research Objectives 36
2.1 Introduction 37
2.1.1 New Zealand fur seal – Life History and Population Numbers 37
2.1.2 Diet 39
2.1.3 Foraging – Time Depth Recorders and Satellite Tracking 39
2.1.4 Stable Isotope Analysis and Foraging Behaviour 40
2.2 Methods 41
2.2.1 Sampling 41
2.2.2 Statistical Analysis 43
2.3 Results 45
2.4 Discussion 59
2.4.1 Diet and Foraging 60
2.4.2 Oceanography and Geography 61
2.4.3 Stable Isotope Values 64
2.4.4 Isotopic Niche Widths 67
2.4.5 Study Constraints and Future Research 69
2.5 Conclusions 71
Chapter 3. The use of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissae to determine the area of origin of stranded individuals in Northland and Hawkes Bay, New Zealand 72
Abstract 72
Research Objectives 74
3.1 Introduction 75
3.2 Methods 78
3.2.1 Vibrissa length calculations 79
3.2.2 Stable Isotope Analysis 80
3.2.3 Statistical Analysis 82
3.3 Results 83
3.3.1 Vibrissa Growth Rates and Estimated Vibrissa Length at Birth 83
3.3.2 Vibrissa widths 90
3.3.3 Stable Isotope Analysis 93

3.3.4 Stable Isotope Bayesian Ellipses in R (SIBER) 98
3.3.5 Estimated Age at Weaning 104
3.4 Discussion 105
3.4.1 Vibrissa Growth Rates and Estimated Vibrissa Length at Birth 105
3.4.2 Stable Isotope Analysis - $\delta^{13}C$ and $\delta^{15}N$ Comparison 109
3.4.3 SIBER – Stable Isotope Bayesian Ellipses in R 110
3.4.4 Stable Isotope Analysis – Time of Weaning 112
3.5 Limitations of the Study and Future Research 116
3.6 Conclusions 118
Chapter 4. General Discussion and Conclusions 119
4.1 Summary of Findings 119
4.2 Ecological Implications of Recolonising New Zealand Fur Seals 120
4.2.1 Diet and Foraging 120
4.2.2 Dispersal 122
4.2.3 Recolonisation 124
4.3 Threats to New Zealand Fur Seals 126
4.3.1 Early Weaning 126
4.3.2 Fisheries Competition and Bycatch 127
4.3.4 Climate Change 128
4.3.5 Highly Pathogenic Avian Influenza 129
4.4 Future Research 130
4.4.1 PIT Tagging – An Alternative to Genetics or SIA 130
4.4.2 Diet and Foraging Studies 131
4.5 Conclusions 132
References 134
Appendix 1 159
Data file for stranded New Zealand fur seal young-of-the-year 159

Tables

Table 1 Monthly distribution of New Zealand fur seal activity by age and sex. Modified from Baird, 2011. 8

Table 2 Latitudes and longitudes of each New Zealand fur seal breeding colony sampled. For Kaikōura North, the coordinates of Ōhau Point were used as the majority of the samples came from there........ 43

Table 3 The number of vibrissae from each location, the number of New Zealand fur seal pups for which sex, body length (cm) and body weight (kg) were recorded, and the number of samples analysed from each location. Samples from Needles Point and Ōhau Point were combined into Kaikōura North........ 45

Table 4 The number of New Zealand fur seal pup vibrissa samples at each location, and the mean and standard deviation for $\delta^{13}C$ and $\delta^{15}N$ values (‰). Kaikōura North combines the results from Needles Point and Ōhau Point........ 46

Table 5 The correlation between $\delta^{13}C$ and $\delta^{15}N$ values in the proximal vibrissa of New Zealand fur seal pups at seven breeding colonies around the coast of New Zealand. Correlation is the Spearman's rank correlation coefficient; n is the number of samples at each location; Strength is the strength of the correlation between $\delta^{13}C$ and $\delta^{15}N$. 51

Table 6 Group metrics for seven fur seal breeding areas in New Zealand. TA is the convex hull area, SEA is the standard ellipse area, and SEA_C is the SEA corrected for sample size effects. Units are ‰^{2}. 56

Table 7 Ellipse areas (‰^{2}) for $\delta^{13}C$ and $\delta^{15}N$ values in vibrissae from stranded New Zealand fur seal pups from three areas around the coast of the North Island, New Zealand. Probability is the probability that the ellipse area at the first site is smaller than that at the second site, expressed as the proportion of posterior draws........ 58

Table 8 Vibrissa growth rates in different species and age classes of otariids........ 77

Table 9 Maximum, minimum and mean estimated vibrissa lengths at birth (EVLB), and vibrissa widths at the base, half, and two-thirds of vibrissa length (mm) for New Zealand fur seal pups at breeding colonies, stranded individuals, and both combined. The stranded individual with the shortest EVLB did not have the normal range of vibrissa lengths, so the next shortest EVLB was used for the minimum (*). The combined width results for the two-thirds vibrissa include the base samples from the breeding colonies and the two-thirds samples from the stranded individuals (^). 87

Table 10 Number of vibrissa samples, means and standard deviations of δ^{13}C and δ^{15}N from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, North Island, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae were sampled at the base and at two-thirds of the length. 94

Table 11 Group metrics for δ^{13}C and δ^{15}N values in vibrissae from New Zealand fur seal pups at seven breeding colonies and from stranded young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Stranded individuals were sampled at two-thirds of the vibrissa length. TA is the convex hull area, SEA is the standard ellipse area, and SEA_C is the SEA corrected for sample size effects. Units are ‰^{2}. 99

Table 12 Group metrics for δ^{13}C and δ^{15}N values in vibrissae from stranded New Zealand fur seal young-of-the-year from locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. TA is the convex hull area, SEA is the standard ellipse area, and SEAC is the SEA corrected for sample size effects. Units are ‰^{2}. 100

Table 13 Ellipse areas (in ‰^{2}) for δ^{13}C and δ^{15}N values in vibrissae from New Zealand fur seal pups from seven breeding colonies around New Zealand, and stranded young-of-the-year from locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae from stranded individuals were sampled at two-thirds of the length to make them comparable to samples taken at breeding colonies. Probability is the probability that the ellipse area at the first site is smaller than that at the second site, expressed as the proportion of posterior draws. 103

Table 14 Ellipse areas (in ‰^{2}) for δ^{13}C and δ^{15}N values in vibrissae from stranded New Zealand fur seal young-of-the-year from locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Probability is the probability that the ellipse area at the first site is smaller than that at the second site, expressed as the proportion of posterior draws. 104

Table 15 Summary of New Zealand fur seal pup weaning ages and dates at colonies in New Zealand and Australia. An * means the weaning age was approximate. 114

Figures

Figure 1 Locations within Aotearoa/New Zealand mentioned in the thesis. 10

Figure 2 The locations of the seven established fur seal breeding areas from which New Zealand fur seal pup vibrissae were sampled, in New Zealand. 42

Figure 3 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in the proximal vibrissa of New Zealand fur seal pups at seven breeding colonies around the coast of New Zealand. Colours represent breeding colonies. 46

Figure 4 Boxplots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (‰) at seven established breeding colonies in New Zealand, showing medians, upper and lower quartiles and ranges. Colonies are ordered clockwise from southwest to southeast. Black dots are outliers... 47

Figure 5 Boxplots of New Zealand fur seal pup vibrissa $\delta^{15}N$ (‰) at seven established breeding colonies in New Zealand, showing medians, upper and lower quartiles and ranges. Colonies are ordered clockwise from southwest to southeast. Black dots are outliers... 48

Figure 6 Scatter plots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (a) and $\delta^{15}N$ (b) values (‰) against latitude. Linear model regression line shown in blue and 95 % confidence intervals in grey shading. 49

Figure 7 Scatter plots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (a) and $\delta^{15}N$ values (b) against longitude. Linear model regression line shown in blue 95 % confidence intervals in grey shading. .. 50

Figure 8 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in the proximal vibrissa of New Zealand fur seal pups at seven established breeding colonies in New Zealand. Correlation line is in blue, and 95 % confidence intervals in grey shading. 51

Figure 9 The proportion of New Zealand fur seal vibrissa samples in each of two clusters at seven breeding areas based on scaled $\delta^{13}C$ and $\delta^{15}N$ values. Cluster one is in light grey and cluster two is in dark grey. Colonies are ordered clockwise from southwest to southeast. 52

Figure 10 $\delta^{13}C$ and $\delta^{15}N$ values of vibrissa samples from New Zealand fur seals. Colours are the locations of the colonies and shape is the cluster number. 53

Figure 11 Scaled $\delta^{13}C$ and $\delta^{15}N$ results for New Zealand fur seal vibrissa samples allocated to two groups. Colour is cluster number and individual points are sample numbers. 53

Figure 12 The proportion of New Zealand fur seal vibrissa samples in each of three clusters at seven breeding areas based on scaled $\delta^{13}C$ and $\delta^{15}N$ values. Cluster one is light grey, cluster two is middle grey and cluster three is dark grey. Colonies are ordered clockwise from southwest to southeast. . 54

Figure 13 $\delta^{13}C$ and $\delta^{15}N$ values of vibrissa samples from New Zealand fur seals. Colours are the locations of the colonies and shape is the cluster number. 55

Figure 14 Scaled $\delta^{13}C$ and $\delta^{15}N$ results for New Zealand fur seal vibrissa samples allocated to three groups. Colour is cluster number and individual points are sample numbers. 55

Figure 15 Bayesian ellipses at 95 % confidence intervals for $\delta^{13}C$ and $\delta^{15}N$ (‰) in vibrissa samples taken from New Zealand fur seal pups at seven established breeding colonies around New Zealand. Each colour represents a different colony. 56

Figure 16 Standard ellipse areas (‰^{2}) of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissa sampled at seven established breeding colonies in New Zealand. Black dot represents the mode and red x represents the SEA_C (standard ellipse area corrected for sample size). Box edges from dark to light are 50 %, 75 % and 95 % CI. Colonies are ordered clockwise from southwest to southeast. 57

Figure 17 The general areas from which vibrissae were collected from stranded New Zealand fur seals in Northland and in Napier, Hawkes Bay, New Zealand. 78

Figure 18 Typical vibrissa from a pup at a colony (a), and typical plucked vibrissa from a stranded young-of-the-year (b). Vibrissae from stranded individuals were sampled at the base (1), half (2), and two-thirds (3) of the length. The base sample was taken 10 mm from the proximal end of the vibrissae to avoid contamination with neural tissue. The sample taken from half the length of the vibrissa was not analysed but kept in reserve. 81

Figure 19 Length of the longest vibrissa (mm) from New Zealand fur seal pups at seven New Zealand breeding colonies, plotted against the number of days from the assumed median pupping date. Linear model regression line is in blue and grey shading represents 95 % confidence intervals. Colour represents the breeding colony. 84

Figure 20 Length of the longest vibrissa (mm) from New Zealand fur seal pups at seven New Zealand breeding colonies, and from stranded young-of-the-year from the east and west coasts of Northland, North Island, and from Napier, Hawkes Bay, North Island, plotted against the number of days from the assumed median pupping date of 16 December, 2022. Linear model regression line is in blue and grey shading represents 95 % confidence intervals. Colour represents the breeding colony or the location of the stranded young-of-the-year. 85

Figure 21 Length of the longest vibrissa (mm) from New Zealand fur seal pups at seven New Zealand breeding colonies, and from stranded young-of-the-year from the east and west coasts of Northland, North Island, and from Napier, Hawkes Bay, North Island, plotted against the number of days from the assumed median pupping date of 16 December, 2022. Regression line is in blue, and grey shading represents 95 % confidence intervals. Peach colour represents pups and turquoise represents stranded young-of-the-year. 86

Figure 22 Length of the longest vibrissa (mm) from stranded New Zealand fur seal young-of-the-year from the east and west coasts of Northland, North Island, and from Napier, Hawkes Bay, North Island, plotted against the number of days from the assumed median pupping date of 16 December, 2022. Regression line is in blue, and grey shading represents 95 % confidence intervals. Colour represents the location. 86

Figure 23 Estimated vibrissa length at birth (mm) for New Zealand fur seal pups from seven breeding colonies, and stranded young-of-the-year from the east and west coasts of Northland, and from Napier, Hawkes Bay, New Zealand. Boxplots show median values and first and third quartiles. Colours are locations. Black dots are outliers. 89

Figure 24 Estimated vibrissa length at birth (mm) for New Zealand fur seal pups from seven breeding colonies, and stranded young-of-the-year from the east and west coasts of Northland, and from Napier, Hawkes Bay, North Island, New Zealand, plotted against the number of days between the assumed median pupping date and date of vibrissa collection. Linear model regression line is in blue and grey shading represents 95 % confidence intervals. 90

Figure 25 Width (mm) of the base of vibrissae of New Zealand fur seal pups sampled at six breeding colonies, and width at two-thirds of the length from the base in stranded New Zealand fur seal young-of-the-year on the east and west coasts of Northland, North Island, and Napier, Hawkes Bay, North Island, New Zealand. Breeding colonies are arranged in order of collection date. Boxplot shows median, and first and third quartiles. Black dots are outliers. 91

Figure 26 Width (mm) of the base of vibrissae of New Zealand fur seal pups sampled at six breeding colonies, and width at two-thirds of the length from the base in stranded New Zealand fur seals on the east and west coasts of Northland, North Island, and Napier, Hawkes Bay, North Island. As vibrissae are oval in cross-section, the width of each vibrissa is calculated by adding the maximum and minimum widths, at the same level, and dividing by two. The x axis is the number of days from the assumed median pupping date of 16 December, 2022. Linear model regression line is in blue and grey shading represents 95 % confidence intervals. 92

Figure 27 Carbon to nitrogen ratios (means and standard error bars) in vibrissa samples from New Zealand fur seal pups at seven breeding colonies and from stranded New Zealand fur seal young-of-the-year on the east and west coasts of Northland, North Island, and from Napier, North Island, New Zealand. 94

Figure 28 δ^{13}C values in the base of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles. Black dots are outliers. 95

Figure 29 δ^{13}C values at two-thirds the length of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles. 95

Figure 30 $\delta^{15}N$ values in the base of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles. Black dots are outliers. 96

Figure 31 $\delta^{15}N$ values at two-thirds the length of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles. Black dots are outliers. 96

Figure 32 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in vibrissae from stranded New Zealand fur seals at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae were sampled at two-thirds of the length, and at the base. The shape is the location and the colour is the vibrissa section............ 97

Figure 33 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in vibrissae from stranded New Zealand fur seals at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae were sampled at two-thirds of the length, and at the base. The colour is the location and the shape is the vibrissa section. Ellipse sizes are 95 % CI............ 99

Figure 34 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in vibrissae from New Zealand fur seal pups at seven breeding colonies in New Zealand, and stranded fur seals at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Pup vibrissae were sampled at the base, and vibrissae from stranded individuals were sampled at two-thirds of the length. The colour is the location and the shape is the vibrissa section. Bayesian ellipse sizes are 95 % CI........ 100

Figure 35 Isotopic niche space shown by 95 % CI bivariate ellipses (SEA_B) of $\delta^{13}C$ and $\delta^{15}N$ values in samples from the base and two-thirds of the length of the longest vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Black dot represents the mode, and red x represents the maximum likelihood estimated SEA_C (standard ellipse area corrected for sample size). Box edges from dark to light are 50 %, 75 % and 95 % CI. Units are $‰^2$............ 101

Figure 36 Isotopic niche space shown by 95 % CI bivariate ellipses (SEA_B) of $\delta^{13}C$ and $\delta^{15}N$ values in samples from the base of the longest vibrissa from New Zealand fur seal pups sampled at seven breeding colonies around New Zealand, and from two-thirds of the length of the longest vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Black dot represents the mode, and red x represents the maximum likelihood estimated SEA_C (standard ellipse area corrected for sample size). Box edges from dark to light are 50 %, 75 % and 95 % CI. Units are $‰^2$. 102

Research Objectives

- Create a database of $\delta^{13}C$ and $\delta^{15}N$ values in the proximal vibrissa section of New Zealand fur seal pups at representative breeding colonies in New Zealand.
- Summarise the known foraging characteristics of New Zealand fur seals and the environmental conditions that might explain the $\delta^{13}C$ and $\delta^{15}N$ values found in pup vibrissae.
- Determine the origin of juvenile New Zealand fur seals stranded in some of the northern parts of the North Island, New Zealand, by comparing their $\delta^{13}C$ and $\delta^{15}N$ values to those of New Zealand fur seal pups from known breeding colonies. All the major New Zealand fur seal breeding colonies are in the South Island except Cape Palliser on the south coast of the North Island, with no known breeding in the North Island north of 37.9721°S on the west coast and 37.8558°S on the east coast.
- Calculate vibrissa growth rates and estimate the vibrissa length at birth for New Zealand fur seals.
- Calculate isotopic niche widths for New Zealand fur seal pups at colonies and for groups of stranded New Zealand fur seal young-of-the-year.
- Clarify weaning times for stranded New Zealand fur seal young-of-the-year and compare these to lactation lengths in the literature.

Chapter 1. Introduction

1.1 Thesis Rationale

Across the world, expanding populations of fur seals appear to be affecting existing species and ecosystems (Haussmann et al., 2013; Makhado et al., 2006; Smith, 1988). Knowledge of New Zealand fur seal/kekeno (*Arctocephalus forsteri*, Lesson, 1828, hereafter 'NZFS') distribution, abundance, foraging behaviour, and dispersal is currently limited (Boren, 2010). To understand the effects of NZFSs on other species, and to assess the anthropogenic risks to NZFSs, a better understanding of foraging and movement ecology is required (Baird, 2011; Carter et al., 2016; Lalas & Bradshaw, 2001).

The existing methods of tracking individuals using external markers or tracking devices have limitations (Bradshaw et al., 2000; Carter et al., 2016; Hobbs & Russell, 1979; Hobson, 1999; Osterrieder et al., 2017; Ramos & González-Solís, 2012; Shaughnessy, 1994; Tomkiewicz et al., 2010; Wilson & McMahon, 2006). Intrinsic biogeochemical markers, such as stable isotopes, can be used to trace foraging ecology and migration (Ramos & González-Solís, 2012). Isotopic niche size can be described statistically and provides ecologically relevant information at an individual, population and community level (Jackson et al., 2011).

In the absence of any known affordable or logistically possible ways to trace NZFS movements around New Zealand, this study investigates the use of stable isotope analysis (SIA) of vibrissae to determine the origin of stranded (deceased) NZFS young-of-the-year (hereafter 'YOY'). δ^{13}C and δ^{15}N values in vibrissae from stranded NZFS YOY are compared to a database of vibrissa samples collected from multiple established breeding colonies in New Zealand. Isotopic niche widths are compared among colonies and stranded groups, and ecologically relevant information on foraging and pup weaning times is provided.

The following abbreviations are used throughout the thesis:

NZFS	New Zealand fur seal
SIA	Stable isotope analysis
YOY	Young-of-the-year
EVLB	Estimated vibrissa length at birth
SEA	Standard ellipse area

1.2 New Zealand Fur Seal

1.2.1 Taxonomy

The NZFS is in the family *Otariidae* (eared seals) which includes all the fur seals and sea lions. In Australia, the species was generally known as the New Zealand fur seal until the vernacular name was changed to the long-nosed fur seal (Shaughnessy & Goldsworthy, 2015). In this thesis, the species will be referred to as the NZFS throughout its range, consistent with its common name in the IUCN listing (Chilvers & Goldsworthy, 2015).

Molecular studies support monophyly (one common ancestor) of *Otariidae* (Arnason et al., 2006; Boessenecker & Churchill, 2015; Churchill et al., 2014; Higdon et al., 2007; Yonezawa et al., 2009), however, relationships within the *Otariidae* remain unresolved (Berta et al., 2018). Early morphological studies suggested there were two subfamilies: *Arctocephalinae* (fur seals) which have smaller bodies and a dense furry pelage, and *Otariinae* (sea lions) which have larger bodies and rely on blubber for insulation (Berta & Demere, 1986). Conversely, combined morphologic and molecular studies identify the northern fur seal (*Callorhinus ursinus*) as the earliest diverging otariid, with the northern sea lions (*Zalophus* and *Eumetopias*) being a sister clade to the southern otariids (Berta et al., 2018).

The genus *Arctocephalus* is thought to be paraphyletic (Berta & Churchill, 2012), and it has been suggested that the genus should be restricted to *Arctocephalus pusillus,* with the genus *Arctophoca* to include *A. australis, A. galapagoensis, A. tropicalis, A. gazella* and *A. philippi* (Berta & Churchill, 2012). Conversely, some molecular data suggest a sister-taxon relationship between *A. tropicalis* and *A. pusillus* (Wynen et al., 2001; Yonezawa et al., 2009), in which case *A. tropicalis* would be included in *Arctocephalus* (Berta & Churchill, 2012). Berta and Churchill (2012) suggested that the NZFS should be reclassified as *Arctophoca australis forsteri*. Conversely, a study on mitochondrial DNA found two deeply divergent NZFS seal clades, with the degree of sequence divergence approaching that between closely related species (Lento et al., 1997). Until there is a consensus on the relationships between members of the current *Arctocephalus* genus, any taxonomic changes are premature (Nyakatura & Bininda-Emonds, 2012).

1.2.2 Biology/life history

The NZFS is native to Aotearoa/New Zealand, inhabiting the rocky coast of New Zealand and the sub-Antarctic islands, mostly south of 40°S (Crawley & Wilson, 1976), although its range is expanding (Lalas & Bradshaw, 2001). Populations also occur in southern and western Australia (Baird, 2011), and it is listed as Least Concern on the IUCN Red List (Chilvers & Goldsworthy, 2015) and Incr/SO (increasing, secure overseas) in the New Zealand Threat Classification Series (Baker et al., 2019). Males weigh up to 154 kg, while females weigh up to 50 kg (Mattlin, 1978a). In a study on diving behaviour in South Australia, the mean length of males was 170.2 ± 6.8 cm and the mean weight was 106.4 ± 18.4 kg, while the mean length of females was 135 ± 4.8 cm and the mean weight was 42.4 ± 5.7 kg (Page et al., 2005b). Pups are approximately 55 cm long and 3.5 kg at birth (Crawley & Wilson, 1976). Males reach sexual maturity at between five and nine years old, and females between four and six years old (Dickie & Dawson, 2003), however, males are generally not socially mature enough to hold a territory until at least 8-10 years of age (Mattlin, 1978a; McKenzie et al., 2007).

1.2.3 Threats

Anthropogenic threats to NZFSs include fisheries (Abraham et al., 2021; Abraham & Berkenbusch, 2017; Hamer & Goldsworthy, 2006; Lalas & Bradshaw, 2001; Thompson et al., 2011), entanglement in man-made debris (Boren, Morrissey, et al., 2006), disturbance by vessels (Cowling et al., 2015), tourism (Boren et al., 2002; Cowling, 2013), and climate change (Roberts & Hendriks, 2022). Early weaning can adversely affect pinnipeds (Beauplet et al., 2005; Davis, 2014; Goldsworthy, 2006; Ono et al., 1987), and might contribute to increased mortality in NZFS YOY.

1.2.3.1 Fisheries and Aquaculture

An estimated 10,824 (95 % c.i. 7737 – 15201) NZFSs were captured in New Zealand trawl fisheries from 2002/03 to 2017/18, and a further 1752 (95 % c.i. 1195 – 2466) were estimated to have been captured in surface long-line fisheries over the same period (Abraham et al., 2021). Fur seal captures peaked in 2004/05 at 1487 (95 % c.i. 964 – 2370), while in the 2017/18 season an estimated 324 NZFSs (95 % c.i. 233 – 462) were caught in the trawl fishery, with 190 (95 % c.i. 128 – 283) of those in the hoki (*Macruronus novaezelandiae*) fishery (Abraham et al., 2021). While 94.7 % of NZFSs caught on surface longlines were released alive, 88.3 % of observed trawl fishery captures died (Abraham & Berkenbusch, 2017). A particular concern is the estimated 2684 NZFSs killed in the Cook Strait hoki fishery from 2002 – 2020 (Pavanato et al., 2023). To quantify the bycatch from different colonies it is necessary to know which colony the bycaught individuals came from (Robertson & Gemmell, 2005).

Australian fur seals (*Arctocephalus pusillus doriferus*) are known to damage nets and prey on farmed fish (Pemberton et al., 1991). There was an inverse square relationship between distance from a hauling ground and the frequency of fur seal predation on fish farms in Australia (Pemberton & Shaughnessy, 1993). An assessment of the risks to marine mammals from aquaculture in Northland, New Zealand, noted that NZFSs attempting to predate farmed finfish can become entangled, and that the expansion of seal populations in Northland increases the potential for interactions with fish farms (Baker, 2005).

1.2.3.2 Early Weaning

Concerns were raised about NZFS mortalities in the Hauraki Gulf/Coromandel area (east coast, northern North Island, New Zealand), in 2021 (Lee, 2022), with stranded YOY being found as early as 15 August (S. Lee, unpublished data). The median lactation length for the NZFS is considered to be 294 ± 6 days (Boren 2005), however, 15 August is only 242 days after the assumed median pupping date of 16 December (Boren, Muller, et al., 2006). There are no known NZFS breeding colonies in the Hauraki Gulf/Coromandel area (Galbraith, 2022).

Mortality rates are high during the period immediately following weaning in many mammals (Reiter et al., 1978). In subantarctic fur seals (*Arctocephalus tropicalis*), mortality was higher in the post-weaning than pre-weaning period, and was significantly influenced by environmental conditions in the first six months after weaning (Beauplet et al., 2005). Higher pre-weaning growth rates improved survival after weaning (Beauplet et al., 2005). Pinnipeds that are weaned earlier can be physiologically different from those weaned later (Davis, 2014), and age at weaning has been shown to affect growth in otariids (Goldsworthy, 2006).

1.2.3.3 Climate Change

Worldwide, climate change is expected to be the greatest threat to pinnipeds (Kovacs et al., 2012). Historically, fur seal species at higher latitudes were subject to seasonal changes that were larger but more predictable, while in tropical zones seasonal changes were smaller but less predictable, with temperate latitudes thought to be intermediate between the extremes (Gentry & Kooyman, 1986). The NZFS inhabits temperate latitudes (Crawley & Wilson, 1976). Anthropogenic climate change is having a range of effects on the New Zealand marine environment, with extreme weather events predicted to increase in frequency and severity (Keegan et al., 2022).

In a study on subantarctic fur seals over seven years, post-weaning survival was negatively correlated with sea surface temperature anomalies (SSTA) in the first six months after weaning (Beauplet et al., 2005). Guadalupe fur seals (*Arctocephalus townsendi*) grew more slowly and had lower survival rates at higher sea temperatures (Gálvez et al., 2020). California sea lion pups (*Zalophus californianus*) had lower growth rates and higher mortality due to lower food availability in El Niño conditions (Ono et al., 1987), and a decline in California sea lion populations was correlated with increased sea surface temperatures (Adame et al., 2020).

In New Zealand, rising sea levels, ocean warming, and ocean acidification will have the greatest impact on the marine environment (Keegan et al., 2022). For the NZFS, rising sea levels are likely to affect the availability of suitable habitat for breeding and hauling out (Roberts & Hendriks, 2022). Primary productivity is likely to decline around the North Island and the west coast of the South Island, with upwellings decreasing in strength (Roberts & Hendriks, 2022). An unpublished study by Best et al., (1998, cited in Roberts and Neale, 2016) found a strong negative correlation between sea surface temperature and pup numbers, and the mass of individual pups. The abundances of some fish species in New Zealand have been correlated with climate, however, relationships are inconsistent and incompletely understood (Dunn et al., 2009).

1.2.3.4 Highly Pathogenic Avian Influenza (HPAI)

HPAI (H5N1 strain) is spreading around the globe, causing mass mortalities in many species, including domestic and wild birds (Chen et al., 2022), and pinnipeds (Leguia et al., 2023; Uhart et al., 2024; Ulloa et al., 2023). HPAI poses a serious risk to New Zealand's native and introduced species (Gartrell et al., 2024), including the NZFS. A large proportion of the fauna on New Zealand's off-shore and subantarctic islands is endemic and/or threatened (Towns et al., 2012), and the entry of HPAI might have a serious impact on populations (Gartrell et al., 2024).

1.2.4 Annual Cycle and Reproduction

Otariids have evolved to breed in colonies, to balance fitness costs and benefits (Cassini, 1999, 2000). NZFS breeding colonies are broadly defined as areas where fur seals breed and give birth (Baird, 2011), however, Bradshaw et al., (1999) designated breeding colonies as locations where more than 10 pups were born each year, and non-breeding colonies as sites with fewer than 10 pups. The Ministry of Fisheries defined a NZFS breeding colony as a location where at least 10 pups are born each year in at least three consecutive years and where offspring return to the same site each year (Baird, 2011). In lieu of regular monitoring, the NABIS distribution (www.nabis.govt.nz) generally just uses the best available information to define breeding colonies (Baird, 2011). Breeding colonies have also been described as aggregations of pups within two kilometres of each other, with clusters of individuals within a colony termed 'subcolonies' (Shaughnessy et al., 1994, 2015).

The NZFS reproductive behavioural strategy is classed as resource-defence polygyny (Carey, 1991b), with adult males occupying territories from mid-October, although permanent territories are not established until the second half of November (Stirling, 1971b). Females come ashore around two (Miller, 1975b) to five (Crawley & Wilson, 1976) days before parturition and give birth between late November and mid-January, peaking in mid-December (Crawley & Wilson, 1976). The generally adopted median pupping date for NZFs in New Zealand is 16 December (Boren, Muller, et al., 2006), with 90 % of pups born within a six-week period (Mattlin, 1978a).

Females are considered to be philopatric (Baird, 2011; Boren, 2005) and do show a high level of fidelity to breeding colonies (Stirling, 1971a). However, genetic studies on NZFSs (Dussex et al., 2016; Robertson & Gemmell, 2005), suggest that the extreme philopatry shown in other fur seal species (Hoffman & Forcada, 2012), may not apply to the NZFS. In New Zealand, new colonies cluster around existing ones, implying philopatry, although this has not been quantified in NZFSs (Bradshaw, 1999; Miller, 1971), and they can disperse over long distances (Boren, Muller, et al., 2006). NZFS pups were tagged in southern Australia in eight consecutive breeding seasons, with the furthest resighting being a juvenile, 1700 km away in Sydney, NSW (Shaughnessy & Goldsworthy, 2020). There has been no evidence of tagged males holding territories outside their natal colony (Shaughnessy & Goldsworthy, 2020). While there were three records of females over four years of age in colonies other than their natal one, none was seen with a pup (Shaughnessy & Goldsworthy, 2020).

Females give birth to one pup, remain with it until they come into oestrus approximately eight days later, and generally mate with the territorial male (Crawley & Wilson, 1976). Implantation of the blastocyst is delayed (Miller, 1975b), and the total gestation period is assumed to be 11 – 12 months, consistent with other *Arctocephalus* species which have been shown to have an embryonic diapause of 3 – 5 months (Atkinson, 1997). Females forage within 200 km of the colony (Smith, 2005) while returning to suckle their pups every few days (Harcourt et al., 2002). Lactation ranges from 238-365 days (Boren, 2005; Goldsworthy, 2006), with a quoted median of 294 ± 6 days (Boren, 2005). Pups can be weaned between late July and early October (Smith, 2005), but are generally weaned in September or October (Goldsworthy, 2006; Harcourt, 2001). At Kaikōura, median weaning age for pups was 325 days in 2003 and 343 days in 2004 (Boren, 2005). In Otago, pups mostly stayed in breeding colonies until November, although some dispersed to adjacent hauling grounds between February and June (Bradshaw et al., 1999).

1.2.5 Distribution

NZFSs may have numbered between 1.5 – 2 million prior to human settlement (Richards, 1994), and they were believed to have inhabited all suitable areas of rocky coastline around New Zealand's North, South, and Stewart Islands (Smith, 1989) and all coastal and subantarctic islands (Falla, 1965). There is archaeological evidence of prehistoric breeding colonies in Foveaux Strait, South Otago, the Otago Peninsula, Cook Strait, the Coromandel Peninsula and northern Northland (Smith, 1989) (Figure 1). Subsistence hunting by early Māori reduced the breeding range to the south and west coasts of the South Island, with seasonal, non-breeding colonies in Cook Strait and on the east coast of the South

Island (Smith, 1989). The species was hunted almost to local extinction (Crawley & Wilson, 1976) by commercial sealing, which started in 1791 or 1792 and had virtually finished by the early 1840s (Smith, 2002). The peak harvest lasted for just over 10 years (Falla, 1962), with an estimated 329,000 NZFSs killed around the New Zealand mainland and adjacent islands (Ling, 1999). Populations have gradually increased (e.g., Falla, 1962; Lalas & Bradshaw, 2001) since the species was first given some legal protection in 1875 (Crawley & Wilson, 1976). It is now fully protected under the Marine Mammals Act 1978 (Baird, 2011).

NZFSs occupy breeding colonies and hauling grounds throughout the year, but the age and sex classes present vary seasonally (Crawley & Wilson, 1976) (Table 1). The modern NZFS non-breeding range is from the Three Kings Islands (34.15°S ’S, 172.14°E) to Macquarie Island (54.62°S, 158.85°E), however, distribution is discontinuous and north of the breeding range NZFSs are only seen in any numbers in winter and spring (Crawley & Wilson, 1976). Lactating females repeatedly return to the colony to provision their pups until weaning, however, many territorial bulls and subadult males move north or south for the winter (Crawley & Wilson, 1976). During the breeding season, non-breeding animals cluster at hauling grounds near the colonies (Smith, 2005).

Table 1 Monthly distribution of New Zealand fur seal activity by age and sex. Modified from Baird, 2011.

New Zealand fur seals	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Breeding Males	At breeding colony				Dispersed at sea or at haulouts							
Breeding Females		At breeding colony			At breeding colony and at sea foraging							At sea
Pups			At breeding colony									At sea
Non-breeders (incl. Yearlings)	Dispersed at sea, at haulouts, or breeding colony periphery											

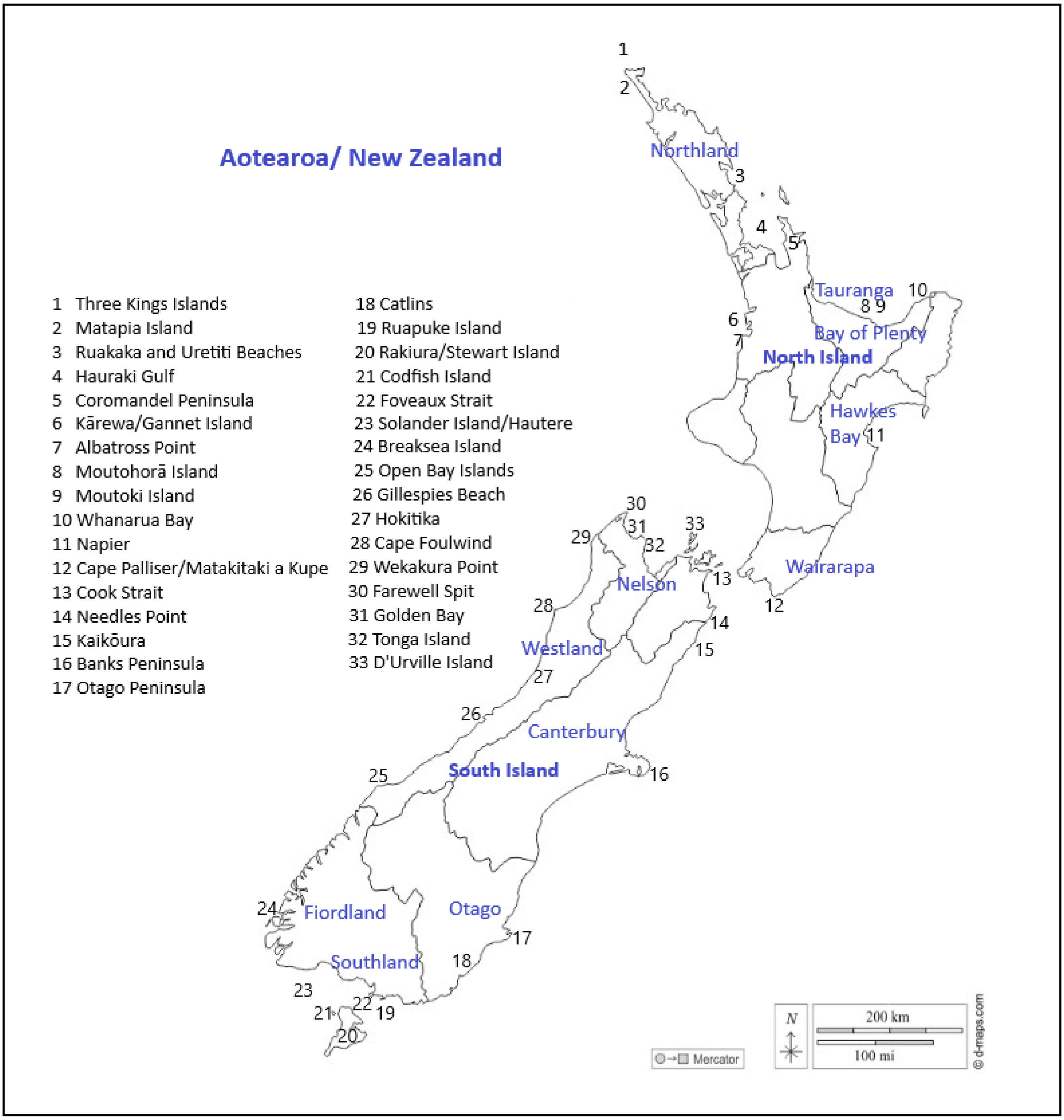
A comprehensive survey in the early 1970s showed that breeding colonies on the New Zealand mainland were present only in Westland, Fiordland, Solander Island, Stewart Island and Ruapuke Island (Wilson, 1981). The breeding range has now expanded around the South Island (Boren, 2005; Lalas & Harcourt, 1995; Lalas & Murphy, 1998; Taylor et al., 1995), and to Cape Palliser in the southern North Island (Dix, 1993).

The northernmost documented west coast breeding colony is at Kārewa/Gannet Island (2 ha, 37.9721°S, 174.5659°E) in the Waikato region (Bouma et al., 2008). Albatross Point (38.1073°S, 174.6841°E) is currently shown as a breeding colony (www.nabis.govt.nz), but Bouma et al., (2008) noted that although Albatross Point and nearby Tirua Point had some suitable breeding habitat there was very little protection against heavy seas.

Moutohorā Island (1.4 km^2, 37.8558°S, 176.9738°E) near Whakatāne is the closest known breeding colony to the Hauraki Gulf (Cowling, 2013). Pup production is thought to have increased there (M. Sothieson, personal communication, 1 April 2022), since at least eight pups were born there in 2011/2012 (Cowling, 2013). NZFSs are present all year round, with up to 140 non-breeding NZFSs of mixed ages counted around Moutohorā Island (Department of Conservation, 2016). On Moutoki Island (0.8 ha, 37.8317°S, 176.8835°E) there were 15-20 adults and two pups seen in January 2020, and other possible but unconfirmed breeding locations include Whanarua Bay (37.6738°S, 177.7918°E) (M. Sothieson, personal communication, 1 April 2022). Some individuals sighted at Moutohorā Island were tagged in Kaikōura and the Nelson region (Department of Conservation, 2016). There was no known NZFS breeding in the Tauranga region (K. McCarthy, personal communication, 23 March 2022).

In Northland, Matapia Island (1.3 ha, 34.6060°S, 172.7986°E), off Ninety Mile Beach, has been classed as a hauling ground (www.nabis.govt.nz). Sixty NZFSs, of all age classes except pups, were counted there in the summer of 1996/97 (Parrish & Anderson, 1999). There is no recent information on fur seal distribution on Matapia Island (P. Mills, personal communication, 7 March 2022), and no known evidence of breeding (K. Matthews, personal communication, 8 December 2023).

Figure 1 Locations within Aotearoa/New Zealand mentioned in the thesis.



1.2.6 Population numbers

Wilson (1981) estimated the total New Zealand, Chatham Islands, and subantarctic population of NZFSs to be 30,000 – 50,000. Lalas and Bradshaw (2001) summarised the other previously published NZFS population estimates and concluded that they were not statistically robust as they did not include values for accuracy and precision. In 1990, a population of 'nearer 100,000' was suggested (Taylor, 1990), with no confidence limits given. The combined population of NZFSs in Australia and

New Zealand was thought to be approximately 200,000, although there were no complete data to determine a total population estimate (Chilvers & Goldsworthy, 2015). The latest estimate for the total New Zealand population, based on pup production estimates is 129,773 – 166,704, and on modelling is 146,094 – 229,179 (A. Hall, unpublished data).

Pup counts are the best way to estimate population size, as pups are the only age-group that is confined to land and readily recognisable (Shaughnessy et al., 1994). Annual pup counts can be used to estimate the rate of population change, although they can be subject to bias if there is density-dependent pre- or post-census mortality (Berkson & DeMaster, 1985). Estimating population numbers from pup counts is difficult (Lalas & Bradshaw, 2001). Multipliers of 4.76 (Goldsworthy & Page, 2007) and 4.9 (Taylor, 1982) have been used to estimate total population from pup counts, however, the demographic information needed to calculate a multiplier will differ between colonies and is unknown for NZFSs generally (Baird, 2011; Chilvers, 2021c).

The colonies at Wekakura Point, Cape Foulwind, and Open Bay Islands, West Coast, South Island, have been monitored annually or biennially since 1990/1991, and were previously thought to produce approximately a third of all pups on the west coast of the South Island (Roberts & Neale, 2016). At all three colonies pup production peaked in the mid-1990s: Open Bay Islands (1,432 pups in 1995), Cape Foulwind (484 pups in 1993), and Wekakura Point (1,097 pups in 1996) (Roberts & Neale, 2016). Mark/recapture pup production estimates in 2022-23 were 638, 93 and 143, respectively (Department of Conservation, unpublished data), constituting declines from peak production of 55 % at Open Bay Islands, 81 % at Cape Foulwind, and 87 % at Wekakura Point.

Other colonies that have had population surveys include Nelson/Marlborough (Taylor et al., 1995), Kaikōura (Boren, 2005; Boren, Muller, et al., 2006), Banks Peninsula (Emami-Khoyi, Hartley, Paterson, Paterson, et al., 2016), Otago Peninsula (Bradshaw, 1999; Lalas & Harcourt, 1995), the Catlins (Lalas & Murphy, 1998), Rakiura/Stewart Island (Watson et al., 2015), Fiordland (Chilvers, 2021c), Kaikōura (Hall et al., 2024), and Cape Palliser (Pavanato et al., 2023; L. Boren, personal communication, 11 September 2023).

In the greater Kaikōura area in 2022/23, estimated pup production was 5703 – 5781, with a total population estimate of 20,944 – 27,518, using a multiplier of 4.76 (Hall et al., 2024). At Ōhau Point, Kaikōura, pup production was 2401 ± 99 in 2022/23 (Hall et al., 2024), but decreased to approximately 1,182 in 2023/24 (J. Weir, unpublished data). Cape Palliser was surveyed in March 2022, with 405 adults/sub-adults and 335 pups seen on direct counts (Pavanato et al., 2023). In February/March 2023, pup production at Cape Palliser was estimated at approximately 600 pups, based on direct counts (L. Boren, personal communication, 11 September 2023). From Ward Beach (41.8451°S, 174.1857°E) to Needles Point (41.9085°S, 174.1146°E), 316 adults/juveniles and 36 pups were counted in September 2022 and the area was thought to be a breeding colony (Pavanato et al., 2023), however, in February 2023 only four pups were found (L Boren, personal communication, 18 February 2023).

Pup production on the Otago Peninsula increased from 20 – 30 pups in two colonies in 1982/83 to at least 673 at 11 colonies in 1993/94 (Lalas & Harcourt, 1995), and was expected to plateau at around 2550 pups for the whole of Otago by about 2010 (Lalas, 2008). Conversely, annual monitoring at Sandymount, Otago Peninsula from 1994 to 2023, showed pup production peaked at 141 – 197 in 2005 (Chapman estimate, 95 % CI) and was down to a low of 28 – 31 in 2023 (P. Seddon, unpublished data).

1.3 Movement Ecology and Animal Identification

Demography is the study of factors that affect birth, death, and dispersal, and is fundamental to biology (Coulson, 2020). The individual organism is the basic biological unit, and individuals should be studied where possible (Coulson, 2020). Individuals can be identified using natural features (Petso et al., 2022), or artificial marks (Gormley et al., 2005), and their movements can be tracked (Carter et al., 2016).

1.3.1 Population estimates and tracking

Identifying individuals allows population numbers to be estimated using mark/recapture techniques (Iijima, 2020; Schwarz & Seber, 1999). Tracking wildlife usually involves tracing individuals using technology such as satellite tracking (Thomas et al., 2011), however, genetic studies (Whiteman, in Bradshaw & Brook, 2010, p.332), or biogeochemical markers are increasingly used to study animal movements (Ramos & González-Solís, 2012). Computerised image recognition and citizen science can also combine to track distinctive individuals over large distances (e.g., https://happywhale.com/home).

1.3.2 Photo-identification Using Natural Markings

Many biological studies require individuals to be identifiable, and both species and individuals can be identified by multiple different features including body patterns, tracks (footprints etc.), facial characteristics, and sound (Petso et al., 2022). Natural markings or acquired injuries can often be used in place of artificial tagging (Slooten et al., 1992). Photo-identification has been widely used in terrestrial species including zebras (*Equus burchelli*), (Peterson, 1972), giraffes (*Giraffa camelopardalis*), (Foster, 1966), elephants (*Loxodonta africana*), (Douglas-Hamilton, 1973), lions (*Panthera leo*), (Schaller, 1972), chimpanzees (*Pan troglodytes*), (Goodall, 1986), wild dogs (*Lycaon* *pictus*), (Frame et al., 1979), and cheetahs (*Acinonyx jubatus*), (Kelly, 2001). Since the 1970s photo-identification has been extensively used in cetaceans (Hammond et al., 1990; Wursig & Jefferson, 1990). A study in humpback whales (*Megaptera novaeangliae*) comparing natural markings and microsatellite DNA showed that photo-identification was a reliable way of identifying individuals (Stevick et al., 2001). Some pinnipeds, such as harbour seals (*Phoca vitulina*), can be identified by pelage markings (Yochem et al., 1990). Computer-assisted matching has been used to distinguish between populations and between individuals in grey seals (*Halichoerus grypus*) (Hiby & Lovell, 1990), and Hawaiian monk seals (*Monachus schauinslandi*) (Harting et al., 2004). Sea otters (*Enhydra lutris*) can be distinguished by acquired marks on their noses (Gilkinson et al., 2007).

Vibrissa spot patterns have been used to identify individual lions (Pennycuick & Rudnai, 1970) and were 98 % accurate in identifying a population of 50 polar bears (*Ursus maritimus*) (Anderson et al., 2007). A study on captive and wild Australian sea lions (*Neophoca cinerea*) showed vibrissa spot patterns could identify members of a population of 50 animals, although reliability estimates dropped if the population was a thousand or more (Osterrieder et al., 2015). A subsequent study in wild Australian sea lions found that individuals could not be reliably identified, however, due to insufficient variability, inconsistent imaging, and differences between observers (Osterrieder et al., 2017).

A study in New Zealand sea lions (*Phocarctos hookeri*) at Otago Peninsula, South Island, used naturally acquired markings to identify 48 individuals (82 % of individuals seen over a 42-month study) (McConkey, 1999). In many cases, pinnipeds do not have sufficiently distinctive markings or population numbers are too high for natural markings to be an effective way to distinguish individuals (Wells, 2009), and both of these constraints are likely to apply to the NZFS.

1.3.3 Identification Using Artificial Marks

Mark/recapture methods were originally developed for studies in birds and small mammals, and generally relied on individual capture and artificial marking (Gormley et al., 2005).

In pinnipeds, temporary marking generally involves using paints, dyes, bleaches, or clipping of the pelage (coat) (Robertson et al., 2006; Erickson et al. 1993, in Wells, 2009). More permanent techniques include flipper marking, freeze branding, hot branding, and applying plastic tags (Erickson et al. 1993, in Wells, 2009). Branding can be a useful way to permanently identify individuals (McMahon et al., 2006), and is more reliable than flipper tagging (Chilvers & MacKenzie, 2010), although it can also be controversial (Jabour & Bradshaw, 2004). A study in New Zealand sea lions over a 10-year period showed that hot branding did not decrease survival, and it provided more reliable resighting data than plastic flipper tagging (Wilkinson et al., 2011).

Artificial tagging can adversely affect some animals; in penguins flipper tags have been shown to increase energy requirements and decrease survival (Jackson & Wilson, 2002). Artificial tags can be lost (Shaughnessy, 1994) or become illegible (McConkey, 1999), and colours can fade to a different colour (Hobbs & Russell, 1979). Double tagging doesn't completely overcome the problem of tag loss, as the probability of losing a tag is higher for individuals that have already lost one tag (Bradshaw et al., 2000). Passive integrated transponder (PIT) tags are long-lasting and inexpensive and have been used in fur seals and sea lions (Chilvers & MacKenzie, 2010; Hoffman & Forcada, 2012), although scanners must be within one metre of the PIT tag to read it (Wells, 2009).

A review of 39 published studies that investigated the effects of artificial marking on marine mammals found short term behavioural and physiological changes attributable to marking, but only internally placed devices have been associated with decreased survival in some species (Walker et al., 2012).

External tagging enables the public to report resightings, which potentially increases the number of reports. However, animal marking programs require substantial time and effort, and resighting rates can be low, particularly away from populated areas (Ramos & González-Solís, 2012). For example, as of June 2024 there were only 189 reported resightings out of more than thirty thousand NZFS pups tagged in West Coast colonies from 1991 to 2020 (https://furseals.dragonfly.co.nz/). In addition, capturing wild animals to apply tags generally causes them considerable short-term stress (Wilson & McMahon, 2006).

1.3.4 Telemetry

Observing and quantifying the at-sea behaviour of air-breathing, diving predators is difficult, however, technological advances in tracking devices have increased our understanding of marine mammal and particularly pinniped movements (Carter et al., 2016). Conventional animal tracking generally uses extrinsic markers and requires individuals to be recovered (Hobson, 1999), and cannot resolve animal dispersal at a population level (Hobson, 2005). Furthermore, most pinniped studies have been carried out on lactating females, but there are marked differences in foraging behaviour and ranges between different age classes (Page et al., 2005a), and pups and juveniles are likely to be more affected by human activities than older individuals (Fowler et al., 2007).

Early studies on pinniped foraging used very high frequency (VHF) radio transmitters, but the animal needs to be in close proximity to an observer, or to receiver stations, and foraging behaviour can only be inferred (Carter et al., 2016). VHF telemetry was used to quantify foraging and colony attendance times in lactating female NZFSs (Boren, 2005).

Archival time-depth recorders (TDRs) have been widely used, and provide useful data on diving behaviour, however, they must be retrieved to access the data so are not suitable for all life stages (Carter et al., 2016). TDRs have been used to study the summer diving behaviour of four lactating female NZFSs in Otago (Harcourt et al., 1995), and the summer/autumn/winter diving behaviour of 18 female NZFSs at Open Bay Islands (Mattlin et al., 1998). Satellite-linked TDRs do not require retrieval and have been used to study foraging in New Zealand sea lions (Chilvers, 2018).

Satellite tracking can be used to study species such as apex marine predators which are otherwise difficult to follow (Block et al., 2011). Satellite trackers have been widely used to study foraging in pinnipeds (e.g., Baylis et al., 2008, 2012; Block et al., 2011; Chilvers et al., 2005; Harcourt et al., 2002; Lowther & Goldsworthy, 2011; Walters et al., 2020; Zeppelin et al., 2019). Various satellite trackers have been developed in response to scientific and commercial demand (Thomas et al., 2011). Telemetry devices may be externally attached (ETD) or internally implanted (FIT), and best practice recommendations have been published for both methods (Horning et al., 2017, 2019). While rapid advances in GPS technology are occurring, they can come at the expense of field testing and reliability (Tomkiewicz et al., 2010). In addition to the potential adverse effects of capture on wild animals, tracking devices can also negatively affect individuals by increasing their energy costs and decreasing their foraging efficiency (Wilson & McMahon, 2006).

Satellite tracking methods and technology are continuing to improve (see Mate et al., 2007, for a summary of satellite tagging progression). Whales can be satellite tracked over long distances, providing invaluable information, however, satellite tracking is expensive and can be used on only a limited number of animals (Olsen et al., 2009). The patterns and drivers of southern elephant seal (*Mirounga leonina*) movements around Antarctica were revealed by analysing large satellite tracking data sets (Rodríguez et al., 2017). A comparison between ARGOS and Fastloc GPS tracking in pinnipeds showed that the ARGOS positions were less accurate, and that species that make shorter dives and spend more time at the surface, such as sea lions and fur seals, have less location error than species that dive deeper, such as elephant seals (Costa et al., 2010).

1.4 DNA

Genetic studies are used to clarify the origin of individuals, and the ecological and evolutionary relationships between populations (Whiteman, in Bradshaw & Brook, 2010, p.332). Mitochondrial and nuclear DNA are commonly used as markers (Arif et al., 2011), while genomic analyses are increasingly used to assist wildlife conservation and management (Hohenlohe et al., 2021). Individuals of unknown origin can be assigned to populations based on genetic analysis, however, the accuracy of the assignment depends on the genetic variability within the species and the statistical method used (Cornuet et al., 1999; Latch et al., 2006). Molecular genetic studies can be easier to perform than behavioural studies and require less time and effort than mark-recapture and telemetry (Gemmell et al., 1997).

Early genetic studies on the NZFS used mitochondrial haplotypes and found high genetic diversity within the overall population (Lento et al., 1997), however, there was no genetic distinction between animals on the east and west coasts of the South Island, New Zealand (Lento et al., 1994). Phylogenetic analysis using mitochondrial DNA showed that NZFS lineages were highly divergent (Wynen et al., 2001). A study on 305 pups from seven breeding colonies around New Zealand used eight microsatellite markers and was able to assign 42 % of individuals to their colony of origin and 70 % to their region of origin (Robertson & Gemmell, 2005). It was expected that adding further microsatellite loci would improve the accuracy of assignment (Robertson & Gemmell, 2005), however, a subsequent study with samples from 397 NZFS pups at 19 breeding colonies used 12 microsatellites but was only able to assign 32 % of individuals to their colony of origin (Dussex et al., 2016). The authors concluded that current microsatellite markers would probably be unable to determine the colony of origin of bycaught NZFSs. The relatively low level of genetic structuring among NZFS colonies was confirmed by a genomic analysis (Stovall, 2016). More recent genomic studies were also unable to assign NZFSs to their colonies of origin (B. Robertson, personal communication*,* 29 May 2024).

1.5 Biochemical tracing methods

Biogeochemical markers can be used to trace the feeding ecology and migration of apex marine predators such as pinnipeds (Ramos & González-Solís, 2012). Stable isotopes, trace elements, persistent organic pollutants (POPs), and lipids can all be used as tracers (Ramos & González-Solís, 2012). Although they don't provide the taxonomic resolution of dietary studies, or the geographic precision of marked or tracked animals, they give information on assimilation (Ramos & González-Solís, 2012), and can reflect dietary intake over days to years (Rubenstein & Hobson, 2004). To maximise the usefulness of intrinsic markers, it is important to select the best tracer and tissue, and an understanding of biogeochemical integration is required to interpret results (Ramos & González-Solís, 2012). Combining results from two or more tracers (Hebert et al., 2009; Herman et al., 2005) or combining tracers and animal tracking (Walters et al., 2020) can increase the information obtained. For example, a combination of scat hard part analysis and DNA metabarcoding, plasma SIA, and GPS and dive data loggers, on northern fur seals (*Callorhinus ursinus*) identified two ecotypes – one shelf-feeding and one pelagic (Jeanniard-Du-Dot et al., 2017).

Fatty acids (FAs) are particularly useful for tracing trophic relationships for several reasons: vertebrates can only carry out limited modifications to FAs; lipids are broken down to FAs during digestion but not completely degraded; and animals store fat in reservoirs (Iverson, 2009). Some long-chain polyunsaturated fatty acids can be traced through multiple trophic levels, as they are predictably absorbed by each consumer from its prey (Ramos & González-Solís, 2012). FA analysis in New Zealand sea lions showed interannual differences, and differences between males and females (Meynier et al., 2008). FA analysis requires sampling a metabolically active tissue that stores energy such as adipose tissue or blubber (Iverson, 2009), so vibrissae are not useful for measuring FAs.

Trace element analysis can be used in conjunction with SIA. Some trace elements, such as mercury, arsenic, cadmium and selenium, bioaccumulate in consumers (Ramos & González-Solís, 2012). An Australian study on little penguin (*Eudyptula minor*) feathers from NZFS scats was able to assign the penguins to their colony (78 %) or region (85 %) using aluminium, titanium, strontium, and magnesium levels, along with $\delta^{13}C$ and $\delta^{15}N$ results (Reinhold et al., 2022).

Persistent organic pollutants (POPs) can bioaccumulate in lipid tissues, indicating the trophic level of the consumer (Ramos & González-Solís, 2012). Organochlorine levels in Greenland sharks (*Somniosus microcephalus*) showed that they were feeding at a higher trophic level than indicated by $\delta^{13}C$ and $\delta^{15}N$ results (Fisk et al., 2002).

1.6 Stable Isotope Analysis

SIA is a powerful tool for exploring animal behaviour and ecology (Crawford et al., 2008), and for tracing the origins and migration patterns of wildlife (Hobson, 1999; Hobson et al., 2010). The stable isotope ratios of different parts of ecosystems vary naturally, and SIA can explain ecological systems over a wide range of spatial and temporal scales (West et al., 2006). SIA is widely used in marine mammals to study foraging ecology, the use of habitat, and migration (Newsome, Clementz, et al., 2010). Stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$ respectively) define the isotopic position in two dimensions, with $\delta^{13}C$ reflecting the foraging habit and $\delta^{15}N$ the trophic level (Cherel et al., 2009). Isotopic signatures are related to food webs rather than genetic or population processes (Hobson, 1999; Webster et al., 2002). Stable isotope ratios in animal tissues give indirect information on diet and foraging locations (Rubenstein & Hobson, 2004). Long-distance dispersal in animals, particularly birds, can be determined using SIA, however, sufficient isotopic differences between source populations are needed for individuals to be definitively assigned to their colony of origin (Hobson, 2005) and samples from multiple individuals are needed (Rubenstein & Hobson, 2004). The ability to detect long-distance dispersal relies on understanding natural isotopic patterns and species ecology, and choosing the appropriate tissue to sample (Hobson, 2005).

Applications of SIA include: determining isotopic gradients and trophic relationships between benthic fauna over wide geographic areas (Dunton et al., 1989), identifying latitudinal gradients using particulate organic matter samples (Espinasse et al., 2019), and combining stable isotope values with other data sets on large marine predators to explore long-term foraging and the effects of climate change in oceanic ecosystems (Dervilleet al., 2023). In an example of a coarse-scale study, a combination of skin sample $\delta^{15}N$ and $\delta^{13}C$ and whaling records since the 18th century showed that southern right whale (*Eubalaena australis*) foraging is more consistent in mid-latitude areas, while prey availability in polar regions is likely to be more influenced by recent climate change (Derville et al., 2023). On a finer scale, in the northern South Island, New Zealand, SIA was used to examine foraging such in the Hector's dolphin (*Cephalorhynchus hectori hectori*) and significant differences were found in the $\delta^{13}C$ and $\delta^{15}N$ values, and the isotopic niche spaces, between eastern and western sites (Ogilvy et al., 2023).

Metabolically active tissues are constantly modified (Rubenstein & Hobson, 2004). Blood plasma and liver isotopes change in hours to days, while bone collagen changes in months to years (Rubenstein & Hobson, 2004). Hair, baleen and vibrissae are made of keratin which is metabolically inert once it has been formed (West et al., 2006). Vibrissae provide a permanent, sequential record of dietary intake (West et al., 2006) and grow continually in otariids, however, growth rates and retention times vary among species (Hirons, Schell, & St Aubin, 2001).

1.6.1 Explanation of Stable Isotopes

Many elements occur in stable and non-stable (radioactive) forms; stable isotopes of an element have the same numbers of protons and electrons, but a different number of neutrons (Ehleringer & Rundel, 1989, p. 1). Heavier isotopes accumulate more than lighter ones within an organism due to isotopic discrimination, which leads to trophic enrichment of the consumer relative to its diet (Rubenstein & Hobson, 2004). The most relevant elements for ecological studies are carbon, nitrogen, sulphur, hydrogen and oxygen (Ramos & González-Solís, 2012). Carbon and nitrogen each have two stable isotopes, with the majority being C^{12} or N^{14}, and very small proportions being C^{13} or N^{15} (Ehleringer & Rundel, 1989, p. 2). To ensure that results are precise, repeatable, and accurate, isotopic ratios are measured relative to a defined standard (Ehleringer & Rundel, 1989, p. 3). The standards used are PeeDee belemnite marine fossil limestone for carbon, and atmospheric air for nitrogen (Ehleringer & Rundel, 1989, p. 3).

The formula for calculating stable isotope ratios is:

$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 10^3$$

where R_{sample} and R_{standard} are the ratios of the heavy to light isotope in the sample and standard, respectively. The result is expressed in delta units (parts per thousand, ‰). Delta units are appropriate for quantifying the variation in abundance of naturally occurring isotopes, however, they are not SI units (Slater et al., 2001).

Fractionation is natural isotopic variation and depends on small differences in physical and chemical properties, which are proportional to the differences between the masses of the isotopes (Broecker and Oversley, 1976, in Ehleringer & Rundel, 1989). The exact nature of fractionation is not completely understood (Hobson et al., 1996). SIA can be used to infer diet, however, the fractionation between a consumer and its diet can only be determined if the diet is known (Crawford et al., 2008). δ^{15}N and δ^{13}C were measured in the diet and in various tissues of captive harp (*Pagophilus groenlandicus*), harbour, and ringed seals (*Pusa hispida*) consuming herring for at least two years (Hobson et al., 1996). In blood, the mean δ^{15}N enrichment was +1.7 ‰ compared to the diet, while for vibrissae it was +2.8 ‰ (Hobson et al., 1996). Blood was enriched in δ^{13}C by +1.7 ‰ relative to the diet, while vibrissae were enriched by +3.2 ‰ (Hobson et al., 1996). δ^{13}C and δ^{15}N were higher in vibrissae than in blood (Hobson et al., 1996), however, in another study on seven species of captive pinnipeds serum and plasma δ^{15}N were higher than vibrissa δ^{15}N (Beltran et al., 2016). In northern fur seals, δ^{15}C was higher in fur than in plasma or red blood cells, while δ^{15}N was higher in plasma than in RBC or fur (Zeppelin & Orr, 2010). Fractionation, therefore, differs with each combination of species, diet, tissue, and environment (Jenkins et al., 2001).

Seasonal cycles in food supply and energy requirements can affect the physiology of isotopic fractionation within an individual (Newsome, Clementz, et al., 2010). Carbon in a consumer's tissues is derived from proteins, fats and carbohydrates in the diet, but δ^{13}C can be reduced if an animal is metabolising its blubber stores (Newsome, Clementz, et al., 2010). The main source of nitrogen in marine mammals is dietary protein, however, δ^{15}N may be enriched if an animal is catabolising its own protein reserves (Newsome, Clementz, et al., 2010).

In marine ecosystems, dissolved inorganic carbon is the main carbon source (Crawford et al., 2008). Inshore δ^{13}C sources are enriched relative to offshore ones, benthic sources are enriched relative to pelagic ones, and lower latitude sources are enriched compared to higher latitude ones (Rubenstein & Hobson, 2004). δ^{13}C often reflects the original carbon source, and is minimally enriched through the food chain (Kelly, 2000). Conversely, metabolism causes δ^{15}N to be enriched by an average of 3 ‰

(1 – 5‰) in consumers relative to their diets (Hobson et al., 1994, 1996; Kelly, 2000; Schoeninger & Deniro, 1984).

Latitudinal and longitudinal isotopic gradients occur. Coarse-scale isoscapes in the southwest Pacific, derived from analysing suspended particulate organic matter (SPOM), show a strong latitudinal gradient with $\delta^{13}C$ decreasing from around -16 ‰ at the Equator to -32 ‰ at the Antarctic shelf, although values around the coast of New Zealand alone range from -32 to -19 ‰ (Graham & Bury, 2019). It is difficult to generate isoscapes for coastal environments due to their dynamic processes and locally variable isotopic sources (Graham & Bury, 2019). Fine-scale isoscapes in the Southern California Bight showed that overall variability was low, but modelling showed chlorophyll *a*, latitude and season were predictors for $\delta^{13}C$, while longitude, season, nitrate and oxygen were predictors for $\delta^{15}N$ (Kurle & McWhorter, 2017). Variable upwelling patterns were likely to be driving some of the changes in SPOM stable isotope values (Kurle & McWhorter, 2017).

1.6.2 Examples of SIA Use in Pinnipeds

SIA is increasingly used as an economical way to study foraging in pinnipeds (Lowther & Goldsworthy, 2011). SIA complements methods like scat or regurgitate analysis, or direct observations (Crawford et al., 2008). There can be considerable variation in foraging among individuals (Chilvers et al., 2005; Drago et al., 2010). SIA on the vibrissae of dependent pinniped pups can provide information on fine-scale geographic variation in maternal foraging (Lowther & Goldsworthy, 2011). To infer maternal diet blood samples from South American sea lion (*Otaria flavescens*) pups were compared to potential prey species (Drago et al., 2010). The pups of females that foraged mostly on pelagic prey grew more quickly than those of females that foraged on benthic coastal prey (Drago et al., 2010). Vibrissa samples from Steller sea lion (*Eumetopias jubatus*) pups were used in conjunction with prey isotopic values to show geographical differences in maternal foraging during gestation (Scherer et al., 2015). Stable isotopes of maternal and offspring blood serum and vibrissae were combined with data from GPS trackers and time-depth-recorders to determine fine-scale foraging differences among female Australian sea lions in three geographically close colonies (Lowther & Goldsworthy, 2011). The authors recommended that telemetry be undertaken before SIA.

Vibrissa SIA and information from satellite data loggers on weaned southern elephant seals from Macquarie Island showed that krill were an important part of the diet, and that individuals that were less than one year old fed at a lower trophic level than older animals (Walters et al., 2014).

Lactating female New Zealand sea lions, studied using dive data loggers and SIA on vibrissae, were classified into two ecotypes based on their distinct foraging strategies, with some being consistent benthic feeders and the rest mesopelagic foragers (Chilvers, 2017, 2019). The two ecotypes were also distinguished by SIA of their pups' vibrissae (Chilvers, 2021a). Whole vibrissa SIA of female New Zealand sea lions at Stewart Island showed individuals had a consistent, life-long foraging strategy in a relatively restricted area (Chilvers, 2023). SIA of vibrissae from Australian sea lion pups, at three different colonies, showed there were two maternal foraging ecotypes at the southern colonies, while in the northern colony individuals had similar $\delta^{15}N$ values to seabirds in the same area (Lowther et al., 2013). Conversely, female Australian sea lions at three South Australian colonies were offshore, inshore, or intermediate foraging ecotypes, determined from SIA on pup vibrissae (Lowther & Goldsworthy, 2011). Distal vibrissa samples from southern (or South American) sea lion (*Otaria flavescens*) pups showed that pregnant females were offshore (43 %), inshore (43 %) or intermediate (14 %) foraging ecotypes (Baylis et al., 2016). Northern elephant seal (*Mirounga angustirostris*) pups from two colonies over 1000 km apart were distinguished by $\delta^{13}C$ and $\delta^{15}N$ in hair samples (Aurioles et al., 2006). SIA on bone collagen and tooth dentine showed the duration of nursing in northern fur seals and in California sea lions (Newsome et al. 2.006). Multi-year foraging strategies of male Antarctic fur seals (*Arctocephalus gazella*) were shown by serial samples along the length of the vibrissae (Cherel et al., 2009). Dive data loggers and SIA on blood and vibrissae were used to compile isotopic gradients, or 'isoscapes' for adult female Antarctic fur seals in the non-breeding season (Walters et al., 2020).

Teeth of male Antarctic fur seals were collected posthumously between 1971 and 2006, and showed that individual males foraged over a higher trophic level as they aged (Hanson et al., 2009). Decreased productivity at the base of the food web was the most likely cause for the decline in $\delta^{13}C$ over the total period (Hanson et al., 2009). A similar decline in $\delta^{13}C$ was seen in bone collagen from wild Steller sea lions, northern fur seals and harbour seals collected from 1951-1997 (Hirons, Schell, & Finney, 2001). Comparisons between two populations of Galapagos sea lions (*Zalophus wollebaeki*) and Galapagos fur seals (*Arctocephalus galapagoensis*) showed that the sea lions were diverging ecologically while the fur seals were not (Wolf et al., 2008).

Blood samples from Australian fur seals showed that while the species is considered to be a generalised predator, individuals can be very specialised in their foraging (Arnould et al., 2011; Kernaléguen et al., 2016). Changes in $\delta^{15}N$ of two-thirds of a trophic level (2 ‰) between some time periods coincided with cooler sea surface temperatures and a change in prey availability (Arnould et al., 2011). Vibrissae from Peruvian/South American fur seals (*Arctocephalus australis*) showed $\delta^{13}C$ and $\delta^{15}N$ fluctuated with variable sea surface temperatures in ENSO (El Niño- La Niña- Southern Oscillation) events (Edwards et al., 2021). Skin biopsy samples showed differences in trophic level foraging between female and male northern fur seals, and also between females in different reproductive states (Kurle & Worthy, 2001).

1.6.4 Isotopic Niche Widths

The concept of the ‘ecological niche’ was first proposed by Hutchinson in 1957, and is fundamental to ecology, although difficult to define (Newsome et al., 2007). The advent of SIA enabled the ‘isotopic niche’ to be quantified as a multivariate space, i.e., $\delta^{13}C$ and $\delta^{15}N$ biplot, which provides information on what an individual consumes (bionomic axis) and where it lives (scenopoetic axis) (Newsome et al., 2007). SIA is, therefore, a valuable tool to assess the ecological characteristics of organisms and to investigate the ecological niche (Newsome et al., 2007). The variance in $\delta^{13}C$ and $\delta^{15}N$ has been suggested as a measure of isotopic niche width (Bearhop et al., 2004). More recently, Bayesian analysis has allowed isotopic niche widths to be defined graphically and quantified (SIBER: Stable Isotope Bayesian Ellipses in R), and the resulting standard ellipse areas (SEAs) compared among communities or groups (Jackson et al., 2011). The authors noted that while the isotopic niche is closely correlated to the trophic niche, they are not identical. However, stable isotopes do provide ecologically relevant information on individuals, populations, and communities (Jackson et al., 2011).

Marine ecosystems are being modified by natural and anthropogenic factors, and a way to monitor the health of trophic systems is required (Ciancio et al., 2021). An example is a study that used blood samples from Magellanic penguins (*Spheniscus magellanicus*) at 12 colonies over seven years, which showed that isotopic niche width increased with decreasing prey abundance (Ciancio et al., 2021). The authors found differences among colonies and years, and concluded that sampling relatively small numbers of high-level predators was an effective way to monitor the state of the base of the trophic web. In a study on flesh-footed shearwaters (*Puffinus carneipes*), the isotopic niche doubled in size over 75 years and the $\delta^{15}N$ decreased by a full trophic level (-3.4 ‰), probably due to changes in climate (Bond & Lavers, 2014).

1.6.5 The Use of Pinniped Pups as Proxies

Pinniped pups are increasingly being used as proxies for maternal foraging (Drago et al., 2010), as pups are easier and safer to sample (Lowther & Goldsworthy, 2011). However, the relationship between maternal and offspring stable isotope values is not necessarily consistent. While $\delta^{13}C$ and $\delta^{15}N$ enrichment or depletion of pups relative to their mothers varies, several studies in different species have shown a correlation between maternal and offspring $\delta^{13}C$ and $\delta^{15}N$ (Cherel et al., 2015; Chilvers, 2017, 2021b; Ducatez et al., 2008; Lowther & Goldsworthy, 2011).

In four southern elephant seal mother-pup pairs the $\delta^{15}N$ and $\delta^{13}C$ values were generally negatively correlated during gestation, however, the relationship was pair-specific (Lübcker et al., 2020). The authors cautioned that foetal physiology should be considered when using foetal tissues as proxies for maternal isotopic composition. In four mother-pup pairs of Steller sea lions the trophic enrichment factor (TEF) from mother to pup vibrissae during gestion for $\delta^{13}C$ was -0.4 (-0.5 to -0.3) and for $\delta^{15}N$ was 0.8 (0.5 – 0.9) (Stricker et al., 2015). During nursing the TEF for $\delta^{13}C$ was -0.1 (-0.6 to -0.3) and for $\delta^{15}N$ was 1.6 (1.2 – 2.1), based on a single sample from each vibrissa (Stricker et al., 2015).

In a study on multiple terrestrial species, milk was depleted in $\delta^{15}N$ and $\delta^{13}C$ compared to maternal plasma, mean offspring plasma $\delta^{13}N$ was only slightly enriched over maternal plasma, and $\delta^{13}C$ showed no difference between the two (Jenkins et al., 2001). A study comparing maternal and pup bloods, and milk samples, in Antarctic and subantarctic fur seals showed that blood $\delta^{13}C$ levels were not significantly different, while $\delta^{15}N$ levels were significantly higher in pups, although not a full trophic level (Cherel et al., 2015). Milk was depleted in both $\delta^{13}C$ and $\delta^{15}N$ compared to maternal blood levels, and pup $\delta^{15}N$ was a full trophic level higher than the milk they were consuming (Cherel et al., 2015). The authors concluded that the 'apparent' $\delta^{15}N$ (the difference between the pup and its mother) was less than the 'real' $\delta^{15}N$ (the difference between the pup and its diet), with the real $\delta^{15}N$ often less than a full trophic level. In New Zealand sea lions, pup serum $\delta^{15}N$ was also enriched relative to maternal serum, but $\delta^{13}C$ was depleted (Chilvers, 2021b). Whole milk was depleted in $\delta^{13}C$, as expected, but slightly enriched in $\delta^{15}N$ relative to both pups and mothers (Chilvers, 2021b). New Zealand sea lion milk is lower in solids and fats than the milk of other otariids (Riet-Sapriza et al., 2012). The real $\delta^{15}N$ seems to be species- and tissue-specific (Cherel et al., 2015), and the relationship between $\delta^{15}N$ and $\delta^{13}C$ in milk and consumer tissues is not consistent (Chilvers, 2021b).

A study on free-ranging Steller sea lion pups and juveniles measured carbon and nitrogen isotope ratios in milk (sampled from stomach contents), serum, and vibrissal roots, and showed that $\delta^{15}N$ and $\delta^{13}C$ levels in serum were enriched over milk, $\delta^{13}C$ was enriched in vibrissal roots over serum, and $\delta^{15}N$ did not differ between vibrissal roots and serum (Stegall et al., 2008). Conversely, adult female New Zealand sea lions showed no significant difference in nitrogen or carbon isotope ratios between blood serum and vibrissae (Chilvers, 2017). Vibrissa samples from mother-pup pairs of Australian sea lions showed pup $\delta^{15}N$ was enriched by +1.27 ‰ over maternal $\delta^{15}N$ (Lowther & Goldsworthy, 2011). For $\delta^{13}C$ there was a very strong linear relationship between mother and pup values but $\delta^{13}C$ was not enriched in pups (Lowther & Goldsworthy, 2011).

In southern elephant seals, maternal and offspring $\delta^{13}C$ and $\delta^{15}N$ were strongly correlated, however, levels of both were higher in pups (Ducatez et al., 2008). In Guadalupe fur seals, the fur of pups was enriched in $\delta^{15}N$ relative to their mothers, but there was no significant difference in $\delta^{13}C$ levels (Elorriaga-Verplancken et al., 2016).

Sequential analysis of South American fur seal pup vibrissae showed that fluctuations in $\delta^{13}C$ likely reflected maternal foraging, particularly the increased diversity of foraging in late pregnancy when females were not lactating (Jones et al., 2020). Conversely, $\delta^{15}N$ levels in vibrissae increased steadily from birth till sampling at approximately 8 months old, probably due to physiological factors relating to suckling and fasting (Jones et al., 2020).

1.7 Foraging Studies

Lactating female otariids are 'central place foragers' (Baylis, 2008) and the duration and distance of their foraging trips are limited by the ability of their offspring to fast between feedings (Harcourt et al., 2002). The information gained from foraging studies can be increased by combining the results from more than one biogeochemical marker (Hebert et al., 2009; Herman et al., 2005), or by combining biogeochemical markers with animal tracking (Walters et al., 2020).

1.7.1 Otariid Foraging Studies

Stable isotope values in vibrissae and blood samples were combined with data from archival loggers on female Antarctic fur seals over the eight-month non-breeding season, to compile $\delta^{13}C$ and $\delta^{15}N$ isotopic gradients or 'isoscapes' (Walters et al., 2020).

Female Antarctic fur seals in South Georgia, feeding predominantly on krill, foraged at two spatial scales (Boyd, 1996). At a fine scale (0.18 – 0.27 km), travel times between krill patches were less than five minutes, while at a coarser scale (1.3 – 1.6 km), travel times were greater than five minutes (Boyd, 1996). Changes in these foraging patterns between years reflected changes in prey availability (Boyd, 1996), and animals appeared to change foraging trip duration and shore attendance times to maximise food delivery to their pups (Boyd, 1998a). Lactating South American fur seals at the Falklands Islands mostly foraged within 25 km of the breeding colony in late summer and autumn (93 % of satellite fixes), while in the winter only 11.5 % of positions were within 25 km (Thompson et al., 2003). Early in the breeding season, most foraging trips were brief and nocturnal (Thompson et al., 2003). Two individuals that foraged northwest, near the colony, and close inshore between 30 April and the end of May suddenly switched, on the same day, to foraging southeast, further away, and over the continental shelf (Thompson et al., 2003). Conversely, a satellite tracking study on three Australian fur seals for 65 – 174 days showed each individual repeatedly returned to the same location (Littnan & Arnould, 2002). Two individuals would travel directly to a foraging area and then return to the colony after feeding, while the other appeared to forage while following a looping route at a lower average speed (Littnan & Arnould, 2002). Australian fur seals (n = 48) in Bass Strait foraged exclusively within the continental shelf, and apparently were all benthic feeders, preferring depths of 60 – 80 m (Arnould & Kirkwood, 2008).

A study in Antarctic fur seals using satellite tracking, TDR and radio transmitters, showed that while individuals varied in their foraging patterns, the trip category accounted for more of the variation between trips than the individual did (Staniland et al., 2004). The authors concluded that while the foraging location is determined by the individual, the diving pattern depends on the prey distribution at that location (Staniland et al., 2004).

TDRs employed on Antarctic fur seals at the Kerguelen Islands identified four different diving behaviour categories: deep divers (n = 60), shallow-active divers (n = 45), shallow divers (n = 9) and daytime divers (n = 3) (Lea et al., 2002). Diving strategies were flexible and changed in response to differing environmental conditions and prey availability (Lea et al., 2002).

Satellite tracked lactating female Antarctic fur seals at Cap Noir, Kerguelen Island, foraged within a relatively narrow arc in three consecutive seasons, although within that arc most animals travelled northeast, to the edge of the continental shelf, with smaller numbers heading east-southeast (Bonadonna et al., 2001). It was suggested that animals know the approximate location of foraging grounds relative to their colony, but also that individuals learn from foraging trips and can return to areas where they have foraged successfully, or try alternative strategies (Bonadonna et al., 2001). The animals that foraged in the northeastern area travelled relatively quickly to and from the colony, and foraged in a small area there, while trips to the east-southeast were longer, and involved more apparent searching for food (Bonadonna et al., 2000). Female Antarctic fur seals at South Georgia foraged at a consistent compass bearing from the colony (Staniland et al., 2004).

Pinnipeds can detect subtle differences in salinity which could help them to navigate in the marine environment (Dehnhardt, 2002). Salinity gradients occur at ocean current boundaries (Baylis et al., 2012; Durante et al., 2021), which are often areas of increased biological productivity (Baylis et al., 2008a).

The relationship between various environmental variables and dive parameters in lactating Antarctic fur seals at Cap Noir, Kerguelen, changed depending on the scale at which they were measured, however, it was suggested that fur seal distribution gave a good indication of their prey distribution (Guinet et al., 2001). The same may not be true for more generalised predators such as NZFSs at Otago Peninsula (Harcourt et al., 2002). A comparison between Antarctic and subantarctic fur seals at the Crozet Islands showed that while they have a similar diet of mainly myctophid fish, the subantarctic fur seals foraged in both deep water and in a shallower area, while the Antarctic fur seals foraged in a different smaller area on the edge of a submarine ridge (Bailleul et al., 2005). Their foraging behaviour was similar, although in different environments the two species show very different foraging behaviours, which implies that fur seal foraging behaviour is mainly determined by environmental factors (Bailleul et al., 2005). Female Antarctic fur seals at South Georgia foraged for longer and made more dives in a season of low krill availability compared to seasons with normal krill numbers (McCafferty et al., 1998). In a year of particularly high krill abundance, the fur seals carried out more shallow dives and daytime dives, consistent with the fact that krill stay closer to the surface in years of high abundance (McCafferty et al., 1998). Foraging effort increased with the age of the pup, probably in response to increased demand (McCafferty et al., 1998).

SIA showed that isotopic niche widths were higher in South American fur seals than in South American sea lions, and the fur seals were generalist individuals while the sea lions were more specialised individuals (Franco-Trecu et al., 2014). Despite breeding in adjacent colonies, isotopic niches of South American and subantarctic fur seals did not overlap (de Albernaz et al., 2017). Niche widths were greater in Antarctic fur seals than in South American and subantarctic fur seals (de Albernaz et al., 2017).

A population of lactating Australian fur seals was shown to be comprised of both generalist and specialist individuals, in a study using animal-borne cameras, TDR/GPS loggers, and SIA of multiple tissues (Kernaléguen et al., 2016).

1.7.2 New Zealand Fur Seal Foraging – Time Depth Recorders (TDR) and Satellite Tracking

In New Zealand, most foraging research has involved using tracking devices on lactating NZFSs (Baird, 2011). The first satellite tracking of NZFSs also included TDRs, and found that females carried out longer foraging trips and dived deeper in autumn than in winter (Harcourt & Davis, 1997).

At Open Bay Islands, TDRs recorded the foraging behaviour of 18 lactating female NZFSs in different seasons (Mattlin et al., 1998). Mean dive depth, duration, and bottom time were shortest in the summer and longest in the winter (Mattlin et al., 1998). In summer and autumn, diving mostly occurred between 1800 – 0600, however, diving was spread over 24 hours in winter (Mattlin et al., 1998). Likewise, in four lactating female NZFSs in Otago in summer, all foraging occurred at night (Harcourt et al., 1995). The dive patterns were consistent with summer feeding on vertically migrating, pelagic prey, such as arrow squid (*Nototodarus sloanii*) (Harcourt et al., 1995; Mattlin et al., 1998).

At Cape Foulwind, lactating females mostly foraged in sea depths between 100 – 200 m, and less than 30 km from shore in April, while they foraged further offshore in deeper water in July (Sinclair & Wilson, 1994). Conversely, at Otago Peninsula, lactating females foraged around the continental shelf and slope in summer (n = 2), in deep water offshore in autumn (n = 3), and inshore again in the winter (n = 2) (Harcourt et al., 2002).

At Kaikōura, foraging trips were longer in the El Niño conditions of the 2004/2005 summer, compared to the previous year (Boren, 2005). Conversely, in Otago over five summers no inter-annual differences in dive behaviour were detected, despite the differences in prey availability among years (Harcourt et al., 2001).

NZFSs at Open Bay Islands were considered to be either relatively shallow or deep divers (Mattlin et al., 1998), which was consistent with findings in sea lions (Chilvers, 2017; Lowther & Goldsworthy, 2011), however, the variation in dive behaviour among seasons was much greater than the variation in dive behaviour among individual seals within a season (Mattlin et al., 1998). Furthermore, the diving bouts of female NZFSs in Otago were classed as 'long', 'shallow' or 'deep', with shallow dives the most common in summer, shallow (in 1995) or deep (in 1994) in autumn, and long and deep in winter (Harcourt et al., 2002), implying a greater level of plasticity in diving strategies in NZFSs than in sea lions.

Satellite tracking of lactating female NZFSs from four breeding colonies in southern Australia in autumn showed that animals travelled to and from their colonies on a consistent, colony-specific, compass-bearing (Baylis et al., 2008a). Individuals from Cape Gantheaume foraged at the consistent Bonney upwelling on the continental shelf, while those at the other three colonies foraged in oceanic waters associated with the subtropical front (Baylis et al., 2008a). Satellite transmitters and TDRs on lactating females showed that while the majority foraged on the continental shelf in autumn, they mostly foraged in oceanic waters in the winter, after the seasonal Bonney upwelling ceased (Baylis et al., 2008b). Individuals showed directional fidelity to their foraging sites, and the foraging site overlap between consecutive trips was greater on the continental shelf than in oceanic areas (Baylis et al., 2012). The distance and duration of foraging trips varied among individuals and colonies, showing that foraging and provisioning strategies were very flexible (Baylis et al., 2012).

More research is still needed for a full understanding of NZFS foraging and diet (Boren, 2010), but previous studies have shown that there can be considerable variation among individuals, seasons, and locations. NZFS colonies may, therefore, not be isotopically distinct.

1.7.3 Biogeochemical Markers in New Zealand fur seals

There have been few studies using biogeochemical markers in NZFSs. Fatty acid analysis of milk samples from NZFSs in southern Australia showed that individuals foraging in oceanic waters could be distinguished from those foraging over the continental shelf (Baylis & Nichols, 2009).

SIA of vibrissae from males, females, and pups at three colonies in the northern South Island, New Zealand, showed differences in $\delta^{13}C$ and $\delta^{15}N$ among locations, age classes and seasons (Noè, 2013).

Vibrissa SIA of lactating female NZFSs showed higher $\delta^{15}N$ at Cape Foulwind than at Kaikōura, and higher $\delta^{13}C$ at Kaikōura than at Cape Foulwind (L. Meynier, unpublished data). Seven out of eight NZFSs sampled in winter at Cape Foulwind had similar isotopic signatures to those sampled in summer (L. Meynier, unpublished data).

1.7.4 New Zealand Fur Seal Diets

NZFSs as a species are generalist predators (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016). Diet varies with season, region, age/sex of NZFS and whether the area is a breeding site or hauling ground (Boren, 2010). NZFSs consume a range of species with arrow squid and octopus (*Octopus maorum*) being the only ones found in all studies (Boren, 2010). The diet of NZFSs in New Zealand has not been exhaustively studied, with only nine published studies prior to 2010 (Boren, 2010). Techniques included examination of stomach contents (Street, 1964), and of hard parts in scats and regurgitates (Allum & Maddigan, 2012; Carey, 1991a; Fea et al., 1999; Holborow, 1999; Willis et al., 2008). Stomach content analysis can identify prey species and distinguish between direct and indirect consumption; however, lethal sampling is needed (Boren, 2010). Scats provide large sample sizes and prey species can be identified, but analysis tends to underestimate the importance of larger prey and cannot distinguish between direct and indirect consumption (Boren, 2010). Regurgitates generally represent less digestible larger prey and cephalopods, and occur only seasonally, with few available during winter (Boren, 2010). DNA sequencing provides information on carnivore diets, however, systematic biases in DNA analysis of scats must be accounted for (Thuo et al., 2019). Next-generation DNA sequencing has been used to study NZFS diets (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016). To minimise bias dietary studies must be well-designed, and those that combine more than one technique tend to be more accurate (Boren, 2010).

There are uncertainties associated with hard-part analysis; in a feeding trial in captive subantarctic fur seals prey recovery rates depended on erosion and passage rates, which varied with prey size (Staniland, 2002). A study in captive South American fur seals and California sea lions showed that while the proportion of different prey species could be estimated if large numbers of scats were analysed, scat analysis could not give an accurate estimate of the biomass or energy consumed (Dellinger & Trillmich, 1988). Scat analysis in captive and wild Australian sea lions was shown to be unreliable, even for a qualitative description of diet (Gales & Cheal, 1992). The clearance rate of different prey species varies (Gales & Cheal, 1992), with 46 % of small (1 mm diameter) markers passed within 6 hours (Richardson & Gales, 1987). In a dye-marked diet study on three species of captive pinniped, the time from ingestion to first defaecation averaged five hours or less (Helm, 1984). Conversely, larger or less digestible components of the diet can be retained in the stomach for six days or more (Richardson & Gales, 1987). Scats collected on shore are likely to be biased towards prey consumed in the previous 48 hours (Gales & Cheal, 1992).

Analysis of stomach contents from 64 NZFSs from five areas in Canterbury, Otago and Southland, New Zealand, showed squid and octopus made up just over half the diet by weight, with barracouta (*Thyrsites atun*) 38 %, and the balance was made up of other fish (Street, 1964). Scat samples collected from colonies at Kaikōura, Cape Foulwind, Open Bay Islands and Gillespies Beach, South Island, New Zealand, between February and August showed that the main fish prey species were lanternfish (*Lampanyctodes hectoris* and *Symbolophorus* spp.) and anchovy (*Engraulis australis*), in varying proportions (Carey, 1991a). Seasonal changes were evident at Cape Foulwind with ahuru (*Auchenoceros punctatus*) decreasing and anchovy increasing in winter, however, at Kaikōura, *Symbolophorus* spp. were the main fish prey throughout sampling, and overall, there were not many seasonal diet fluctuations (Carey, 1991a). The study did not assess any cephalopod component of the diet and was not comparable to studies using different methodologies (Carey, 1991a).

At a breeding colony on the Otago Peninsula, scats and regurgitates were collected between July 1993 and September 1994 (Fea et al., 1999). Arrow squid predominated in summer and autumn, while barracouta, mackerel (*Trachurus* spp.) and New Zealand octopus were more common in winter and spring (Fea et al., 1999). Over six seasons at Otago Peninsula in 1994/1995, analysis of scats and regurgitates in summer, autumn, and winter showed arrow squid and myctophid fish were important components of the diet in summer and autumn, while ahuru was the main contributor by estimated biomass in winter (Harcourt et al., 2002). At five sites in southern New Zealand, scat and regurgitate analysis showed NZFSs fed on a variety of mostly mesopelagic prey, with octopus the only important benthic species (Holborow, 1999). Prey composition varied with region and season (Holborow, 1999).

At Tonga Island, Abel Tasman National Park, South Island, New Zealand, scats and regurgitates were collected in winter and spring (Willis et al., 2008). Arrow squid, anchovy, pilchard (*Sardinops neopilchardus*), and jack mackerel (*Trachurus spp.*) predominated (Willis et al., 2008). In winter the colony consisted mostly of lactating females and pups, while in spring it contained mostly territorial males, however, diet composition did not vary markedly between seasons (Willis et al., 2008). At Banks Peninsula, examination of scats and regurgitates showed that arrow squid predominated all year round (>90 %) followed by lanternfish (4 %) and barracouta (2.6 %) (Allum & Maddigan, 2012).

At Cape Gantheaume, South Australia, analysis of scats and regurgitates from adult male, adult female, and juvenile NZFSs, and adult male Australian fur seals, showed there were differences in foraging between the four groups (Page et al., 2005a). Adult females were generalist predators, but consumed mostly large squid and medium sized fish over the continental shelf or the shelf break, while juveniles mostly foraged on small fish in pelagic waters (Page et al., 2005a, 2006). Adult male NZFSs consumed the largest prey items, including birds, with their most important prey being little penguins (*Eudyptula minor*) (Page et al., 2005a). Adult male and female NZFSs consumed a greater proportion of fish in the winter, while there were no seasonal consumption patterns in juvenile NZFSs (Page et al., 2005a).

DNA analysis of scat samples from five locations from the Bay of Plenty to Codfish Island, New Zealand, identified diverse NZFS prey species, with a single colony yielding up to 46 fish species and 18 cephalopod species (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016). Only *Architeuthis dux*, *Sepia officinalis*, *Nototodarus gouldi*, *Martia liahyadesi*, *Spirula spirula*, *Nototodarus sloanii*, and *Callorhinchus milii* were common to all colonies (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016). There was little overlap in the species present at Kaikōura in summer and winter (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016). Approximately 10.6 % of prey species found in NZFS scats were commercial species (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016).

1.8 Vibrissae – Structure, Function, and Growth Rates

Vibrissae (whiskers) are made of keratin which is metabolically inert once it has been formed and provides a permanent, sequential record of dietary consumption (West et al., 2006). Vibrissae are present in most mammalian species, and they are particularly long and sensitive in some nocturnal, arboreal species, and also in aquatic species (Grant & Goss, 2022). Mystacial (muzzle) vibrissae are the most obvious ones, but pinnipeds also have superciliary (above the eyes) and, in some cases, rhinal and submental vibrissae (King, 1983). NZFSs have 0-2 superciliary vibrissae and 22-31 mystacial vibrissae on each side, arranged in five or six horizontal rows (Miller, 1975a). Pups are usually born with black mystacial vibrissae, although some have a single white vibrissa on each side (Miller, 1975a), which is often the longest (L. Boren, personal communication, 18 February 2023). Vibrissae are tapered, with an oval cross-sectional shape in otariids and most phocids (Ginter et al., 2012), and consist of a cuticle, cortex and medulla (Voges et al., 2012). The surface of the vibrissa is smooth in otariids and wavy in some phocids (Ginter et al., 2012). The longest recorded pinniped vibrissa was from an Antarctic fur seal, and measured 480 mm (Bonner, 1968, in King 1983). The shaft of the vibrissa transmits vibrotactile stimuli from the environment to mechanoreceptors in the follicle-sinus complex (Ginter et al., 2012). Vibrissae are innervated and under voluntary muscle control (Hirons et al., 2001b). The tactile sensory and hydrodynamic information provided by vibrissae (Dehnhardt et al., 1998), is useful for individuals that live in complex environments and hunt mobile prey (Grant & Goss, 2022). Vibrissae are also used for social communication (Miller, 1975a).

In otariids, vibrissae grow continually and are retained for at least two years (Hirons, Schell, & St Aubin, 2001). Vibrissa growth rates have been measured in various pinniped species and age classes using different techniques, including cut/regrowth, glycine injection, and annual oscillations (Table 8). Growth rates calculated from seasonal oscillations assume that these conform exactly to annual fluctuations (Hirons, Schell, & St Aubin, 2001), however, that may not be the case (Rea et al., 2015). Vibrissa growth rates vary among species and age-classes and cannot necessarily be extrapolated from one group to another (Foo et al., 2019). Vibrissa growth rates also vary considerably among individuals within an age-class or species (Chilvers, 2019; Walters et al., 2020). Most relevant to the present study, in adult female NZFSs in Australia, vibrissa growth rates were 0.18 mm/day (Foo et al., 2019), with Steller sea lion YOY having vibrissa growth rates that were double those of adult conspecifics (Rea et al., 2015).

1.9 Summary of Stable Isotope Analysis and Foraging Behaviour

It is difficult to observe the behaviour of pinnipeds at sea (Carter et al., 2016), and biogeochemical markers, such as stable isotopes, can be used to trace feeding ecology and migration (Crawford et al., 2008; Hobson, 1999; Hobson et al., 2010; Ramos & González-Solís, 2012). Studies on NZFSs in Australia and New Zealand, and on closely related species, have shown a range of foraging strategies and SIA results.

In some colonies, individuals forage in a consistent direction from the colony (Bailleul et al., 2005; Baylis et al., 2008a, 2012; Bonadonna et al., 2001; Staniland et al., 2004), however, the limited tracking data for foraging NZFSs in New Zealand are not consistent with that behaviour (Harcourt et al., 1995, 2002; Harcourt & Davis, 1997; L. Meynier, unpublished data). In some otariid studies, foraging area fidelity changed with season (Baylis et al., 2012; Harcourt et al., 2002; Mattlin et al., 1998; Sinclair & Wilson, 1994; Thompson et al., 2003), or year (Boren, 2005), although in other cases seasonal or inter-annual differences were not detected (Harcourt et al., 2001; Littnan & Arnould, 2002). Likewise, diving strategies can vary among individuals, seasons, years, and locations (Bailleul et al., 2005; Baylis et al., 2008b, 2008a, 2012; Boyd, 1998a; Harcourt et al., 2002; Mattlin et al., 1998; McCafferty et al., 1998; Sinclair & Wilson, 1994; Staniland et al., 2004; Thompson et al., 2003).

Different components of ecosystems have different stable isotope ratios (West et al., 2006), and SIA can provide information from coarse scales (Derville et al., 2023) to fine ones (Ogilvy et al., 2023). While isotopic gradients can be determined over wide areas (Dunton et al., 1989; Espinasse et al., 2019), coastal ecosystems are constantly changing (Graham & Bury, 2019). Carbon is minimally enriched through the food chain, whereas nitrogen is enriched by 3 – 5 ‰ at each trophic level (Kelly, 2000). Baseline $\delta^{13}C$ and $\delta^{15}N$ values can differ among areas and species (Hansen et al., 2012). In addition, for $\delta^{13}C$, there are latitudinal (Cherel & Hobson, 2007), benthic/pelagic, and inshore/offshore gradients (Rubenstein & Hobson, 2004). Isotopes fractionate differently between the diet and different tissues in the consumer (Hobson et al., 1996), and between lactating females and their pups (Cherel et al., 2015; Chilvers, 2021b). Physiological processes, related to food supply and energy needs, also affect stable isotope values in individuals (Newsome, Clementz, et al., 2010). All the above factors may complicate the interpretation of $\delta^{13}C$ and $\delta^{15}N$ values in individuals from different colonies.

Thesis Aims and Plan

The structure of this thesis is as follows:

Chapter 1: General introduction

This chapter summarises the biology, life cycle, distribution, and population numbers of the NZFS in New Zealand. Previous research on movement ecology and animal tracking is discussed, including individual identification and telemetry techniques. Genetic analysis and biochemical tracers are considered. Stable isotope analysis (SIA) is explained, and examples of its use in marine mammals generally, and pinnipeds in particular, are provided. Isotopic niche widths are defined and discussed. Diet and foraging studies on NZFSs and some related species are summarised. The structure and function of vibrissae are explained.

Chapter 2: Stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissae at seven established breeding areas in New Zealand

This chapter describes the first attempt to develop a database of NZFS pup vibrissa $\delta^{13}C$ and $\delta^{15}N$ values. The results of analysis of proximal vibrissa samples are discussed with reference to local bathymetry and other factors that may influence the results. Cluster analysis is used to define how samples from known breeding areas group isotopically. Isotopic niche widths are described and compared using Bayesian ellipse areas.

Chapter 3: The use of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissae to determine the area of origin of stranded individuals in Northland and Hawkes Bay, New Zealand

In this chapter, the $\delta^{13}C$ and $\delta^{15}N$ values in vibrissa samples taken from weaned NZFS young-of-the-year (YOY) stranded in Northland or in Hawkes Bay, New Zealand, are compared to the database of values in vibrissae sampled from pups at known breeding colonies (Chapter 2) to try to determine the origin of the stranded individuals. $\delta^{13}C$ and $\delta^{15}N$ values in a sample taken at two-thirds of the length of the vibrissa in stranded YOY are compared to values in the proximal section of the vibrissa samples from pups at breeding colonies. Vibrissa growth rates and estimated vibrissa lengths at birth are calculated.

Isotopic niche widths are described using Bayesian ellipses, and niche width sizes are compared before and after weaning for stranded individuals. Isotopic niche widths are also compared among breeding colonies (Chapter 2) and the three groups of stranded YOY.

Chapters two and three were written as manuscripts to be submitted for publication so there is some unavoidable repetition of material in the introductions and discussions of these chapters.

Chapter 4: General Discussion and Conclusions

This chapter summarises the main findings of this study, and discusses the role of SIA in monitoring foraging, dispersal, and recolonisation of NZFSs. Threats to the NZFS, including fisheries, exotic disease incursions, and climate change, are discussed. The role of SIA, and its benefits and limitations, are examined. Recommendations for future research to increase the understanding of NZFS ecology are made.

Chapter 2. Stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissae at seven established breeding areas in New Zealand

Abstract

The New Zealand fur seal/kekeno (*Arctocephalus forsteri*, NZFS) is native to Aotearoa/New Zealand. Its original range in New Zealand waters included the entire coast of mainland New Zealand, and New Zealand's offshore and subantarctic islands. Having been almost extirpated by hunting, it is recolonising its former range, however, little is known about the dispersal of the species around New Zealand in the non-breeding season. To understand the ecological implications of recolonisation it is necessary to know the life history (demographics), abundance, distribution, and movement patterns of the species. Traditionally, population demographic studies identified individuals from natural or artificial marks. Increasingly, intrinsic substances such as DNA or biochemical markers, including stable isotope analysis (SIA), are being used to study individuals and populations, and to trace foraging ecology and migration. Studies in many marine mammal species have used SIA to provide information on diet, trophic level, and movement patterns. Isotopic niche size can be described statistically and provides ecologically relevant information on diet at an individual, population, and community level.

Otariid pup vibrissae (whiskers) provide a sequential record of nutrient intake derived from maternal milk, and can, therefore, be used as proxies for maternal foraging.

In this study, vibrissae from NZFS pups were collected from seven established breeding areas around the coast of New Zealand between 39 and 84 days after the assumed median pupping date. $\delta^{13}C$ and $\delta^{15}N$ values in the proximal vibrissa were measured. Colonies were not sufficiently isotopically distinct for pups to be identified to their colony of origin.

The $\delta^{13}C$ and $\delta^{15}N$ values were also used to calculate isotopic niche widths (standard ellipse areas, 'SEAs') for each colony, which indicate the diversity of maternal foraging. Isotopic niche widths were larger at Open Bay Islands and Cape Foulwind than at the other colonies.

Research Objectives

- Create a database of $\delta^{13}C$ and $\delta^{15}N$ values from the proximal vibrissa of New Zealand fur seal (NZFS) pups at representative established breeding colonies in New Zealand.
- Quantify isotopic niche widths represented by NZFS pup vibrissae.
- Summarise the known foraging characteristics of the NZFS and the environmental conditions that might explain the $\delta^{13}C$ and $\delta^{15}N$ results.

2.1 Introduction

There is little known about New Zealand fur seal/kekeno (*Arctocephalus forsteri,* Lesson, 1828, hereafter 'NZFS') dispersal around New Zealand in the non-breeding season. While lactating females forage close to the breeding colony for most of the year while provisioning their pups, non-breeding females and other age-classes disperse around the coast (Crawley & Wilson, 1976). NZFS pup production is declining in some colonies (Roberts & Neale, 2016), and increasing in others (A. Hall, unpublished data). Declining populations could be due either to emigration, or to threats to NZFSs varying by region. It is necessary to be able to distinguish between individuals from different areas to assess the threats to NZFS populations in different regions.

2.1.1 New Zealand fur seal – Life History and Population Numbers

The NZFS is in the family *Otariidae* (eared seals). It is native to Aotearoa/New Zealand, and inhabits the rocky coast of New Zealand and its sub-Antarctic islands (Crawley & Wilson, 1976), as well as southern and western Australia (Baird, 2011). It is classified as 'Least Concern' on the IUCN Red List (Chilvers & Goldsworthy, 2015) and Increasing, Secure Overseas in the New Zealand Threat Classification Series (Baker et al., 2019), however, it is susceptible to anthropogenic threats including fisheries bycatch (Abraham et al., 2021; Abraham & Berkenbusch, 2017; Hamer & Goldsworthy, 2006; Lalas & Bradshaw, 2001; Thompson et al., 2011), aquaculture (Baker, 2005), entanglement (Boren, Morrissey, et al., 2006), disturbance (Cowling et al., 2015), tourism (Boren et al., 2002; Cowling, 2013), and climate change (Roberts & Hendriks, 2022).

Prior to human settlement, populations may have been 1.5 – 2 million (Richards, 1994), and NZFSs were distributed around the main and subantarctic islands of New Zealand (Falla, 1965; Smith, 1989). Māori subsistence hunting (Smith, 1989) and European commercial sealing (Ling, 1999) almost extirpated the NZFS population from the New Zealand mainland (Lalas & Bradshaw, 2001), however, it has increased (e.g., Falla, 1962; Lalas & Bradshaw, 2001) since 1875 when it was first given some legal protection (Crawley & Wilson, 1976). It is now completely protected under the Marine Mammals Act 1978 (Baird, 2011). NZFS populations have not been comprehensively surveyed recently (Chilvers & Goldsworthy, 2015). Pup counts are used to estimate population numbers (Shaughnessy et al., 1994), and rates of population change (Berkson & DeMaster, 1985), however, it can be difficult to estimate total population numbers from pup counts (Lalas & Bradshaw, 2001). The demographic information necessary to calculate a multiplier differs among colonies, and is generally unknown for the NZFS (Baird, 2011; Chilvers, 2021c; Watson et al., 2015). The latest estimate for the total New

Zealand population is 129,773 – 166,704, based on pup production estimates, and 146,094 – 229,179, based on modelling (A. Hall, unpublished data).

NZFS breeding colonies have been variously defined as areas where fur seals breed and give birth (Baird, 2011), locations where more than 10 pups are born each year (Bradshaw, 1999), and aggregations of pups within two kilometres of each other (Shaughnessy et al., 1994, 2015). From a few sites in the south and west of the South Island, New Zealand, in the 1970s (Wilson, 1981), the breeding range has now expanded around the South Island (Boren, 2005; Lalas & Harcourt, 1995; Lalas & Murphy, 1998; Taylor et al., 1995), and to Cape Palliser in the southern North Island (Dix, 1993). NZFS breeding has also been recorded as far north as Kārewa/Gannet Island (37.9721°S, 174.5659°E) (Bouma et al., 2008) and Albatross Point (38.1073°S, 174.6841°E) (www.nabis.govt.nz) on the west coast of the North Island, and Moutohorā Island (37.8558°S, 176.9738°E) (Cowling, 2013) on the east coast of the North Island.

The breeding colonies in the present study have differing population trajectories. The colonies at Open Bay Islands, Cape Foulwind, and Wekakura Point have been counted regularly by staff from the Department of Conservation (DOC) since 1990/1991. Pup production at Open Bay Islands peaked at 1,432 in 1995 (Roberts & Neale, 2016) and was down to 638 in 2022/23 (DOC, unpublished data). At Cape Foulwind, pup production peaked at 484 in 1993 (Roberts & Neale, 2016) and was 93 in 2022/23 (DOC, unpublished data), while Wekakura Point peaked at 1,097 pups in 1996 (Roberts & Neale, 2016) and produced 143 pups in 2022/23 (DOC, unpublished data). At Cape Palliser, breeding was first confirmed when at least 13 pups were counted in the 1991/92 season (Dix, 1993). Pup production has increased considerably since then, with approximately 600 pups born in 2022/23 (L. Boren, personal communication, 11 September 2023). Cape Palliser has not been surveyed regularly so it is not clear whether pup production is continuing to increase (L. Boren, personal communication, 11 July 2024). Pups were first seen at Ōhau Point, Kaikōura, in 1990 and pup production was nearly 600 in 2005 (Boren, 2005). In 2014/15 an estimated 2,471 pups were born at Ōhau Point (Gooday, 2016). In 2022/23 pup production was 2,401 ± 99 (Hall et al., 2024), however, in 2023/24 it had dropped to approximately 1,182 (J. Weir, unpublished data). The 7.8 magnitude earthquake in November 2016 caused considerable disruption to the breeding habitat at Ōhau Point and is likely to have affected pup production (Hall et al., 2024). Pup production south of the Kaikōura Peninsula was estimated to be 923 ± 17 in 2022/23 (Hall et al., 2024). In the greater Kaikōura area, total pup production was estimated to be 5703 – 5781 in 2022/23 (Hall et al., 2024). The colony at Sandymount, Otago, has been counted annually since March 1994, with pup production peaking at 141 to 197 in 2005 and declining to a low of 28 to 31 in 2023 (P. Seddon, unpublished data).

The NZFS breeding strategy is categorised as resource-defence polygyny (Carey, 1991b). Male NZFSs establish territories from mid-November (Stirling, 1971b), while females arrive from late November and give birth to a single pup a few days later (Crawley & Wilson, 1976). Females show a high level of fidelity to breeding colonies (Stirling, 1971a), and new colonies cluster around existing ones (Bradshaw, 1999). Pinniped breeding colonies are often distant from foraging grounds (Boyd, 1998b), however, female NZFSs must forage relatively close to the breeding colony as they return to feed their pups every few days (Harcourt et al., 2002). The time of weaning varies among studies: from late July to early October (Smith, 2005), September or October (Goldsworthy, 2006; Harcourt, 2001), or November (Boren, 2005; Bradshaw et al., 1999). The numbers, ages and sex-classes at breeding colonies and hauling grounds vary seasonally (Baird, 2011).

2.1.2 Diet

Foraging in marine generalist predator species can vary markedly between individuals (Chilvers et al., 2005; Drago et al., 2010). The NZFS is considered to be a generalist predator (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016). Season, region, breeding or non-breeding site, and age/sex of NZFSs are all known to affect foraging behaviour and, therefore, diet (Boren, 2010). Studies on NZFSs have been done on stomach contents (Street, 1964), and the hard parts of regurgitates and scats (Allum & Maddigan, 2012; Carey, 1991a; Fea et al., 1999; Holborow, 1999; Willis et al., 2008), with arrow squid (*Nototodarus sloanii*) and octopus (*Octopus maorum*) the only species found in all studies (Boren, 2010). DNA analysis of scats showed differences in foraging between seasons and between regions (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016).

2.1.3 Foraging – Time Depth Recorders and Satellite Tracking

Foraging research on NZFSs in New Zealand has mostly been done on lactating females, using VHF radio tracking (Boren, 2005; Mattlin et al., 1998; Sinclair & Wilson, 1994), satellite-linked transmitters (Harcourt et al., 2002; Harcourt & Davis, 1997), or Time Depth Recorders (TDRs) (Harcourt et al., 1995, 2001, 2002; Mattlin et al., 1998). Dive behaviour varied among individuals, regions, and seasons (Harcourt et al., 2002; Mattlin et al., 1998; Sinclair & Wilson, 1994). Interannual changes in dive behaviour were not detected at Otago Peninsula (Harcourt et al., 2001), however, at Kaikōura, foraging trip duration increased in El Niño conditions (Boren, 2005). Telemetry and vibrissa SIA on lactating female NZFSs at Cape Foulwind and Ōhau Point, Kaikōura, showed that foraging areas generally did not overlap, and animals were probably feeding at a higher trophic level at Cape Foulwind (L. Meynier, unpublished data). Of eight animals sampled in the winter at Cape Foulwind, seven had similar isotopic signatures to those sampled in the summer (L. Meynier, unpublished data).

In a study using satellite tracking to follow lactating female NZFSs in southern Australia, foraging trip distances and durations varied among individuals and among colonies, reflecting a high level of plasticity in foraging and provisioning strategies (Baylis et al., 2012).

2.1.4 Stable Isotope Analysis and Foraging Behaviour

Biogeochemical markers, such as stable isotopes, can be used to trace feeding ecology and migration (Crawford et al., 2008; Hobson, 1999; Hobson et al., 2010; Ramos & González-Solís, 2012), overcoming the difficulty of observing the behaviour of pinnipeds at sea (Carter et al., 2016). Stable isotope ratios in animal tissues reflect diet and nutrient assimilation (Ramos & González-Solís, 2012), provide indirect information on diet and foraging locations (Rubenstein & Hobson, 2004), and can be used to determine an individual's area of origin (Hobson, 1999; Webster et al., 2002). Samples from multiple individuals are required (Rubenstein & Hobson, 2004), however, and source populations must be isotopically distinct (Hobson, 1999).

Vibrissae are an appropriate tissue to sample as they are metabolically inert once formed and provide a permanent, sequential record of dietary consumption (West et al., 2006). Vibrissae in otariids grow continually and are retained for at least two years (Hirons, Schell, & St Aubin, 2001). Vibrissa growth rates and retention times vary among species (Hirons, Schell, & St Aubin, 2001).

Studies on NZFSs in Australia and New Zealand, and on closely related species, have shown a range of foraging strategies and stable isotope analysis (SIA) results. In some cases, individuals repeatedly forage in the same direction from the colony (Bailleul et al., 2005; Baylis et al., 2008a, 2012; Bonadonna et al., 2001; Staniland et al., 2004). There is limited tracking data for foraging NZFSs in New Zealand, but foraging in a consistent direction has not been noted (Harcourt et al., 1995, 2002; Harcourt & Davis, 1997; L. Meynier, unpublished data). In some otariid studies, foraging area fidelity changed with season (Baylis et al., 2012; Harcourt et al., 2002; Mattlin et al., 1998; Sinclair & Wilson, 1994; Thompson et al., 2003), or year (Boren, 2005). Conversely, in other studies, seasonal or inter-annual differences were not detected (Harcourt et al., 2001; Littnan & Arnould, 2002). Likewise, diving strategies can vary among individuals, seasons, years, and locations (Bailleul et al., 2005; Baylis et al., 2008b, 2008a, 2012; Boyd, 1998a; Harcourt et al., 2002; Mattlin et al., 1998; McCafferty et al., 1998; Sinclair & Wilson, 1994; Staniland et al., 2004; Thompson et al., 2003).

Otariid pup vibrissa $\delta^{13}C$ and $\delta^{15}N$ values are related to maternal foraging (Ducatez et al., 2008; Lowther and Goldsworthy, 2011; Cherel, Hobson and Guinet, 2015; Chilvers, 2017, 2021b). In this study, samples from the vibrissae of NZFS pups in seven breeding areas in New Zealand were used to construct a database of $\delta^{13}C$ and $\delta^{15}N$ values, and to determine the isotopic the niche size for each colony (Jackson et al., 2011).

2.2 Methods

2.2.1 Sampling

Vibrissa sampling was carried out between 25 January and 10 March 2023, which is 39 – 84 days after the assumed median pupping date. Based on estimated vibrissa growth rates (Chapter 3) all sampled vibrissae would have been formed in the post-natal period. As each colony was sampled only once, it was not possible to determine if there were any changes in maternal foraging over the sampling period. Vibrissae were taken from NZFS pups in seven areas: Open Bay Islands, Cape Foulwind, Wekakura Point (all West Coast, South Island), Kaikōura North (Needles Point and Ōhau Point combined), Kaikōura South, Sandymount (Otago Peninsula), and Cape Palliser (North Island), New Zealand (Figure 2, Table 2). The colonies have been ordered clockwise from southwest to southeast so that the geographically closest colonies are adjacent for comparison. All the colonies were well-established and/or well-documented, and were selected largely for logistical reasons because pups were being caught as part of mark/recapture population surveys at each location. At Wekakura Point, Cape Foulwind and Open Bay Islands, pups were sampled by DOC staff, as part of their on-going monitoring programme (data available at https://furseals.dragonfly.co.nz/). Counts at Cape Palliser (Matakitaki a Kupe) were carried out by DOC staff, members of the Rangitāne and Ngāti Kahungunu iwi, and volunteers (L. Boren, personal communication, 11 June 2024). At Kaikōura, vibrissae were collected in conjunction with a population analysis (Hall et al., 2024). At Sandymount, samples were collected from pups that were being caught as part of a long-running population survey by the Zoology Department, Otago University (Ethics permit: AUP-20-156: Fur seal monitoring for Wildlife Management).

For sampling, pups were restrained by two people. The longest vibrissa on the left side of the animal was cut as close to the skin as possible, using scissors. Vibrissae were then stored in plastic bags. All vibrissae were collected with the approval of DOC, and under Massey University Animal Ethics Permit AEC 22/60. A single vibrissa was collected from between 20 and 50 pups at each location, and the sex, body length, and body weight, were recorded for most of the individuals sampled (Table 3).

Vibrissae were individually cleaned in distilled water for five minutes, followed by 96 % ethanol for five minutes then distilled water for a further five minutes (Chilvers, 2017). All samples were examined under a stereomicroscope and any residual dirt or tissue found was scraped off using a scalpel blade and the samples rinsed again, then all samples were left to dry overnight (Chilvers, 2017). Vibrissae were stored in individual plastic bags prior to weighing. To achieve the optimum sample weight of 0.6 mg, a section approximately 1 mm long was cut from the proximal end of each vibrissa and weighed using a semi-micro analytical balance (A&D Instruments, GR-202, or equivalent scales, accurate to 0.1 mg). Each sample weighed between 0.3 and 0.8 mg (mean = 0.5 ± 0.15 mg), and was packed into an individual tin container (Cherel et al., 2009).

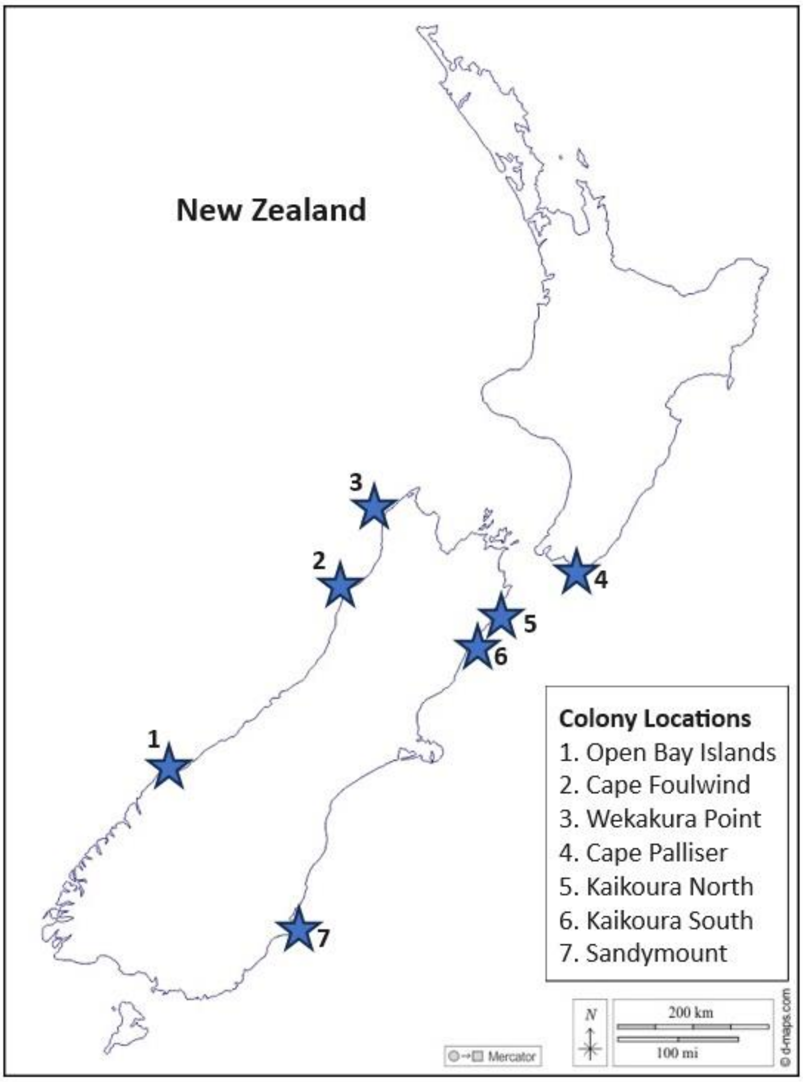


Figure 2 The locations of the seven established fur seal breeding areas from which New Zealand fur seal pup vibrissae were sampled, in New Zealand.

Samples were analysed at the Stable Isotope Laboratory at GNS Science, Upper Hutt, New Zealand, by combustion on a Eurovector elemental analyser coupled to an Isoprime mass spectrometer. Results were reported with respect to VPDB and N-Air, normalised to an internal standard; Leucine (-28.3 ‰ for $\delta^{13}C$, 6.5 ‰ for $\delta^{15}N$). The analytical precision for these measurements is 0.2 ‰ for $\delta^{13}C$ and 0.3 ‰

for $\delta^{15}N$. A series of reference materials, in duplicate, was run at the beginning and end of each sequence. A drift standard and rotating calibration standards were run after every 10 samples.

Table 2 Latitudes and longitudes of each New Zealand fur seal breeding colony sampled. For Kaikōura North, the coordinates of Ōhau Point were used as the majority of the samples came from there.

Location	**Latitude**	**Longitude**
Open Bay Islands	43.8592°S	168.8833°E
Cape Foulwind	41.7459°S	171.4872°E
Wekakura Point	40.9157°S	172.0937°E
Cape Palliser	41.6131°S	175.2732°E
Kaikōura North	42.2495°S	173.8267°E
Kaikōura South	42.4502°S	173.5741°E
Sandymount	45.8908°S	170.6841°E

2.2.2 Statistical Analysis

Statistical analysis of the $\delta^{13}C$ and $\delta^{15}N$ results from the NZFS vibrissa samples was carried out in R Studio v. 4.3.2, and all plots were visually examined for trends. As the data did not meet the requirement of homogeneity of variance (Levene's test: $\delta^{13}C$: F value 1.83, $p = 0.09$; $\delta^{15}N$: F value 2.22, $p = 0.04$), and data transformation failed to correct the problem, a permutational multivariate analysis of variance (PerMANOVA) was used (adonis2, package: 'vegan', method: 'euclidian', permutations = 999).

Linear models for $\delta^{13}C$ and $\delta^{15}N$ by latitude and longitude were constructed, with post-model checking showing the residuals were adequate but the data failed the Durbin-Watson test for autocorrelation.

The correlation between $\delta^{13}C$ and $\delta^{15}N$ values was explored using Spearman's rank correlation coefficient, as the data were not normally distributed.

Cluster analysis in R was used to group results and to compare these groups to the sampled colonies. The Shapiro-Wilk test on the overall dataset showed that $\delta^{13}C$ was normally distributed (stat 0.99, $p = 0.19$), while $\delta^{15}N$ was not (stat 0.917, $p < 10^{-7}$). The Shapiro-Wilk test applied to each colony individually showed that $\delta^{13}C$ and $\delta^{15}N$ were normally distributed in all colonies, except for $\delta^{15}N$ at Kaikōura North which was not normally distributed (stat 0.90, $p = 0.04$). The results from Ōhau Point ($n=20$) did not differ significantly from Needles Point ($n = 4$), which is approximately 48 km northeast of Ōhau Point, so these locations were combined into 'Kaikōura North'. The overall data set had no outliers, but eight data points were identified as being more than 1.5 times the interquartile range for either $\delta^{13}C$ or $\delta^{15}N$ at an individual colony (two at Kaikōura South, two at Open Bay Islands, two at Cape Foulwind, and two at Wekakura Point). If the sample weight is not within the correct range, then nitrogen saturation can prevent the carbon and nitrogen percentages (C % and N %) from being measured correctly. However, as long as the nitrogen is not completely saturated, $\delta^{13}C$ and $\delta^{15}N$ are independent of sample weight (C. Wood, personal communication, 25 January 2024). All outliers were checked for C % and N % and only one was missing the C % and N % value; in this case the sample had a low $\delta^{13}C$. In all cases outliers were either $\delta^{13}C$ or $\delta^{15}N$, but not both. There was no compelling reason to exclude any of the data points, so all were retained for analysis. The package SIBER (Stable Isotope Bayesian Ellipses in R) v. 2.1.9 (Jackson et al., 2011) was used to compare isotopic niche widths between the seven colonies. Bivariate ellipses of $\delta^{13}C$ and $\delta^{15}N$ values, with 95 % credible intervals, were plotted. Bayesian standard ellipse areas (SEA_B) were calculated using the default priors; Inverse Wishart prior on the covariance matrix, and a vague normal prior on the means, and fitted using JAGS. Standard ellipse areas (SEA_C) were corrected for sample size. Ellipse areas are measured in ‰^{2}. While normal distribution of the data is an assumption of SIBER analysis (Stable Isotope Bayesian Ellipses in R), the fact that the data do not meet the criterion of a multivariate normal distribution does not completely preclude analysis with SIBER, and may reflect underlying ecologically interesting processes (Jackson et al., 2011).

2.3 Results

In total, 147 pup vibrissa samples were analysed from the seven breeding areas. The number of samples from each location and the number with associated information (sex, animal length, animal weight) are shown in Table 3. The range in $\delta^{13}C$ values (-17.7 to -15.7 ‰) was less than the range in $\delta^{15}N$ values (14 to 18.5 ‰) (Figure 3). The mean $\delta^{13}C$ value for all samples was -16.8 ± 0.41 ‰, and mean $\delta^{15}N$ was 16.3 ± 1.16 ‰ (Table 4). The colony with the highest mean $\delta^{13}C$ was Kaikōura South (-16.1 ± 0.20 ‰), and the lowest was at Open Bay Islands (-17.0 ± 0.28 ‰), followed by Cape Foulwind (-16.9 ± 0.31 ‰) and Sandymount (-16.8 ± 0.16 ‰). The highest mean $\delta^{15}N$ was at Wekakura Point (17.6 ± 0.48 ‰) and the lowest was at Sandymount, Otago Peninsula (14.6 ± 0.42 ‰), followed by Open Bay Islands (15.0 ± 0.66 ‰). Mean $\delta^{15}N$ values at Cape Foulwind, Kaikōura North, Kaikōura South and Cape Palliser only ranged from 16.7-16.9 ‰, which is within the quoted laboratory analytical precision for $\delta^{15}N$ of 0.3 ‰.

The carbon to nitrogen ratio (C:N) can be used as a control for keratin quality(Newsome et al., 2009). In this study the C:N ratios were 2.90 – 2.95 (mean 2.93 ± 0.02).

Table 3 The number of vibrissae from each location, the number of New Zealand fur seal pups for which sex, body length (cm) and body weight (kg) were recorded, and the number of samples analysed from each location. Samples from Needles Point and Ōhau Point were combined into Kaikōura North.

Location	**Samples**	**Sex**	**Length**	**Weight**	**Analysed**
Open Bay Islands	50	50	50	50	23
Cape Foulwind	28	28	28	28	20
Wekakura Point	39	39	39	39	20
Cape Palliser	20	20	0	0	20
Needles Point	4	4	0	0	4
Ōhau Point	20	20	20	20	20
Kaikōura South	20	0	0	0	20
Sandymount	23	15	15	15	20

Table 4 The number of New Zealand fur seal pup vibrissa samples at each location, and the mean and standard deviation for δ^{13}C and δ^{15}N values (‰). Kaikōura North combines the results from Needles Point and Ōhau Point.

Location	**n**	**Mean δ^{13}C**		**sd**	**Mean δ^{15}N**		**sd**
Open Bay Is	23	-17.0	±	0.28	15.0	±	0.66
Cape Foulwind	20	-16.9	±	0.31	16.7	±	0.82
Wekakura Point	20	-16.7	±	0.18	17.6	±	0.48
Cape Palliser	20	-16.5	±	0.23	16.9	±	0.24
Kaikōura North	24	-16.4	±	0.19	16.8	±	0.48
Kaikōura South	20	-16.1	±	0.20	16.8	±	0.53
Sandymount	20	-16.8	±	0.16	14.6	±	0.42
Total samples	**147**	**-16.8**	±	**0.41**	**16.3**	±	**1.16**

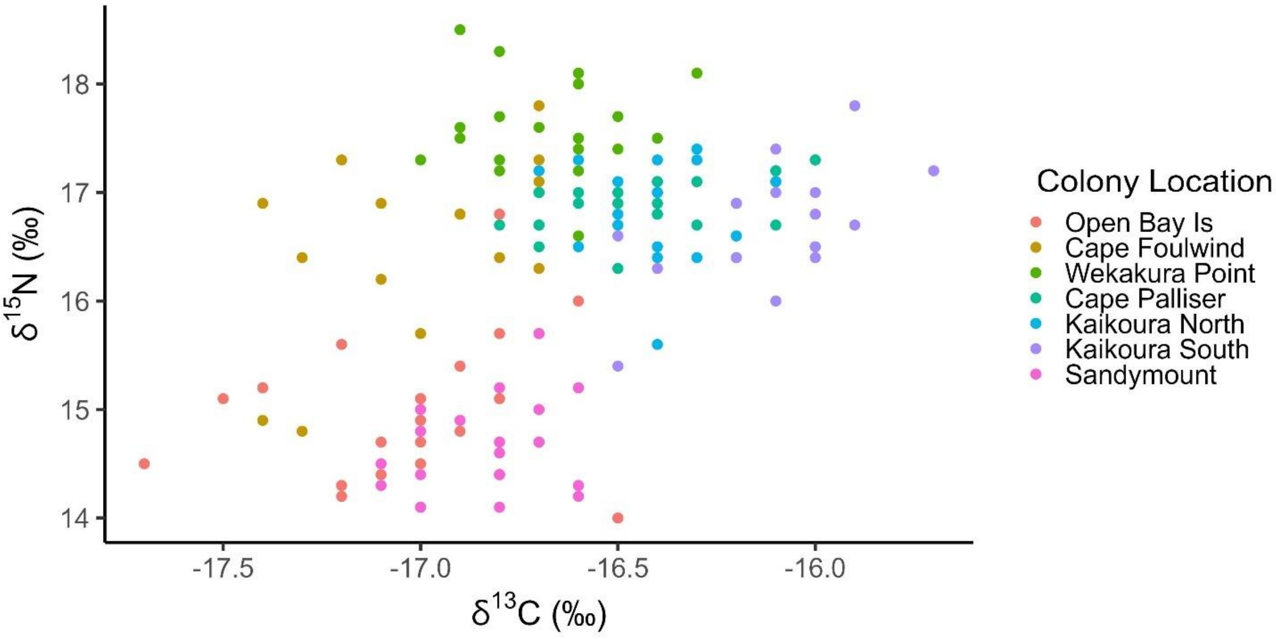


Figure 3 δ^{13}C and δ^{15}N values (‰) in the proximal vibrissa of New Zealand fur seal pups at seven breeding colonies around the coast of New Zealand. Colours represent breeding colonies.

While $\delta^{13}C$ values increased from Cape Palliser to Kaikōura North to Kaikōura South, $\delta^{15}N$ values were almost identical at the three colonies (Figure 4, Figure 5). Conversely, on the west coast $\delta^{13}C$ increased slightly from south to north, but $\delta^{15}N$ markedly increased from south to north. It is approximately 132 km from Cape Palliser to Kaikōura North, and a further 40 km around the coast to Kaikōura South. The distances between the west coast colonies are greater; approximately 327 km from Open Bay Islands to Cape Foulwind and just over 100 km between Cape Foulwind and Wekakura Point.

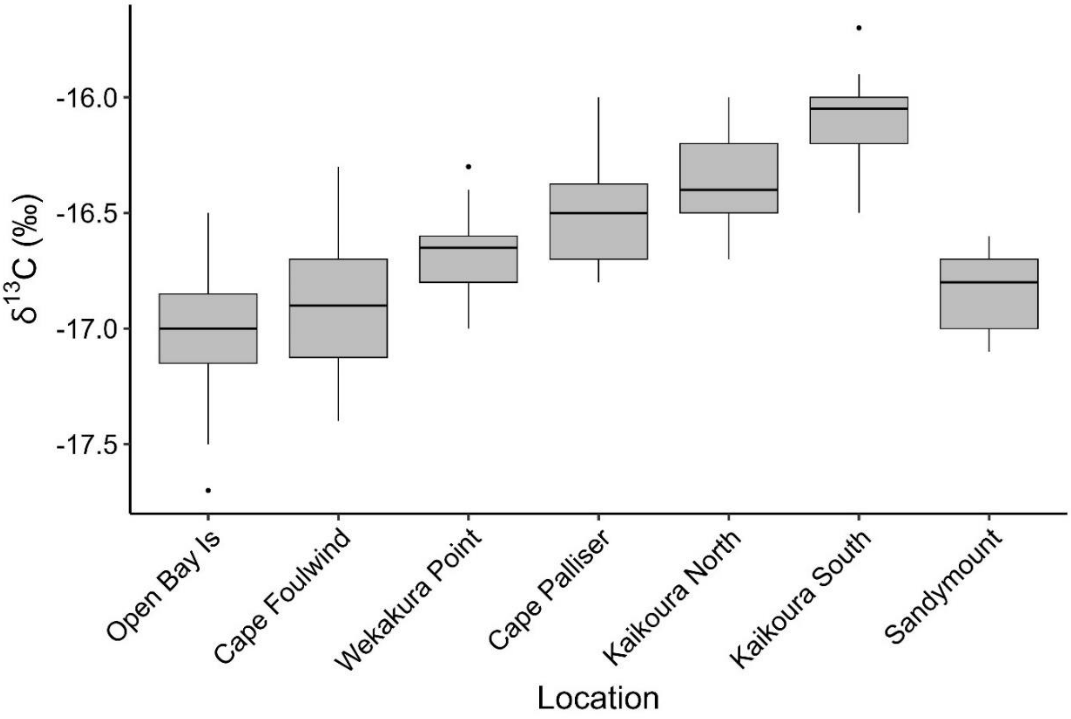


Figure 4 Boxplots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (‰) at seven established breeding colonies in New Zealand, showing medians, upper and lower quartiles and ranges. Colonies are ordered clockwise from southwest to southeast. Black dots are outliers.

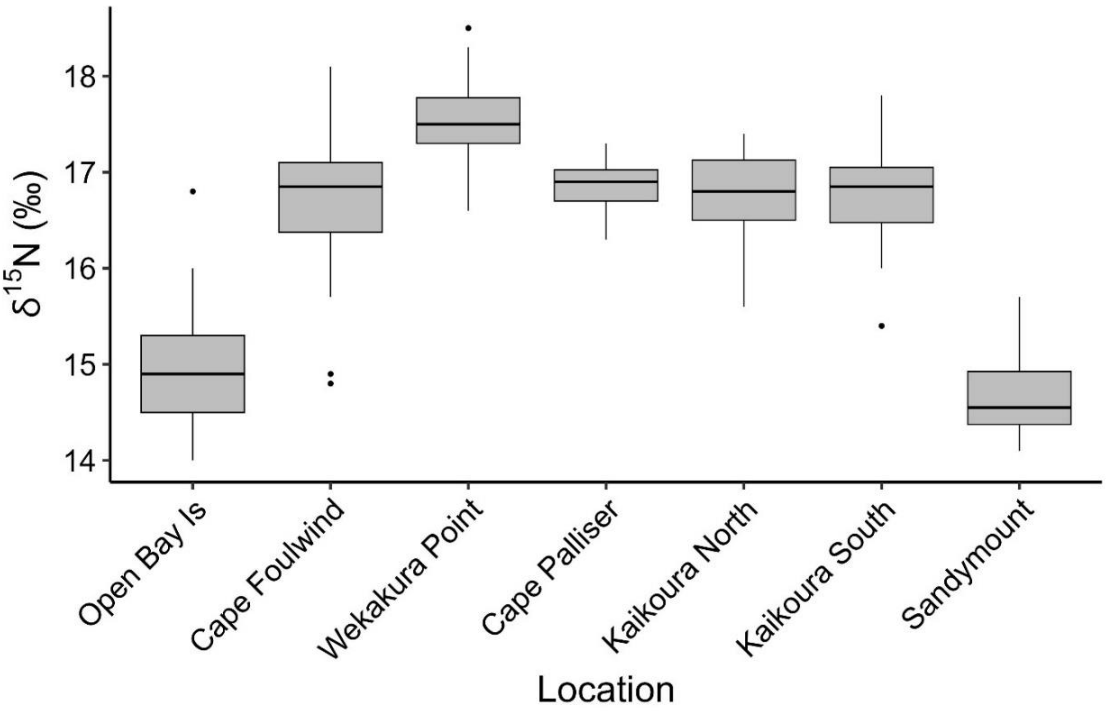


Figure 5 Boxplots of New Zealand fur seal pup vibrissa $\delta^{15}N$ (‰) at seven established breeding colonies in New Zealand, showing medians, upper and lower quartiles and ranges. Colonies are ordered clockwise from southwest to southeast. Black dots are outliers.

Permutational MANOVA analysis at the seven breeding colonies showed that location had a significant effect on $\delta^{13}C$ and $\delta^{15}N$ ($F = 76.02$, $p < 0.001$, $R^2 = 0.77$). Pairwise comparisons varied with different permutations of the analysis. The colony pairs that consistently had no significant difference were Open Bay Islands and Sandymount; Kaikōura North and Cape Palliser; and Kaikōura North and Kaikōura South (p adjusted > 0.05). In some permutations, Cape Foulwind and Cape Palliser, and Kaikōura South and Cape Palliser, were not significantly different, consistent with the overlap in $\delta^{13}C$ and $\delta^{15}N$ values in those areas (Figure 3, Figure 13). It was not possible to identify pups to their colony of origin as colonies were not sufficiently isotopically distinct.

Permutational MANOVA showed that latitude ($F = 249.65$, $p < 0.001$, $R^2 = 0.63$) and longitude ($F = 94.75$, $p < 0.001$, $R^2 = 0.40$) were significant predictors for $\delta^{13}C$ and $\delta^{15}N$. Linear modelling showed that $\delta^{13}C$ values decrease with increasing latitude ($t = 3.72$, slope -0.07, $p < 0.001$, adjusted R-squared = 0.08), and increase with increasing longitude ($t = 10.69$, slope = 0.12, $p < 10^{-15}$, adjusted R-squared = 0.44) (Figure 6, Figure 7). $\delta^{15}N$ values also decrease with increasing latitude ($t = 18.08$, slope = -0.61, $p < 10^{-15}$, adjusted R-squared = 0.69), and increase with increasing longitude ($t = 9.63$, slope = 0.35, $p < 10^{-15}$, adjusted R-squared = 0.39) (Figure 6, Figure 7).

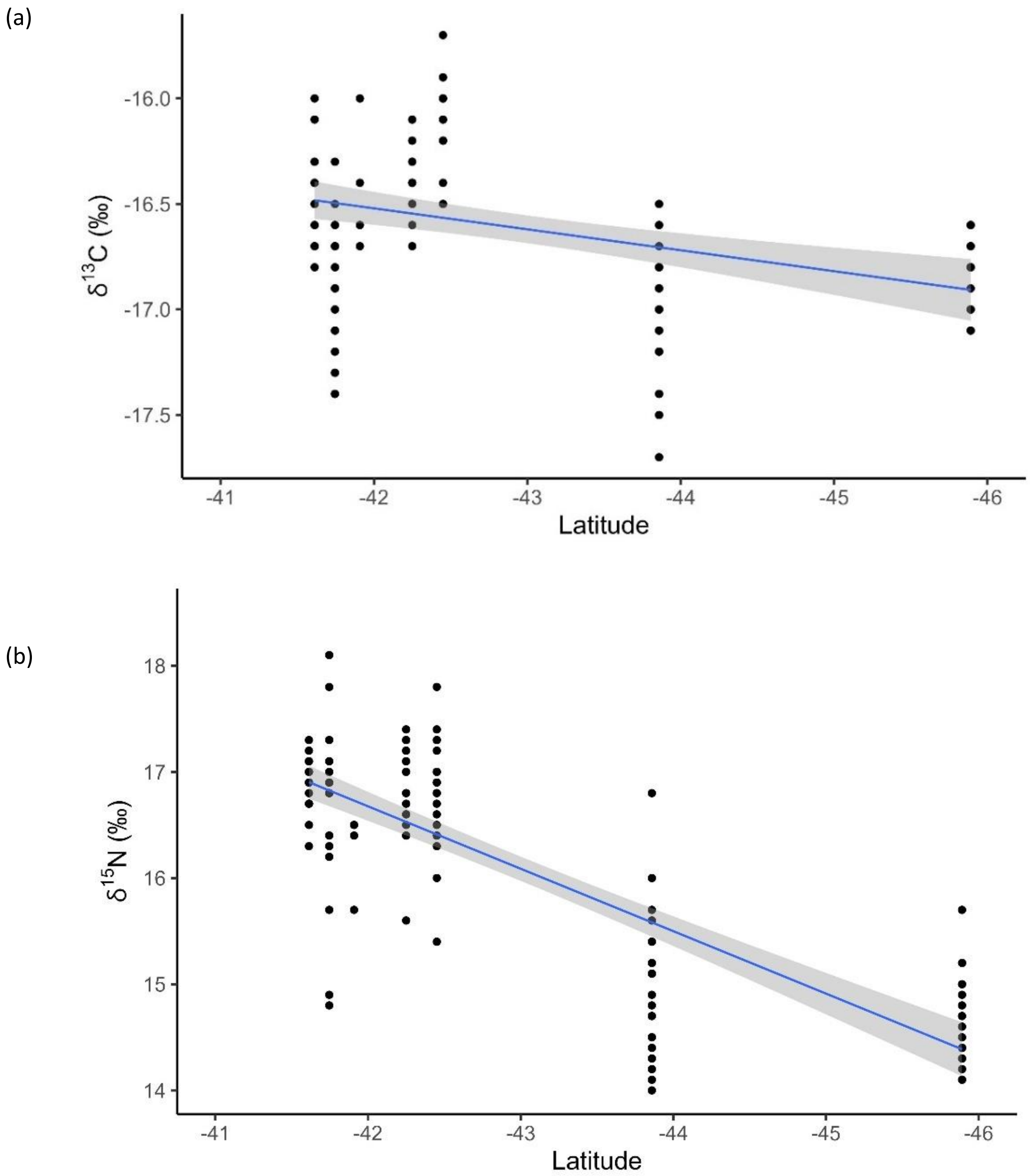
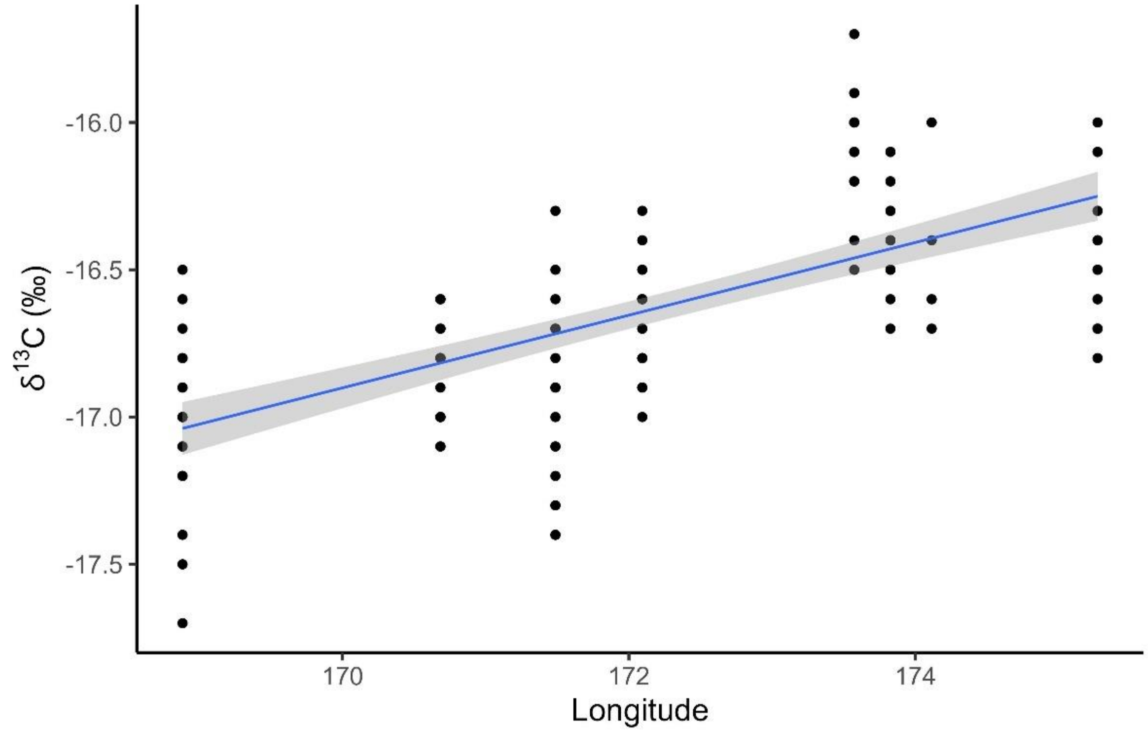


Figure 6 Scatter plots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (a) and $\delta^{15}N$ (b) values (‰) against latitude. Linear model regression line shown in blue and 95 % confidence intervals in grey shading.

(a)



(b)

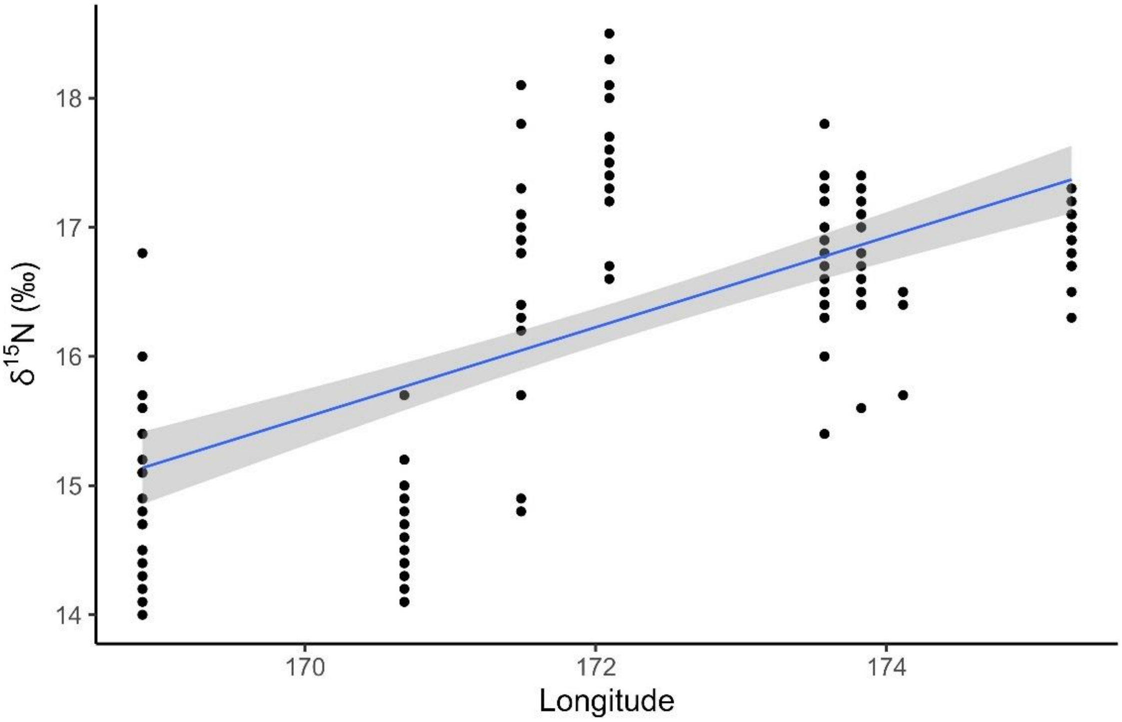


Figure 7 Scatter plots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (a) and $\delta^{15}N$ values (b) against longitude. Linear model regression line shown in blue 95 % confidence intervals in grey shading.

In the total dataset there appears to be a moderate correlation between $\delta^{13}C$ and $\delta^{15}N$ values (r = 0.44, $p < 10^{-7}$, Figure 8), however, when each colony is analysed individually, $\delta^{13}C$ and $\delta^{15}N$ values were significantly correlated only at Cape Foulwind and Kaikōura South, and borderline at Cape Palliser (Table 5).

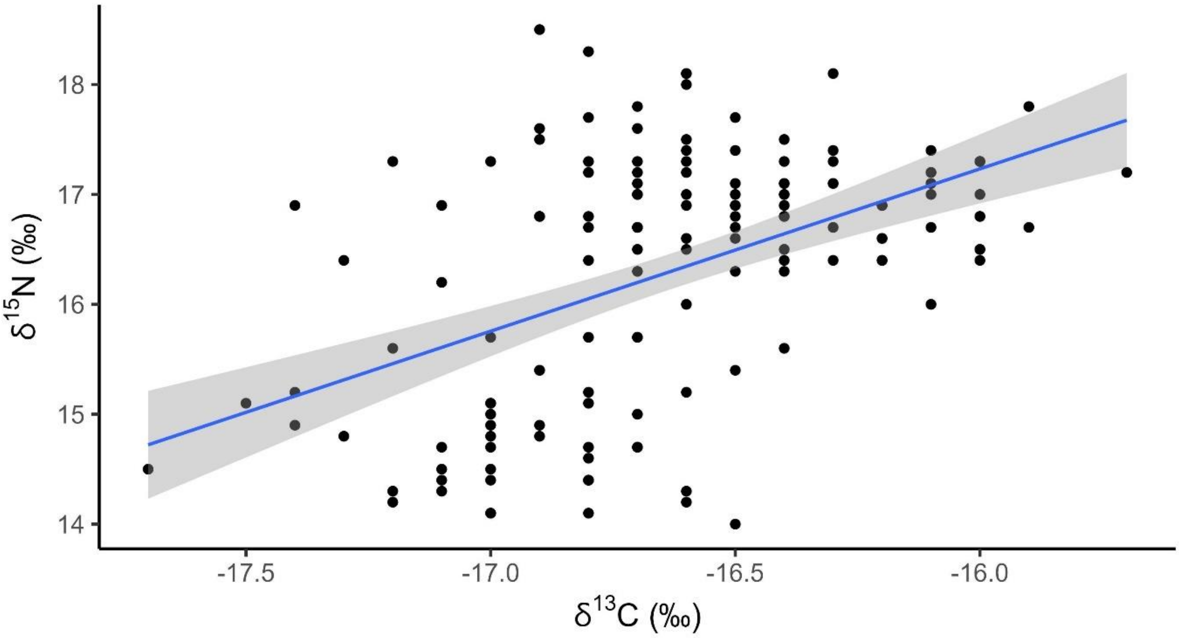


Figure 8 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in the proximal vibrissa of New Zealand fur seal pups at seven established breeding colonies in New Zealand. Correlation line is in blue, and 95 % confidence intervals in grey shading.

Table 5 The correlation between $\delta^{13}C$ and $\delta^{15}N$ values in the proximal vibrissa of New Zealand fur seal pups at seven breeding colonies around the coast of New Zealand. Correlation is the Spearman's rank correlation coefficient; n is the number of samples at each location; Strength is the strength of the correlation between $\delta^{13}C$ and $\delta^{15}N$.

Location	**n**	**Correlation**	**Strength**	**p Value**	**Significance**
Open Bay Islands	23	0.26	Weak	0.22	
Cape Foulwind	20	0.56	Strong	0.01	*
Wekakura Point	20	0.03	None	0.92	
Cape Palliser	20	0.44	Moderate	0.05	.
Kaikōura North	24	0.03	Weak	0.87	
Kaikōura South	20	0.47	Moderate	0.04	*
Sandymount	20	0.16	Weak	0.50	
All Colonies	**147**	**0.44**	**Moderate**	**$<10^{-8}$**	*******

Cluster analysis in R showed that the optimum number of clusters was either two (using within sums of squares) or three (using gap statistic). If the data were grouped into two clusters, the southern colonies on both coasts (Open Bay Islands and Sandymount) were differentiated from the northern ones. If the data were grouped into three clusters, the southern colonies remained in one cluster, while the northern colonies were distinguished on their $\delta^{13}C$ values, with the Kaikōura colonies and Cape Palliser having generally higher values than the colonies at Wekakura Point and Cape Foulwind (Figure 9 – 14). When the values are divided into two clusters, Cape Palliser and Wekakura Point samples are all in cluster one, along with most of the Kaikōura North and South samples, with mostly higher $\delta^{15}N$ values (Figures 8 – 10). Cluster two comprises all of the Sandymount samples, most of the Open Bay Islands ones and approximately a third of Cape Foulwind, with generally lower $\delta^{15}N$ values. There are 98 samples in cluster one and 49 in cluster two.

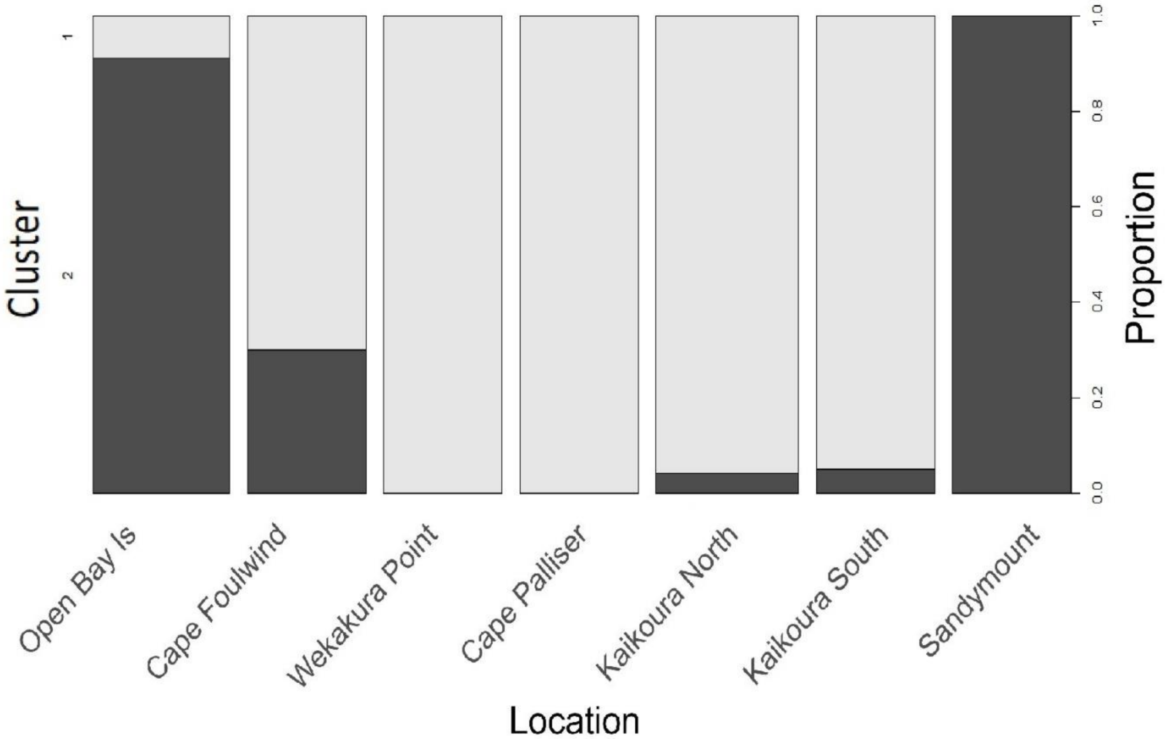


Figure 9 The proportion of New Zealand fur seal vibrissa samples in each of two clusters at seven breeding areas based on scaled $\delta^{13}C$ and $\delta^{15}N$ values. Cluster one is in light grey and cluster two is in dark grey. Colonies are ordered clockwise from southwest to southeast.

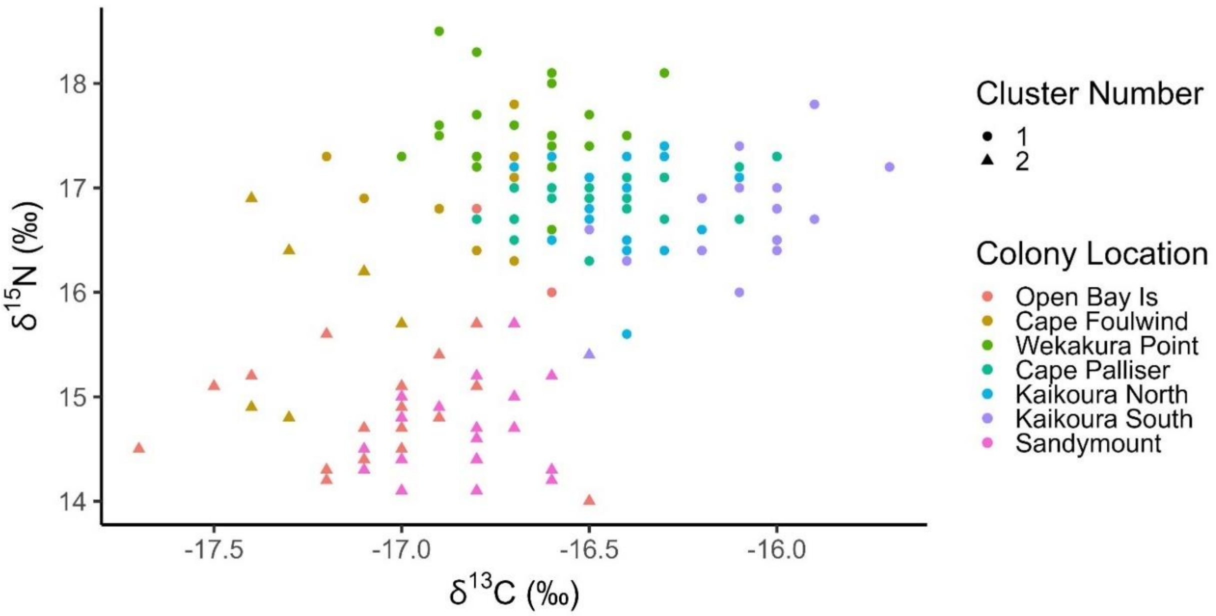


Figure 10 $\delta^{13}C$ and $\delta^{15}N$ values of vibrissa samples from New Zealand fur seals. Colours are the locations of the colonies and shape is the cluster number.

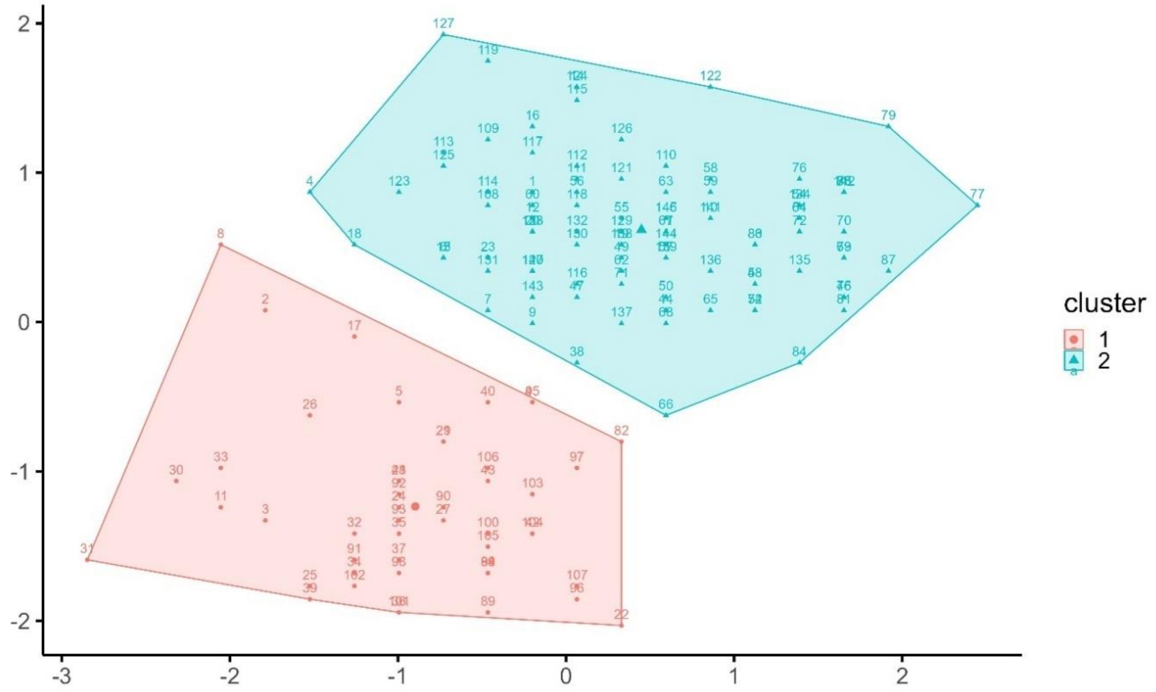


Figure 11 Scaled $\delta^{13}C$ and $\delta^{15}N$ results for New Zealand fur seal vibrissa samples allocated to two groups. Colour is cluster number and individual points are sample numbers.

Selecting three clusters gives cluster sizes of 54, 46, and 47 samples. Sandymount and Open Bay Islands remain largely in the same cluster (now cluster three), but Kaikōura North and Kaikōura South have the greatest proportions of samples in cluster two, with relatively higher $\delta^{13}C$ values, while Cape Foulwind and Wekakura Point samples are mostly in cluster one, with lower $\delta^{13}C$ values (Figure 12 – 14).

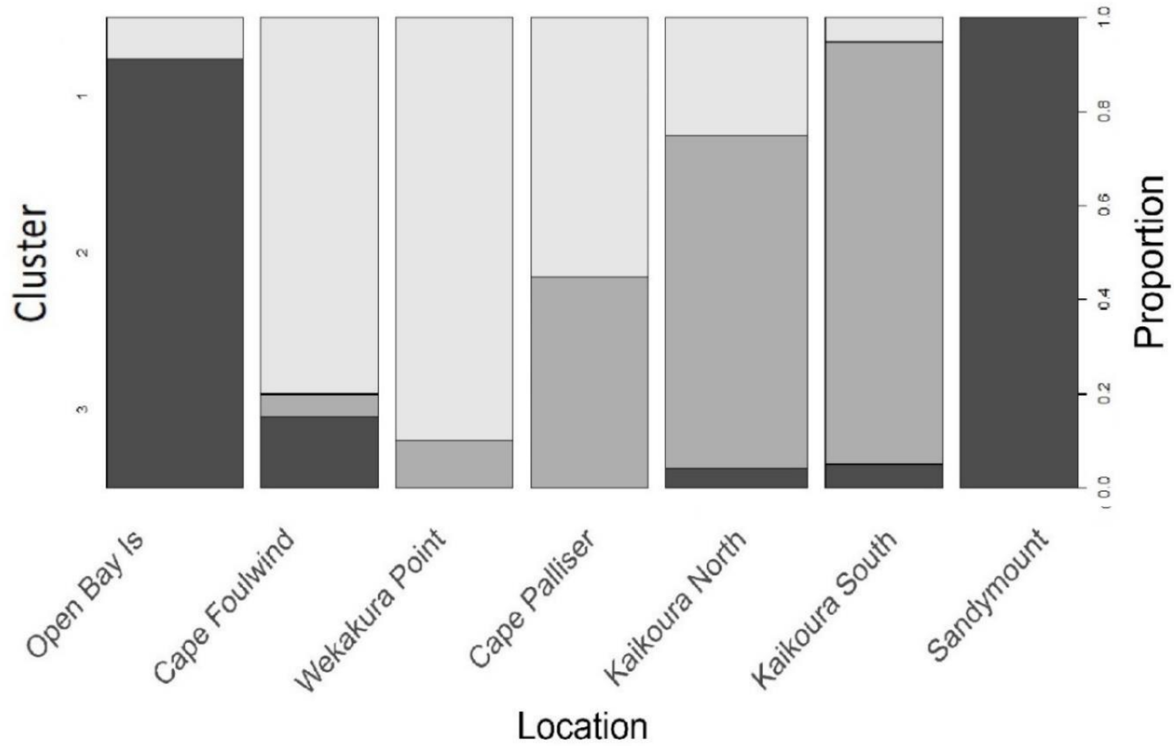


Figure 12 The proportion of New Zealand fur seal vibrissa samples in each of three clusters at seven breeding areas based on scaled $\delta^{13}C$ and $\delta^{15}N$ values. Cluster one is light grey, cluster two is middle grey and cluster three is dark grey. Colonies are ordered clockwise from southwest to southeast.

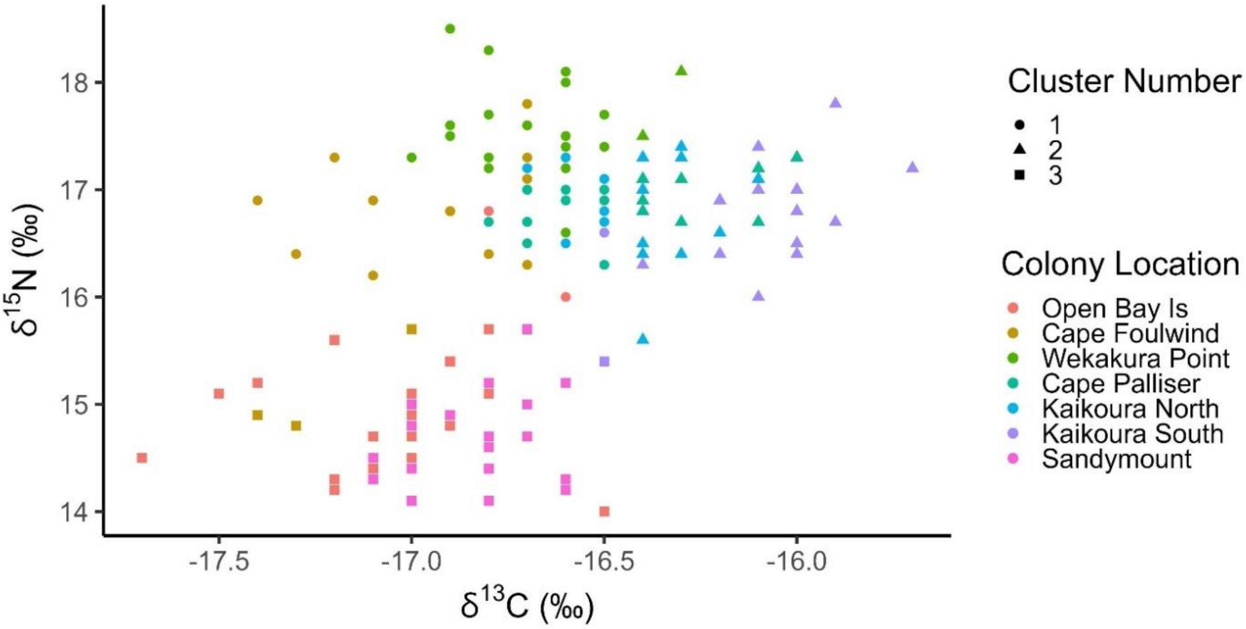


Figure 13 $\delta^{13}C$ and $\delta^{15}N$ values of vibrissa samples from New Zealand fur seals. Colours are the locations of the colonies and shape is the cluster number.

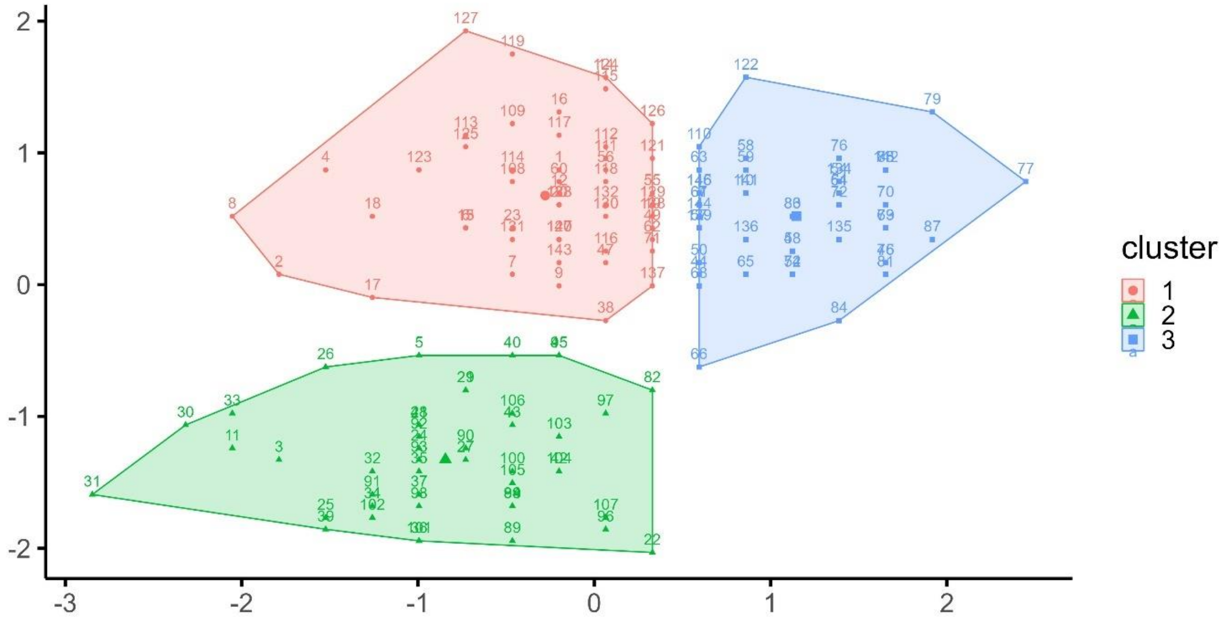


Figure 14 Scaled $\delta^{13}C$ and $\delta^{15}N$ results for New Zealand fur seal vibrissa samples allocated to three groups. Colour is cluster number and individual points are sample numbers.

The isotopic niche size can be shown graphically (Figure 15, Figure 16) and also described quantitatively (Table 6) (Jackson et al., 2011). The standard ellipse area (SEA or SEA_B) represents the size of the isotopic niche, with the SEA reaching an asymptote at n = 30. The SEA_C is corrected for sample size (Table 6). Cape Foulwind has the largest niche size (SEA_C = 0.69 ‰^{2}), with Open Bay Islands next (SEA_C = 0.59 ‰^{2}). Cape Palliser the smallest niche size (SEA_C = 0.17 ‰^{2}), with Sandymount next (SEA_C = 0.22 ‰^{2}). Isotopic niche widths can be compared among locations, and the probability that the niche at one site is smaller than another site is estimated (Table 7).

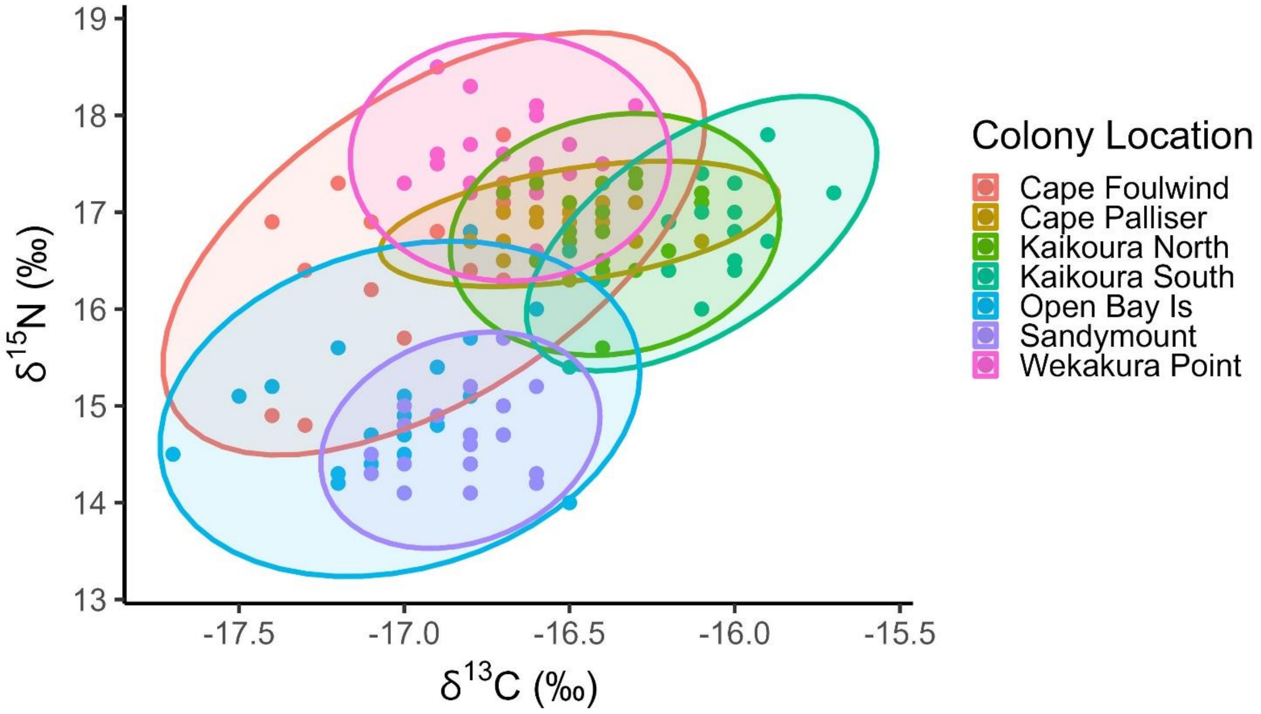


Figure 15 Bayesian ellipses at 95 % confidence intervals for $\delta^{13}C$ and $\delta^{15}N$ (‰) in vibrissa samples taken from New Zealand fur seal pups at seven established breeding colonies around New Zealand. Each colour represents a different colony.

Table 6 Group metrics for seven fur seal breeding areas in New Zealand. TA is the convex hull area, SEA is the standard ellipse area, and SEA_C is the SEA corrected for sample size effects. Units are ‰^{2}.

	Open Bay Islands	Cape Foulwind	Wekakura Point	Cape Palliser	Kaikōura North	Kaikōura South	Sandymount
TA	1.88	1.89	0.82	0.45	0.96	0.90	0.56
SEA	0.56	0.66	0.27	0.16	0.28	0.27	0.21
SEAc	0.59	0.69	0.29	0.17	0.30	0.29	0.22

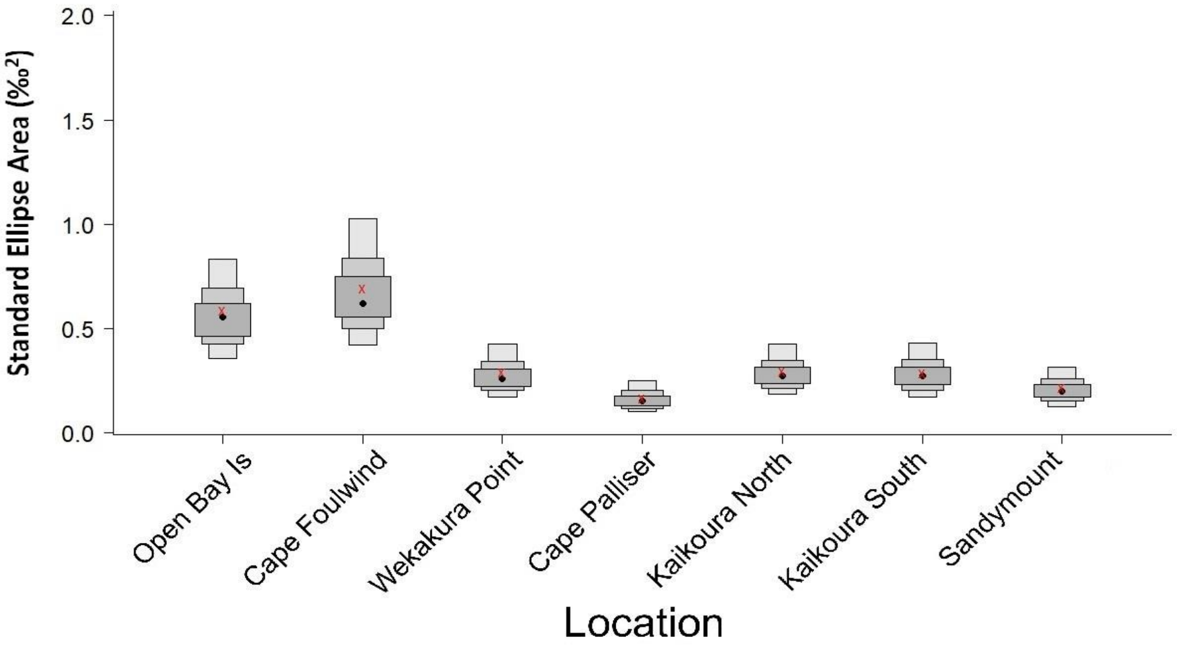


Figure 16 Standard ellipse areas (‰^{2}) of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissa sampled at seven established breeding colonies in New Zealand. Black dot represents the mode and red x represents the SEA_C (standard ellipse area corrected for sample size). Box edges from dark to light are 50 %, 75 % and 95 % CI. Colonies are ordered clockwise from southwest to southeast.

Table 7 Ellipse areas (‰^{2}) for $\delta^{13}C$ and $\delta^{15}N$ values in vibrissae from stranded New Zealand fur seal pups from three areas around the coast of the North Island, New Zealand. Probability is the probability that the ellipse area at the first site is smaller than that at the second site, expressed as the proportion of posterior draws.

First Location	**Area (‰^{2})**	**Second Location**	**Area (‰^{2})**	**Probability**
Open Bay Islands	0.56	Cape Foulwind	0.66	0.72
Open Bay Islands	0.56	Wekakura Point	0.27	0.01
Open Bay Islands	0.56	Cape Palliser	0.16	0.00
Open Bay Islands	0.56	Kaikōura North	0.28	0.01
Open Bay Islands	0.56	Kaikōura South	0.27	0.01
Open Bay Islands	0.56	Sandymount	0.21	0.00
Cape Foulwind	0.66	Wekakura Point	0.27	0.00
Cape Foulwind	0.66	Cape Palliser	0.16	0.00
Cape Foulwind	0.66	Kaikōura North	0.28	0.00
Cape Foulwind	0.66	Kaikōura South	0.27	0.00
Cape Foulwind	0.66	Sandymount	0.21	0.00
Wekakura Point	0.27	Cape Palliser	0.16	0.04
Wekakura Point	0.27	Kaikōura North	0.28	0.54
Wekakura Point	0.27	Kaikōura South	0.27	0.52
Wekakura Point	0.27	Sandymount	0.21	0.19
Cape Palliser	0.16	Kaikōura North	0.28	0.97
Cape Palliser	0.16	Kaikōura South	0.27	0.96
Cape Palliser	0.16	Sandymount	0.21	0.78
Kaikōura North	0.28	Kaikōura South	0.27	0.48
Kaikōura North	0.28	Sandymount	0.21	0.15
Kaikōura South	0.27	Sandymount	0.21	0.17

2.4 Discussion

To understand the ecological implications of the NZFS recolonising its former range, it is necessary to know how individuals disperse and which colony they originated from. Genetic studies have not provided sufficient resolution to distinguish colony of origin reliably (Dussex et al., 2016; Robertson & Gemmell, 2005), and both tagging and resighting rates are too low to provide useful data (see: www.dragonfly.co.nz). This study develops a library of SIA values from fur seal pups in seven established breeding areas in New Zealand to investigate whether the colony of origin of NZFSs can be determined from SIA of their vibrissae. Additionally, isotopic niche widths are calculated for each colony and compared between colonies.

In the seven colonies sampled, the mean $\delta^{13}C$ for each location ranged from -17.0 to -16.1 ‰, with the lowest at Open Bay Islands (-17.0 ± 0.28 ‰) and highest at Kaikōura South (-16.1 ± 0.20 ‰) (Table 4). The lowest mean $\delta^{15}N$ values were at Sandymount (14.6 ± 0.42 ‰) and Open Bay Islands (15.0 ± 0.66 ‰), the most southern colonies, while the highest was at Wekakura Point (17.6 ± 0.48 ‰), the most northern. Mean $\delta^{15}N$ values at Cape Foulwind, Kaikōura North, Kaikōura South and Cape Palliser only ranged from 16.7 – 16.9 ‰.

There were trends in $\delta^{13}C$ and $\delta^{15}N$ with changes in latitude and longitude. $\delta^{13}C$ and $\delta^{15}N$ both declined with increasing latitude and increased with increasing longitude (Figure 6, Figure 7).

The isotopic niche can be used to provide information about the ecological niche of an organism (Newsome et al., 2007). Isotopic niche widths were largest, and most variable, at Cape Foulwind and Open Bay Islands, and smallest at Cape Palliser and Sandymount (Figure 15, Figure 16, Table 6). $\delta^{13}C$ and $\delta^{15}N$ vary, depending on isotopic baseline values (Hansen et al., 2012), and physiological processes such as fractionation (Hobson et al., 1996), lactation (Cherel et al., 2015), and metabolism relating to food supply and energy requirements (Newsome, Clementz, et al., 2010).

While some of the findings, such as the similarities between Kaikōura North and South and Cape Palliser, were expected, other findings, such as the fact that Cape Foulwind is more similar to Kaikōura and Cape Palliser than it is to Wekakura Point, and the overlap between Sandymount and Open Bay Islands were unexpected. Isotopic baselines can be similar in different habitats, which can confound SIA results (Ogilvy et al., 2023). Cetaceans consuming different prey in different habitats have yielded similar SIA results (Riccialdelli et al., 2010). Oceanographic factors that could affect primary production are not well understood due to a lack of data around New Zealand (Stevens et al., 2021), and isoscapes for coastal environments are difficult to generate due to dynamic processes and fine-scale variation in isotope sources (Graham & Bury, 2019). Likewise, larger scale trends in δ^{13}C and δ^{15}N related to latitude and longitude would not necessarily be expected to hold in an inshore environment (Graham & Bury, 2019).

2.4.1 Diet and Foraging

Like other otariids, NZFSs are 'central place foragers' (Baylis, 2008), however, they are also generalised predators (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016, Harcourt et al., 2002). Lactating females alternate trips to sea with periods ashore feeding their pups, with the duration of foraging trips increasing as the pups get older (Crawley & Wilson, 1976). When foraging, pinnipeds must solve the trade-off between the quality of the prey and the distance from the colony at which it is found (Boyd, 1998b). Colony-specific foraging areas have been noted in other fur seal species (Bailleul et al., 2005; Bonadonna et al., 2001; Staniland et al., 2004), and in NZFSs in Australia (Baylis et al., 2008a, 2012), however it is not known whether NZFS at the colonies in the present study forage in specific areas.

NZFSs in southern Australia tend to feed near oceanographic fronts or upwellings, as these produce a reliable food source (Baylis et al., 2012). In New Zealand, NZFSs are thought to forage at all levels in the water column, and from inshore areas out as far as the 200 m depth contour (Harcourt et al., 1995).

There have been relatively few studies on NZFS foraging in New Zealand (Boren, 2010). At Otago Peninsula the maximum foraging distance from the colony was 78 km in summer (n = 2 individuals), 178 km in autumn (n = 3), and 162 km in winter (n = 4) (Harcourt et al., 2002). Overnight foraging trips of less than 12 hours were more common in summer than in other seasons (Harcourt et al., 2001).

There have been limited studies on NZFS diet at the present study locations, particularly in the summer. Studies on scats and regurgitates showed that squid tended to predominate in the summer at the Otago Peninsula (Fea et al., 1999; Harcourt et al., 2002). Analysis of stomach contents found barracouta (*Thyrsites atun*), octopus, and squid were the main species found at the Otago Peninsula, while barracouta, miscellaneous fish, and squid predominated at Kaikōura (Street, 1964). In the 64 NZFSs at all locations combined, squid were more commonly found in the summer and octopus in the winter (Street, 1964), however, these data were not shown for each location separately.

Scat samples collected monthly at Kaikōura between April and August 1991, showed the majority of fish species consumed were lanternfish (*Symbolophorus spp.*), but the study did not include any cephalopod component (Carey, 1991a), and only covered the autumn and winter months, whereas the diet of lactating female NZFSs in summer would be more relevant to the present study. A study using massive parallel sequencing (also known as next-generation sequencing) on scat samples from five locations around New Zealand found that Cape Palliser and Kaikōura, both sampled in winter, had the greatest overlap of prey species (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016), which is consistent with their similar isotopic values in the present study. There was little overlap in species between summer and winter diets in Kaikōura (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016), indicating seasonal variation. Cape Palliser was not sampled in the summer in that study.

Previous studies have taken samples from Ōhau Point to be representative of the whole Kaikōura area, however, the present study showed that samples from Kaikōura South (-16.1 ‰) had higher mean $\delta^{13}C$ values than Kaikōura North (-16.4 ‰), despite being only 40 km south of Ōhau Point (ANOVA: $F = 19.78$, $p < 0.0001$). Individuals from Kaikōura South may, therefore, be foraging in different areas to those from Kaikōura North. Kaikōura North and South were sampled only a few days apart, so vibrissa SIA values should be comparable. However, the West Coast colonies were sampled 35 days before Cape Palliser and 45 days before Sandymount, so there might have been changes in the diets of female NZFSs over that time which could complicate interpretation of the differences between colonies.

There is currently insufficient data on NZFSs in the study colonies to draw any firm conclusions about diet and foraging behaviour. DNA analysis of scats throughout the year and baseline SIA of prey would help to clarify NZFS diets.

2.4.2 Oceanography and Geography

The geographically closest colonies are Kaikōura North and South, approximately 40 km apart, measured around the coast, while Cape Palliser is approximately 132 km from Kaikōura North (Figure 2). Wekakura Point is approximately 340 km from both Cape Palliser and Needles Point, with Cape Foulwind a further 100 km away, and Open Bay Islands approximately 327 km from Cape Foulwind. Sandymount is approximately 460 km from Kaikōura South, and over 720 km from Open Bay Islands.

As the colonies at Cape Palliser, Kaikōura North, and Kaikōura South are geographically close and have similar isotopic results, they will be discussed together. Combined $\delta^{13}C$ and $\delta^{15}N$ values did not differ significantly between Kaikōura North and Kaikōura South, or between Kaikōura North and Cape Palliser. The Kaikōura Canyon extends to within 500 m of shore, bringing oceanic waters close inshore (Benoit-Bird et al., 2004). The 200 m contour is approximately five kilometres from shore at Cape Palliser, 12 – 25 km at Kaikōura North, and two km at Kaikōura South, with the 1000 m depth contour approximately 10 km from shore at Cape Palliser, 20 – 30 km at Kaikōura North, and 4.5 km at Kaikōura South (https://wetmaps.co.nz). The Wairarapa Coastal Current is likely to be derived from the D'Urville and Southland Currents, and the Hikurangi Eddy also affects circulation in this area (Stevens et al., 2021). Despite high tidal flows in the Greater Cook Strait (GCS) there is still considerable stratification of the waters in that area, with cool, nutrient-rich water from the Kahurangi Shoals (approximately 28 km north of Wekakura Point) known to be carried into the GCS (Stevens et al., 2021). The Kaikōura Peninsula and Canyon are a demarcation point, with the canyon providing a pathway for nutrients on seasonal upwelling currents (Reid et al., 2011). The variability in deeper temperatures at Kaikōura is primarily determined by upwelling, while variability in sea surface temperature is determined by currents along the shore (Stevens et al., 2021). A study comparing the Kaikōura Canyon (Kaikōura) and the Hokitika Canyon (West Coast, South Island, approximately 120 km south of Cape Foulwind) showed that there was a greater contribution of terrestrial sediment in the Hokitika Canyon, and the sediment was transported further out to sea, compared to Kaikōura (Gibbs et al., 2020). The distribution of sediments also depends on longshore currents (Gibbs et al., 2020; Reid et al., 2011; Stevens et al., 2021). The overlap in $\delta^{13}C$ and $\delta^{15}N$ values among individuals from Cape Palliser, Kaikōura North, and Kaikōura South may be due to similar isotopic baseline values in the trophic web, however, the difference in $\delta^{13}C$ between Kaikōura North, and Kaikōura South could also indicate fine-scale differences in baseline $\delta^{13}C$ over a relatively small area.

Of the three colony pairs that did not differ significantly, Open Bay Islands and Sandymount are the most ecologically surprising, with the values for Sandymount being a subset of Open Bay Islands, despite the colonies being over 720 km apart, around the coast, and on opposite coasts of the lower South Island. While Sandymount and Open Bay Islands were not isotopically distinct, they can be differentiated on the basis of isotopic niche width. The probability that the isotopic niche width of Open Bay Islands was greater than that of Sandymount was 1.0 (Table 7).

Off Otago, the subantarctic surface water current comes to within 28-40 km of the coast in summer and 35-50 km in winter (Jones et al., 2013) and there are many submarine canyons along the shelf break (Durante et al., 2021). Along the coast from one to 16 km offshore is a band of Neritic Water (NW) flowing northwards, characterised by lower salinity due to freshwater runoff from Fiordland and southern rivers (Hawke, 1992). NW mixes with Subtropical Water (STW) to form modified Subtropical Water (mSTW) which also flows northwards, with a low-salinity inshore band (1 – 16 km offshore) and a high-salinity offshore component (16 – 30 km offshore) (Murdoch et al., 1990). The mSTW mixes with Subantarctic Surface Water (SASW) approximately 30 km offshore, forming the Southland Front (SF, a local area of the Subtropical Front (STF)) (Chiswell et al., 2015), which has enhanced temperature and salinity gradients (Durante et al., 2021). At Cape Saunders, Otago Peninsula, the 100 m contour is approximately 10 km from the coast, and the 200 m contour between 14 – 24 km from the coast (https://wetmaps.co.nz). At Otago Peninsula in the summer, female NZFSs foraged in water shallower than the 200 m contour, and mostly at night (Harcourt et al., 1995). Two females tracked with satellite transmitters were found to be foraging up to 78 km from the colony, but always in water less than 200 m deep (Harcourt et al., 1995), so they would be feeding in NW or mSTW. The majority of NZFS prey on the east coast are pelagic or demersal species, so the recorded dive pattern of deeper, V-shaped dives at dawn and dusk, and then shallower U-shaped dives while foraging overnight is consistent with feeding on these vertically migrating species (Harcourt et al., 1995). Octopus are nocturnal, benthic, and found from inshore waters out to the 200 m depth contour (Harcourt et al., 1995). Short, nocturnal foraging trips by lactating females may reflect foraging on octopus (Harcourt et al., 1995), however, in Otago, octopus were more common in winter and spring, and arrow squid predominated in summer and autumn (Fea et al., 1999). In a study in southeastern Australia, pelagic cephalopods such as squid had lower δ^{13}C and higher δ^{15}N values than mobile benthic species such as octopus (Davenport & Bax, 2002). It is not known whether squid and octopus in New Zealand would have the same relative values.

On the West Coast, South Island, the continental shelf width varies from approximately 30 km in the north to just a few metres off Fiordland (Stevens et al., 2021). The dynamics of the inner shelf are a balance between upwelling and coastal propagation, and it is a complicated and variable system (Stevens et al., 2021). Rainfalls are high, and river catchments steep, leading to a predominance of terrigenous (derived from the earth) sediments, particularly in the area affected by the Hokitika River (Stoffers et al., 1984).

Open Bay Islands is also subject to the STF, however, the current is weaker in the Tasman and forms the southward flowing Southland Current approximately 23 km southwest of Open Bay Islands, with the more variable, probably wind-driven, Westland Current flowing northeast from there (Stanton, 1976). The colony at Open Bay Islands has access to waters ranging from relatively shallow ones along the coast to water more than 2000 m deep, so that may partly explain the wide range in δ^{13}C and δ^{15}N values. At Open Bay Islands the 200 m contour is between 10 – 22 km from the colony, with the 1000 m contour a minimum of 26 km from the colony. In a study on lactating female NZFSs at Open Bay Islands, mean dive depth in summer was 30 ± 37 m, while the maximum recorded dive depth was 274 m (in autumn) (Mattlin et al., 1998). During the summer lactating female NZFSs foraged mostly at night, and the shallow dive pattern was consistent with them feeding on pelagic, vertically migrating species such as arrow squid (Mattlin et al., 1998). Scat analysis at Open Bay Islands in May 1991 showed that lanternfish species were the predominant prey, although sample sizes were small and any cephalopod component of the diet was not determined (Carey, 1991a). In a study analysing prey

DNA from scats, Breaksea Island, Fiordland (-45.5780°S, 166.6385°E), approximately 280 km southwest of Open Bay Islands, had the greatest prey diversity of the five sites in that study (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016), which is consistent with the wide isotopic niche found in the present study, however, NZFSs at Open Bay Islands are unlikely to be foraging as far south as Breaksea Island.

At Cape Foulwind the 200 m depth contour is around 52 km from shore, and the 1000 m contour over 140 km from shore, with Wekakura Point similar at 48 km and over 200 km, respectively (https://wetmaps.co.nz). Female NZFSs at Cape Foulwind, tracked using radio-telemetry, foraged mostly in depths from 100 – 200 m, less than 30 km from shore in April, and in deeper water further offshore in July (Sinclair & Wilson, 1994). Scat analysis from samples collected at Cape Foulwind monthly from February to August 1991 showed that anchovy (*Engraulis australis*), a shallow, coastal water species, was most commonly found, followed by ahuru (*Auchenoceros punctatus*) (Carey, 1991a). Anchovy was the major prey species from May, while ahuru consumption declined from April (Carey, 1991a). There have been no recent studies on NZFS foraging at Cape Foulwind, and no studies at all at Wekakura Point. Given the wide, relatively shallow shelf, and the fact that Cape Foulwind and Wekakura Point are only around 100 km apart it would be expected that their isotopic values might be similar, but that was not the case. Mean δ^{13}C and δ^{15}N values were both higher at Wekakura Point than Cape Foulwind (Table 4), with Wekakura Point having the highest mean δ^{15}N of all the colonies. Conversely, δ^{13}C and δ^{15}N values at Cape Foulwind were more similar to those at Cape Palliser and Kaikōura North, than they were to Wekakura Point. Cape Foulwind had the widest isotopic niche of the colonies studied (0.69 ‰^{2}), while the niche width at Wekakura Point was only 0.29 ‰^{2}, implying either a greater diversity of isotopic baselines or a wider range of foraging at Cape Foulwind than at Wekakura Point.

2.4.3 Stable Isotope Values

The relationships between species and marine habitats can be complex and difficult to understand (Ballance et al., 2006). While some studies have shown differences in SIA values over small geographical scales (Ogilvy et al., 2023), there can also be overlaps in δ^{13}C and δ^{15}N values among species foraging in different locations and consuming different prey (Riccialdelli et al., 2010).

In this study, locations were selected for sampling largely for logistical reasons, and latitude and longitude were not sampled consistently enough to draw firm conclusions about their effects. Nevertheless, some trends in δ^{13}C and δ^{15}N values are consistent with other studies, particularly the decrease in $\delta^{13}C$ with increasing latitude (Graham & Bury, 2019). Both $\delta^{13}C$ and $\delta^{15}N$ tended to decline with increasing latitude and increase with increasing longitude (Figure 6, Figure 7).

The northernmost colony was Wekakura Point (latitude 40.9158°S) and the southernmost was Sandymount (latitude 45.8909°S). On a smaller scale the trends were not consistent, with an increase in $\delta^{13}C$ from Wekakura Point to Kaikōura South (Table 4, Figure 4). $\delta^{13}C$ values at Cape Foulwind, West Coast, were lower than at comparable latitudes on the east coast. In a fine-scale North American study on particulate organic matter, $\delta^{13}C$ increased with increasing latitude (Kurle & McWhorter, 2017). Locally variable conditions tend to predominate in coastal ecosystems (Graham & Bury, 2019).

Cape Palliser is the easternmost colony (longitude 175.2732°E) and Open Bay Islands is the westernmost colony (longitude 168.8833°E). There was a trend for both $\delta^{13}C$ and $\delta^{15}N$ to increase from west to east, consistent with the findings in a North American study (Kurle & McWhorter, 2017).

$\delta^{13}C$ and $\delta^{15}N$ are correlated ($r = 0.44$, $p < 0.0001$, Figure 8) in the total dataset, however, when each colony is considered individually the correlation is significant only at Cape Foulwind and Kaikōura South, and borderline at Cape Palliser (Table 5). A similar pattern is seen in Hector's dolphins (*Cephalorhynchus hectori hectori*) in the northern South Island, where there appears to be a correlation between $\delta^{13}C$ and $\delta^{15}N$ (Ogilvy et al., 2023). New Zealand sea lions at Auckland Islands (subantarctic New Zealand), were mostly either benthic feeders, with generally lower $\delta^{13}C$ and $\delta^{15}N$ values, or mesopelagic feeders, with generally higher $\delta^{13}C$ and $\delta^{15}N$ (Chilvers, 2019). Generally, benthic sources of $\delta^{13}C$ are enriched relative to pelagic sources, and inshore sources enriched relative to offshore ones (Rubenstein & Hobson, 2004), so a negative correlation between $\delta^{13}C$ and $\delta^{15}N$ might be expected, but that does not seem to be the most common pattern.

In a trophic study of a marine ecosystem in southeastern Australia, fur seals had the highest $\delta^{15}N$ values, followed by penguins, fish, pelagic cephalopods, and mobile benthos (including octopus) (Davenport & Bax, 2002). Davenport and Bax (2002) found that species with higher $\delta^{15}N$ values appeared to have higher $\delta^{13}C$. A cluster analysis showed five groups of fish species, with high trophic-level pelagic predators and benthic feeders appearing to show a relationship between $\delta^{13}C$ and $\delta^{15}N$. Conversely, three other groups (those feeding on benthic and pelagic invertebrates and fish, those consuming pelagic zooplankton and fish, and pelagic planktivores) did not seem to show that relationship (Davenport & Bax, 2002). Pelagic planktivores include some lanternfish (Davenport & Bax, 2002), and lanternfish have been shown to be an important component of the NZFS diet at Banks Peninsula (Allum & Maddigan, 2012), and at Open Bay Islands, Cape Foulwind and Kaikōura (Carey, 1991a). Base-line isotope values and a comprehensive diet analysis would be needed in order to draw firm conclusions about contemporary NZFS diets in New Zealand.

There are few studies with which to compare the current findings. A study along the top of the South Island on skin samples from Hector's dolphins showed that $\delta^{13}C$ values were significantly higher in the eastern part and $\delta^{15}N$ values were higher in the west, however, median $\delta^{13}C$ and $\delta^{15}N$ values differed by less than 1 ‰ (Ogilvy et al., 2023). In the present study, mean $\delta^{13}C$ differed by less than 1 ‰ among colonies, and mean $\delta^{15}N$ differed by up to 3 ‰. The bathymetry and biogeochemistry of the top of the South Island were thought to vary widely at a fine scale (Ogilvy et al., 2023), and the area is not directly comparable to any areas in the present study. The western part of Ogilvy et al.'s (2023) study area was Golden Bay (approximate location: 40°S, 173°E), which is east of Farewell Spit, whereas Cape Foulwind is over 200 km southwest of Farewell Spit. Hector's dolphins are generalist predators (Ogilvy et al., 2023), live in relatively shallow water, have small home ranges of 50 – 60 km, and show high levels of site fidelity (Bräger & Bräger, 2018; Rayment et al., 2009).

In an unpublished study using vibrissae from lactating female NZFSs at Ōhau Point, Kaikōura (n = 25), and Cape Foulwind (n = 29), there appeared to be minimal overlap between the colonies on a $\delta^{13}C$ and $\delta^{15}N$ biplot (L. Meynier, unpublished data). The $\delta^{13}C$ values were higher at Ōhau Point and the $\delta^{15}N$ values higher at Cape Foulwind, however, the authors noted that the difference in $\delta^{13}C$ between the two colonies was < 1 ‰ (L. Meynier, unpublished data). Analysis of proximal vibrissa segments of 69 NZFSs, including live and dead animals and a range of ages and sexes, showed $\delta^{13}C$ was significantly higher at Kaikōura than Cape Foulwind and $\delta^{15}N$ was significantly higher at Cape Foulwind than Kaikōura (Noè, 2013). In the present study, mean $\delta^{13}C$ was higher at Kaikōura North than at Cape Foulwind (Table 4, Figure 4, ANOVA: F = 51.7, $p < 0.0001$, Levene test: p = 0.03). Mean $\delta^{15}N$ was also slightly higher at Kaikōura North than at Cape Foulwind (Table 4, Figure 5), however, the difference was not significant (ANOVA: p = 0.63; Levene's test: p = 0.19). $\delta^{15}N$ at Wekakura Point was higher than at Cape Palliser (ANOVA: F = 32.0, $p < 0.0001$, Levene's test: p = 0.05), which is more consistent with other studies finding higher $\delta^{15}N$ values further west.

Cluster analysis groups the combined $\delta^{13}C$ and $\delta^{15}N$ values (Figure 9 – 14). Ideally, the number of clusters would have corresponded with the number of colonies, and there would have been minimal overlap in $\delta^{13}C$ and $\delta^{15}N$ values among colonies, however, the data formed either two or three clusters, and there was substantial overlap between $\delta^{13}C$ and $\delta^{15}N$ values. With two clusters, the higher $\delta^{13}C$ and $\delta^{15}N$ tended to be in cluster one (n = 98), and lower $\delta^{13}C$ and $\delta^{15}N$ in cluster 2 (n = 49). The group sizes were more even with three clusters (n = 46, 47 or 48), and the cluster with relatively higher $\delta^{13}C$ and $\delta^{15}N$ values is divided into two based on higher or lower $\delta^{13}C$ values.

When the data were divided into two clusters, both Cape Palliser and Wekakura Point samples were exclusively in cluster one, and Sandymount and the majority of Open Bay Islands were in cluster two (Figure 9). The higher δ^{15}N values at Cape Palliser, Wekakura Point, and the Kaikōura colonies imply that either the baseline δ^{15}N is higher in these NZFS foraging areas or that individuals at these colonies are foraging at a higher trophic level. It is very unlikely that individuals from Wekakura Point and Cape Palliser would be foraging in the same areas, so the overlap in values between these two colonies might be due to similar isotopic baselines in their respective foraging areas. Sandymount and Open Bay Islands are approximately 700 km apart and on opposite coasts, so foraging areas during the breeding season would not overlap. Their δ^{13}C and δ^{15}N values could reflect isotopic baseline similarities or a combination of differing isotopic baselines and diets leading to a coincidental overlapping of values.

If the data are allocated to one of three clusters, then some of the colonies that are geographically closest together have very comparable cluster allocations. Kaikōura North and Kaikōura South are 40 km apart and have 5 – 25 % of values in cluster one. Cape Foulwind and Wekakura Point are 100 km apart and approximately 90 % of Wekakura Point samples and 80 % of Cape Foulwind samples are in cluster one. Cape Palliser has an intermediate cluster allocation. δ^{13}C and δ^{15}N values at Sandymount and Open Bay Islands continue to cluster together.

2.4.4 Isotopic Niche Widths

The isotopic niche quantitatively represents the spread of δ^{13}C and δ^{15}N values in a group (Newsome et al., 2007). Isotopic niche widths represent diversity of foraging, are correlated to trophic niches, and can be a useful way to compare groups (Jackson et al., 2011).

Isotopic niche widths are shown quantitatively and graphically in Table 6 and Figure 16. The widest niche sizes were at Cape Foulwind (0.69 $‰^2$) and Open Bay Islands (0.59 $‰^2$). The niche width at Wekakura Point, also on the west coast of the South Island, was only 0.29 $‰^2$. While NZFSs at Open Bay Islands have access to a greater range of water depths, those at Cape Foulwind would be expected to be foraging more consistently in shallower water. The bathymetry at Cape Foulwind and Wekakura Point are similar, and yet δ^{13}C and δ^{15}N values and isotopic niche widths differ between the two colonies. SIBER (Stable Isotope Bayesian Ellipses in R) analysis assumes normal distribution of the data, although this is a general guide and not an absolute rule (Jackson et al., 2011). While δ^{13}C values were normally distributed in the present study (Shapiro-Wilk test $p = 0.19$), δ^{15}N values were not ($p < 10^{-7}$). When the Shapiro-Wilk test was applied to each colony individually, however, only δ^{15}N at

Kaikōura North was not normally distributed. There was no evidence of a bimodal distribution in the data at any of the colonies.

Pinniped pup tissues can be used as proxies for maternal foraging (Cherel et al., 2015; Chilvers, 2017, 2021b; Ducatez et al., 2008; Lowther & Goldsworthy, 2011). However, ecological and physiological processes vary, so offspring isotopic profiles will be tissue- and species-specific (Jenkins et al., 2001). While NZFS pup vibrissa δ^{13}C and δ^{15}N values are likely to be closely related to maternal δ^{13}C and δ^{15}N values, it is not possible to draw firm conclusions on maternal foraging from the present study.

After weaning the previous pup, female NZFSs feed at sea for several weeks to build up body reserves before returning to the colony to give birth (Crawley & Wilson, 1976). Milk production for approximately the first 10 days must be from body reserves, before females go on their first post-partum foraging trip. Female Antarctic fur seals (*Arctocephalus gazella*) returning from foraging stored most of the nutrients to produce milk as body lipid and protein reserves, transporting a relatively small amount as concentrated milk in the mammary glands (Arnould & Boyd, 1995). The majority (42 – 79 %) of the energy delivered to their pups was produced while ashore, from maternal body reserves (Arnould & Boyd, 1995).

In a study on Hector's dolphins in which SIBER analysis was carried out, neither δ^{13}C nor δ^{15}N values were normally distributed (Ogilvy et al., 2023). In that study, the niche widths at Golden Bay, further west, were greater than those at Queen Charlotte Sound and Cloudy Bay. Niche widths in the present study were largest at Cape Foulwind and Open Bay Islands, while nearby Wekakura Point had one of the smaller niche widths. The locations are not directly comparable between studies, as the Hector's dolphins were sampled at locations along the top of the South Island (Ogilvy et al., 2023), whereas the NZFSs were sampled on the east and west coasts of the South Island.

SIBER analysis of niche widths reaches an asymptote at a sample size of 30 (Jackson et al., 2011). In the present study there were 20 – 24 samples per colony, so increasing the number of samples could have refined the niche width, however, the $\mathrm{SEA_C}$ (standard ellipse area – corrected for sample size) was only 0.01 to 0.03 ‰^{2} greater than the $\mathrm{SEA_B}$ (not corrected for sample size) at each colony so it is unlikely that increasing the sample size would have greatly affected the overall results (Table 6). There were two outliers at Cape Foulwind with low δ^{15}N, and removing these could reduce the niche width there, however, there was no convincing reason to exclude those data points.

2.4.5 Study Constraints and Future Research

NZFS demographic parameters and foraging ecology are not completely understood, therefore, there are several limitations to this study.

It is important that the vibrissa tissue sampled grew after birth, as the relationship between maternal and foetal $\delta^{13}C$ and $\delta^{15}N$ values has not been studied in NZFSs and appears to be pair-specific in other pinnipeds (Lübcker et al., 2020). Pups sampled at Open Bay Islands, Cape Foulwind and Wekakura Point could have had a median age of six to seven weeks, based on an assumed median pupping date of 16 December (Boren, Muller, et al., 2006). In a previous study it was noted that contamination of the proximal 5 mm of the vibrissa with neural tissue indicated that 5 mm of the vibrissa was below skin level (Noè, 2013), although presumably the neural tissue would be derived from the follicle-sinus complex in the subcutaneous tissue, not the epidermis. In Steller sea lions (*Eumetopius jubatus*), 6 – 12 mm of vibrissa was below the epidermis, which was 3 – 5 % of the total vibrissa length (Rea et al., 2015). In the present study, several vibrissae plucked from stranded NZFSs (Chapter 3) were visibly discoloured for the proximal 10 mm, indicating that there could be 10 mm of vibrissa below the level of the epidermis in animals eight to nine months of age, or older. As pups are smaller, if it is assumed that vibrissae cut at the level of the skin omit the proximal 5 mm of vibrissa, and if the growth rate is assumed to be 0.29 mm/day, then that 5 mm would represent around 17 days of growth, so samples taken from the proximal vibrissa would represent post-natal growth. If there was 10 mm of the vibrissa below the level of the epidermis and it grew at only 0.22 mm/day (the growth rate from Jones et al., 2020) then that would represent 45 days of growth. It is likely that growth rates of young pups are higher than the average for an eight-month-old pup (Rea et al., 2015), and that the length of the proximal section of vibrissa is less than 10 mm. As pups were sampled at 39 – 84 days after the assumed median pupping date, the $\delta^{13}C$ and $\delta^{15}N$ in their vibrissae should reflect maternal body reserves derived from feeding in late spring and possibly early summer. As it was not possible to collect all the samples at the same time, there could be changes in maternal foraging, for example between early and late summer, that are not accounted for in this study. In a study on South American fur seal (*Arctocephalus australis*) young-of-the-year, $\delta^{15}N$ increased steadily along the vibrissa length from birth to at least eight months of age, probably due to the increased duration of fasting while the mothers were foraging (Jones et al., 2020). Conversely, in the present study the highest $\delta^{15}N$ was at Wekakura Point, one of the first colonies sampled, and the lowest was at Sandymount, the last colony sampled. Considerable intra-individual variation was shown from analysing 160 random vibrissa sections from four males and four females at Kaikōura (Noè, 2013), but it was not possible to assess intra-individual variation in the present study, as only one sample was analysed from each animal.

This study was the first to create a database of δ^{13}C and δ^{15}N values in NZFS pup vibrissae. While it is unlikely that this database can be used to determine the origin of stranded or bycaught animals, it could be used as a baseline with which to compare future samples to assess trends in maternal foraging. Sea surface temperature anomalies are known to affect prey availability (Fraser & Lalas, 2004; Ono et al., 1987; Page et al., 2005a) and the survival of high-level predators (Adame et al., 2020; Beauplet et al., 2005; Gálvez et al., 2020), and vulnerable coastal species are increasingly subject to the effects of climate change (Bond & Lavers, 2014; Keegan et al., 2022; Roberts & Hendriks, 2022). Ongoing measurement of δ^{13}C and δ^{15}N values in pup vibrissae, and comparison of isotopic niche widths among groups over multiple seasons, would, therefore, be a valuable and cost-effective way to monitor the ecological impacts of changing climate on the NZFS.

2.5 Conclusions

- A database of δ^{13}C and δ^{15}N values of NZFS pup vibrissae from seven established breeding areas was compiled.
- The combined δ^{13}C and δ^{15}N values differed significantly among most of the sampled NZFS colonies in New Zealand.
- The most similar δ^{13}C and δ^{15}N values did not necessarily occur in the geographically closest colonies.
- There was a trend for δ^{13}C and δ^{15}N values to decrease with increasing latitude and increase with increasing longitude, however, this was not consistent at a fine scale.
- Isotopic niche widths varied among colonies, being larger at two of the three west coast colonies.
- There appears to be insufficient data on oceanography, baseline δ^{13}C and δ^{15}N values, and NZFS foraging and physiology, to draw firm conclusions about what NZFSs are feeding on.
- There is likely to be insufficient separation of δ^{13}C and δ^{15}N values among colonies to determine the colony of origin of stranded or bycaught individuals solely from SIA.

Chapter 3. The use of δ^{13}C and δ^{15}N values in New Zealand fur seal pup vibrissae to determine the area of origin of stranded individuals in Northland and Hawkes Bay, New Zealand

Abstract

The New Zealand fur seal/kekeno (*Arctocephalus forsteri,* NZFS) is a marine predator native to Aotearoa/New Zealand. After being almost eradicated by hunting, it is recolonising its former range, however, little is known about its dispersal around New Zealand in the non-breeding season. As an alternative to external marking, intrinsic biogeochemical markers can be used to trace foraging ecology and migration. Stable isotope analysis (SIA) is increasingly being used to study diet, trophic level, and movement patterns in marine mammals.

Vibrissae from stranded (deceased) NZFS young-of-the-year (hereafter 'YOY') were collected opportunistically from non-breeding sites on the east and west coasts of parts of Northland, and Napier, Hawkes Bay, New Zealand. δ^{13}C and δ^{15}N values in the proximal vibrissa and in a section two-thirds of the length from the base were measured, and the values compared to results from samples taken from pups at seven established breeding colonies (Chapter 2) to establish whether stranded animals could be identified to their colony of origin. Values from stranded animals overlapped almost completely with those from pups at the breeding colonies, so it was not possible to determine their colony of origin.

Isotopic niche widths represent diversity of foraging and can be quantified as standard ellipse areas (SEAs). SEAs were calculated for the east and west coasts of Northland and for Napier and compared to the SEAs at the colonies. Isotopic niche widths were greater for stranded individuals than for pups at colonies, and, for stranded individuals, greater for samples at the base of the vibrissa than for samples two-thirds along the length, implying that the weaned NZFS pups in this study foraged more diversely than their mothers.

To interpret sequential values along the vibrissa, it is necessary to know an accurate, age-specific vibrissa growth rate. It is useful to be able to calculate the vibrissa length at birth to help distinguish between stranded YOY and non-pups. Vibrissa growth rates and estimated vibrissa lengths at birth were calculated using linear regression on the colony and stranded samples, with a mean growth rate of 0.21 mm/day for colony samples and 0.24 mm/day for all samples combined. Consistent with other otariid studies, there is likely to be a wide range of individual growth rates. The estimated vibrissa

length at birth for all samples was 55 ± 11 mm (range: colony samples 30 – 78 mm; stranded samples 22 – 84 mm).

In this study, the decrease in mean $\delta^{15}N$ between samples from two-thirds of the vibrissa length and samples from the base was 4.7 ‰, which is equivalent to a trophic level, and consistent with pups being weaned in the intervening period. Based on the median pupping date, the estimated maximum age at weaning is 223 to 247 days, which is less than any of the published lactation lengths for NZFSs.

SIA is relatively non-invasive and cost-effective technique. Quantifying isotopic niche width provides useful information on the ecology of this mobile and variable species.

Research Objectives

- Measure lengths of vibrissae from pups at colonies and from stranded young-of-the-year to estimate vibrissa growth rate, and vibrissa length at birth.
- Collect vibrissae from stranded New Zealand fur seals in northern New Zealand and analyse these for $\delta^{13}C$ and $\delta^{15}N$. Compare values from the base of the vibrissa to values from a section at two-thirds of the length, corresponding to the period when young-of-the-year would have been at the natal colony.
- Compare the $\delta^{13}C$ and $\delta^{15}N$ values at two-thirds of the vibrissa length to a database of samples taken from New Zealand fur seal pups at seven breeding colonies (Chapter 2).
- Calculate and compare isotopic niche widths among stranded groups and colonies.
- Use the results from the base section to estimate the latest possible weaning date of stranded young-of-the-year and compare that to the literature.

3.1 Introduction

The New Zealand fur seal/kekeno (*Arctocephalus forsteri*, Lesson, 1828, hereafter 'NZFS') is a mobile, high-level predator, dispersing from breeding colonies in the South Island and southern North Island, New Zealand, to sites as far north as Three Kings Islands and as far south as Macquarie Island in the non-breeding season (Crawley & Wilson, 1976). Despite their expanding range (Lalas & Bradshaw, 2001), and apparently increasing population (Baker et al., 2019), they are still vulnerable to anthropogenic threats, (Abraham et al., 2021; Abraham & Berkenbusch, 2017; Hamer & Goldsworthy, 2006; Lalas & Bradshaw, 2001). Furthermore, the increasing effects of climate change are expected to be the greatest threat to pinnipeds worldwide (Kovacs et al., 2012).

A Citizen Science study in 2021 (Lee, 2022), identified that a number of stranded NZFSs were being found in the Hauraki Gulf/Coromandel area (east coast, northern North Island, New Zealand), including young-of-the-year (hereafter 'YOY'), from as early as 15 August 2021 (S. Lee, unpublished data). August 15th is only 242 days from the median pupping date, while the median weaning time for the species is considered to be 294 days (Boren 2005). There are no known breeding locations in the Hauraki Gulf/Coromandel area (Galbraith, 2022), so these YOY were either from unidentified breeding locations in northern New Zealand, or had travelled to the area after weaning. Little is known about NZFS fine-scale dispersal outside the breeding season, and the suspicion that NZFS pups may be weaning earlier than expected warranted further investigation. This study, therefore, uses stable isotope analysis (SIA) to explore NZFS dispersion in northern New Zealand, possible weaning dates, and isotopic niche widths.

As an alternative to external marking, intrinsic biogeochemical markers, such as stable isotopes, can be used to trace foraging ecology and migration (Newsome, Clementz, et al., 2010; Ramos & González-Solís, 2012). Furthermore, isotopic niche size can be described statistically and provides ecologically relevant information on individuals, populations, and communities (Jackson et al., 2011).

Fur seal pup vibrissae are metabolically inert, relatively easy to sample, and provide a sequential record of nutrient intake derived from maternal milk (Jones et al., 2020). In this study, SIA was used on vibrissa samples from NZFS pups at colonies, and from stranded (deceased) YOY in northern New Zealand, to compare δ^{13}C and δ^{15}N values and isotopic niche widths. δ^{13}C and δ^{15}N values in sections from the base and from two-thirds of the length of the vibrissa (hereafter 'two-thirds') (Figure 18) in stranded individuals were compared. The latest possible weaning date for stranded individuals was calculated.

Vibrissae are one of the tissues increasingly being used for SIA, but it is necessary to know an accurate, age-specific growth rate in order to interpret sequential values along the vibrissa (Rea et al., 2015). Vibrissa growth rates have been measured in various pinniped species and age classes using different techniques, including cut/regrowth, glycine injection, and annual oscillations (e.g., Rea et al., 2015, Foo et al., 2019; Table 8). When using oscillations to calculate vibrissa growth rates, it is assumed that large isotopic oscillations along a vibrissa are annual (Hirons, Schell, & St Aubin, 2001), although that may not be the case (Rea et al., 2015). Growth rates vary, so caution should be used if applying these rates to different species and age-classes of animals (Foo et al., 2019).

Although the length of vibrissae at birth has not been documented for pinnipeds, the majority of the growth is thought to occur in the third trimester, and Steller sea lion (*Eumetopias jubatus*) vibrissae were an estimated 77.9 ± 12.5 mm at birth (Scherer et al., 2015). South American fur seal (*Arctocephalus australis*) vibrissae measured 92.8 ± 3.8 mm at approximately 8 months of age, and grew at about 0.22 ± 0.04 mm/day, based on the minimum $\delta^{15}N$ value in the vibrissa occurring around the time of birth (Jones et al., 2020). Within a species and age-class there is a relatively wide range of growth rates, with female Antarctic fur seal (*Arctocephalus gazella*) vibrissa growth rates outside the breeding season varying from 0.04 – 0.21 mm/d (Walters et al., 2020). Table 8 shows the most relevant growth rates for NZFSs are 0.18 mm/d for adult females (Foo et al., 2019) with Steller sea lion YOY having a vibrissa growth rate approximately twice that of adults (Rea et al., 2015).

In many mammals, mortality rates are high during the period immediately following weaning (Reiter et al., 1978). Post-weaning mortality was higher than pre-weaning mortality in subantarctic fur seals (*Arctocephalus tropicalis*) (Beauplet et al., 2005). Post-weaning survival increases with higher pre-weaning growth rates and is negatively correlated with sea surface temperature anomalies (SSTA) in the first six months after weaning (Beauplet et al., 2005). Earlier weaned California sea lions (*Zalophus californianus*) lost more muscle mass and took longer to recover that muscle than later weaned individuals (Davis, 2014). In El Niño conditions, California sea lion pups grew more slowly and had higher mortality rates (Ono et al., 1987). A decrease in California sea lion populations was correlated with higher sea surface temperatures (Adame et al., 2020).

Table 8 Vibrissa growth rates in different species and age classes of otariids

Species	Age Class	Number	Technique	Growth Rate	Reference
Steller sea lion	Subadult (captive)	2	Cut/regrowth	0.14 and 0.17 mm/d	Hirons, Schell, & St Aubin, 2001
Steller sea lion	Adult (captive)	2	Glycine injection	0.05 to 0.07 mm/d	Hirons, Schell, & St Aubin, 2001
Steller sea lion	Adult + Subadult (wild)	30	Seasonal oscillation	0.08-0.15 mm/d	Hirons, Schell, & St Aubin, 2001
Steller sea lion	Adult	18	Seasonal oscillation	0.44 ± 0.15 cm/month	Rea et al., 2015
Steller sea lion	Subadult	11	Seasonal oscillation	0.61 ± 0.10 cm/month	Rea et al., 2015
Steller sea lion	Young of year	43	Cut/regrowth	0.87 ± 0.28 cm/month	Rea et al., 2015
Steller sea lion	Foetus	4	Inferred from maternal growth	0.73 ± 0.05 cm/ month	Rea et al., 2015
Antarctic fur seal	Adult female (wild)	8	Cut/regrowth	0.14 ± 0.04 mm/d	Walters et al., 2020
Antarctic fur seal	Adult female (wild)	24	Cut/regrowth	0.11 ± 0.04 mm/d	Walters et al., 2020
Antarctic fur seal	Adult female (wild)	20	Cut/regrowth	0.10 ± 0.04 mm/d	Walters et al., 2020
Antarctic fur seal	Adult male (wild)	10	Seasonal oscillation	0.13 ± 0.02 mm/d	Cherel et al., 2009
New Zealand fur seal	Adult female (wild)	18	Cut/regrowth	0.18 ± 0.04 mm/d	Foo et al., 2019
New Zealand fur seal	Adult female (wild)	8	Glycine injection	0.19 ± 0.05 mm/d	Foo et al., 2019
New Zealand sea lion	Adult female (wild)	35	Known age	0.03 (0.01-0.05) mm/d	Chilvers, 2019
South American fur seal	Pup (wild)	10	$\delta^{15}N$ nadir at birth	0.67 ± 0.14 cm/month	Jones et al., 2020
Australian fur seal	Adult female (wild)	10	Seasonal oscillation	0.09 ± 0.03 mm/d	Kernaléguen, et. al., 2016

3.2 Methods

Vibrissae were collected opportunistically from a total of 30 stranded NZFSs on the east and west coasts of Northland between 16 September and 7 October 2023, and from seven NZFSs at Napier, Hawkes Bay, between 7 September and 1 October 2023. Vibrissae were collected from between 35.5822°S, 173.4011°E and 36.1557°S, 173.9187°E on the west coast of Northland; between 35.7866°S, 174.5509°E and 36.0207°S, 174.5006°E on the east coast of Northland; and between 39.3772°S, 176.8944°E and 39.4800°S, 176.8880°E at Napier, Hawkes Bay.

The general areas in which samples were collected are shown in Figure 17. Of the 30 stranded animals from the east and west coasts of Northland, 22 were initially identified as YOY, five as adults, and three as unknown. To try to ensure that YOY were distinguished from other age classes, all stranded animals were visually assessed for appearance and photographed, and, where possible, their curvilinear lengths were measured. The longest vibrissa was measured, and the estimated vibrissa length at birth (EVLB) calculated.

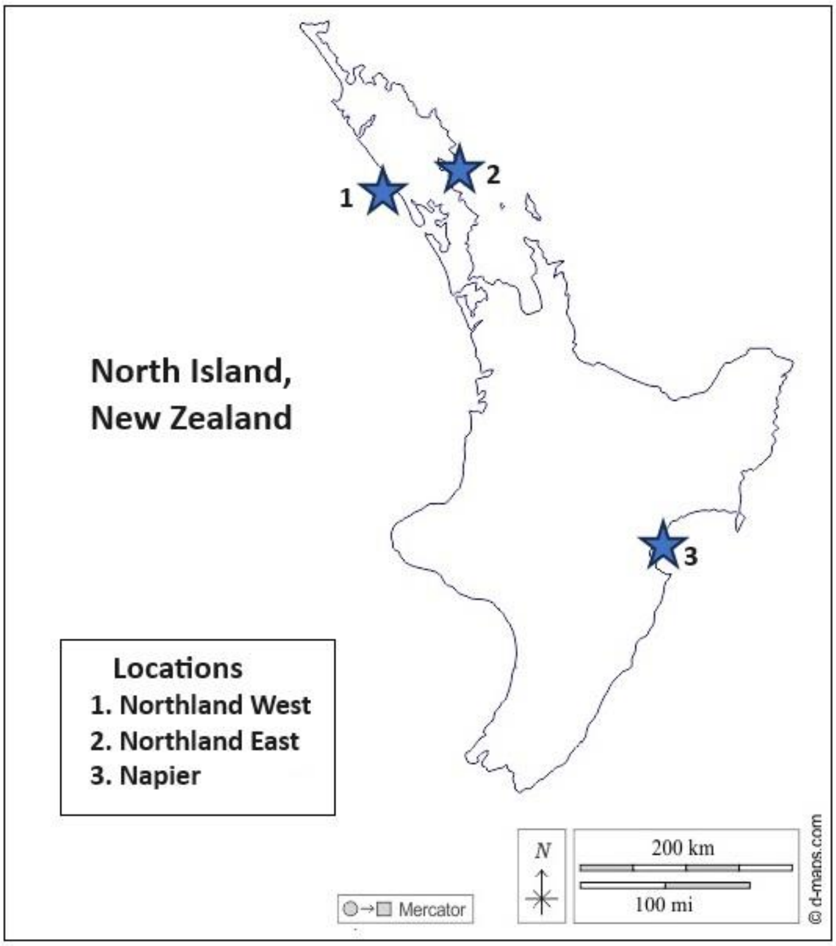


Figure 17 The general areas from which vibrissae were collected from stranded New Zealand fur seals in Northland and in Napier, Hawkes Bay, New Zealand.

3.2.1 Vibrissa length calculations

All vibrissae collected were measured prior to cleaning, and 10 mm was subtracted from the length of each plucked vibrissa to make it comparable to the length of a cut vibrissa. The vibrissa length at birth was estimated and compared to that of the samples from the breeding colonies, as described below.

The vibrissa growth rates from all colony samples, and from the combined colony and stranded samples, were calculated using linear regression in R Studio. The growth rates derived from linear modelling were used to calculate the estimated vibrissa length at birth (EVLB) for each individual.

One of the criteria for determining whether stranded animals were YOY or not was whether their estimated vibrissa length at birth (EVLB) was consistent with the EVLB of pups sampled at the breeding colonies. As far as is known, there are no data on the length of vibrissae at birth in the NZFS, and this study constitutes the first attempt to estimate vibrissa growth rates, and to calculate EVLB in this species.

In addition, vibrissa growth rates were calculated using linear regression on several subsets of the dataset: Sandymount and Open Bay Islands (45 days between samplings), combined West Coast colonies and combined Kaikōura colonies (22 – 28 days between samplings), and Sandymount and combined Kaikōura colonies (17 – 21 days between samplings). The combinations were chosen to increase the sample size by combining vibrissa lengths of pups from colonies that were sampled within a few days of each other, and colony pairs were chosen to maximise the number of days between samples, to increase the accuracy of the calculated growth rates. The three West Coast colonies were sampled over a three-day period, and the three Kaikōura colonies were sampled up to four days apart. Open Bay Islands was the first colony sampled, and Sandymount the last, 45 days later.

To calculate the estimated vibrissa length at birth:

$$\text{EVLB} = \text{Vibrissa length} - (\text{Days post} \times \text{Vibrissa growth rate})$$

where vibrissa length is the length of the vibrissa from skin level to the tip, days post is the number of days from median pupping date to collection date, and vibrissa growth rate is the growth rate derived from linear regression analysis.

In Northland, all vibrissae were plucked from stranded YOY, with the exception of one vibrissa which was cut at the level of the skin (ID: 218). Seven vibrissae were collected by Department of Conservation (DOC) staff from stranded animals near Napier, Hawkes Bay, of which six were cut and one (ID: 240) was plucked. A previous study on NZFSs showed that the proximal 1 – 5 mm of vibrissae was below the skin surface (Noè, 2013), however, in the present study the proximal 9 – 10 mm of several vibrissae was discoloured, consistent with that part of the vibrissa being subcutaneous. For the purposes of calculating growth rates and EVLBs, 10 mm was subtracted from each of the plucked samples.

NZFSs usually have a range of vibrissa lengths, with caudal vibrissae longer than rostral ones (Miller, 1975a). The individual with the shortest calculated EVLB only had very short vibrissae present, rather than the expected range of lengths including the longer, caudal vibrissae, therefore it was excluded from the vibrissa length analysis and the individual with the next shortest EVLB was used as the minimum EVLB (Table 9).

3.2.2 Stable Isotope Analysis

Vibrissae were individually cleaned in distilled water for five minutes, including gentle scraping with a scalpel blade to remove gross contamination, followed by soaking in 96 % ethanol for five minutes, then distilled water for a further five minutes (Chilvers, 2017). All samples were examined under a stereomicroscope; any residual dirt or tissue found was scraped off using a scalpel blade, and the samples rinsed again then left to dry overnight (Chilvers, 2017). Vibrissae were stored in individual plastic bags prior to sampling.

Two sections were submitted per vibrissa. Firstly, the proximal 10 mm of each plucked vibrissa was discarded due to the risk of contamination with nerve tissue which could affect the $\delta^{13}C$ and $\delta^{15}N$ values (Noè, 2013) and the 'base sample' cut (Figure 18). The base sample represents recent nutrient intake. Secondly, to try to ensure that the more distal section of vibrissa sampled from the stranded YOY corresponded to the same sampling period as the pups at the colonies, measurements were taken as follows. Vibrissae were taken from pups at breeding colonies between 39 and 84 days after the assumed median pupping date (see Chapter 2). Otariid vibrissae are oval in cross section (Ginter et al., 2012). Minimum and maximum width measurements were taken at the base of 60 vibrissae collected from breeding colonies around New Zealand (10 samples from each of six different areas), using a micrometer, and the mean width was determined for each vibrissa (hereafter 'width'). The maximum and minimum widths of each vibrissa from stranded animals were measured at the base, halfway along its length, and at two-thirds of the length from the base sample, and the mean width calculated at each site. Based on the expected vibrissa widths between 39 and 84 days of age, it was decided to sample the vibrissae at two-thirds of the length from the base, in addition to the base. A further sample was taken at half the length and held for future analysis if required.

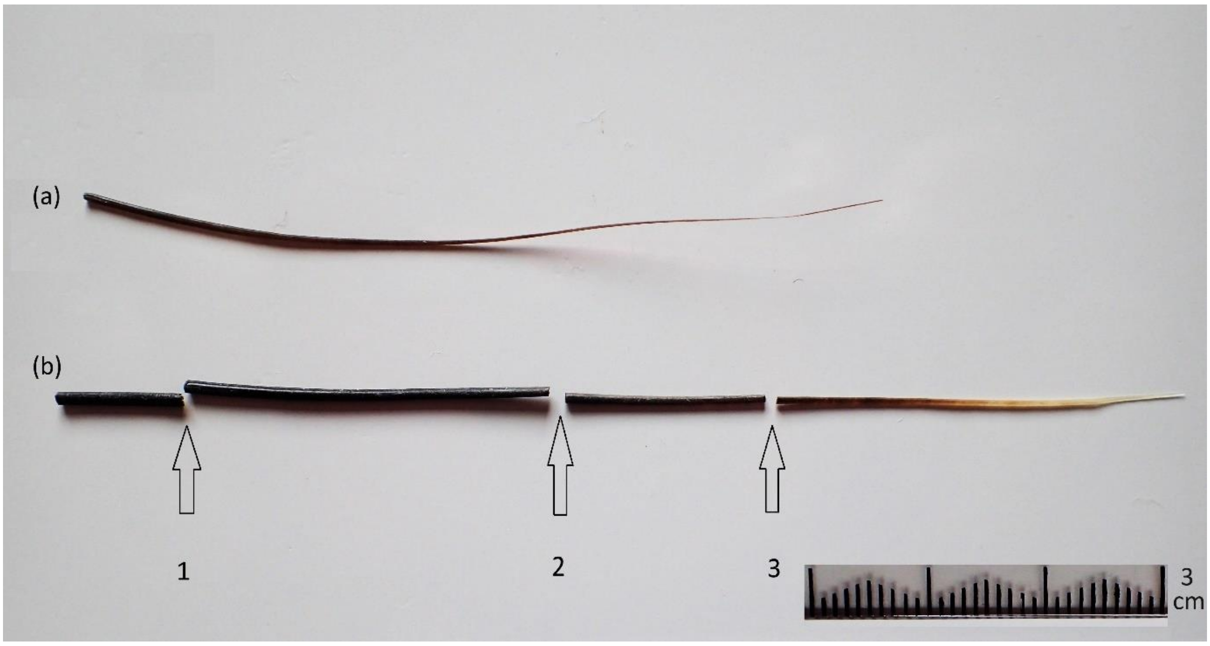


Figure 18 Typical vibrissa from a pup at a colony (a), and typical plucked vibrissa from a stranded young-of-the-year (b). Vibrissae from stranded individuals were sampled at the base (1), half (2), and two-thirds (3) of the length. The base sample was taken 10 mm from the proximal end of the vibrissae to avoid contamination with neural tissue. The sample taken from half the length of the vibrissa was not analysed but kept in reserve.

To achieve the optimum sample weight of 0.6 mg, a section approximately 1 mm long was cut from each vibrissa and weighed using a semi-micro analytical balance (A&D Instruments, GR-202, accurate to 0.1 mg). Each sample weighed between 0.3 and 0.8 mg (mean 0.59 ± 0.14 mm), and was packed into an individual tin container (Cherel et al., 2009).

Samples were analysed at the Stable Isotope Laboratory at GNS Science, Upper Hutt, New Zealand, by combustion on a Eurovector elemental analyser coupled to an Isoprime mass spectrometer. Results were reported with respect to VPDB and N-Air, normalised to an internal standard; Leucine (-28.3 ‰ for $\delta^{13}C$, 6.5 ‰ for $\delta^{15}N$). The analytical precision for these measurements is 0.2 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$. A series of reference materials, in duplicate, is run at the beginning and end of each sequence, and a drift standard, and rotating calibration standards, are run after every 10 samples.

The carbon to nitrogen ratio (C:N) can be used as a control for keratin quality (Newsome et al., 2009), and C:N was calculated, graphed, and analysed by location.

3.2.3 Statistical Analysis

Statistical analysis was carried out in R Studio v 4.3.1, and all plots were visually examined for trends. Analysis of variance (ANOVA) was used to compare vibrissa widths at the base of the breeding colony vibrissae and at two-thirds of the stranded vibrissae samples. Estimated vibrissa lengths at birth (EVLBs) were calculated using growth rates derived from linear modelling of vibrissa lengths from pups at breeding colonies and from stranded individuals that were confirmed to be YOY. Vibrissa growth rates were estimated using linear regression. Model checking showed the data met the assumptions of linear regression based on assessing residuals and determining independence (Durbin-Watson test: $p = 0.93$ for the combined colony and stranded samples, and $p = 0.52$ for the colony samples). Multivariate analysis of variance (MANOVA, Pillai's trace method) was used to assess differences in $\delta^{13}C$ and $\delta^{15}N$ among the three general locations; Northland West, Northland East and Napier, and between the vibrissa sections; base and two-thirds. Non-parametric analysis (PerMANOVA) was used to compare carbon to nitrogen ratios between samples from pups at colonies and stranded YOY.

The package SIBER (Stable Isotope Bayesian Ellipses in R) v. 2.1.9 (Jackson et al., 2011) was used to calculate isotopic niche widths at each location, and in both vibrissa sections at each location in the case of the stranded samples. Histograms of $\delta^{13}C$ and $\delta^{15}N$ values at each location were plotted and checked for unimodal distribution. Bivariate ellipses of $\delta^{13}C$ and $\delta^{15}N$ results, with 95 % credible intervals, were plotted. Bayesian standard ellipse areas (SEA or SEA_B), and ellipse areas corrected for sample size (SEA_C) were calculated using the default priors; Inverse Wishart prior on the covariance matrix, and a vague normal prior on the means, and fitted using JAGS. The Shapiro-Wilks test was used to assess normality of distribution. While SIBER analysis assumes multivariate normal distribution of the data, failure to meet this assumption does not rule out the use of this analysis (Jackson et al., 2011). Isotopic niche widths were compared by calculating the probability that one SEA_B was smaller than the other for each possible pair combination.

Code and further explanation can be found at: https://andrewcparnell.github.io/simms_course/aj-content/practicals/siber-comparing-populations.nb.html.

3.3 Results

Of the 60 samples submitted for analysis, from 30 individuals, 56 yielded values for both δ^{13}C and δ^{15}N. Five individuals were outliers for either δ^{13}C or δ^{15}N, and one was an outlier for both. One individual from Northland's west coast (ID: 208) physically looked like an adult, although its vibrissa length was within the range of the pup vibrissa lengths, so the sample was submitted for analysis. At two-thirds of the vibrissa length its δ^{15}N was low, and there was only 0.7 ‰ decrease in δ^{15}N from two-thirds to the base. Given that the two-thirds sample was expected to correspond to the vibrissa at a similar time to the colony sampling, and there should be a significant drop in δ^{15}N at weaning, this individual was excluded from the analysis. One of the individuals from Napier (ID: 239) was an outlier for both δ^{13}C and δ^{15}N, and was the only one to have a higher δ^{15}N at the base than at two-thirds of the vibrissa, making it unlikely to have been weaned between samples, so it was also excluded from statistical analysis. The remaining individual with a low δ^{15}N at the two-thirds sample also had a low δ^{15}N at the base, and the difference between the two was comparable to the other samples, so it was not excluded from the study. Of the three remaining individuals that were outliers for δ^{13}C (two high and one low) there was no obvious biological reason to exclude them, so they were retained.

3.3.1 Vibrissa Growth Rates and Estimated Vibrissa Length at Birth

Prior to cleaning, the length of each vibrissa was measured. To compensate for the fact that most stranded samples were plucked rather than cut, 10 mm was subtracted from the length of each plucked sample when calculating growth rates and EVLBs. For vibrissae collected at breeding colonies the mean ± s.d. was 66 ± 10.1 mm (range 42 – 85 mm) (Figure 19). For vibrissae collected from stranded YOY the mean was 120 ± 1.4 (range 87 – 148 mm) (Figure 20).

Using linear modelling, the growth rate of vibrissae at colonies was 0.21 mm/day (95 % C.I. 0.13 – 0.29 mm/day; $t = 5.31$, $p < 2\text{x}10^{-16}$), while the growth rate of vibrissae from the combined colony and stranded samples was 0.24 mm/day (95 % C.I. 0.22 – 0.26 mm/day; $t = 23.51$, $p < 2\text{x}10^{-16}$) (Figure 19, Figure 20). Regression analysis of the combined dataset showed the relationship between vibrissa length and the number of days from the assumed median pupping date was not linear (Figure 21). The growth rate calculated from linear regression on the stranded samples alone was 0.06 mm/day (95 % C.I. -0.88 – 1.00; $t = 0.13$, $p = 0.90$), however, the relationship between vibrissa length and the number of days from the assumed median pupping date was clearly non-linear in the stranded YOY (Figure 22). The mean vibrissa length at Sandymount was 77 ± 10.6 mm and at Open Bay Islands it was 64 ± 8.5 mm, giving an estimated growth rate of 0.25 mm/day (95 % C.I. 0.18 – 0.39 mm/day). Comparing the combined West Coast colonies (mean vibrissa length 64 ± 8.6 mm) to the combined Kaikōura ones (mean vibrissa length 66 ± 10.5 mm) gave an estimated growth rate of 0.07 mm/day (95 % C.I -0.05 – 0.20). Comparing Sandymount to the combined Kaikōura colonies gave an estimated growth rate of 0.64 mm/day (95 % C.I 0.36 – 0.91). The marked variation in these growth rates shows the difficulty of calculating a growth rate from vibrissae from different colonies, particularly over a relatively short timescale.

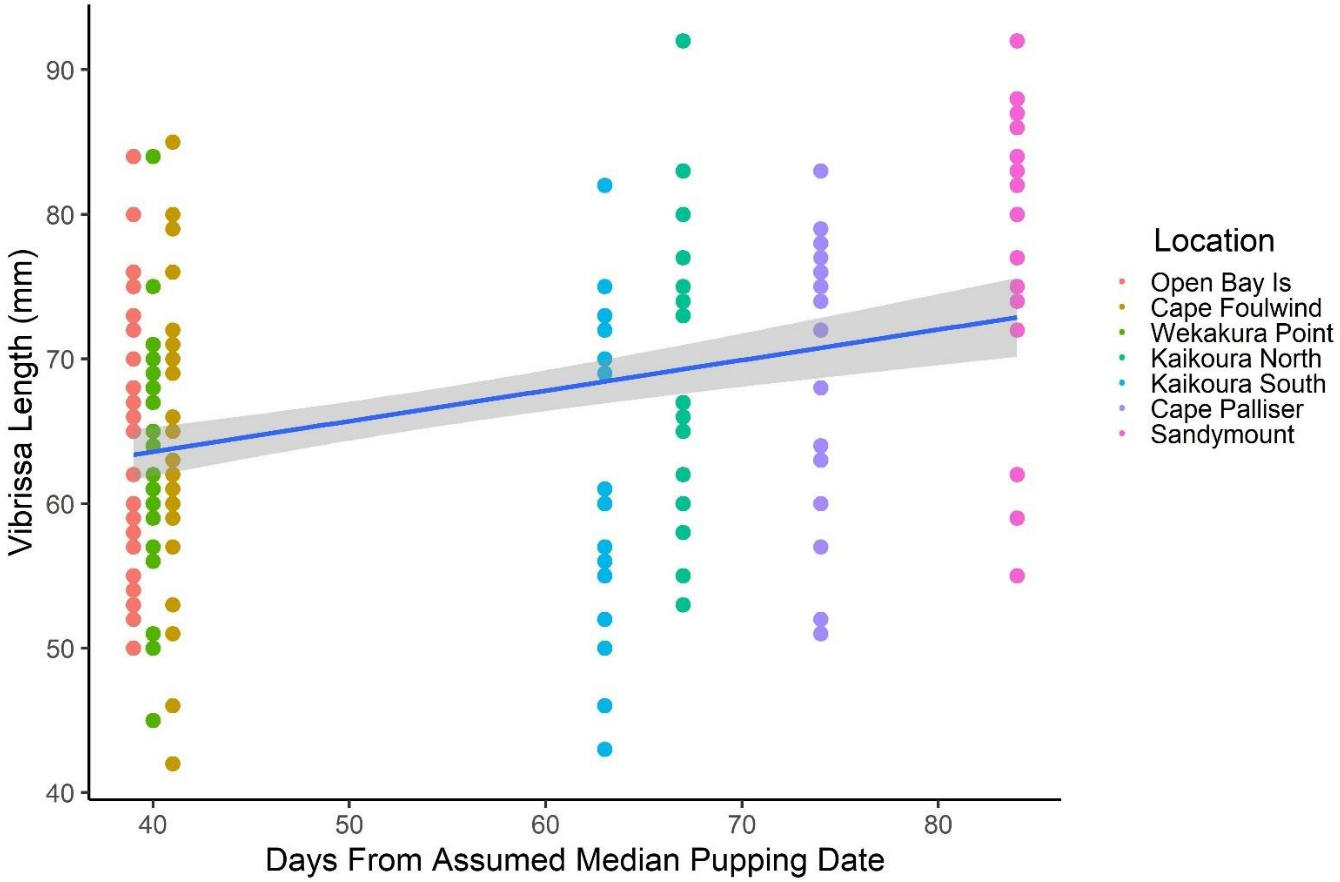


Figure 19 Length of the longest vibrissa (mm) from New Zealand fur seal pups at seven New Zealand breeding colonies, plotted against the number of days from the assumed median pupping date. Linear model regression line is in blue and grey shading represents 95 % confidence intervals. Colour represents the breeding colony.

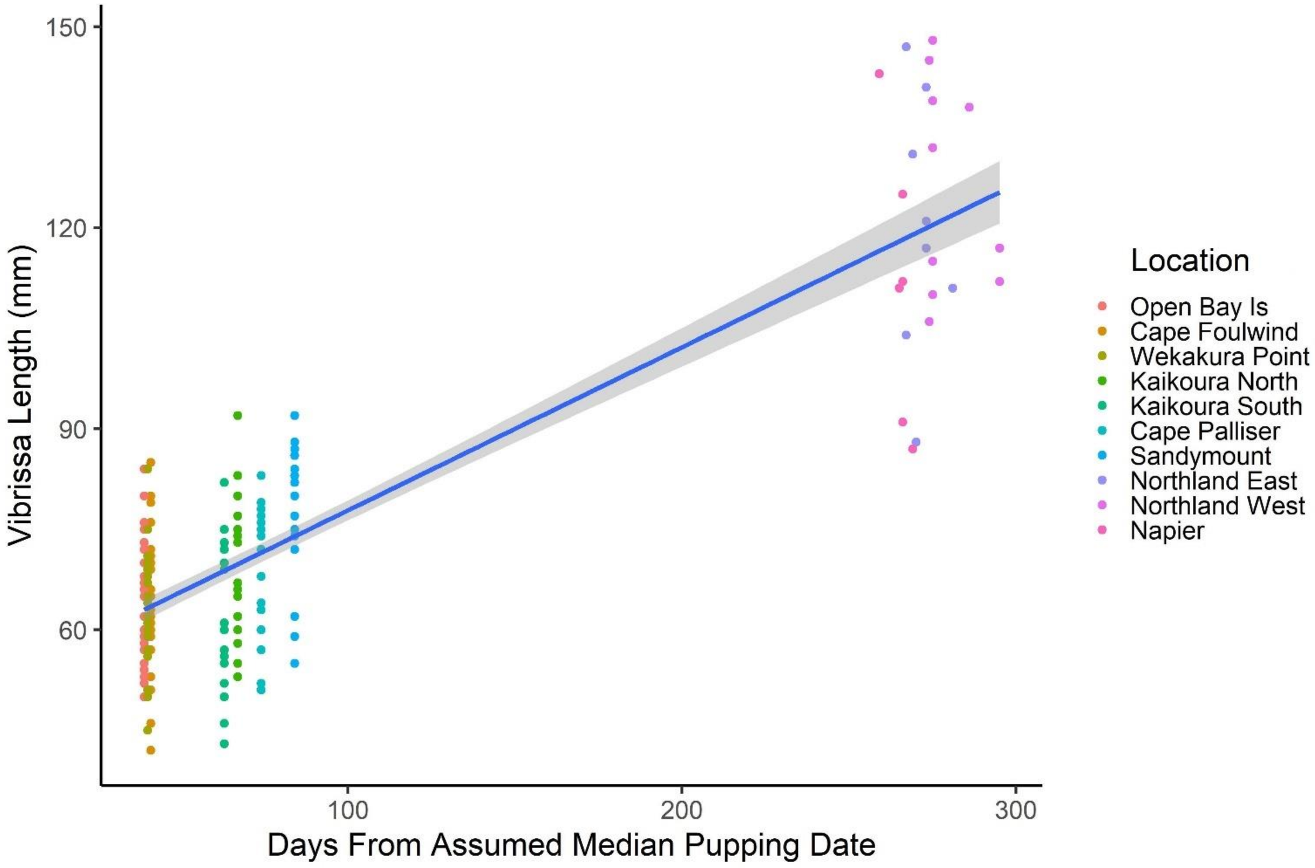


Figure 20 Length of the longest vibrissa (mm) from New Zealand fur seal pups at seven New Zealand breeding colonies, and from stranded young-of-the-year from the east and west coasts of Northland, North Island, and from Napier, Hawkes Bay, North Island, plotted against the number of days from the assumed median pupping date of 16 December, 2022. Linear model regression line is in blue and grey shading represents 95 % confidence intervals. Colour represents the breeding colony or the location of the stranded young-of-the-year.

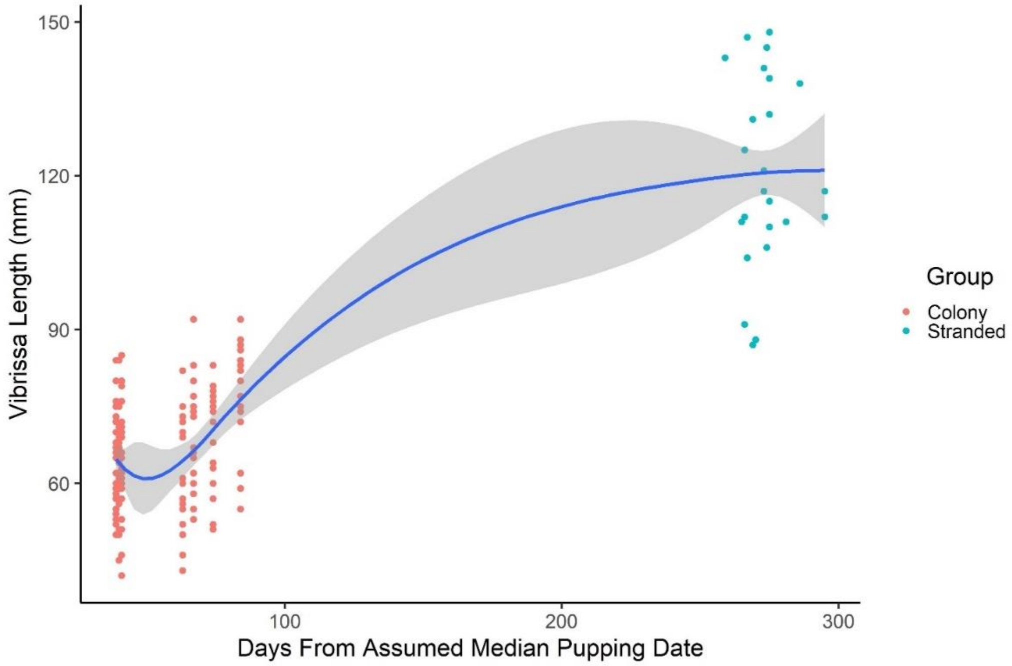


Figure 21 Length of the longest vibrissa (mm) from New Zealand fur seal pups at seven New Zealand breeding colonies, and from stranded young-of-the-year from the east and west coasts of Northland, North Island, and from Napier, Hawkes Bay, North Island, plotted against the number of days from the assumed median pupping date of 16 December, 2022. Regression line is in blue, and grey shading represents 95 % confidence intervals. Peach colour represents pups and turquoise represents stranded young-of-the-year.

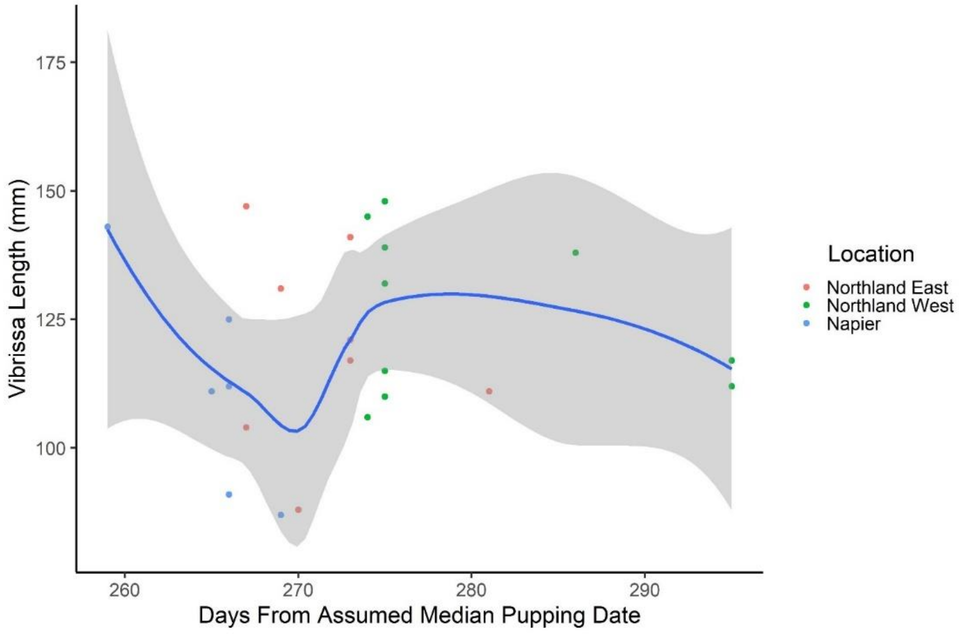


Figure 22 Length of the longest vibrissa (mm) from stranded New Zealand fur seal young-of-the-year from the east and west coasts of Northland, North Island, and from Napier, Hawkes Bay, North Island, plotted against the number of days from the assumed median pupping date of 16 December, 2022. Regression line is in blue, and grey shading represents 95 % confidence intervals. Colour represents the location.

The EVLB for each individual was calculated using an assumed median pupping date for all colonies of 16 December (Boren, Muller, et al., 2006), and growth rates of 0.21 mm/day for pups at breeding colonies, and 0.24 mm/day for stranded animals, based on linear modelling in R Studio. The growth period was calculated as the number of days from the median pupping date to the date of sample collection, as it was not possible to determine the exact date of death for the stranded animals. The EVLB for stranded animals was compared to the EVLB of the pups sampled at the colonies between 24 January and 10 March, 2023. The mean calculated EVLB for all samples was 55 ± 11.3 mm (Table 9), while from the linear model the intercept was 55.2 mm for colony samples and 53.6 mm for all samples combined. The calculated EVLB for stranded YOY is 104 mm (95 % C.I. -154 – 362 mm).

Table 9 Maximum, minimum and mean estimated vibrissa lengths at birth (EVLB), and vibrissa widths at the base, half, and two-thirds of vibrissa length (mm) for New Zealand fur seal pups at breeding colonies, stranded individuals, and both combined. The stranded individual with the shortest EVLB did not have the normal range of vibrissa lengths, so the next shortest EVLB was used for the minimum (*). The combined width results for the two-thirds vibrissa include the base samples from the breeding colonies and the two-thirds samples from the stranded individuals (^).

	Colonies	**Stranded**	**Combined**
Maximum estimated vibrissa length at birth (mm)	78	83	84
Minimum estimated vibrissa length at birth (mm)	30	22*	22*
Mean estimated vibrissa length at birth ± sd (mm)	**55 ± 9.5**	**54 ± 18.6**	**55 ± 10.8**
Maximum vibrissa width at base (mm)	0.78	1.43	
Minimum vibrissa width at base (mm)	0.34	0.99	
Mean vibrissa width at base ± sd (mm)	**0.59 ± 0.090**	**1.16 ± 0.115**	
Maximum vibrissa width at half vibrissa length (mm)		1.06	
Minimum vibrissa width at half vibrissa length (mm)		0.61	
Mean vibrissa width at half vibrissa length ± sd (mm)		**0.80 ± 0.103**	
Maximum vibrissa width at two-thirds vibrissa length (mm)		1.03	1.03 ^
Minimum vibrissa width at two-thirds vibrissa length (mm)		0.39	0.34 ^
Mean vibrissa width at two-thirds vibrissa length ± sd (mm)		**0.63 ± 0.136**	**0.60 ± 0.106^**

Of the 30 stranded individuals, five were initially classified as adults, four as unknowns, and 21 as pups, based on appearance. Individuals that were more than one year old all had body lengths of greater than 100 cm, with the exception of one (ID: 209) which was 98 cm long, but had a vibrissa length of 205 mm. The longest YOY was 93 cm (ID: 210) and the shortest was 75 cm (ID: 232), which was less than the longest pup measured at a colony (ID: 101; 81 cm at Ōhau Point). For comparison, mean curvilinear body lengths of 235-day old pups were 81 cm for males and 77 cm for females (in 1975) and 86 cm for males and 83 cm for females (in 1976) (Mattlin, 1981).

Four of the suspected adults and three of the unknowns had an EVLB of at least 112 mm, so could be confirmed as being older than YOY. Six individuals had an EVLBs between 81 and 87 mm. One of the suspected adults (ID: 208) had an EVLB of 84 mm, and a body length of over one metre. It was subsequently determined to be a non-pup as there was a negligible decrease in $\delta^{15}N$ between the two-thirds and the base samples, whereas pups have a marked decline in $\delta^{15}N$ at weaning (Cherel et al., 2015). The remaining unknown (ID: 223) had an EVLB of 82 mm and a body length of 85 cm, and the drop in $\delta^{15}N$ between the two-thirds and the base samples was consistent with it being a pup. The longest EVLB in an individual thought to be a pup was 87 mm (ID: 217), but as SIA failed to give a $\delta^{15}N$ result at the base and the two-thirds sample, it was excluded from the analysis. Three other individuals identified as YOY at the time of sampling had EVLBs of greater than 80 mm (ID: 211; 83 mm, ID: 218; 84 mm, ID: 241; 81 mm). IDs: 211 and 241 had a drop in $\delta^{15}N$ values between the two-thirds and base samples consistent with being weaned between those samples. Number 218 did not yield a $\delta^{15}N$ for the base sample, but body length was consistent with it being a pup (92 cm) and none of the other values were outliers.

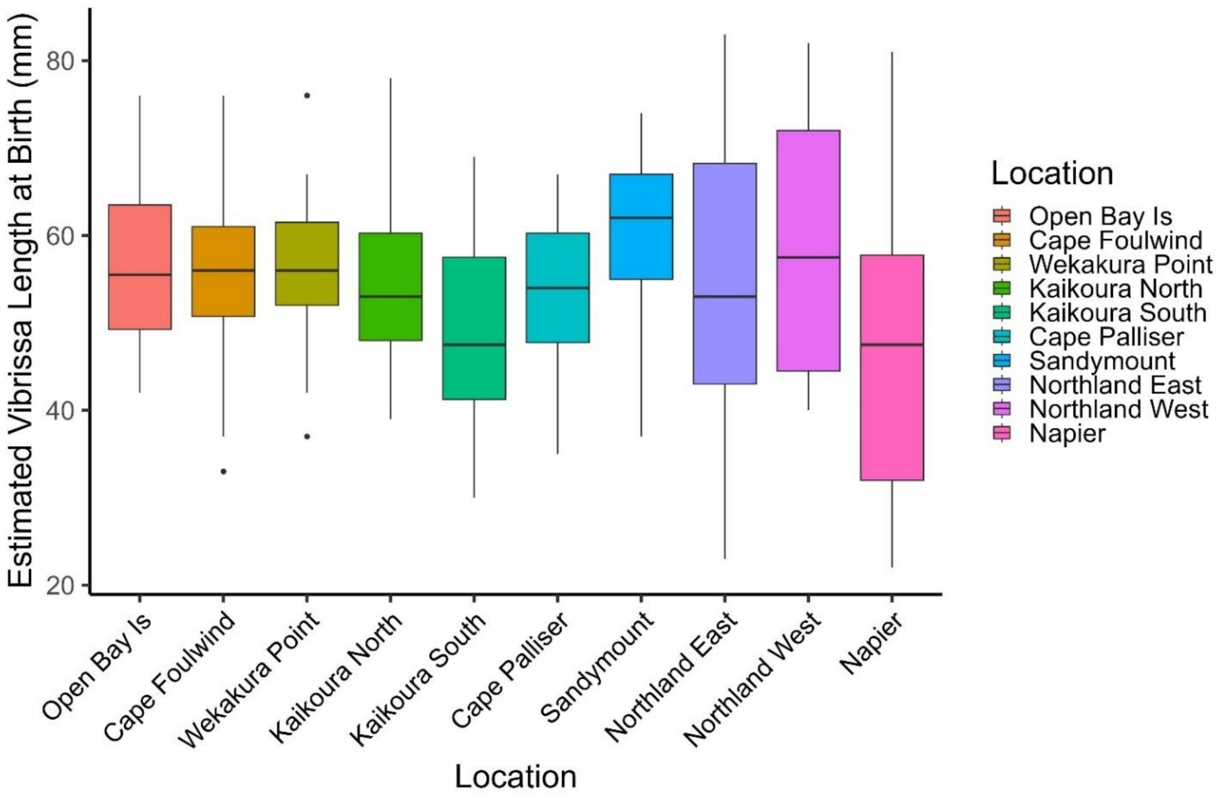


Figure 23 Estimated vibrissa length at birth (mm) for New Zealand fur seal pups from seven breeding colonies, and stranded young-of-the-year from the east and west coasts of Northland, and from Napier, Hawkes Bay, New Zealand. Boxplots show median values and first and third quartiles. Colours are locations. Black dots are outliers.

The seven vibrissae from Napier, Hawkes Bay, were all classed as pups/juveniles by the DOC staff collecting them. Photographs of the animals and vibrissa lengths were all consistent with them being YOY. A body length measurement was only available for one individual. One individual (ID: 239) was subsequently ruled out at the $\delta^{15}N$ at two-thirds of the vibrissa was extremely low, and substantially lower than the value at the base of the vibrissa, which is not consistent with the animal being weaned between those samples. It was an outlier for $\delta^{13}C$ and $\delta^{15}N$.

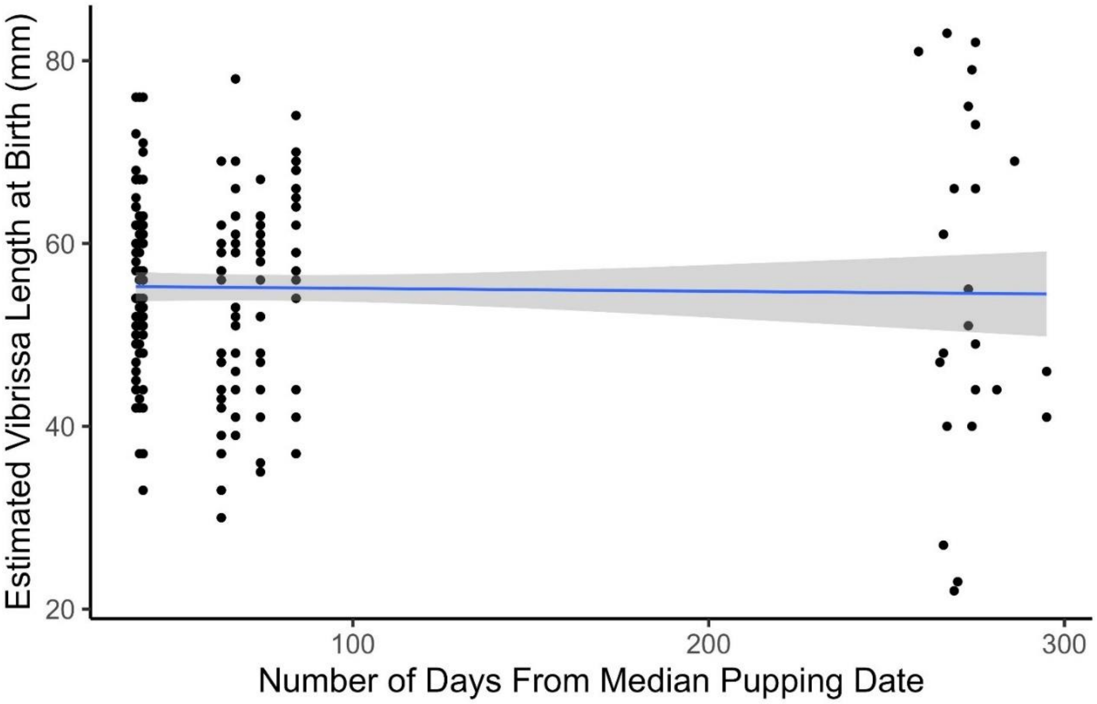


Figure 24 Estimated vibrissa length at birth (mm) for New Zealand fur seal pups from seven breeding colonies, and stranded young-of-the-year from the east and west coasts of Northland, and from Napier, Hawkes Bay, North Island, New Zealand, plotted against the number of days between the assumed median pupping date and date of vibrissa collection. Linear model regression line is in blue and grey shading represents 95 % confidence intervals.

Looking at EVLB among colonies, if the vibrissa growth rate of 0.21 mm/day was adopted for all samples then analysis of variance showed that there were significant differences among colonies ($F = 2.73$, $p < 0.01$), however, the data failed the Levene's test for homogeneity of variance ($F = 5.10$, $p < 10^{-5}$) (Figure 23). The only colony pairs that differed significantly were Northland East and Kaikōura South ($p < 0.01$), and Northland West and Kaikōura South ($p = 0.04$). If the vibrissa growth rate of 0.21 mm/day was used for the colony samples and 0.24 mm/day for the stranded samples, as determined by linear regression (Figure 19, Figure 20), then there were no significant differences between any of the locations ($p = 0.14$). There is a considerable range of vibrissa lengths at any given time, but the slope of the linear regression line when plotting all EVLBs against the number of days from the assumed median pupping date is 0.003 (Figure 24). EVLBs for the stranded individuals are therefore consistent with EVLBs for pups at breeding colonies.

3.3.2 Vibrissa widths

The widths of the bases of 60 vibrissae collected at six colonies (10 per colony) were measured, and the results used to determine which part of the vibrissa to sample from stranded individuals. The breeding colony with the greatest mean vibrissa width was Kaikōura North, with 0.68 ± 0.05 mm (collected on 17 February 23 and 21 February 2023) and the smallest mean vibrissa width was at Open Bay Islands, with 0.51 ± 0.09 mm (collected on 24 January 2023).

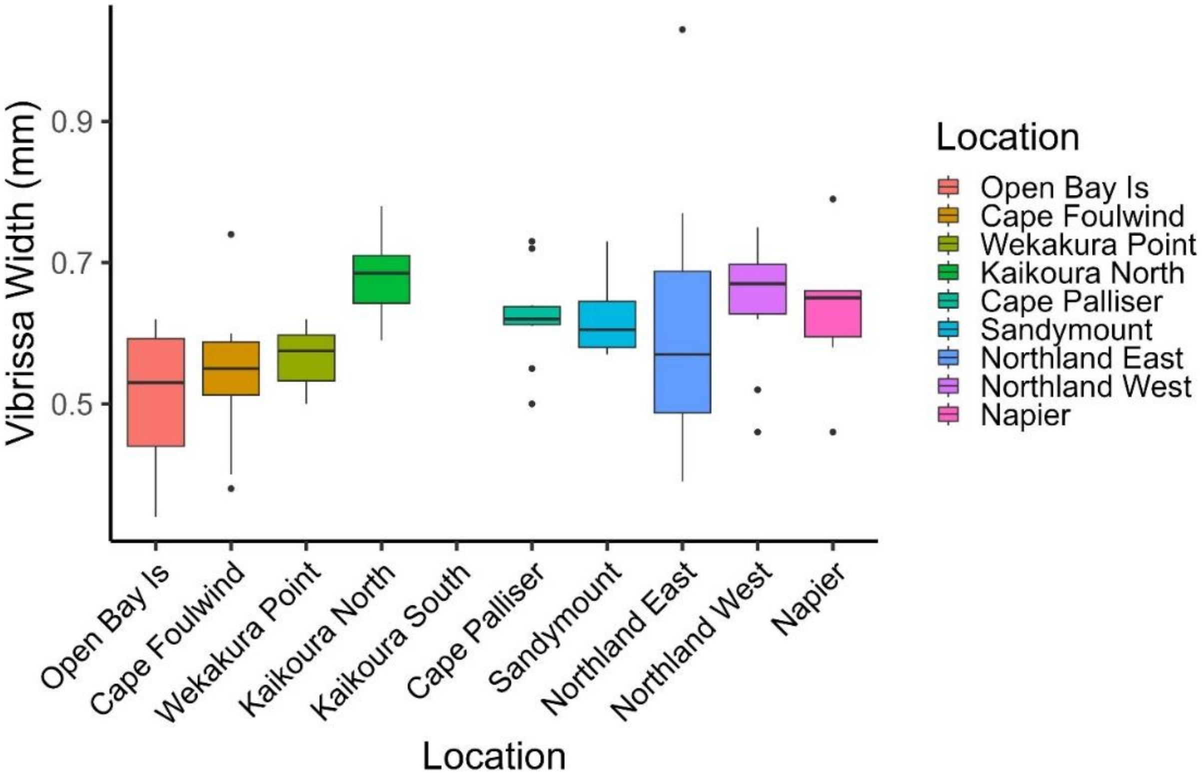


Figure 25 Width (mm) of the base of vibrissae of New Zealand fur seal pups sampled at six breeding colonies, and width at two-thirds of the length from the base in stranded New Zealand fur seal young-of-the-year on the east and west coasts of Northland, North Island, and Napier, Hawkes Bay, North Island, New Zealand. Breeding colonies are arranged in order of collection date. Boxplot shows median, and first and third quartiles. Black dots are outliers.

Vibrissa widths varied among colonies (ANOVA: $F = 6.247$, $p < 10^{-4}$), with a large effect size (partial eta squared = 0.41) (Table 9, Figure 25). The data passed the Levene's test for homogeneity of variance ($p = 0.34$). Tukey HSD post hoc tests showed that mean vibrissa width was greater at Kaikōura North than at Open Bay Islands ($p < 10^{-4}$), Cape Foulwind ($p < 0.01$), and Wekakura Point ($p = 0.02$), and greater at Cape Palliser ($p = 0.02$) and Sandymount ($p = 0.03$) than at Open Bay Islands. Kaikōura North was sampled 22 – 28 days after Open Bay Islands, Cape Foulwind and Wekakura Point, but only around seven days before Cape Palliser and 17 days before Sandymount. Vibrissa lengths also differed significantly between the breeding areas (ANOVA: $F = 7.443$, $p < 10^{-6}$), but only Sandymount vibrissae differed significantly from the other colonies, being highly significantly longer than vibrissae at Open

Bay Islands, Cape Foulwind and Wekakura Point ($p < 10^{-4}$), and significantly longer than at Kaikōura North ($p = 0.03$).

When measurements from the base of the vibrissae at breeding colonies and from two-thirds of the length of stranded samples were combined, vibrissa widths ranged from 0.34 to 1.03 mm, with a mean of 0.61 ± 0.107 mm. Median vibrissa widths for each location are shown in Figure 25. ANOVA of vibrissa widths at all locations showed location was significant ($F = 3.25$, $p < 0.01$), with a partial eta squared of 0.25. The data failed the Levene's test ($p = 0.03$). The Tukey HSD showed only Open Bay Islands versus Kaikōura North ($p < 0.01$) and Open Bay Islands vs Northland West ($p = 0.02$) were significantly different. Linear modelling gave a regression coefficient of 0.0002, indicating that the vibrissa widths at two-thirds of the vibrissa length were largely comparable to the vibrissa base widths of the colony samples (Figure 26).

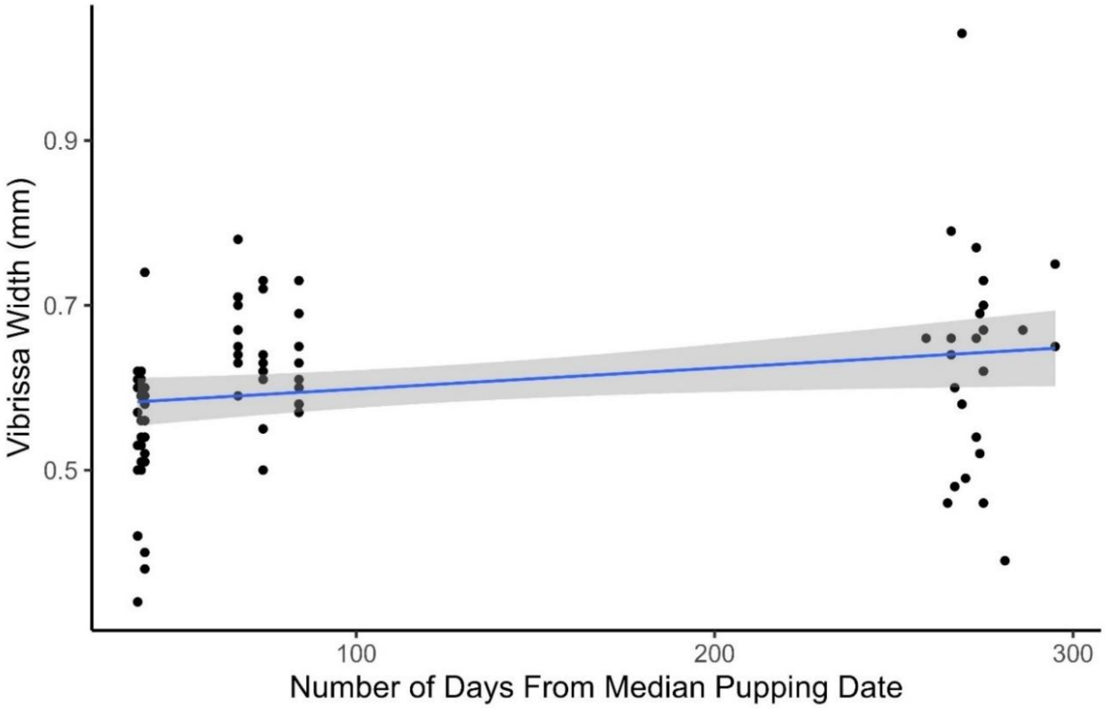


Figure 26 Width (mm) of the base of vibrissae of New Zealand fur seal pups sampled at six breeding colonies, and width at two-thirds of the length from the base in stranded New Zealand fur seals on the east and west coasts of Northland, North Island, and Napier, Hawkes Bay, North Island. As vibrissae are oval in cross-section, the width of each vibrissa is calculated by adding the maximum and minimum widths, at the same level, and dividing by two. The x axis is the number of days from the assumed median pupping date of 16 December, 2022. Linear model regression line is in blue and grey shading represents 95 % confidence intervals.

3.3.3 Stable Isotope Analysis

Complete $\delta^{13}C$ and $\delta^{15}N$ results for the base and two-thirds of the length of the vibrissa were available for 24 individuals: eight from Northland East, 10 from Northland West and six from Napier (Table 10). The $\delta^{13}C$ values for all stranded individuals ranged from -19.7 to -15.7 ‰, with a mean of -17.1 ± 0.83 ‰, and the $\delta^{15}N$ values from 8.3 to 17.8 ‰, with a mean of 13.9 ± 2.73 ‰. Mean $\delta^{13}C$ in base samples was -17.5 ± 0.95 ‰, and in two-thirds samples -16.6 ± 0.36 ‰, while mean $\delta^{15}N$ in base samples was 11.5 ± 1.53 ‰, and in two-thirds samples it was 16.2 ± 1.26 ‰. In this study, the mean $\delta^{15}N$ between samples from two-thirds of the vibrissa length and samples from the base decreased by 4.7 ‰, which is equivalent to a trophic level (Chilvers, 2021a; Hobson et al., 1996; Kelly, 2000; Minagawa & Wada, 1984), and is consistent with pups being weaned in the intervening period.

Means and standard deviations at each location are shown in Table 10. For base vibrissa sections $\delta^{13}C$ was highest at Northland West and lowest at Northland East, while for two-thirds sections it was highest at Napier with Northland East and West values the same, although none of the differences were significant. For $\delta^{15}N$, Napier was highest for the base and two-thirds sections, although the differences were not significant. Boxplots of $\delta^{13}C$ and $\delta^{15}N$ values for the at two-thirds sample at each location are shown in Figure 28 – 31.

The carbon to nitrogen ratio (C:N) gives an indication of keratin quality (Newsome et al., 2009). The mean C:N for all samples combined was 2.91 ± 0.056 (range 2.76 to 3.15). The mean C:N for samples from stranded YOY was 2.87 ± 0.077 (range 2.76 to 3.07), while for samples from pups at colonies it was 2.92 ± 0.040 (range 2.81 to 3.15).

Non-parametric analysis (PerMANOVA) showed that C:N in pup samples was significantly higher than in YOY samples ($F = 28.54$, $R^2 = 0.15$, $p = 0.001$) (Figure 27).

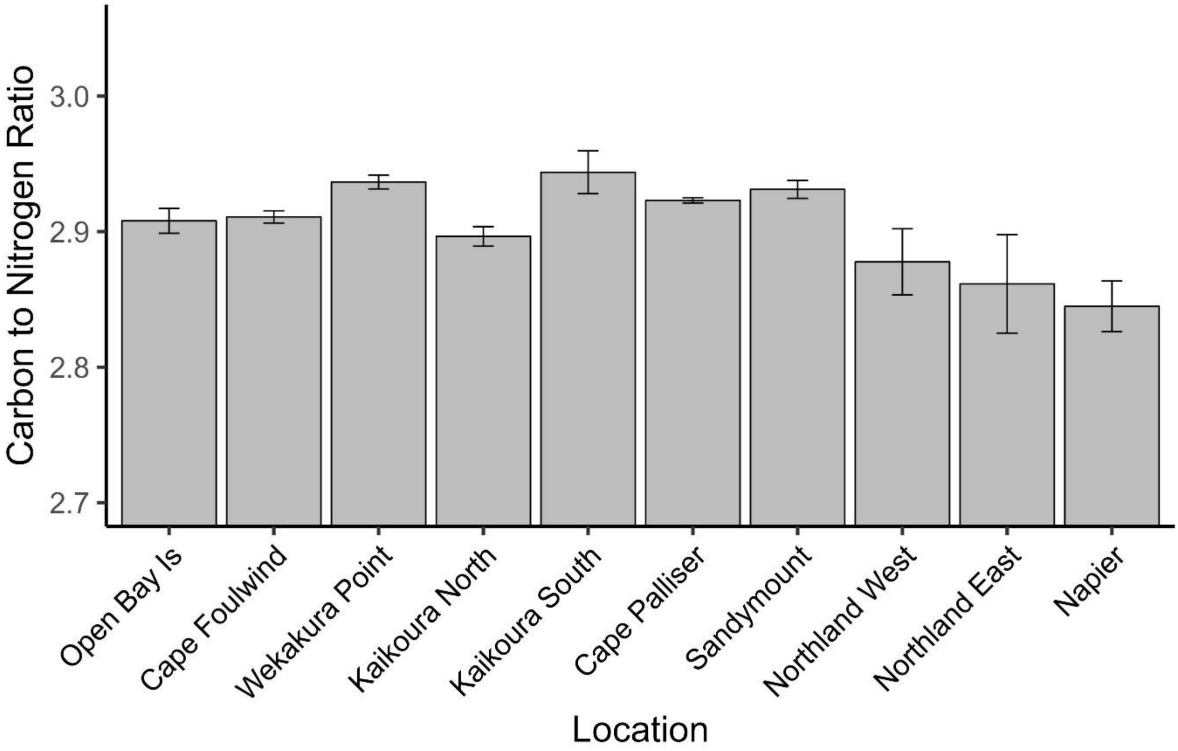


Figure 27 Carbon to nitrogen ratios (means and standard error bars) in vibrissa samples from New Zealand fur seal pups at seven breeding colonies and from stranded New Zealand fur seal young-of-the-year on the east and west coasts of Northland, North Island, and from Napier, North Island, New Zealand.

Table 10 Number of vibrissa samples, means and standard deviations of δ^{13}C and δ^{15}N from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, North Island, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae were sampled at the base and at two-thirds of the length.

Location	**n**	**Mean δ^{13}C**		**sd**	**Mean δ^{15}N**		**sd**
Northland West - Base	10	-17.1	±	1.06	11.8	±	1.56
Northland East - Base	8	-17.8	±	0.86	10.9	±	1.55
Napier - Base	6	-17.6	±	0.75	11.9	±	1.43
Base Vibrissae	**24**	**-17.5**	**±**	**0.95**	**11.5**	**±**	**1.53**
Northland West – Two-thirds	10	-16.7	±	0.37	16.4	±	1.35
Northland East – Two-thirds	8	-16.8	±	0.25	15.8	±	1.27
Napier – Two-thirds	6	-16.3	±	0.33	16.5	±	1.16
Total samples	**24**	**-16.6**	**±**	**0.36**	**16.2**	**±**	**1.26**

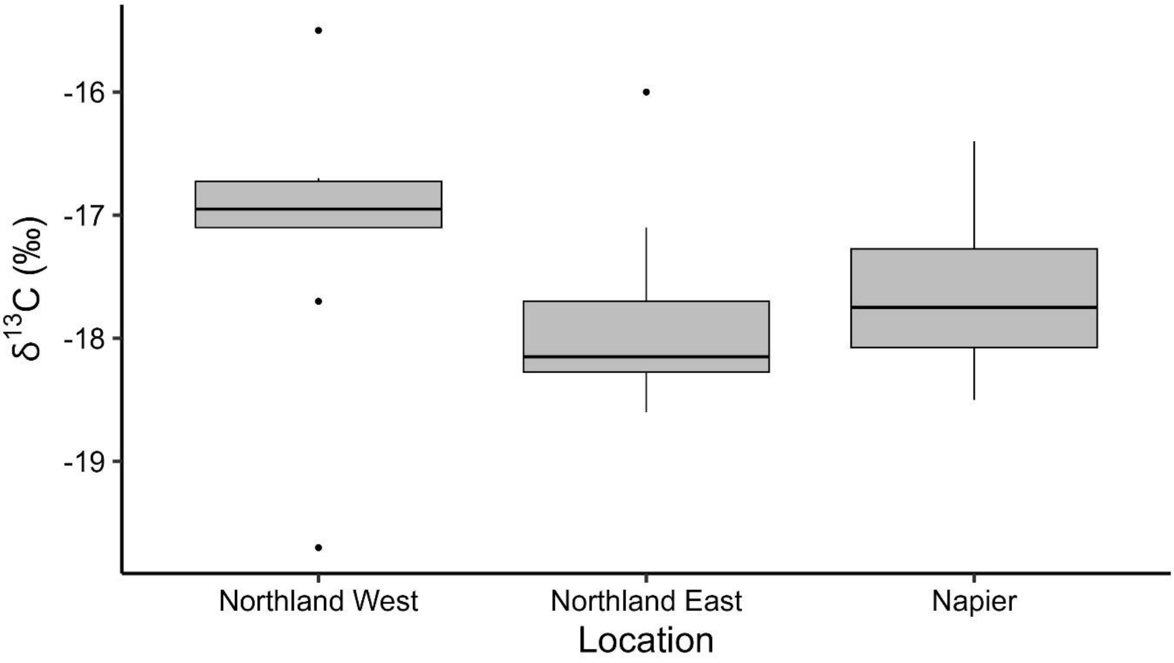


Figure 28 $\delta^{13}C$ values in the base of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles. Black dots are outliers.

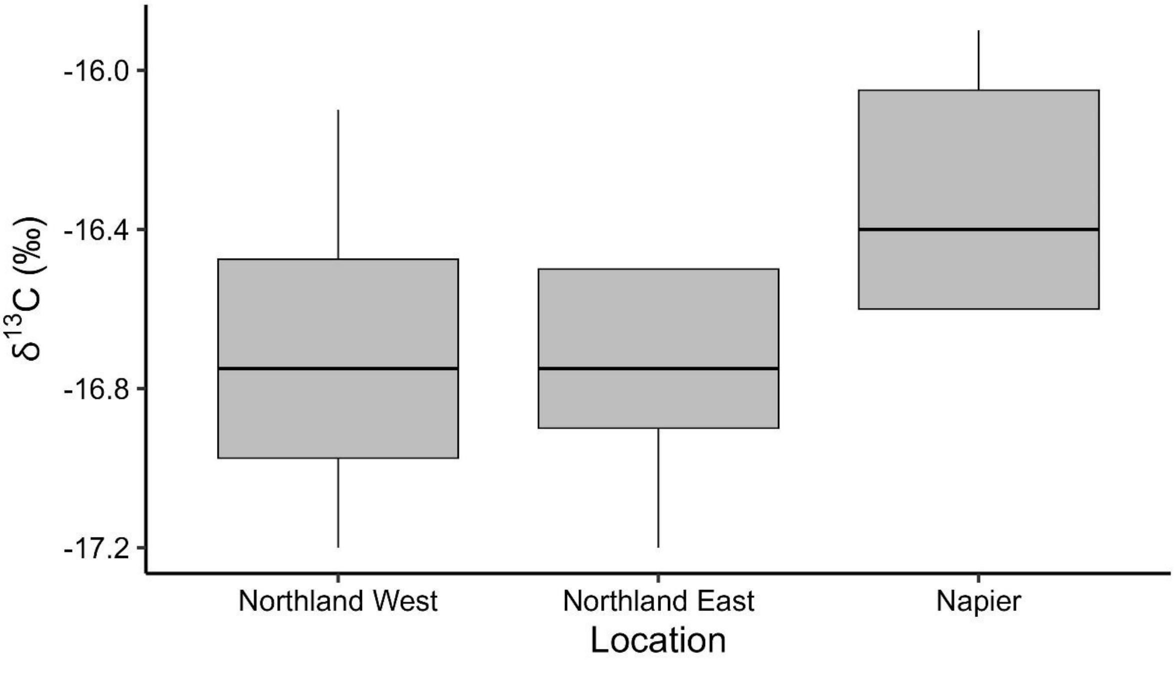


Figure 29 $\delta^{13}C$ values at two-thirds the length of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles.

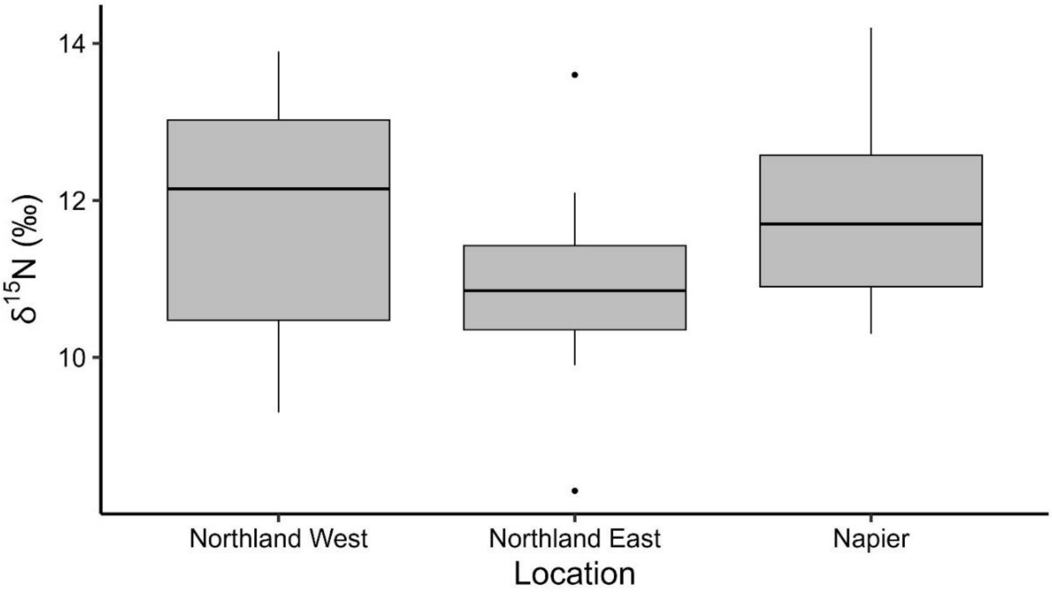


Figure 30 $\delta^{15}N$ values in the base of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles. Black dots are outliers.

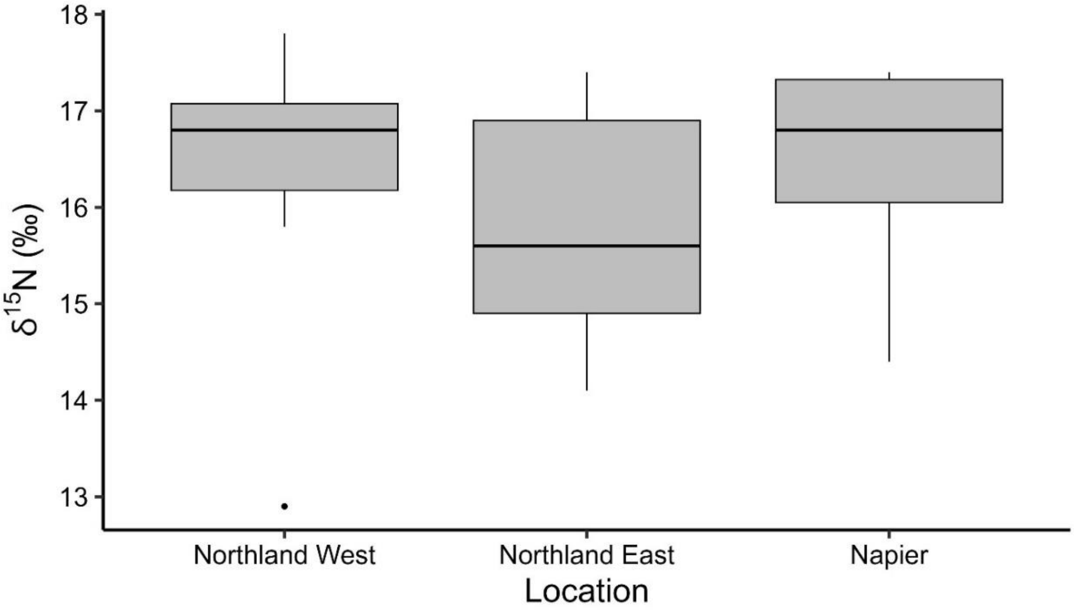


Figure 31 $\delta^{15}N$ values at two-thirds the length of the vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Boxplot shows median, and first and third quartiles. Black dots are outliers.

Multivariate analysis of variance (MANOVA) comparing the three locations showed no significant differences at the base ($F = 1.32$, $p = 0.28$) or two-thirds section ($F = 1.91$, $p = 0.13$). The $\delta^{13}C$ and $\delta^{15}N$ data met the requirements for homogeneity of variance (Levene's test, $\delta^{13}C$: $F = 0.83$, $p = 0.44$, and $\delta^{15}N$: $F = 0.045$, $p = 0.96$). When the three locations were combined there was a highly significant difference between the base and two-thirds sections ($F = 82.3$, $p < 10^{-15}$) and a large effect size (eta squared = 0.77) (Figure 32), with the two-thirds sections being generally higher in $\delta^{13}C$ and $\delta^{15}N$ than the base sections. However, while $\delta^{15}N$ met the requirements for homogeneity of variance (Levene's test: $F = 1.17$, $p = 0.29$), $\delta^{13}C$ did not (Levene's test: $F = 16.7$, $p < 0.001$). Permutational multivariate analysis of variance (PerMANOVA) also showed that section was highly significant for the combined $\delta^{13}C$ and $\delta^{15}N$ results ($F = 108.4$, $p = 0.001$).

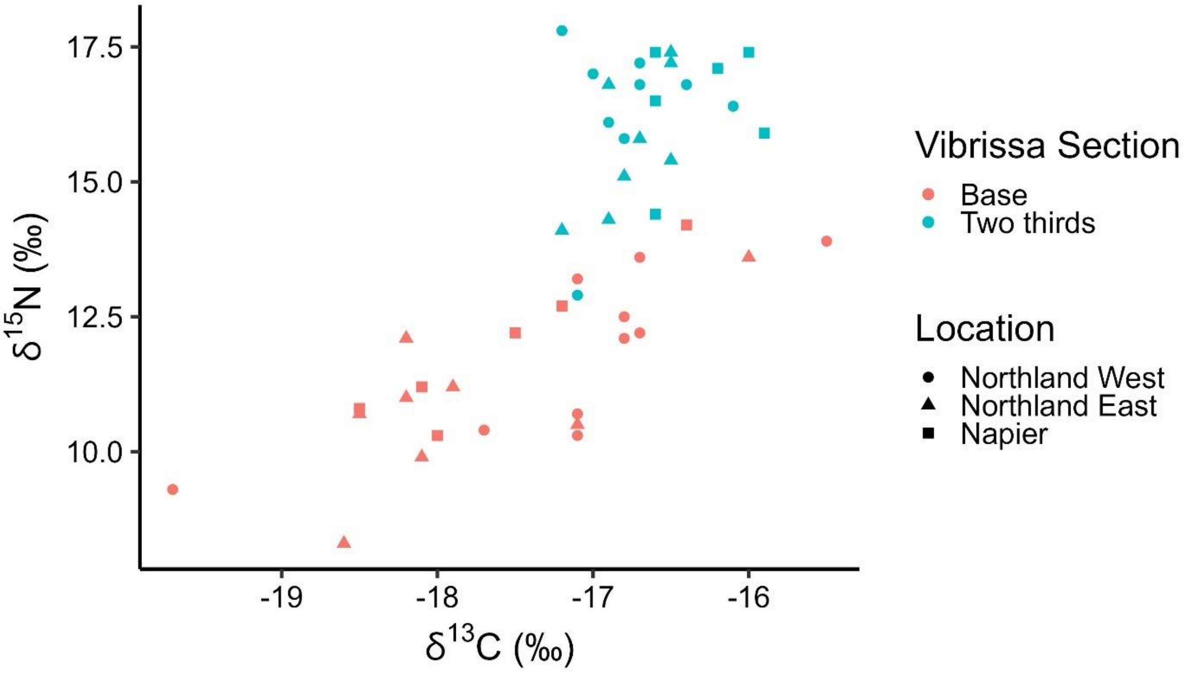


Figure 32 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in vibrissae from stranded New Zealand fur seals at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae were sampled at two-thirds of the length, and at the base. The shape is the location and the colour is the vibrissa section.

3.3.4 Stable Isotope Bayesian Ellipses in R (SIBER)

Isotopic niche widths are represented graphically by ellipses (Figure 33, Figure 34) and quantitatively by ellipse areas in ‰^{2} (Table 11, Table 12, Figure 35, Figure 36). The isotopic data did not meet the recommendations for normality of distribution (Jackson et al., 2011). For the colony samples combined with the two-thirds stranded vibrissa samples, both δ^{13}C (stat = 0.93, p = 0.01) and δ^{15}N (stat = 0.929, p = 0.006) failed the Shapiro-Wilks test. However, when each of the locations was considered separately, only δ^{15}N at Kaikōura North (stat = 0.908, p = 0.03) and Northland West (stat = 0.769, p = 0.006) failed the Shapiro-Wilks test. The plotting code for standard ellipse areas assumes unimodal distributions (Jackson et al., 2011). Histograms of δ^{13}C and δ^{15}N at each location were examined, and δ^{13}C at Cape Foulwind, Cape Palliser, Sandymount, and Northland East was not clearly unimodal.

The standard ellipse area (SEA or SEA$_B$) represents the size of the isotopic niche, reaching an asymptote at n = 30. The SEA$_C$ is the standard ellipse area corrected for sample size (Table 11, Table 12).

The largest colony SEA$_B$ was Open Bay Islands (0.66 ‰^{2}), and the smallest was Cape Palliser (0.16 ‰^{2}) (See Chapter 2 for further details on colony niche sizes), while the largest for North Island two-thirds samples was Northland West (1.54 ‰^{2}) and the smallest was Northland East (0.73 ‰^{2}) (Table 11). The base SEA$_B$ values ranged from Northland West (3.18 ‰^{2}) to Napier (1.12 ‰^{2}).

For ellipse areas corrected for sample size (SEA$_C$), Northland West has the largest niche size at both the base (3.57 ‰^{2}) and two-thirds samples (1.73 ‰^{2}) with Northland East next largest for base (3.54 ‰^{2}), and Napier for two-thirds (1.44 ‰^{2}) (Table 12). In colony samples, SEA$_C$ ranged from 0.17 – 0.69 ‰^{2}, while the smallest SEA$_C$ in the stranded samples was 0.85 ‰^{2} at Northland East. Ellipses for SEA$_B$ at the base and two-thirds vibrissa sections from stranded individuals are shown in Figure 33. The probability that one isotopic niche width is smaller than another can be determined statistically. For each pair of locations, the probability that the SEA$_B$ of the first location was smaller than the second location is shown in Table 13. Cape Foulwind and Open Bay Islands had the largest isotopic niche sizes among the colonies (SEA$_B$ 0.66 and 0.56 ‰^{2}, respectively) and the probabilities that their SEA$_B$ values were greater than those of the other colonies were at least 99 %. The probability that Open Bay Islands had a smaller niche size than Cape Foulwind was 72 %. Comparing the largest breeding colony niche width to the three North Island locations, Cape Foulwind was 99 % likely to be smaller than Northland West, 69 % likely to be smaller than Northland East, and 91 % likely to be smaller than Napier.

Among the North Island locations, the probability that SEA$_B$ in base samples was larger at Northland West than Northland East was 44 %, but in two-thirds samples it was only 9 % (Table 14). Comparing the SEA_B at each North Island location the base was between 16 % (Napier) and 0 % (Northland East) likely to be smaller than the two-thirds sample.

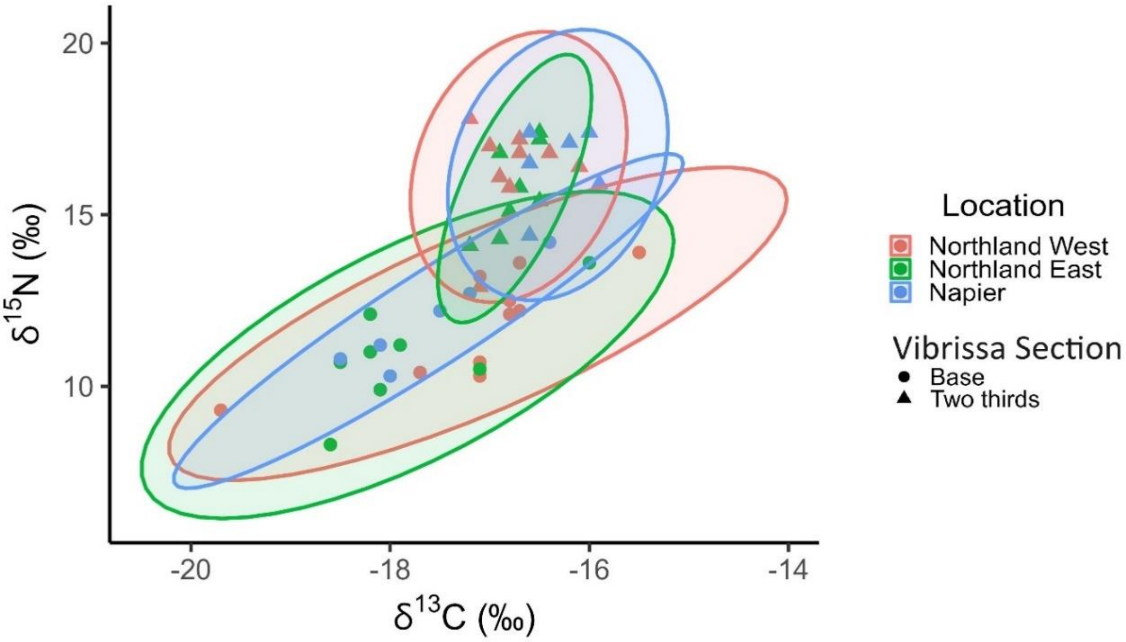


Figure 33 δ^{13}C and δ^{15}N values (‰) in vibrissae from stranded New Zealand fur seals at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae were sampled at two-thirds of the length, and at the base. The colour is the location and the shape is the vibrissa section. Ellipse sizes are 95 % CI.

Table 11 Group metrics for δ^{13}C and δ^{15}N values in vibrissae from New Zealand fur seal pups at seven breeding colonies and from stranded young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Stranded individuals were sampled at two-thirds of the vibrissa length. TA is the convex hull area, SEA is the standard ellipse area, and SEA_C is the SEA corrected for sample size effects. Units are ‰^{2}.

	Open Bay Islands	**Cape Foulwind**	**Wekakura Point**	**Cape Palliser**	**Kaikōura North**	**Kaikōura South**	**Sandy-mount**	**Northland West**	**Northland East**	**Napier**
TA	1.88	1.89	0.82	0.45	0.96	0.90	0.56	2.94	1.28	1.50
SEA	0.56	0.66	0.27	0.16	0.28	0.27	0.21	1.54	0.73	1.15
SEAc	0.59	0.69	0.29	0.17	0.30	0.29	0.22	1.73	0.85	1.44

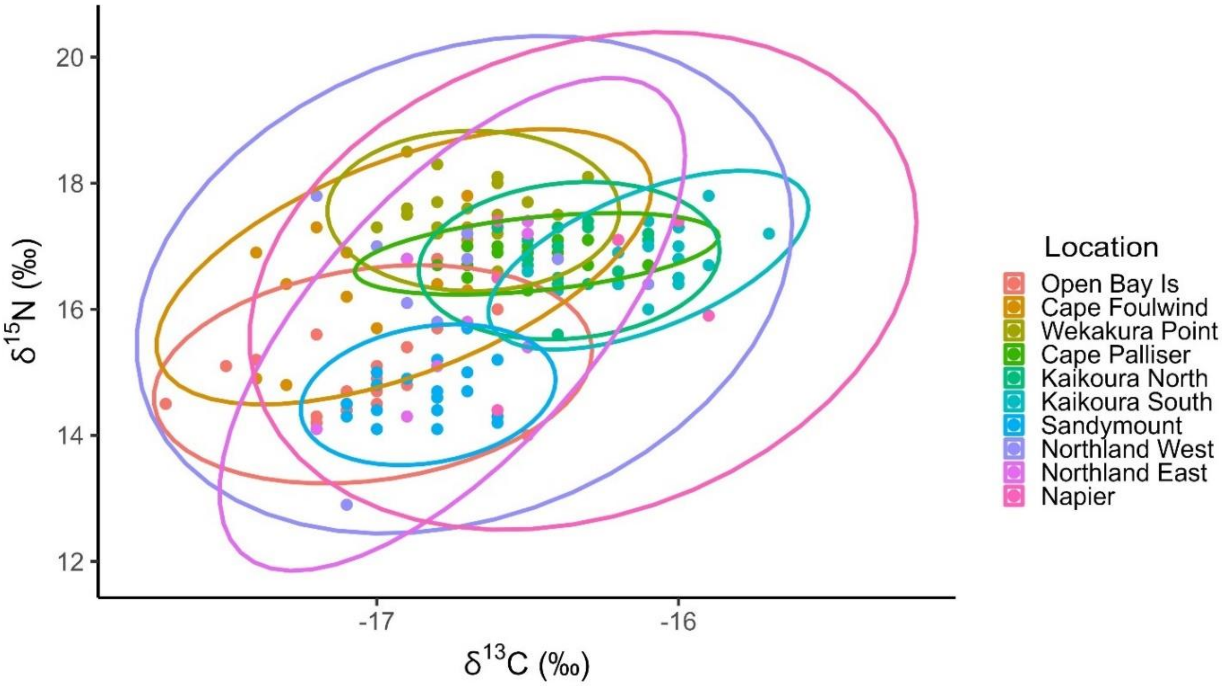


Figure 34 $\delta^{13}C$ and $\delta^{15}N$ values (‰) in vibrissae from New Zealand fur seal pups at seven breeding colonies in New Zealand, and stranded fur seals at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Pup vibrissae were sampled at the base, and vibrissae from stranded individuals were sampled at two-thirds of the length. The colour is the location and the shape is the vibrissa section. Bayesian ellipse sizes are 95 % CI.

Table 12 Group metrics for $\delta^{13}C$ and $\delta^{15}N$ values in vibrissae from stranded New Zealand fur seal young-of-the-year from locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. TA is the convex hull area, SEA is the standard ellipse area, and SEAC is the SEA corrected for sample size effects. Units are ‰^{2}.

Base	**Northland West**	**Northland East**	**Napier**
TA	6.27	5.29	1.38
SEA	3.18	3.03	1.12
SEAc	3.57	3.54	1.40
Two-thirds			
TA	2.94	1.28	1.50
SEA	1.54	0.73	1.15
SEAc	1.73	0.85	1.44

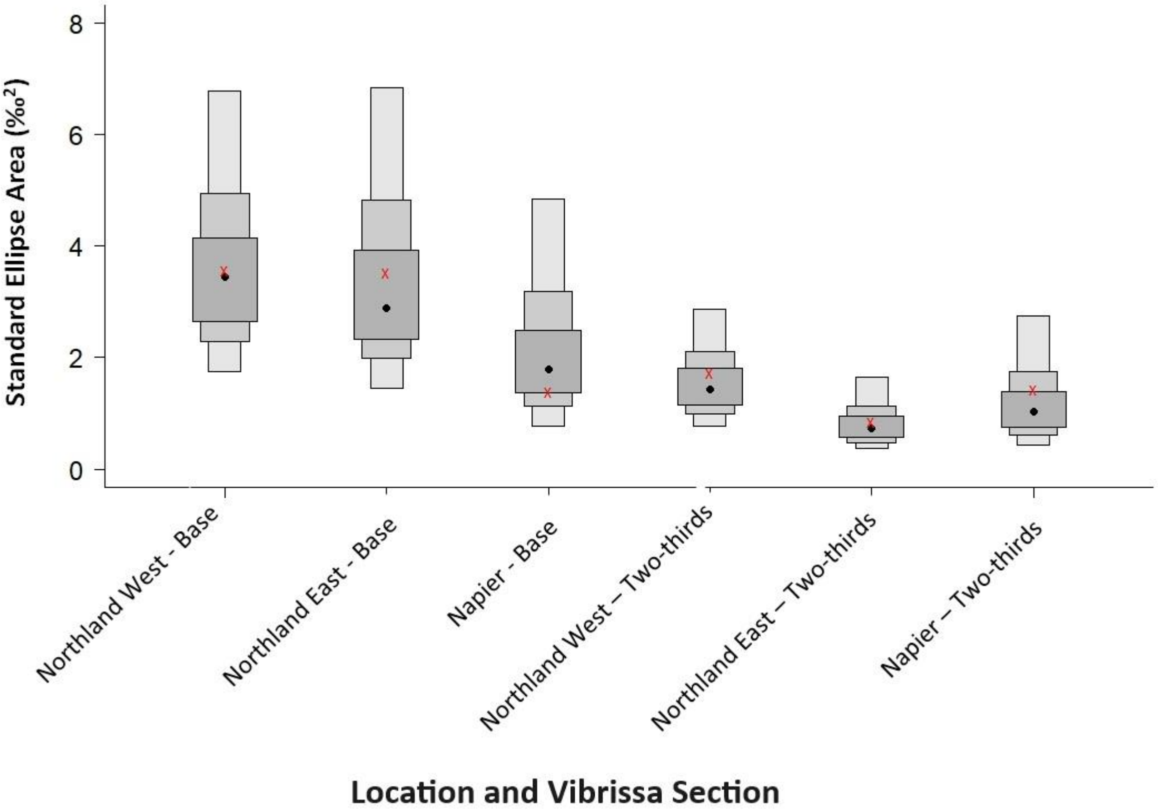


Figure 35 Isotopic niche space shown by 95 % CI bivariate ellipses (SEA_B) of $\delta^{13}C$ and $\delta^{15}N$ values in samples from the base and two-thirds of the length of the longest vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Black dot represents the mode, and red x represents the maximum likelihood estimated SEA_C (standard ellipse area corrected for sample size). Box edges from dark to light are 50 %, 75 % and 95 % CI. Units are ‰².

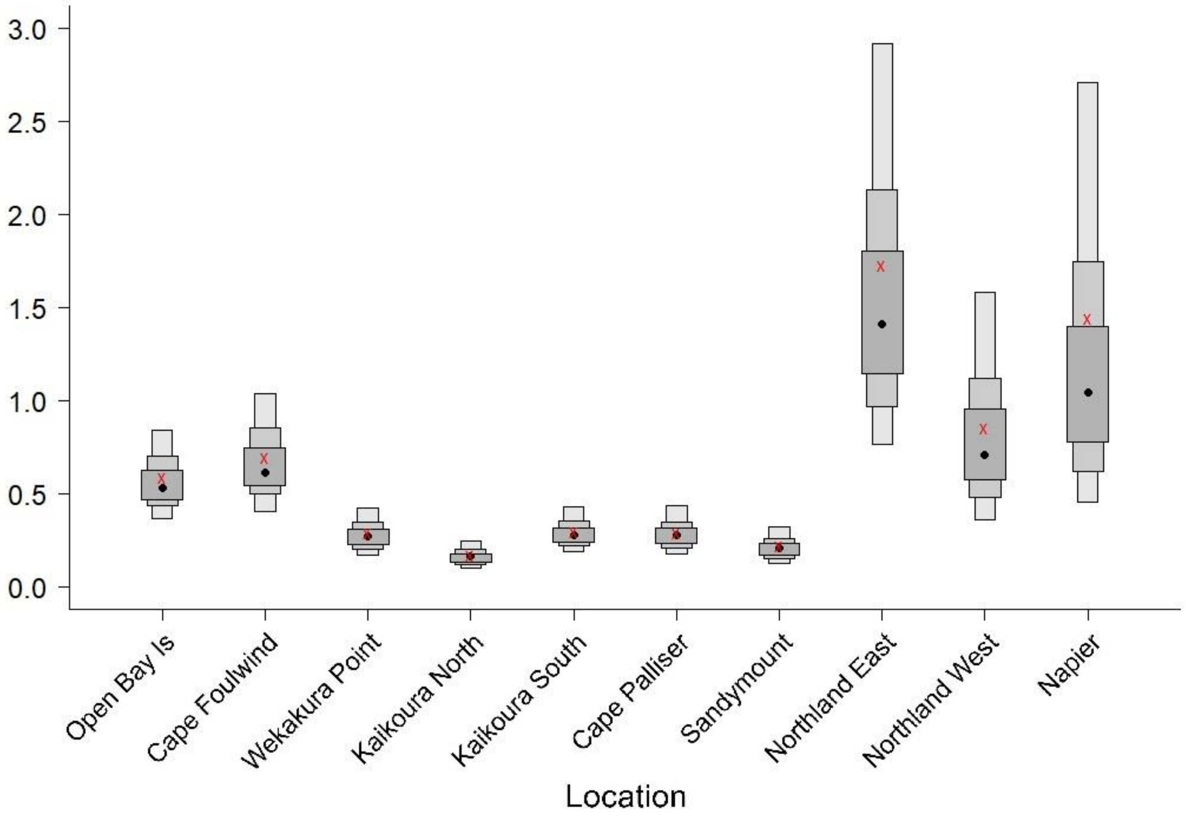


Figure 36 Isotopic niche space shown by 95 % CI bivariate ellipses (SEA_B) of $\delta^{13}C$ and $\delta^{15}N$ values in samples from the base of the longest vibrissa from New Zealand fur seal pups sampled at seven breeding colonies around New Zealand, and from two-thirds of the length of the longest vibrissa from stranded New Zealand fur seal young-of-the-year at locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Black dot represents the mode, and red x represents the maximum likelihood estimated SEA_C (standard ellipse area corrected for sample size). Box edges from dark to light are 50 %, 75 % and 95 % CI. Units are ‰^{2}.

Table 13 Ellipse areas (in ‰^{2}) for $\delta^{13}C$ and $\delta^{15}N$ values in vibrissae from New Zealand fur seal pups from seven breeding colonies around New Zealand, and stranded young-of-the-year from locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Vibrissae from stranded individuals were sampled at two-thirds of the length to make them comparable to samples taken at breeding colonies. Probability is the probability that the ellipse area at the first site is smaller than that at the second site, expressed as the proportion of posterior draws.

First Location	Area (‰^{2})	Second Location	Area (‰^{2})	Probability
Open Bay Islands	0.56	Cape Foulwind	0.66	0.72
Open Bay Islands	0.56	Wekakura Point	0.27	0.01
Open Bay Islands	0.56	Cape Palliser	0.16	0.00
Open Bay Islands	0.56	Kaikōura North	0.28	0.01
Open Bay Islands	0.56	Kaikōura South	0.27	0.01
Open Bay Islands	0.56	Sandymount	0.21	0.00
Open Bay Islands	0.56	Northland West	1.54	1.00
Open Bay Islands	0.56	Northland East	0.73	0.83
Open Bay Islands	0.56	Napier	1.15	0.96
Cape Foulwind	0.66	Wekakura Point	0.27	0.00
Cape Foulwind	0.66	Cape Palliser	0.16	0.00
Cape Foulwind	0.66	Kaikōura North	0.28	0.00
Cape Foulwind	0.66	Kaikōura South	0.27	0.00
Cape Foulwind	0.66	Sandymount	0.21	0.00
Cape Foulwind	0.66	Northland West	1.54	0.99
Cape Foulwind	0.66	Northland East	0.73	0.69
Cape Foulwind	0.66	Napier	1.15	0.91
Wekakura Point	0.27	Cape Palliser	0.16	0.04
Wekakura Point	0.27	Kaikōura North	0.28	0.54
Wekakura Point	0.27	Kaikōura South	0.27	0.52
Wekakura Point	0.27	Sandymount	0.21	0.19
Wekakura Point	0.27	Northland West	1.54	1.00
Wekakura Point	0.27	Northland East	0.73	1.00
Wekakura Point	0.27	Napier	1.15	1.00
Cape Palliser	0.16	Kaikōura North	0.28	0.97
Cape Palliser	0.16	Kaikoura South	0.27	0.96
Cape Palliser	0.16	Sandymount	0.21	0.78
Cape Palliser	0.16	Northland West	1.54	1.00
Cape Palliser	0.16	Northland East	0.73	1.00
Cape Palliser	0.16	Napier	1.15	1.00
Kaikōura North	0.28	Kaikōura South	0.27	0.48
Kaikōura North	0.28	Sandymount	0.21	0.15
Kaikōura North	0.28	Northland West	1.54	1.00
Kaikōura North	0.28	Northland East	0.73	1.00
Kaikōura North	0.28	Napier	1.15	1.00
Kaikōura South	0.27	Sandymount	0.21	0.17
Kaikōura South	0.27	Northland West	1.54	1.00
Kaikōura South	0.27	Northland East	0.73	1.00
Kaikōura South	0.27	Napier	1.15	1.00
Sandymount	0.21	Northland West	1.54	1.00
Sandymount	0.21	Northland East	0.73	1.00
Sandymount	0.21	Napier	1.15	1.00
Northland West	1.54	Northland East	0.73	0.10
Northland West	1.54	Napier	1.15	0.31
Northland East	0.73	Napier	1.15	0.75

Table 14 Ellipse areas (in ‰^{2}) for $\delta^{13}C$ and $\delta^{15}N$ values in vibrissae from stranded New Zealand fur seal young-of-the-year from locations on the east and west coasts of Northland, and at Napier, Hawkes Bay, North Island, New Zealand. Probability is the probability that the ellipse area at the first site is smaller than that at the second site, expressed as the proportion of posterior draws.

First Site	**Vibrissa Section**	**Area (‰^{2})**	**Second Site**	**Vibrissa Section**	**Area (‰^{2})**	**Probability**
Northland West	Base	3.18	Northland East	Base	3.03	0.44
Northland West	Base	3.18	Napier	Base	1.12	0.16
Northland East	Base	3.03	Napier	Base	1.12	0.21
Northland West	Two-thirds	1.54	Northland East	Two-thirds	0.73	0.09
Northland West	Two-thirds	1.54	Napier	Two-thirds	1.15	0.31
Northland East	Two-thirds	0.73	Napier	Two-thirds	1.15	0.75
Northland West	Base	3.18	Northland West	Two-thirds	1.54	0.03
Northland East	Base	3.03	Northland East	Two-thirds	0.73	0.00
Napier	Base	1.12	Napier	Two-thirds	1.15	0.16

3.3.5 Estimated Age at Weaning

Stranded individuals were found from 7 September to 7 October 2023, although they would have died a variable time before that. There was no attempt to estimate the time between individuals dying and being found, as decomposition rates were unknown. The mean vibrissa growth rate of 0.24 mm/day was determined from linear regression (Figure 20). The latest possible weaning dates for the stranded individuals were estimated to be 27 July to 20 August, 2023. Based on the assumed median pupping date of 16 December, 2022, the estimated maximum age at weaning is 223 – 247 days, which is less than any of the lactation lengths in the published literature.

3.4 Discussion

Stable isotope analysis is a powerful tool for studying foraging ecology and dispersal of mobile species (Crawford et al., 2008; Hobson, 1999, 2005; Hobson et al., 2010; Newsome, Clementz, et al., 2010), and is increasingly used as a cost-effective way to understand pinniped foraging (Lowther & Goldsworthy, 2011). The information gained from SIA can be enhanced by combining it with results from other biogeochemical markers, such as trace elements, persistent organic pollutants, or lipids, or with animal tracking (Hebert et al., 2009; Herman et al., 2005; Walters et al., 2020).

Vibrissae are metabolically inert once formed (West et al., 2006), relatively easy to sample (Jones et al., 2020), and widely used for SIA in pinnipeds (Baylis et al., 2016; Chilvers, 2017, 2019, 2021a; Lowther et al., 2013; Lowther & Goldsworthy, 2011; Scherer et al., 2015; Walters et al., 2014). To compare values from individuals sampled at different times, it is necessary to know an accurate, age-specific vibrissa growth rate (Rea et al., 2015), but growth rates in YOY are likely to vary widely among individuals (Rea et al., 2015).

This study measured vibrissae from pups at seven breeding colonies (Chapter 2), and from stranded YOY in the northern North Island, and calculated vibrissa growth rates based on linear regression, adding to the existing database of otariid vibrissa growth rates derived from cut/recut or biochemical markers (Table 8). Calculated growth rates were used to derive the first known estimate of vibrissa length at birth (EVLB) for NZFSs. In this study, the EVLB was used as a screening tool on stranded samples to help to confirm that vibrissae sampled were from YOY.

$\delta^{13}C$ and $\delta^{15}N$ values were compared among base and two-thirds vibrissa samples from stranded individuals and among two-thirds samples from stranded individuals and base samples from pups at breeding colonies. Isotopic niche widths were quantified and compared among the samples to give an indication of maternal diet and, therefore, foraging behaviour, and a comparison between pre-weaned and weaned pups of the year. The latest possible date of weaning was estimated for stranded individuals and compared to weaning times in the literature.

3.4.1 Vibrissa Growth Rates and Estimated Vibrissa Length at Birth

Vibrissa growth rates have been measured in different pinniped species, with techniques including cut/regrowth, glycine injection with SIA, annual oscillation, and $\delta^{15}N$ nadir at birth (Table 8). Growth rates vary with species and life-stage (Foo et al., 2019). It is necessary to know an accurate, age-specific growth rate in order to interpret sequential values along the vibrissa (Rea et al., 2015), or to be able to model growth rates using known growth parameters (Rogers et al., 2016). Ideally, vibrissa lengths and growth rates, and pup dates of birth, would be combined to calculate the EVLB, but accurate growth rates and dates of birth are not available for NZFSs.

In this study, individuals were sampled only once, so it was not possible to measure vibrissa growth rates within an individual. Vibrissa lengths at birth, median pupping dates, and vibrissa growth rates may all have varied between colonies. The first pup samples taken were from Open Bay Islands and the last from Sandymount, Otago Peninsula, so they may have different median pupping dates (see Chapter 2). The mean pupping date at Open Bay Islands was determined to be 9 December (Mattlin, 1978b) and at the Otago Peninsula the median pupping date was 24 December (Lalas & Harcourt, 1995), however, both these studies were carried out some time ago and there is no recent information on mean or median pupping dates at those locations. More recently, the median pupping date at Kaikōura was 16 December (Boren, 2005). Based on various studies, a median pupping date for NZFS colonies in New Zealand was estimated to be 16 December (Boren, Muller, et al., 2006).

Adult female NZFSs in Australia had vibrissa growth rates of 0.18 ± 0.04 mm/day based on a glycine spike (n = 8), and 0.19 ± 0.05 mm/day based on cut/recut (n = 18) (Foo et al., 2019), although the range in growth rates between individuals was not given. The glycine injection technique is independent of wear at the vibrissa tip, whereas in the cut/recut technique the distal vibrissa could be subject to damage or abrasion, so the growth rate derived from the glycine injection measurement might have been expected to be greater than the cut/recut, but that was not the case (Foo et al., 2019). Based on seasonal oscillation, the growth rates of female Antarctic fur seals (*Arctocephalus gazella*) at three colonies ranged from 0.04 – 0.21 mm/day (Walters et al., 2020), a five-fold difference between individuals. Vibrissae at one colony grew significantly faster than vibrissae at the other two colonies (Walters et al., 2020). Changes in the timing of migration or in seasonal environmental fluctuations could affect the accuracy of growth rates derived from annual oscillations (Rea et al., 2015). In a study on 35 adult female New Zealand sea lions (*Phocarctos hookeri*) of known age, vibrissa growth rates ranged from 0.01 to 0.05 mm/day, although this should be considered a minimum rate as it did not take into account possible wear at the vibrissa tip (Chilvers, 2019). The length of the vibrissa at birth is not mentioned in this study, but the minimum age of individuals captured was seven years, and the vibrissa formed *in utero* would presumably have been abraded by then (Rea et al., 2015), so the length of the vibrissa at birth could safely be ignored. In Steller sea lions (*Eumetopias jubatus*), the mean vibrissa growth rate in YOY was approximately double that of adults, but there was considerable individual variation in each age class (Rea et al., 2015). YOY had the widest range of vibrissa growth rates, from 0.19–1.92 cm/month (equivalent to 0.06 – 0.64 mm/day) (Rea et al., 2015), which is a 10-fold variation. Captive sub-adult Steller sea lions (0.14 and 0.17 mm/day) had vibrissa growth rates double that of adults (0.05 and 0.07 mm/day), although the study only involved two individuals of each age class (Hirons, Schell, & St Aubin, 2001).

The majority of samples from stranded individuals in the present study were plucked, and all the samples from pups at colonies were cut, so it was necessary to correct the plucked vibrissae for the portion that would have been below the epidermis. In a previous study on NZFSs the section of vibrissa below the epidermis was determined to be 1 – 5 mm (Noè, 2013). Conversely, in the present study, several of the plucked vibrissae were discoloured for the proximal 10 mm, which was thought likely to correspond to the part below the epidermis. In Steller sea lions the length of the vibrissa under the epidermis was 17.4 ± 3.4 mm (range 6 – 20 mm) (Rea et al., 2015). Regression analysis showed it was more accurately an addition of 3 – 5 % to the length of the vibrissa above the skin (Rea et al., 2015), however, as that study was in sea lions, the proportion of vibrissa under the skin surface in NZFSs may well be different. The length of the vibrissa under the epidermis could be determined by measuring the vibrissae of recently deceased NZFS. In the present study, if 5 % of the total vibrissa length was subtracted, the difference for each vibrissa length ranged from -5 – +8 mm, compared to subtracting 10 mm off each vibrissa, but the mean EVLBs and the calculated growth rates were almost identical (53.6 mm vs 53.2 mm, and 0.241 mm/day versus 0.248 mm/day). Vibrissa width was the main criterion used to select the section to sample for this study, and the vibrissae were sampled at a proportion of their length, which should help to compensate for the differing growth rates.

The vibrissae in adult female New Zealand sea lions ranged in length from 60 – 145 mm, and there was no correlation between vibrissa length and age of the individual (Chilvers, 2019). In a study on vibrissa morphology, which found no difference in vibrissa length among age classes, the mean length of the longest mystacial vibrissa in fur seals was 83.0 ± 20.3 mm, while in sea lions it was 90.7 ± 11.3 mm (Ginter et al., 2012). The longest recorded pinniped vibrissa was 480 mm in a male Antarctic fur seal (Bonner, 1968, in King 1983). South American fur seal (*Arctocephalus australis*) vibrissae measured 92.8 ± 3.8 mm at approximately 8 months of age, and grew at about 0.22 ± 0.04 mm/day, based on the minimum δ^{15}N value in the vibrissa occurring around the time of birth (Jones et al., 2020). Non-YOY (of unknown sex) vibrissae in the current study ranged in length from 148 – 250 mm, while vibrissae from stranded YOY ranged from 88 – 158 mm, so there was some overlap between the vibrissa lengths of YOY at approximately 8 – 10 months of age and non-YOY.

Another difficulty with estimating vibrissa length at birth is the loss of the fine foetal vibrissae at different times (Rea et al., 2015). Six out of 43 Steller sea lions captured at five months of age had isotopic evidence of wear or breakage at the vibrissa tip, whereas 34 had wear or breakage when they were recaptured at less than 12 months of age (Rea et al., 2015). The authors noted that the fine, foetal vibrissae could have been lost in both compared vibrissae before the first capture (Rea et al., 2015). Loss of the foetal vibrissae could explain the fact that estimated vibrissa lengths at birth were 7.8 ± 0.1 cm for Steller sea lion pups, while for individuals caught at around five and nine months of age they were 5.9 ± 2.30 cm. Conversely, in a study on 10 South American fur seals vibrissa SIA were apparently determined as far back as very early gestation, however, the proportion of vibrissa remaining from in-utero growth varied among individuals (Jones et al., 2020). In another study, the majority of *in utero* vibrissa growth was thought to occur in the third trimester (Scherer et al., 2015). There is a $\delta^{15}N$ nadir at birth which can be determined by sequential analysis of vibrissa segments (Rea et al., 2015), however, in the present study it was not possible to analyse the entire vibrissa.

The vibrissa growth rates calculated for the stranded individuals alone were not useful for estimating EVLBs, probably due to the large variation in vibrissa lengths and the relatively short period over which they were collected (Figure 22). There was no attempt to estimate the date of death, despite the fact that stranded individuals ranged from relatively freshly dead to quite decomposed, as the rate of decomposition was unknown. If the foetal vibrissae had been lost between the time of sampling on the colony and the time of sampling the stranded individuals then the stranded vibrissae should have been relatively shorter and the apparent growth rate lower, as seen in Steller sea lions (Rea et al., 2015). In fact, the growth rate including the stranded samples was 0.24 mm/day while that of the colony samples was 0.21 mm/day. The estimated growth rates are comparable to the mean vibrissa growth rate in South American fur seals of 0.67 ± 0.14 cm/month (0.22 ± 0.04 mm/day) in live individuals sampled at around eight months of age (Jones et al., 2020). Somatic growth rates in NZFSs between birth and 300 days of age are almost half the rates between birth and 50 days of age (Goldsworthy, 2006). Body growth rates of NZFS pups in Tasmania were 78 – 138 g/day from 0 – 50 days of age, and 52 – 86 g/day from 0 – 147 days of age (Lea & Hindell, 1997). It is not known whether vibrissa growth rates vary in the same way. Two adult male Steller sea lions that were emaciated at necropsy had the lowest vibrissa growth rates in that study (Rea et al., 2015). Given that the stranded individuals in the present study are most likely to have starved, their vibrissa growth rates could be expected to be lower than growth rates in healthy individuals. Vibrissa growth rates could be modelled more accurately if there were more samples from YOY and if they were sampled over a longer period.

Overall, there is likely to be considerable variation in vibrissa growth among individuals, and caution should be used when extrapolating growth rates, particularly without internal validation such as the use of the $\delta^{15}N$ minimum at birth (Rea et al., 2015). The calculated growth rates based on stranded individuals may not apply to live individuals. The lack of consistency between vibrissa lengths in stranded individuals and pups at colonies supports the decision to use vibrissa widths to determine the optimum proportion of the vibrissa length to sample, so the $\delta^{13}C$ and $\delta^{15}N$ values among stranded and colony samples could be compared.

3.4.2 Stable Isotope Analysis – $\delta^{13}C$ and $\delta^{15}N$ Comparison

The primary aim of the study was to determine the origin of stranded individuals by comparing the $\delta^{13}C$ and $\delta^{15}N$ values in their vibrissae to a database of values from pups at seven breeding colonies around New Zealand. Samples from the section of vibrissa likely to represent the time that stranded individuals were at their natal colony were compared to the breeding colony values. Although there were significant differences in $\delta^{13}C$ and $\delta^{15}N$ among many of the breeding colonies (see Chapter 2), the isotopic differences were not sufficient to assign individuals definitively to a source population (Hobson, 2005). Vibrissae from stranded individuals were also sampled near the base, to give an indication of weaning time and to quantify isotopic niche widths in YOY.

As vibrissa samples from dead individuals were being compared to live ones, an analysis of C:N ratios in all samples was carried out as an indication of keratin quality. Newsome et al., (2010) state that it is essential to include C:N values and their associated errors in results, as they are a proxy for data quality and enable results to be compared among studies. The C:N of keratin has been described as approximately 3.0 (Newsome, Clementz, et al., 2010). California sea otter (*Enhydra lutris nereis*) vibrissa C:N ratios varied from 3.3 – 3.5 (Newsome et al., 2009). In the present study, keratin C:N was slightly lower (2.91 ± 0.056) and ranged more widely (2.76 – 3.15) than in previous studies (Newsome, Bentall, et al., 2010; Newsome et al., 2009). C:N was lower in samples from stranded YOY than in samples from pups at colonies, which could possibly reflect poorer keratin quality in under-nourished individuals or post mortem vibrissa deterioration. However, as the calculation of carbon and nitrogen percentages depends on sample weight (C. Wood, personal communication, 25 January 2024), the range of values is not surprising given the difficulty of cutting and weighing a sample of 0.6 mg. Vibrissae from YOY were wider and, therefore, more difficult to cut accurately. Due to the possibly fluctuating sample sizes, there is no clear indication to reject any results based on the C:N ratios. $\delta^{13}C$ and $\delta^{15}N$ are independent of sample weight, as long as nitrogen is not completely saturated (C. Wood, personal communication, 25 January 2024).

$\delta^{13}C$ and $\delta^{15}N$ values did not differ significantly among the three different North Island areas. Given the overlap in $\delta^{13}C$ and $\delta^{15}N$ values among colonies on the east and west coasts, and stranded YOY in all three North Island areas, it is not possible to tell if, for example, animals that stranded on the west coast of the North Island originated on the west coast of the South Island. The 95 % C.I. ellipse for Northland West encompassed all the ellipses for the colonies, and the ellipses for Northland East and

Napier were also much larger than any of the colony ones (Figure 34). Isotopic niche widths are discussed further in the next section.

$\delta^{13}C$ and $\delta^{15}N$ values differed significantly between the base and two-thirds vibrissa samples, with both $\delta^{13}C$ and $\delta^{15}N$ values tending to be lower in the base than in the two-thirds samples (Figure 33). The relationship between maternal and pup $\delta^{13}C$ values is inconsistent among otariid species, and while $\delta^{13}C$ values in pups were similar to those of their mothers in two studies (Cherel et al., 2015; Lowther & Goldsworthy, 2011), at least one study has shown lower $\delta^{13}C$ values in pups (Chilvers, 2021b). The lower $\delta^{15}N$ would be expected in the base samples, both due to the drop in $\delta^{15}N$ at weaning (Cherel et al., 2015), and because other studies have shown that younger pinnipeds feed at a lower trophic level than older conspecifics (Hanson et al., 2009; Page et al., 2005a; Walters et al., 2014). $\delta^{13}C$ tends to be lower in pelagic species, and juvenile NZFSs in Australia have been shown to feed on small, pelagic fish species (Page et al., 2005a), however, information on foraging in juvenile NZFSs in New Zealand is not available. $\delta^{13}C$ would be expected to increase at lower latitudes (Graham & Bury, 2019), and in colony samples there was a slight but significant decline in $\delta^{13}C$ values with increasing latitude ($t = 3.72$, slope 0.07, $p < 0.001$, adjusted R-squared = 0.08, see Chapter 2). As there is no way of knowing where the stranded individuals had been foraging, analysis of $\delta^{13}C$ and $\delta^{15}N$ by latitude and longitude were not undertaken for the stranded individuals, but if they had been foraging further north than the breeding colonies for some time their $\delta^{13}C$ values could be expected to be higher.

3.4.3 SIBER – Stable Isotope Bayesian Ellipses in R

The concept of ecological niche is fundamental to ecology, although it can be difficult to define and measure (Newsome et al., 2007). SIA can provide the information needed to quantify an individual's habitat and resource use, and therefore help to describe its ecological niche (Newsome et al., 2007). The development of new statistical techniques has improved the understanding of isotopic niches, and enabled comparisons among communities (Jackson et al., 2011).

In this study, isotopic niche widths corrected for samples size (SEA_C) are greater in the base vibrissa samples (range 1.40 – 3.57 ‰^{2}) than in the two-thirds samples (range 0.85 – 1.73 ‰^{2}), which could be consistent with weaned pups foraging over a wider area and opportunistically feeding at a wider range of trophic levels (Table 14, Figure 35). As samples were only available from stranded individuals, there is no way of knowing whether healthy pups would have had similar or different isotopic niche widths. In the two-thirds samples from YOY, the SEA_C ranged from 0.85 – 1.73 ‰^{2}, while at colonies it was 0.17 – 0.69 ‰^{2} (Table 6). The larger niche widths for YOY are consistent with the stranded individuals in all three areas coming from a variety of colonies, rather than originating from just one colony.

Isotopic niche widths reach an asymptote at around n = 30 (Jackson et al., 2011). Larger sample sizes could help refine the isotopic niche size for the North Island areas, as the differences between SEA_B and SEA_C in the stranded samples are greater than the differences between SEA_B and SEA_C in the colony samples (Table 11). However, even with the current sample sizes, there is a clear difference in niche widths.

Niche widths in the present study were greater after weaning than prior to weaning, when the isotopic niche reflects maternal foraging (Cherel et al., 2015; Chilvers, 2017, 2021a; Ducatez et al., 2008; Jones et al., 2020; Lowther & Goldsworthy, 2011; Lübcker et al., 2020; Stricker et al., 2015). A study on the taxa consumed by adult female NZFSs in Australia showed 27 fish taxa, eight cephalopod, two avian, and one crustacean, while juveniles consumed 21 fish taxa, five cephalopod, and one avian (Page et al., 2005a). In grey seals (*Halichoerus grypus*), SEAs were smaller in juveniles than in adults (Hanson et al., 2018). Conversely, in a study on South American, subantarctic, and Antarctic fur seals isotopic niche widths were greater in juveniles than in adults (de Albernaz et al., 2017).

The relatively wide isotopic niches in juveniles in this study could be because YOY were foraging over a wider geographical area, or because they were consuming a greater range of prey species, or both (Bearhop et al., 2004). Additionally, isotopic niche width can be negatively correlated to prey availability (Ciancio et al., 2021; Ogilvy et al., 2022). In a study on skin SIA values in Māui dolphins (*Cephalorhynchus hectori maui*) over 28 years, a reduction in isotopic niche width was observed after a marine mammal sanctuary was introduced, possibly due to an increase in prey availability (Ogilvy et al., 2022). A study on Magellanic penguins (*Spheniscus magellanicus*), monitored at multiple colonies over several years, showed that isotopic niche widths were negatively correlated with the biomass of their prey fish, with a particularly marked isotopic niche expansion during a La Niña weather pattern (Ciancio et al., 2021). New Zealand was subject to a La Niña weather pattern from spring 2020 until January 2023 (www.niwa.co.nz), which could be expected to have increased the isotopic width, but there are no samples from other years available for comparison. In stranded YOY, isotopic niche widths were greater in the base samples (after weaning) than in the two-thirds samples (before weaning) (Figure 33), consistent with decreased prey availability. However, sampling in multiple years with different climatic conditions would be needed to assess the role of prey availability in NZFS isotopic niche width. Sampling live pups at breeding colonies at the same time as sampling stranded individuals in non-breeding areas would also help clarify the influence of food availability on isotopic niche width.

The ability to quantify isotopic niche widths improves the ability to compare values between different groups. Sampling across different seasons would allow a comparison between isotopic niche widths and climatic conditions in different years.

3.4.4 Stable Isotope Analysis – Time of Weaning

The marked decline in $\delta^{15}N$ values between the base and two-thirds samples is consistent with YOY being weaned between the two samples (Cherel et al., 2015). Pups are effectively feeding off their mother's tissue reserves until weaning (Arnould & Boyd, 1995), so they are feeding at a higher trophic level (Cherel et al., 2015). Mean $\delta^{15}N$ was 16.2 ± 1.26 ‰ in the two-thirds samples and 11.5 ± 1.53 ‰ in the base samples, a drop of 4.7 ‰, consistent with a change in trophic level (Chilvers, 2021b; Hobson et al., 1996; Kelly, 2000; Minagawa & Wada, 1984). In a study on South American fur seals at around eight months of age, sequential analysis of the vibrissae showed a steady increase in $\delta^{15}N$ with age, probably due to physiological processes such as fasting over-riding the maternal $\delta^{15}N$ signature (Jones et al., 2020). It was not possible to determine the maximum $\delta^{15}N$ in the present study, as only two vibrissa sections were analysed, so it is possible that maximum $\delta^{15}N$ levels may subsequently have been higher than at the two-thirds section. Ontogenetic variations in foraging occur, with an SIA study on the tooth dentine of adult male Antarctic fur seals showing that as they age, they tend to forage on prey of a higher trophic level (Hanson et al., 2009), with similar findings in NZFSs in Australia (Page et al., 2005a). This tendency may also have increased the apparent difference between samples from the two-thirds vibrissa, where pups were feeding on milk, and the base samples, which reflected their own foraging at perhaps a lower trophic level to their mothers, as seen in several pinniped species (Hanson et al., 2009; Page et al., 2005a; Walters et al., 2014). In South Australia, some NZFS pups were foraging as early as five to six months old, based on TDRs and scat analysis (Baylis et al., 2005). The relatively low foraging efficiency of YOY was thought to be likely to lead to high mortality as they transitioned to full nutritional independence (Baylis et al., 2005).

The drop in $\delta^{15}N$ in the present study between the two-thirds sample and the base sample was used to confirm that individuals were YOY. One individual (ID: 208) with a high index of suspicion that it was an adult was ruled out of the analysis as there was only a 0.7 ‰ drop in $\delta^{15}N$ between the two-thirds and the base sections. Another individual initially identified as a pup at Napier (ID: 239) was an outlier for both $\delta^{13}C$ and $\delta^{15}N$ and had an increase in $\delta^{15}N$ from two-thirds to the base, which was inconsistent with it being a pup, so it was excluded from the analysis (vibrissa length was 140 mm, and EVLB was 76 mm, so within the range for a pup). The only other possibility is that it was weaned before the two-thirds section, although that would imply that it had survived for perhaps five months after weaning, having been weaned as early as four months of age, which would seem unlikely.

Notwithstanding the variation in vibrissa growth discussed above, it is clear that all the YOY were weaned sometime prior to the formation of the vibrissa section 10 mm distal to the proximal end of the vibrissa.

In a different study of nine juvenile or subadult NZFSs necropsied between August and November 2023, two died from traumatic injuries and the rest were in poor body condition with findings consistent with starvation (S. Hunter, personal communication, 16 April 2024). Although it was not possible to determine the causes of death in the present study, there were no obvious external signs of trauma and individuals may well have died of starvation. Vibrissa growth rates tend to be lower in emaciated individuals than in ones in normal body condition (Rea et al., 2015), so 10 mm of vibrissa may well represent more than 42 days of growth. Stranded individuals were found from 7 September to 7 October 2023, however, they would have died a variable time before that. Assuming the average vibrissa growth rate of 0.24 mm/day, and disregarding the time between individuals dying and being found, the latest dates that the stranded individuals could have been weaned are 27 July to 20 August 2023.

To assess the significance of the weaning dates it is necessary to know the date of birth and the normal lactation length for NZFSs. At Open Bay Islands in 1971, live fur seal births occurred from 18 November to 29 December (42 days) with 76.9 % of births occurring between 29 November and 19 December (22 days) (Miller, 1975b). In 1974/75 and 1975/76 the overall mean pupping date at Open Bay Islands was 10 December, with the first live pups born on 19 and 15 November, respectively, and 90 % born within a six-week period (Mattlin, 1978a). At Kaikōura, over three breeding seasons, the first live birth was on 26 November, 13 November, and 17 November, while the last live birth was 29 December for both the latter two seasons (Boren, 2005). Median pupping dates were 16 December, 5 December and 7 December, respectively (Boren, 2005). At Kaikōura, the first pup was recorded on 8 December 2021, and on 9 December 2022 (Hall et al., 2024). On the Otago Peninsula in 1993/94, the median pupping date was 24 December, with the first pup born on 18 November and 90 % born between 29 November and 21 January (55 days) (Lalas & Harcourt, 1995). The generally adopted median pupping date for NZFSs in New Zealand is 16 December (Boren, Muller, et al., 2006). If 90 % of pups are born within six weeks (Mattlin, 1978a), then 90 % would be expected to be born between 25 November and 6 January. The timing of pupping in harbour seals has been shown to vary according to maternal nutritional status (Cordes & Thompson, 2013), however, there is no recent information on median pupping dates in NZFSs.

The date range of latest possible weaning dates in the current study is 27 July to 20 August, which is 223 – 247 days from median pupping date, and 256 – 280 days from even the earliest previously recorded date of birth for a fur seal pup in New Zealand (13 November, Boren, 2005). If 90 % of pups are born from 25 November to 6 January, that is 244 – 268 days prior to the latest calculated weaning dates in this study. In one Australian study, a single tagged pup was found approximately 70 km from its natal colony on 8 August, leading the authors to suggest some pups may be weaned as early as eight months (243 days) of age, but the 95 % confidence intervals for weaning age in the same study were 269 – 311 days (Goldsworthy, 2006) (Table 15). Boren, (2005), indicated that a median lactation of 294 ± 6 days is the most common figure quoted for the NZFS, with weaning occurring in September to October.

Table 15 Summary of New Zealand fur seal pup weaning ages and dates at colonies in New Zealand and Australia. An * means the weaning age was approximate.

Location	**Year**	**Weaning Age (days)**	**Weaning date**	**Reference**
Kangaroo Island, South Australia	1988-90	285 (269-311)	2 October (16 September -28 October	Goldsworthy, 2006
South Australia		294		Haase, 2005
Open Bay Islands, New Zealand	1974/75, 1975/76	300*		Mattlin, 1978a
Kaikōura, New Zealand	2002, 2003, 2004	352, 325, 343		Boren, 2005
Kangaroo Island, South Australia	2001		26 October ± 16 days	Haase, 2007
Kangaroo Island, South Australia	2002		18 October ± 17 days	Haase, 2007
Kangaroo Island, South Australia	2003		13 October ± 11 days	Haase, 2007

It should be noted that in the current study individuals may be younger than the median age, and that the estimated date of vibrissa sampling is the latest possible weaning date; they may well have been weaned earlier than that. If, for example, the stranded individuals were the last ones born, at around 29 December, then the latest they could have been weaned is 210 – 234 days old. Also, if vibrissa growth rates are less than the mean calculated rate, then the vibrissa base sample would be earlier than 27 July to 20 August. Based on the median pupping date, the estimated maximum age at weaning is 223 – 247 days, which is less than any of the lactation lengths in the published literature.

Individuals sampled in 2023 were unlikely to have been the first animals to strand that year. On 22 June 2024, a stranded YOY (body length: 77 cm) was found at Ruakaka Beach, east coast of Northland (approximate location: 35.910°S, 174.4610°E), and on 23 June 2024, another stranded YOY (body length: 78 cm; length of longest vibrissa: 123 mm) was found at Uretiti Beach, east coast of Northland (approximate location: 35.9628°, 174.4691°) (P. Miller, personal communication, 23 June 2024). June 22 is only 189 days after the assumed median pupping date of 16 December. A further stranded YOY and two live YOY in poor body condition were seen in similar areas on 11 – 12 July 2024 (P. Miller, personal communication, 13 July 2024).

In pinnipeds, weaning constitutes the end of any maternal investment in the pup, and mortality rates are often high in the post-weaning period (Reiter et al., 1978). Juveniles are more susceptible to predation and must learn to forage effectively (Reiter et al., 1978), despite being smaller and having less diving capacity than more mature conspecifics (Page et al., 2006). Diving ability is critical to transitioning successfully to nutritional independence, but pups must balance the need to develop foraging skills with the need to maintain body reserves (Baylis et al., 2005). The age and condition of pinniped pups at weaning and the environmental conditions after weaning affect pup growth and survival (Beauplet et al., 2005; Davis, 2014; Goldsworthy, 2006; Ono et al., 1987).

The effects of climate fluctuations on fish species in New Zealand were incompletely understood (Dunn et al., 2009), however, a study on blue penguins showed that the small pelagic fish over the continental shelf that they forage on were more abundant in El Niño conditions, and likely to be less abundant in La Niña conditions (Fraser & Lalas, 2004). Juvenile NZFSs in South Australia fed mostly on small pelagic fish (Page et al., 2005a), and the La Niña weather pattern predominated in New Zealand from spring 2020 until January 2023 (www.niwa.co.nz).

The findings of the present study are consistent with stranded YOY being weaned earlier than the optimum, and having lower survival rates due to lack of food, although the scope of the study is not sufficient to prove this.

3.5 Limitations of the Study and Future Research

Like many studies, this research raises more questions, and was subject to limitations.

One obvious limitation in this study was the small sample sizes from the stranded individuals in the three North Island areas. Samples were collected opportunistically, and ideally more areas would have been surveyed and surveys would have started earlier. More frequent surveys could have overcome the problem of individuals missing their vibrissae due to decomposition, as did happen on some occasions. There were logistical constraints on the number of surveys, and the length of coast, that could be covered by the author. Department of Conservation staff in the Napier area sampled stranded NZFSs, but samples were not available from other areas. The study could have been improved by a more coordinated approach to sample collection over a wider area.

The fact that only dead individuals were sampled is a limitation. Relatively few live juveniles were seen in the surveyed areas, and eight- to nine-month-old NZFSs are difficult to catch. It would be better to sample at breeding colonies at the same time of year as the stranded YOY were sampled, to get a cohort of live YOY for comparison. There should be a greater density of pups still at breeding colonies than around the coast of the North Island at that time of year, and it would be easier to assemble the necessary small team of people in a more circumscribed area. Vibrissa analysis could then determine whether YOY at the colonies had been weaned or not, and whether isotopic niche widths were larger or smaller in YOY at breeding colonies.

Financial constraints limited the number of sections that could be analysed from each vibrissa, and also necessitated a greater level of sample preparation by the author. Professional SIA laboratories run duplicates of each sample, which is a check for any discrepancies in results (C. Wood, personal communication, 25 January 2024). Of the 131 samples originally tested from NZFS pups at colonies (Chapter 2), seven were saturated in nitrogen, so did not yield a $\delta^{15}N$. The vibrissae were resampled and all yielded a $\delta^{15}N$ value at the second testing. Of the 60 samples from the 30 stranded individuals, five were saturated in nitrogen, due to sample weights not being sufficiently precise, and therefore, did not yield a $\delta^{15}N$ result. For logistical reasons it was not possible to reanalyse the samples so the four individuals were removed from the analysis (in one individual the nitrogen was saturated in both samples). The carbon to nitrogen ratios would have been more reliable if the sample weights had been more precise, however, nitrogen saturation did not affect the $\delta^{13}C$ and $\delta^{15}N$ values, which were the main data from this study. The ability to analyse multiple sections per vibrissa would have helped refine the estimated weaning time, and, if the $\delta^{15}N$ nadir at birth could have been accurately determined, could have greatly improved the estimated vibrissa length at birth, and the estimated vibrissa growth rates.

The breeding colonies sampled were largely determined by logistical constraints, as all pups that were sampled were being caught for mark/recapture studies. It would have been helpful to be able to sample colonies in Fiordland and Rakiura/Stewart Island as these areas also have substantial pup production (Chilvers, 2021c; Watson et al., 2015), however, there was no mark/recapture monitoring of those areas in the 2022/23 breeding season and both areas are difficult to get to and to undertake research in.

The study would benefit from sampling over multiple years and different climatic conditions. Niche widths in high-level predators have been shown to be a predictor of fish biomass (Ciancio et al., 2021), and monitoring isotopic niche width in NZFSs has the potential to be a useful tool for ecological monitoring.

3.6 Conclusions

- The use of regression analysis on samples from NZFS pups at colonies, and from stranded YOY, to estimate growth rate and vibrissa length at birth, constitutes the first attempt to do so for NZFSs in New Zealand, and adds to the existing pinniped literature on growth rates and vibrissa lengths at birth. As with other otariids, vibrissa growth rate appears to be individually variable.
- The $\delta^{13}C$ and $\delta^{15}N$ values of samples from stranded NZFSs in northern New Zealand differed significantly between the base and two-thirds of the vibrissae length, but there were no significant differences among the geographical locations for either section.
- The $\delta^{13}C$ and $\delta^{15}N$ values at the two-thirds vibrissa sample of stranded individuals were comparable to those of samples taken from NZFS pups at seven breeding colonies (see Chapter 2 for details). The stranded samples largely overlapped with all the colony samples, which is consistent with the stranded individuals coming from known breeding locations, although it does not preclude them from having been born elsewhere. $\delta^{13}C$ and $\delta^{15}N$ values in vibrissa samples from colonies and from stranded YOY were not sufficiently isotopically distinct to identify stranded YOY to their colony of origin.
- Isotopic niche widths were greater for two-thirds samples from stranded individuals than from colony samples, and greater for base than for two-thirds samples. The greater niche widths could be due to individuals foraging on a wider range of species or in more wide-spread areas, or to wider baseline isotopic ranges. Lack of prey availability can lead to wider isotopic niche widths.
- The calculated latest possible weaning date of stranded YOY was earlier than the observed weaning dates in the literature. Early weaning could contribute to increased mortality.

Chapter 4. General Discussion and Conclusions

This chapter summarises the findings from chapters two and three and discusses the broader implications of NZFS dispersal and the role of the species in the ecosystem. The present study proposes a novel approach to monitoring the NZFS using SIA and identifies a role for isotopic niche width calculation as an ecologically relevant parameter. In this chapter, the advantages and limitations of the study are discussed, with particular reference to the practical application of SIA to improve the understanding and management of this charismatic and under-studied species. Future research is suggested.

4.1 Summary of Findings

In Chapter two, vibrissa samples were collected from seven established NZFS breeding colonies in New Zealand. $\delta^{13}C$ and $\delta^{15}N$ isotope ratios were measured in the proximal vibrissa and compared between the colonies, and cluster analysis and isotopic niche analysis were carried out. Although the colonies were not sufficiently isotopically distinct to confidently distinguish between them, southern South Island colonies clustered relative to northern ones, and the northern South Island/Southern North Island colonies clustered east versus west. Isotopic niche widths, expressed as standard ellipse areas, were substantially larger in the two southwestern colonies than in the remaining colonies, with a high probability that the differences were repeatable.

In Chapter three, vibrissae were collected from stranded (deceased) NZFSs in three areas of the North Island, New Zealand. For the first time, for the NZFS, vibrissa growth rates were calculated for pups at colonies and stranded young-of-the-year (hereafter 'YOY'). Accurate vibrissa growth rates are needed to interpret sequential $\delta^{13}C$ and $\delta^{15}N$ values along a vibrissa (Rea et al., 2015). Vibrissa lengths varied widely among individuals, consistent with other studies that showed wide variations in vibrissa growth rates among pinnipeds (Chilvers, 2019; Rea et al., 2015; Walters et al., 2020). The estimated vibrissa length at birth was calculated and used as a screening test to confirm that sampled vibrissae were from YOY. There was some overlap in absolute vibrissa length between YOY and non-pups.

$\delta^{13}C$ and $\delta^{15}N$ values were determined for sections from the base of the vibrissa, and at two-thirds of the length in YOY. Isotopic niche widths were greater in the groups of stranded NZFSs than at colonies, and greater at the base of the vibrissa than at two-thirds of the length, implying greater diversity of foraging in weaned YOY than in pups before weaning. The latest possible date of weaning was calculated for stranded individuals, with the documented lactation period, therefore, being shorter than any in the literature for the NZFS. Early weaning has been shown to negatively affect pinnipeds (Beauplet et al., 2005; Davis, 2014; Goldsworthy, 2006; Ono et al., 1987), however, it was not possible to quantify the effects of early weaning on NZFS in this study.

In the following sections, the ecological implications of recolonisation and some threats to the NZFS are discussed, with particular reference to the role of stable isotope analysis (SIA) in increasing the understanding of NZFS ecology.

4.2 Ecological Implications of Recolonising New Zealand Fur Seals

Many aspects of marine mammal ecology are still unknown, but marine mammal distribution and abundance can affect entire ecosystems (Bowen, 1997; Haussmann et al., 2013; Makhado et al., 2006; Smith, 1988). Marine ecosystem health can be assessed by monitoring marine sentinel organisms (Bossart, 2011). The ideal marine sentinel organism is charismatic, lives a relatively long time, feeds at a high trophic level, is resident in coastal areas long-term, and stores toxins and pollutants in its body fat reserves (Bossart, 2011), and the NZFS meets most of those criteria. The NZFS is recolonising its historic range (Crawley & Wilson, 1976; Lalas & Bradshaw, 2001), and populations appear to be increasing (A. Hall, unpublished data), after the species was almost eradicated by hunting (Crawley & Wilson, 1976). NZFSs are subject to multiple anthropogenic threats (Abraham et al., 2021; Abraham & Berkenbusch, 2017; Hamer & Goldsworthy, 2006; Lalas & Bradshaw, 2001; Thompson et al., 2011), with climate change increasingly adding to the risks of habitat loss and changes in prey availability (Keegan et al., 2022; Roberts & Hendriks, 2022). The NZFS is also at risk from emerging diseases such as highly pathogenic avian influenza (HPAI, H5N1) (Gartrell et al., 2024).

4.2.1 Diet and Foraging

The life history patterns of fur seal species are determined by seasonality, and by the amount of environmental uncertainty (Gentry & Kooyman, 1986). Fur seals in temperate regions generally depend on upwelling systems or productive ocean currents for food (Baylis et al., 2008b; Gentry & Kooyman, 1986). Environmental uncertainty is increased by sea surface temperature anomalies (SSTA) (Gentry & Kooyman, 1986). The NZFSs is a generalised predator (Arnould et al., 2011; Harcourt et al., 2002), however, relatively few studies have examined diet and foraging of the NZFS in New Zealand (Allum & Maddigan, 2012; Boren, 2010; Carey, 1991a; Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016; Fea et al., 1999; Harcourt et al., 1995, 2001, 2002; Holborow, 1999; Street, 1964; Willis et al., 2008). A wide range of foraging and provisioning strategies has been demonstrated in the NZFS in

Australia (Baylis et al., 2005; Page et al., 2005a, 2006), and in related species in other locations (Arnould et al., 2011; Arnould & Kirkwood, 2008; Bailleul et al., 2005; Bonadonna et al., 2000; Boyd, 1996, 1998a; Guinet et al., 2001; Lea et al., 2002; Littnan & Arnould, 2002; McCafferty et al., 1998; Staniland et al., 2004; Thompson et al., 2003; Walters et al., 2020). One consistent thread in fur seal foraging studies is that individuals show a high level of behavioural plasticity (Baylis et al., 2012), and foraging is generally driven by environmental conditions (Bailleul et al., 2005; Bonadonna et al., 2001; Boyd, 1996; Lea et al., 2002; Staniland et al., 2004; Thompson et al., 2003). SIA studies in sea lions generally indicate two distinct foraging strategies, sometimes with an additional intermediate ecotype (Chilvers, 2017, 2018, 2019, 2021a, 2023; Lowther & Goldsworthy, 2011), however, in a study comparing sympatric South American fur seals (*Arctocephalus australis*) and sea lions (*Otaria flavescens*) the fur seals were generalist individuals while the sea lions were individually more specialised (Franco-Trecu et al., 2014). Cluster analysis of results from the present study (Chapter 2) concurs with previous studies (Arnould et al., 2011; Harcourt et al., 2002) suggesting that NZFS individuals are generalist predators.

Role of SIA

SIA is only an indirect indicator of diet and foraging location (Rubenstein & Hobson, 2004). Cetaceans known to be foraging in different areas and consuming different prey can be isotopically indistinguishable (Ogilvy et al., 2023; Riccialdelli et al., 2010). Conversely, some relatively small-scale studies have shown marked differences between populations over small geographic areas (Ogilvy et al., 2022, 2023). Even in areas with overlapping $\delta^{13}C$ and $\delta^{15}N$ values, the isotopic niche widths of different groups can be quantified and compared (Jackson et al., 2011). In juvenile grey seals (*Halichoerus grypus*), isotopic niche widths were smaller than those of adults (Hanson et al., 2018). Conversely, in a study on three species of fur seals, isotopic niche widths were greater in juveniles than in adults (de Albernaz et al., 2017). $\delta^{13}C$ and $\delta^{15}N$ values in otariid vibrissa samples from dependent pups are thought to reflect maternal foraging (Cherel et al., 2015; Chilvers, 2017, 2021b; Ducatez et al., 2008; Lowther & Goldsworthy, 2011). Values from NZFSs sampled as pups at breeding colonies and as stranded YOY (at two-thirds of the vibrissa) should, therefore, be related to foraging by their mothers. In the present study, isotopic niche widths are greater for stranded YOY groups than for pups at colonies, and greater at the base of the vibrissa than at two-thirds of the length in stranded groups (Chapters 2 and 3), implying a greater niche width for stranded YOY than for their mothers.

The greater niche widths in the Open Bay Islands and Cape Foulwind breeding colonies compared to the other colonies (Chapter 2) may reflect differences in baseline $\delta^{13}C$ and $\delta^{15}N$ values in the prey in those areas (Bearhop et al., 2004; Ogilvy et al., 2023), or decreased prey availability leading to wider isotopic niches (Ciancio et al., 2021; Ogilvy et al., 2022; Ratcliffe et al., 2018). Primary productivity is expected to decline in the West Coast, South Island, marine area with increasing sea temperatures (Roberts & Hendriks, 2022), however, it is not clear whether that is already affecting the NZFS. Being able to quantify, and statistically compare, isotopic niche widths is useful for comparing the foraging of different groups.

4.2.2 Dispersal

A primary aim of this study was to clarify the dispersal of NZFSs in northern New Zealand in the non-breeding season, using SIA. SIA can be used to trace migration patterns in some species (Crawford et al., 2008; Hobson, 1999; Hobson et al., 2010; Ramos & González-Solís, 2012). As there was considerable overlap in $\delta^{13}C$ and $\delta^{15}N$ values among the breeding colonies (Chapter 2) and complete overlap between the samples from stranded individuals and those from breeding colonies (Chapter 3), it was not possible to assign individuals to their colony of origin using SIA alone.

Genetic studies are frequently used to identify an individual's population of origin (Bradshaw & Brook, 2010), but their accuracy depends on the genetic variability within the species and the statistical method used (Cornuet et al., 1999; Latch et al., 2006). Genetic studies on NZFSs have mostly focussed on identifying the colony of origin of bycaught individuals (Dussex et al., 2016; Robertson & Gemmell, 2005). The loss of adult females has the greatest effect on a pinniped population (Meyer et al., 2015; Robertson & Chilvers, 2011), however, adult male NZFSs are over-represented in bycatch (Pavanato et al., 2023). Despite the apparently divergent NZFS lineages (Wynen et al., 2001), the currently available microsatellite markers appear to be insufficient to determine the colony of origin of NZFSs (Dussex et al., 2016; Robertson & Gemmell, 2005). Recent genomic studies have also been unable to assign NZFSs to their colony of origin (B. Robertson, personal communication*,* 29 May 2024).

Combining genetic sampling and SIA might yield better results than either individually. A study using eight microsatellite markers correctly assigned approximately 42 % of individuals to their colony of origin and approximately 70 % to their area of origin (Robertson & Gemmell, 2005). Combining microsatellite analysis with SIA on colony samples may differentiate Sandymount (east coast, South Island) from Open Bay Islands (west coast, South Island), however, when using SIA alone Sandymount samples formed a subset of Open Bay Islands ones. Likewise, it was difficult to distinguish Cape Foulwind samples from the colonies at Cape Palliser, Kaikōura North and Kaikōura South, but microsatellite analysis could help distinguish between west and east coasts (Robertson & Gemmell, 2005). The South Island colonies have been divided into two genetic clusters; one containing West Coast and northern east coast colonies, and the other containing Fiordland to Banks Peninsula colonies (Dussex et al., 2016; Salis et al., 2016). The lack of genetic structuring in NZFS populations limits the effectiveness of genetic analysis in assigning individuals to a colony, or even an area, of origin (B. Robertson, personal communication, 29 May 2024).

Role of SIA

One difficulty with combining SIA and genetics to determine the colony of origin of bycaught individuals is determining which part of the vibrissa to sample. Ideally, a section would be taken from the adult's vibrissa that would correspond to the time when it was at the colony as a pup, but that section of vibrissa may no longer be present (Rea et al., 2015). Even if the appropriate part of the vibrissa is still present, it may not be possible to identify it, given that the exact age and vibrissa growth rate of the individual are likely to be unknown. SIA values may differ between age- and sex- groups at the same colony. For example, at a colony in South Australia, adult male and female NZFS and juvenile NZFS foraged in different areas and consumed different prey (Page et al., 2005a). Both female and, to a lesser extent, male fur seals are thought to be philopatric (King, 1983; Miller, 1971), however, immigration does occur (Bradshaw, 1999), so adults sampled at a breeding colony might not have returned to their natal colony. Furthermore, territorial males do not feed during the breeding season (Crawley & Wilson, 1976; Miller, 1975b), so their isotopic signatures would not necessarily reflect the isoscape near the colony. Conversely, lactating females tend to forage relatively close to their breeding colonies while provisioning their pups (Crawley & Wilson, 1976).

While dependent otariid pup $\delta^{13}C$ and $\delta^{15}N$ values are related to those in their mothers (Cherel et al., 2015; Chilvers, 2017, 2021b; Ducatez et al., 2008; Lowther & Goldsworthy, 2011), the actual maternal values would be different, particularly $\delta^{15}N$, which would be expected to be lower in maternal than pup tissues (Cherel et al., 2015; Chilvers, 2021b). Physiological differences, including fractionation of isotopes, affect isotope values in different tissues and individuals (Hobson et al., 1996; Jenkins et al., 2001).

The complexity of SIA in such a mobile and generalised predator, combined with the lack of both isotopic baseline data and specific foraging data, and the low resolution of genetic analysis, indicate that a combination of SIA and genetic analysis is unlikely to have widespread use in identifying the origin of bycaught individuals. A useful application of SIA would be to calculate the isotopic niche width of a group of bycaught samples, which would give an indication of diversity of foraging among individuals.

4.2.3 Recolonisation

When high level predators such as NZFSs recolonise areas from which they have been largely absent for several hundred years (Smith, 1989), it provides both opportunities and challenges (Bonner, 1958; Bowen, 1997).

Charismatic, long-lived, top predators such as the NZFS make suitable sentinel organisms for monitoring marine ecosystem health (Bossart, 2011). As NZFSs recolonise their historic range (Crawley & Wilson, 1976; Lalas & Bradshaw, 2001), and populations increase (A. Hall, unpublished data), NZFS interactions with humans are likely to increase, particularly in the more populated areas such as the Hauraki Gulf/Coromandel and the coast of Northland. Additionally, NZFSs have advocacy and tourism value, however, tourism can disturb NZFSs both in the water and at breeding colonies (Boren et al., 2002; Cowling, 2013; Cowling et al., 2015).

The colonisation of new breeding areas by NZFSs depends on spatial and temporal parameters of the terrestrial and marine environments, population demographics, and individual behaviour (Bradshaw, 1999). While the current non-breeding range, from the Three Kings Islands, north of the North Island, to Macquarie Island, in the subantarctic, does not appear to have changed since the 1970s (Crawley & Wilson, 1976), anecdotally the numbers of NZFSs occupying northern parts of New Zealand in the non-breeding season seem to have increased (personal observation; R. Chappell, personal communication, 11 February 2022; E. Davies, personal communication, 7 January 2022), however, systematic surveys have not been carried out. Counting pups is the only way to estimate pinniped populations (Shaughnessy et al., 1994), therefore, accurate population estimates are not possible in non-breeding areas (Bradshaw et al., 1999). There is less evidence of an expansion in the breeding range. The first modern record of NZFS breeding in the North Island, New Zealand, was at Cape Palliser in the early 1990s (Dix, 1993). Cape Palliser remains the only North Island colony to produce more than a few pups each year, with approximately 600 counted there in the 2022/23 season (L. Boren, personal communication, 11 September 2023).

Harvesting by early Polynesian settlers reduced the breeding range of NZFSs to the southwestern South Island, however, NZFSs were still found throughout the coast in the non-breeding season (Smith, 1989). Near extirpation by European sealers did not further diminish the breeding range, but did decrease the non-breeding range (Smith, 1989). It is, therefore, possible that the apparent modern increase in NZFSs in northern areas in the non-breeding season has been driven by population recovery. A recent estimate puts NZFS abundance at approximately 146,000 – 229,000 (A. Hall, unpublished data), up from 30,000 – 50,000 approximately 45 years ago (Wilson, 1981). Rapid increases in pup production have been documented for some NZFS breeding colonies (Boren, 2005;

Bradshaw, 1999), with immigration likely to be contributing to population growth (Bradshaw, 1999). Conversely, philopatry may have contributed to NZFSs remaining at established colonies even if habitat quality has decreased (Hall et al., 2024). Substantial population declines have been recorded in West Coast, South Island, colonies (Roberts & Neale, 2016), and at Otago Peninsula (P. Seddon, unpublished data). While pup production at Cape Palliser is higher now than in the early 1990s, counts have not been sufficiently frequent to determine whether pup production is currently increasing or decreasing there (L. Boren, personal communication, 11 July 2024).

Role of SIA

SIA can be used to trace migration and foraging ecology (Crawford et al., 2008; Hobson, 1999; Hobson et al., 2010; Ramos & González-Solís, 2012). NZFSs are highly mobile, generalised predators (Arnould et al., 2011; Harcourt et al., 2002), and SIA values vary along the length of the fur seal vibrissa (Walters et al., 2020). Baseline SIA values also vary throughout the marine area and are mostly unknown around New Zealand (Graham & Bury, 2019). Sequential $\delta^{13}C$ and $\delta^{15}N$ values from multiple samples along a vibrissa could be used to track foraging by individuals, however, the cost of analysing a full vibrissa would be substantial. Rather than using $\delta^{13}C$ and $\delta^{15}N$ values directly to try to track foraging, calculating standard ellipse areas (Jackson et al., 2011), and comparing them among groups would give a good indication of the isotopic width, which gives useful ecological information (Bearhop et al., 2004; Newsome et al., 2007).

4.3 Threats to New Zealand Fur Seals

4.3.1 Early Weaning

Pinniped mortality is often high in the period after weaning (Reiter et al., 1978), as pups must transition from being dependent on their mothers to foraging successfully for themselves (Baylis et al., 2005). Higher pre-weaning growth rates (Beauplet et al., 2005), greater size at weaning (Bowen et al., 2015), and later weaning (Davis, 2014; Goldsworthy, 2006), are advantageous in pinnipeds. In six pinniped species, weaning occurred when pups were approximately 40 % of the mean adult of female body weight, however, the timing of weaning depended on food availability, seasonality, migration, and environmental predictability for each species (Gentry et al., 1986). In a rapidly expanding NZFS colony at Kaikōura, lactation lengths ranged from 325 to 352 days (Boren, 2005). Despite reaching weaning weights by four to six months of age, NZFS pups at Kaikōura were weaned later than at many other colonies, suggesting that the consistent food supply at the Kaikōura Canyon enabled females to have longer lactations while still maintaining body condition (Boren, 2005). Kaikōura is an area with rapidly expanding NZFS populations (Hall et al., 2024), implying a high level of reproductive success, however, in 2023/24 pup production at Ōhau Point dropped to approximately 1,182 (J. Weir, unpublished data) from 2401 ± 99 the previous season (Hall et al., 2024). The cause of the marked decline in pup production between 2022/23 and 2023/24 is unknown.

The median lactation length of NZFSs is thought to be 294 ± 6 days (Boren, 2005), however, in the present study the latest possible weaning date was only 210 to 234 days after the assumed median pupping date. Furthermore, stranded YOY were seen in Northland as early as 189 days after the median pupping date in 2024 (P. Miller, personal communication, 23 June 2024). Given the known adverse effects of early weaning on pinnipeds (Beauplet et al., 2005; Davis, 2014; Goldsworthy, 2006; Ono et al., 1987), weaning times in NZFSs require further investigation.

Role of SIA

The present study provided evidence that stranded individuals were weaned earlier than any of the weaning dates in the literature. The marked decrease in $\delta^{15}N$ that occurs at the time of weaning (Cherel et al., 2015) could be used to determine which section of the vibrissa was formed at that time, however, the variation in vibrissa growth rates between individual fur seals means that it would not be possible to determine the exact time of weaning (Rea et al., 2015). The probable timing of weaning could be refined by analysing multiple sections per vibrissa, and determining the nitrogen nadir which indicates the time of birth in fur seals (Jones et al., 2020). Vibrissa measurements could then be used to calculate a more accurate growth rate for each individual, based on the median pupping date.

One limitation of the present study was that only stranded individuals were able to be sampled. Ideally, YOY at each of the breeding colonies sampled (Chapter 2), would also be sampled. It would then be possible to determine whether YOY still at colonies had been weaned or not.

4.3.2 Fisheries Competition and Bycatch

Globally, there is evidence that fisheries are adversely affecting many protected species (Burgess et al., 2018), including marine mammals (Kovacs et al., 2012; Read, 2008). The 'ecosystem approach' to managing fisheries has been recommended to mitigate bycatch, manage multi-species, and protect vulnerable ecosystems (Morishita, 2008). New Zealand's fisheries management has been described as a 'first-level ecosystem approach' (Cryer et al., 2016). However, protected seabird, marine mammal, and turtle species are incidentally captured in the New Zealand commercial fishery (Abraham et al., 2021). Among New Zealand pinnipeds, there is particular concern about the negative effect of fisheries on the New Zealand sea lion (Augé et al., 2012, 2014; Meyer et al., 2015; Robertson & Chilvers, 2011). Conversely, fishers often consider pinnipeds to be competitors for fish (Jusufovski et al., 2019). In some countries, recovering pinniped populations are thought to be affecting some fish stocks to the point where predator control is being proposed (Rossi et al., 2021). Similar calls have been made in New Zealand (Lalas & Bradshaw, 2001), however, historically, claims of the adverse effects of NZFSs on commercial fish stocks have been overstated (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016; Street, 1964). Predator-prey relationships are too complicated simply to assume that culling predators will increase prey stocks (Bowen & Lidgard, 2013).

The overlap between NZFS prey species and commercially important species is thought to be low (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016; Street, 1964), however, it is difficult to quantify the amount of non-target fish bycatch in the commercial fishery (Cryer et al., 2016). Observer coverage on fishing boats is low (Cryer et al., 2016), particularly in the in-shore fishery (Baird, 2011). Reported bycatch differs significantly between fishing boats with independent observers and those without (Bremner et al., 2009). Fishery intensity has been correlated with population decline in some pinnipeds (Hennen, 2006).

The NZFS is the most commonly bycaught marine mammal in New Zealand (Abraham et al., 2021), with an estimated 10,000 deaths between 1990 – 2000, over half of those in the West Coast hoki fishery (Robertson & Gemmell, 2005). Nearly 11,000 NZFSs were estimated to have been captured in trawl fisheries between 2002/03 and 2017/18 (Abraham et al., 2021), with an 88 % mortality rate (Abraham & Berkenbusch, 2017). Trawl fisheries off the coast of Westland, from approximately Hokitika northwards, and in the sea area east and north-east of Banks Peninsula, appear to have high numbers of bycaught NZFSs (Abraham & Berkenbusch, 2017). Out of an estimated 324 NZFS captures in the trawl fishery in 2017/18, 59 % were in the hoki fishery, with 36 % of the total in the Cook Strait hoki fishery alone (Abraham et al., 2021), which is a particular area of concern (Pavanato et al., 2023).

Role of SIA

SIA can be used to study diet (Newsome, Clementz, et al., 2010), but baseline isotope values in the prey are needed (Ogilvy et al., 2023), and an understanding of isotopic fractionation within the predator (Hobson et al., 1996; Jenkins et al., 2001; Newsome, Clementz, et al., 2010; Rubenstein & Hobson, 2004). In studies using pups as proxies for their mothers, an understanding of fractionation between mother and pup is also required (Cherel et al., 2015; Chilvers, 2017, 2021b; Ducatez et al., 2008; Lowther & Goldsworthy, 2011). In the absence of complete isotopic baseline and fractionation data, a more useful and relevant application of SIA in the NZFS would be to use isotopic niche width (Chapters 2 and 3) as a proxy for food availability (Ciancio et al., 2021; Ogilvy et al., 2022). Isotopic niche widths could be compared between years and related to fishing intensity and/or fish stocks, to determine whether fisheries were having a direct effect on NZFS prey availability.

4.3.4 Climate Change

Seasonal changes are larger but more predictable at higher latitudes, and smaller but much more unpredictable at tropical latitudes (Gentry & Kooyman, 1986). Fur seals at temperate latitudes, such as in New Zealand, were thought to be intermediate between the high and low latitude extremes, however, tending towards the tropical group (Gentry et al., 1986). Anthropogenic climate change is affecting New Zealand’s marine environment, with rising sea levels, ocean warming, and marine acidification having the greatest overall effect (Keegan et al., 2022). An increase in extreme weather events and a decrease in ocean productivity are also associated with climate change in New Zealand (Keegan et al., 2022). Oceanographic features such as upwellings and surface currents are expected to be affected by climate change, with a general decrease in primary productivity particularly around the North Island and the west coast of the South Island (Roberts & Hendriks, 2022). Fur seals in tropical regions compensate for the increased environmental uncertainty by increasing their lactation lengths (Gentry et al., 1986), but it is not clear whether that would be possible for the NZFS.

In other parts of the world, post-weaning pup survival has been negatively correlated with sea surface temperature anomalies (Beauplet et al., 2005; Gálvez et al., 2020; Ono et al., 1987), and a decline in California sea lion (*Zalophus californianus*) populations was correlated with increased sea surface temperatures (Adame et al., 2020). It is not clear exactly how SSTA affect New Zealand fish species (Dunn et al., 2009). Juvenile NZFSs in Australia have been shown to feed mostly on small pelagic fish

(Page et al., 2005a). Small pelagic fish were less abundant in New Zealand in La Niña conditions (Fraser & Lalas, 2004), and the La Niña weather pattern predominated from spring 2020 until January 2023 (www.niwa.co.nz).

NZFSs show a high level of behavioural plasticity in their foraging strategies (Baylis et al., 2012), however, it is not clear whether pinnipeds generally will be able to adapt to the rate of climate-induced environmental change (Kovacs et al., 2012).

Role of SIA

SIA provides indirect information on trophic level, food web productivity, and isotopic niche width which can be a proxy for prey availability (Ciancio et al., 2021). Sampling of long-term specimen collections in other top marine predators has shown changes in $\delta^{13}C$ and $\delta^{15}N$ values related to ecosystem changes (Bond & Lavers, 2014; Hanson et al., 2018). Continuing to monitor stable isotope values is fundamental to understanding the effects of climate change. Regular sampling of vibrissae from NZFS pups at colonies and stranded YOY would allow a comparison between years and could be compared to climate fluctuations over the same period.

4.3.5 Highly Pathogenic Avian Influenza

Emerging diseases such as highly pathogenic avian influenza (HPAI) are a risk to the NZFS (Gartrell et al., 2024), having already caused substantial mortality overseas in birds (Chen et al., 2022) and in pinnipeds (Leguia et al., 2023; Uhart et al., 2024; Ulloa et al., 2023). HPAI is also zoonotic (able to be spread from animals to humans) (Gartrell et al., 2024). The transmission rate is low, but the mortality rate in humans is high (Gartrell et al., 2024). NZFSs could potentially spread HPAI around New Zealand and transmit it to other species, as has been shown in southern elephant seals (*Mirounga leonina*) in South America (Uhart et al., 2024). The current lack of knowledge about NZFS dispersal outside the breeding season would limit our ability to understand or manage an HPAI outbreak in NZFSs.

4.4 Future Research

4.4.1 PIT Tagging – An Alternative to Genetics or SIA

Given the limitations of SIA and genetics to explain NZFS dispersion, an alternative would be a large-scale tagging programme using passive integrated transponder (PIT) tags, ideally combined with flipper tags (Galimberti et al., 2000). PIT tags have been widely used in otariids (Chilvers & MacKenzie, 2010; Hoffman & Forcada, 2012) and are long-lasting and relatively inexpensive (Wells, 2009). A scanner is required to read them, and it must be within 1 m of the tag (Wells, 2009), so in practical terms it would only be useful for stranded and bycaught individuals. PIT tags overcome the problems of tag loss and illegibility (Bradshaw et al., 2000; Hobbs & Russell, 1979; McConkey, 1999; Shaughnessy, 1994). Recorded resightings of flipper tagged NZFS in New Zealand have been relatively low, with fewer than 200 recorded out of over thirty thousand pups tagged at West Coast colonies over nearly 30 years (https://furseals.dragonfly.co.nz/). Flipper tags are no longer being used at those colonies (L. Boren, personal communication, 13 June 2024).

A large-scale study on NZFS dispersal would be logistically challenging. The latest pup production estimates for NZFSs are 27,525 – 34,265 per year, however, many areas have not been recently surveyed (A. Hall, unpublished data). A substantial number of individuals would, therefore, need to be tagged to achieve sufficient coverage and ensure an adequate number of resightings. Many NZFS breeding areas are relatively inaccessible and it can be difficult to manually catch pups in some terrain. Additionally, the cost of such a study would be difficult to justify as the species is classified as Least Concern by the IUCN (Chilvers & Goldsworthy, 2015).

A more feasible option would be a targeted study on the northern West Coast and Cook Strait areas, where the effect of fisheries on the species is a particular concern (Abraham et al., 2021; Abraham & Berkenbusch, 2017; Pavanato et al., 2023). Pups could be PIT tagged at Cape Foulwind, Wekakura Point, Tonga Island and Cape Palliser, ideally in more than one breeding season. Scanners would have to be available and used on all fishing boats in the relevant fishing areas. The majority of bycaught NZFS are adult males (Pavanato et al., 2023), so monitoring on fishing boats would have to be continued for some years to ensure sufficient records were obtained.

If substantial numbers of NZFS were PIT tagged, citizen scientists could be used to gather data from stranded individuals. Groups carrying out existing coastal monitoring, such as bird surveys, could be issued with Bluetooth enabled microchip scanners, or cheaper scanners requiring manual data entry. Scanning for PIT tags has the advantage that it is not necessary to handle deceased animals. Useful information on NZFS dispersal could be gained at minimal cost.

4.4.2 Diet and Foraging Studies

There have been limited diet and foraging studies on NZFSs in New Zealand (Boren, 2010), and most were carried out some time ago. Ideally, diet studies incorporating scat and regurgitate analysis, and DNA on faecal samples, would be carried out in multiple areas in New Zealand, over different seasons and years. SIA of multiple NZFS tissues would be combined with SIA from examples of prey, to give an accurate picture of NZFS foraging. Any conflicts or overlaps between fisheries and NZFSs would be clarified, and management strategies changed accordingly.

As the NZFS has a New Zealand Threat Classification of increasing/secure overseas (Baker et al., 2019), it is unlikely that funding would be forthcoming to carry out all the work proposed above. Simply monitoring bulk NZFS faecal samples from different areas for prey DNA would be a relatively simple measure that would provide useful information on NZFS diets over time. A basic understanding of NZFS diets in different areas would aid the interpretation of SIA results.

4.5 Conclusions

The present study was the first to use stable isotope analysis of vibrissae to attempt to determine the colony of origin of an otariid, and the first to calculate vibrissa growth rates and estimated vibrissa lengths at birth for NZFSs. Although there was insufficient separation among the $\delta^{13}C$ and $\delta^{15}N$ values to distinguish between colonies, the study provided some ecologically useful findings.

The NZFS is an important component of the ecosystem it occupies and meets the criteria for an indicator species for ecosystem health (Bossart, 2011). While overall population numbers have increased substantially over the past 40 years (A. Hall, unpublished data), some closely monitored colonies have declined alarmingly over the past 20 years (Roberts and Neale, 2016; P. Seddon, unpublished data), so overall the current population trajectory is unknown. Breeding colonies at Kaikōura, Banks Peninsula, and Otago Peninsula have re-established and expanded since around 1990, however, with the exception of Cape Palliser there is still minimal breeding around the North Island, despite apparently suitable habitat there. The diet and foraging strategies of the NZFS are still poorly understood (Baird, 2011; Boren, 2010), which limits our ability to mitigate the impacts of anthropogenic threats.

The most important anthropogenic threats to NZFSs are likely to be fisheries and climate change. Fishery bycatch may be disproportionately affecting some colonies, however, most bycaught NZFSs are male (Pavanato et al., 2023), so the impact on populations is likely to be less than if adult females were being caught, as is the case with New Zealand sea lions (Meyer et al., 2015; Robertson & Chilvers, 2011). Nevertheless, the number of bycaught NZFSs will be higher than the number reported (Bremner et al., 2009), and ongoing bycatch may be having an impact on populations that are already subject to other stressors. The overlap between species consumed by NZFSs and commercially harvested species is only approximately 10 % (Emami-Khoyi, Hartley, Paterson, Boren, et al., 2016), however, commercial fishers catch substantial volumes of non-target species (Cryer et al., 2016) so competition from fisheries could be reducing available fish stocks for NZFSs. Climate change is a threat to NZFSs both in terms of habitat loss due to sea level rise and increasing storms and decreased food availability due to warming seas and changing currents (Keegan et al., 2022; Roberts & Hendriks, 2022). Isotopic niche width can be a proxy for food availability (Ciancio et al., 2021), and ongoing monitoring of isotopic niche widths would provide valuable ecological information about NZFSs and their wider ecosystem.

Early weaning is likely to compromise post-weaning growth and survival (Beauplet et al., 2005; Bowen et al., 2015; Davis, 2014; Goldsworthy, 2006) and the present study demonstrated that all stranded animals were weaned a maximum 223 – 247 days after the median pupping date, while the quoted median lactation length is 294 days (Boren, 2005). In 2024, stranded YOY were found as early as 189 days from the median pupping date (P. Miller, personal communication, 23 June 2024). The period after weaning is a vulnerable time (Reiter et al., 1978), and a combination of early weaning and insufficient prey availability (Fraser & Lalas, 2004; Page et al., 2005a) could lead to increased mortality in YOY.

Highly pathogenic avian influenza (HPAI) is a serious threat to wildlife worldwide (Chen et al., 2022; Leguia et al., 2023; Uhart et al., 2024; Ulloa et al., 2023), and may cause substantial NZFS mortality (Gartrell et al., 2024). The particular concern is that HPAI could be devastating to a species that is already stressed by the anthropogenic threats discussed above.

To address the knowledge gaps about NZFSs and to provide information on the wider ecosystem, targeted and cost-effective studies are required. Bulk faecal analysis in multiple locations and seasons would provide invaluable data on NZFS diets. Large-scale PIT tagging, ideally combined with flipper tagging, would refine population estimates, quantify bycatch at individual colonies, and clarify dispersal in the non-breeding season. Ongoing monitoring of isotopic niche widths is an indirect, but valuable, way to assess foraging and prey availability.

References

Abraham, E. R., & Berkenbusch, K. (2017). Estimated captures of New Zealand fur seal, New Zealand sea lion, common dolphin, and turtles in New Zealand commercial fisheries,1995-96 to 2014-15. *New Zealand Aquatic Environment and Biodiversity Report 188*. Ministry for Primary Industries.

Abraham, E. R., Tremblay-Boyer, L., & Berkenbusch, K. (2021). Estimated captures of New Zealand fur seal, common dolphin, and turtles in New Zealand commercial fisheries, to 2017-18. *New Zealand Aquatic Environment and Biodiversity Report No. 258*.

Adame, K., Elorriaga-Verplancken, F. R., Beier, E., Acevedo-Whitehouse, K., & Pardo, M. A. (2020). The demographic decline of a sea lion population followed multi-decadal sea surface warming. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-67534-0

Allum, L. L., & Maddigan, F. W. (2012). Unusual stability of diet of the New Zealand fur seal (*Arctocephalus forsteri*) at Banks Peninsula, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *46*(1), 91–96. https://doi.org/10.1080/00288330.2011.604336

Anderson, C. J. R., Roth, J. D., & Waterman, J. M. (2007). Can whisker spot patterns be used to identify individual polar bears? *Journal of Zoology*, *273*, 333–339.

Arif, I. A., Khan, H. A., Bahkali, A. H., Al Homaidan, A. A., Al Farhan, A. H., Al Sadoon, M., & Shobrak, M. (2011). DNA marker technology for wildlife conservation. *Saudi Journal of Biological Sciences,* 18(3),219–225. https://doi.org/10.1016/j.sjbs.2011.03.002

Arnason, U., Gullberg, A., Janke, A., Kullberg, M., Lehman, N., Petrov, E. A., & Väinölä, R. (2006). Pinniped phylogeny and a new hypothesis for their origin and dispersal. *Molecular Phylogenetics and Evolution*, *41*(2), 345–354. https://doi.org/10.1016/j.ympev.2006.05.022

Arnould, J. P. Y., & Boyd, I. L. (1995). Temporal patterns of milk production in Antarctic fur seals (*Arctocephalus gazella*). *Journal of Zoology*, *237*(1), 1–12. https://doi.org/10.1111/j.1469-7998.1995.tb02741.x

Arnould, J. P. Y., Cherel, Y., Gibbens, J., White, J. G., & Littnan, C. L. (2011). Stable isotopes reveal inter-annual and inter-individual variation in the diet of female Australian fur seals. *Marine Ecology Progress Series*, *422*, 291–302. https://doi.org/10.3354/meps08933

Arnould, J. P. Y., & Kirkwood, R. (2007). Habitat selection by female Australian fur seals (*Arctocephalus pusillus doriferus*). *Aquatic Conservation: Marine and Freshwater Ecosystems*, *17*(SUPPL. 1), 853–867. https://doi.org/10.1002/aqc.908

Atkinson, S. (1997). Reproductive biology of seals. *Reviews of Reproduction*, *2*, 175–194.

Augé, A. A., Chilvers, B. L., Moore, A. B., & Davis, L. S. (2014). Importance of studying foraging site fidelity for spatial conservation measures in a mobile predator. *Animal Conservation*, *17*(1), 61–71. https://doi.org/10.1111/acv.12056

Augé, A. A., Moore, A. B., & Chilvers, B. L. (2012). Predicting interactions between recolonising marine mammals and fisheries: Defining precautionary management. *Fisheries Management and Ecology*, *19*(5), 426–433. https://doi.org/10.1111/j.1365-2400.2012.00861.x

Aurioles, D., Koch, P. L., & Le Boeuf, B. J. (2006). Differences in foraging location of Mexican and California elephant seals: Evidence from stable isotopes in pups. *Marine Mammal Science*, *22*(2), 326–338. https://doi.org/10.1111/j.1748-7692.2006.00023.x

Bailleul, F., Luque, S., Dubroca, L., Arnould, J. P., & Guinet, C. (2005). Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. *Marine Ecology Progress Series*, *293*, 273–282.

Baird, S. J. (2011). New Zealand fur seals-summary of current knowledge. *New Zealand Aquatic Environment and Biodiversity Report No. 72*.

Baker, A. N. (2005). Sensitivity of marine mammals found in Northland waters to aquaculture activities. *Report to the Department of Conservation, Northland Conservancy*.

Baker, C. S., Boren, L. J., Childerhouse, S., Constantine, R., Van Helden, A., Lundquist, D., Rayment, W., & Rolfe, J. R. (2019). Conservation status of New Zealand marine mammals, 2019. *New Zealand Threat Classification Series 29*. https://www.doc.govt.nz/globalassets/documents/science-and-technical/nztcs29entire.pdf

Ballance, L. T., Pitman, R. L., & Fiedler, P. C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in Oceanography*, *69*(2–4), 360–390. https://doi.org/10.1016/j.pocean.2006.03.013

Baylis, A. M. M. (2008). *Seasonal and colony differences in the foraging ecology of New Zealand fur seals (Arctocephalus forsteri).* PhD thesis. University of Adelaide.

Baylis, A. M. M., Kowalski, G. J., Voigt, C. C., Orben, R. A., Trillmich, F., Staniland, I. J., & Hoffman, J. I. (2016). Pup vibrissae stable isotopes reveal geographic differences in adult female southern sea lion habitat use during gestation. *PLoS ONE*, *11*(6). https://doi.org/10.1371/journal.pone.0157394

Baylis, A. M. M., & Nichols, P. D. (2009). Milk fatty acids predict the foraging locations of the New Zealand fur seal: continental shelf versus oceanic waters. *Marine Ecology Progress Series*, *380*, 271–286. https://doi.org/10.3354/meps07919

Baylis, A. M. M., Page, B., & Goldsworthy, S. D. (2008a). Colony-specific foraging areas of lactating New Zealand fur seals. *Marine Ecology Progress Series*, *361*, 279–290. https://doi.org/10.3354/meps07258

Baylis, A. M. M., Page, B., & Goldsworthy, S. D. (2008b). Effect of seasonal changes in upwelling activity on the foraging locations of a wide-ranging central-place forager, the New Zealand fur seal. *Canadian Journal of Zoology*, *86*(8), 774–789. https://doi.org/10.1139/Z08-055

Baylis, A. M. M., Page, B., McKenzie, J., & Goldsworthy, S. D. (2012). Individual foraging site fidelity in lactating New Zealand fur seals: Continental shelf vs. oceanic habitats. *Marine Mammal Science*, *28*(2), 276–294. https://doi.org/10.1111/j.1748-7692.2011.00487.x

Baylis, A. M. M., Page, B., Peters, K., McIntosh, R., McKenzie, J., & Goldsworthy, S. D. (2005). The ontogeny of diving behaviour in New Zealand fur seal pups (*Arctocephalus forsteri*). *Canadian Journal of Zoology*, *83*, 1149–1169.

Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., & Macleod, H. (2004). Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology 73*(5), 1007–1012. https://doi.org/10.1111/j.0021-8790.2004.00861.x

Beauplet, G., Barbraud, C., Chambellant, M., & Guinet, C. (2005). Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: Influence of pup sex, growth rate and oceanographic conditions. *Journal of Animal Ecology*, *74*(6), 1160–1172. https://doi.org/10.1111/j.1365-2656.2005.01016.x

Beltran, R. S., Peterson, S. H., McHuron, E. A., Reichmuth, C., Hückstädt, L. A., & Costa, D. P. (2016). Seals and sea lions are what they eat, plus what? Determination of trophic discrimination factors for seven pinniped species. *Rapid Communications in Mass Spectrometry*, *30*(9), 1115–1122. https://doi.org/10.1002/rcm.7539

Benoit-Bird, K. J., Würsig, B., & McFadden, C. J. (2004). Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: Active acoustic detection of dolphins and their prey. *Marine Mammal Science*, *20*(2), 215–231. https://doi.org/10.1111/j.1748-7692.2004.tb01152.x

Berkson, J. M., & DeMaster, D. P. (1985). Use of Pup Counts in Indexing Population Changes in Pinnipeds. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 873–879.

Berta, A., & Churchill, M. (2012). Pinniped taxonomy: Review of currently recognized species and subspecies, and evidence used for their description. In *Mammal Review* (Vol. 42, Issue 3, pp. 207–234). Blackwell Publishing Ltd. https://doi.org/10.1111/j.1365-2907.2011.00193.x

Berta, A., Churchill, M., & Boessenecker, R. W. (2018). The Origin and Evolutionary Biology of Pinnipeds: Seals, Sea Lions, and Walruses. *Annual Review of Earth and Planetary Sciences*, *46*, 203–228. https://doi.org/10.1146/annurev-earth-082517

Berta, A., & Demere, T. (1986). *Callorhinus gilmorei* n. sp., (Carnivora: Otariidae) from the San Diego Formation (Blancan) and its implications for otariid phylogeny. *Transactions of the San Diego Society of Natural History*, *21*, 111–126.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A. L., Ganong, J. E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B. R., Shillinger, G. L., Schaefer, K. M., Benson, S. R., Weise, M. J., … Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*(7354), 86–90. https://doi.org/10.1038/nature10082

Boessenecker, R. W., & Churchill, M. (2015). The oldest known fur seal. *Biology Letters*, *11*(2). https://doi.org/10.1098/rsbl.2014.0835

Bonadonna, F., Lea, M. A., Dehorter, O., & Guinet, C. (2001). Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazella*. *Marine Ecology Progress Series, 223*, 287-297.

Bonadonna, F., Lea, M.-A., & Guinet, C. (2000). Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders. *Polar Biology*, *23*, 149–159.

Bond, A. L., & Lavers, J. L. (2014). Climate change alters the trophic niche of a declining apex marine predator. *Global Change Biology*, *20*(7), 2100–2107. https://doi.org/10.1111/gcb.12554

Bonner, W. N. (1958). Notes on the southern fur seal in South Georgia. *Proceedings of the Zoological Society of London*, *130*(2), 241–252. https://doi.org/10.1111/j.1096-3642.1958.tb00571.x

Boren, L. J. (2005). *New Zealand fur seals in the Kaikoura region: colony dynamics, maternal investment and health.* PhD thesis. University of Canterbury, Christchurch.

Boren, L. J. (2010). Diet of New Zealand fur seals (*Arctocephalus forsteri*): a summary. *DOC Research & Development Series 319*. Pub. Team, Dept. of Conservation.

Boren, L. J., Gemmell, N. J., & Barton, K. J. (2002). Tourist disturbance on New Zealand fur seals *Arctocephalus forsteri*. *Australian Mammalogy*, *24*(1), 85–95. https://doi.org/10.1071/AM02085

Boren, L. J., Morrissey, M., Muller, C. G., & Gemmell, N. J. (2006). Entanglement of New Zealand fur seals in man-made debris at Kaikoura, New Zealand. *Marine Pollution Bulletin*, *52*(4), 442–446. https://doi.org/10.1016/j.marpolbul.2005.12.003

Boren, L. J., Muller, C. G., & Gemmell, N. J. (2006). Colony growth and pup condition of the New Zealand fur seal (*Arctocephalus forsteri*) on the Kaikoura coastline compared with other east coast colonies. *Wildlife Research*, *33*(6), 497–505. https://doi.org/10.1071/WR05092

Bossart, G. D. (2011). Marine mammals as sentinel species for oceans and human health. *Veterinary Pathology*, *48*(3), 676–690. https://doi.org/10.1177/0300985810388525

Bouma, S., Hickman, G., & Taucher, D. (2008). Abundance and reproduction of the New Zealand fur seal (*Arctocephalus forsteri*) along the west coast of the Waikato region, New Zealand. *Journal of the Royal Society of New Zealand*, *38*(2), 89–96. https://doi.org/10.1080/03014220809510548

Bowen, W. D. (1997). Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series*, *158*, 267–274.

Bowen, W. D., den Heyer, C. E., McMillan, J. I., & Iverson, S. J. (2015). Offspring size at weaning affects survival to recruitment and reproductive performance of primiparous gray seals. *Ecology and Evolution*, *5*(7), 1412–1424. https://doi.org/10.1002/ece3.1450

Bowen, W. D., & Lidgard, D. (2013). Marine mammal culling programs: Review of effects on predator and prey populations. *Mammal Review 43*(3), 207–220. https://doi.org/10.1111/j.1365-2907.2012.00217.x

Boyd, I. L. (1996). Temporal Scales of Foraging in a Marine Predator. *Ecology 77*(2), 426–434.

Boyd, I. L. (1998a). Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behavioral Ecology*, *10*(2), 198–208.

Boyd, I. L. (1998b). Time and energy constraints in pinniped lactation. *American Naturalist*, *152*(5), 717–728. https://doi.org/10.1086/286202

Bradshaw, & Brook, B. W. (2010). The conservation biologist’s toolbox - principles for the design and analysis of conservation studies. In *Conservation Biology For All* (pp. 313–339). Oxford University Press.

Bradshaw, C. J. A. (1999). *Population dynamics and colonisation modelling of New Zealand fur seals.* PhD thesis. University of Otago, Dunedin.

Bradshaw, C. J. A., Barker, R., & Davis, L. (2000). Modeling Tag Loss in New Zealand Fur Seal Pups. *Journal of Agricultural, Biological, and Environmental Statistics*, *5*(4), 475–485. https://www.jstor.org/stable/1400661

Bradshaw, C. J. A., Lalas, C., Perriman, L., & Harcourt, R. G. (1999). Seasonal oscillation in shore attendance and transience of New Zealand fur seals. *Canadian Journal of Zoology*, *77*, 814–833.

Bräger, S., & Bräger, Z. (2018). Range utilization and movement patterns of coastal Hector's dolphins (*Cephalorhynchus hectori*). *Aquatic Mammals*, *44*(6), 633–642. https://doi.org/10.1578/AM.44.6.2018.633

Bremner, G., Johnstone, P., Bateson, T., & Clarke, P. (2009). Unreported bycatch in the New Zealand West Coast South Island hoki fishery. *Marine Policy*, *33*(3), 504–512. https://doi.org/10.1016/j.marpol.2008.11.006

Burgess, M. G., McDermott, G. R., Owashi, B., Reeves, L. E. P., Clavelle, T., Ovando, D., Wallace, B. P., Lewison, R. L., Gaines, S. D., & Costello, C. (2018). Protecting marine mammals, turtles, and birds by rebuilding global fisheries. *Science*, *359*, 1255–1258. https://www.science.org

Carey, P. W. (1991a). Fish prey species of the New Zealand fur seal (*Arctocephalus forsteri*, Lesson). *Science & Research Internal Report No.115*.

Carey, P. W. (1991b). Resource-defense polygyny and male territory quality in the New Zealand fur seal. *Ethology*, *88*, 63–79.

Carter, M. I. D., Bennett, K. A., Embling, C. B., Hosegood, P. J., & Russell, D. J. F. (2016). Navigating uncertain waters: A critical review of inferring foraging behaviour from location and dive data in pinnipeds. *Movement Ecology 4*(25) https://doi.org/10.1186/s40462-016-0090-9

Cassini, M. H. (1999). The evolution of reproductive systems in pinnipeds. *Behavioral Ecology*, *10*(5), 612–616.

Cassini, M. H. (2000). A model on female breeding dispersion and the reproductive systems of pinnipeds. *Behavioural Processes*, *51*(1–3), 93–99. https://doi.org/10.1016/S0376-6357(00)00121-2

Chen, W., Zhang, X., Zhao, W., Yang, L., Wang, Z., & Bi, H. (2022). Environmental factors and spatiotemporal distribution characteristics of the global outbreaks of the highly pathogenic avian influenza H5N1. *Environmental Science and Pollution Research*, *29*(29), 44175–44185. https://doi.org/10.1007/s11356-022-19016-1

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

Cherel, Y., Hobson, K. A., & Guinet, C. (2015). Milk isotopic values demonstrate that nursing fur seal pups are a full trophic level higher than their mothers. *Rapid Communications in Mass Spectrometry*, *29*(16), 1485–1490. https://doi.org/10.1002/rcm.7243

Cherel, Y., Kernaléguen, L., Richard, P., & Guinet, C. (2009). Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals. *Biology Letters*, *5*(6), 830–832. https://doi.org/10.1098/rsbl.2009.0552

Chilvers, B. L. (2017). Stable isotope signatures of whisker and blood serum confirm foraging strategies for female New Zealand sea lions (*Phocarctos hookeri*) derived from telemetry. *Canadian Journal of Zoology*, *95*(12), 955–963. https://doi.org/10.1139/cjz-2016-0299

Chilvers, B. L. (2018). Preliminary assessment of the foraging behaviour and population dynamics of a cryptic population of the endangered New Zealand sea lion. *New Zealand Journal of Ecology*, *42*(1), 48–57. https://doi.org/10.2307/26538095

Chilvers, B. L. (2019). Whisker stable isotope values indicate long-term foraging strategies for female New Zealand sea lions. *Endangered Species Research*, *38*, 55–66. https://doi.org/10.3354/ESR00934

Chilvers, B. L. (2021a). Identifying female foraging ecotype and fisheries impacts through pup whisker stable isotopes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(8), 2204–2216. https://doi.org/10.1002/aqc.3589

Chilvers, B. L. (2021b). Isotope values from milk and blood serum in New Zealand sea lions: are pups feeding on milk a trophic level higher than their mothers? *Marine Biology*, *168*(1). https://doi.org/10.1007/s00227-020-03817-4

Chilvers, B. L. (2021c). Pup numbers, estimated population size, and monitoring of New Zealand fur seals in Doubtful/Pateā, Dusky and Breaksea Sounds, and Chalky Inlet, Fiordland, New Zealand 2021. *New Zealand Journal of Marine and Freshwater Research*. https://doi.org/10.1080/00288330.2021.1962921

Chilvers, B. L. (2023). Whisker stable isotope analysis used for proactive management of recolonising New Zealand sea lion population. *Endangered Species Research*, *52*, 177–188.

Chilvers, B. L., & Goldsworthy, S. D. (2015). *Arctocephalus forsteri. The IUCN Red List of Threatened Species 2015*. https://doi.org/10.2305/IUCN.UK.2015-2.RLTS.T41664A45230026.en

Chilvers, B. L., & MacKenzie, D. I. (2010). Age- and sex-specific survival estimates incorporating tag loss for New Zealand sea lions, *Phocarctos hookeri*. *Journal of Mammalogy*, *91*(3), 758–767. https://doi.org/10.1644/09-MAMM-A-285.1

Chilvers, B. L., Wilkinson, I. S., Duignan, P. J., & Gemmell, N. J. (2005). Summer foraging areas for lactating New Zealand sea lions, *Phocarctos hookeri*. *Marine Ecology Progress Series 304:*235–247.

Chiswell, S. M., Bostock, H. C., Sutton, P. J. H., & Williams, M. J. (2015). Physical oceanography of the deep seas around New Zealand: A review. *New Zealand Journal of Marine and Freshwater Research*:49(2), 286–317. https://doi.org/10.1080/00288330.2014.992918

Churchill, M., Boessenecker, R. W., & Clementz, M. T. (2014). Colonization of the Southern Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined evidence phylogenetic and Bayesian biogeographical analysis. *Zoological Journal of the Linnean Society*, *172*(1), 200–225. https://doi.org/10.1111/zoj.12163

Ciancio, J. E., Yorio, P., Buratti, C., Colombo, G. Á., & Frere, E. (2021). Isotopic niche plasticity in a marine top predator as indicator of a large marine ecosystem food web status. *Ecological Indicators*, *126*. https://doi.org/10.1016/j.ecolind.2021.107687

Cordes, L. S., & Thompson, P. M. (2013) Variation in breeding phenology provides insights into drivers of long-term population change in harbour seals. *Proceedings of the Royal Society B 280*:20130847

Cornuet, J.-M., Piry, S., Luikart, G., Estoup, A., & Solignac, M. (1999). New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics*, *153*.

Costa, D. P., Robinson, P. W., Arnould, J. P. Y., Harrison, A. L., Simmons, S. E., Hassrick, J. L., Hoskins, A. J., Kirkman, S. P., Oosthuizen, H., Villegas-Amtmann, S., & Crocker, D. E. (2010). Accuracy of ARGOS locations of pinnipeds at-sea estimated using fastloc GPS. *PLoS ONE*, *5*(1). https://doi.org/10.1371/journal.pone.0008677

Coulson, T. (2020). Ecology and Evolution Is Hindered by the Lack of Individual-Based Data. In Dobson A, Tilman D, & Holt RD (Eds.), *Unsolved problems in ecology* (pp. 107–114). Princeton University Press.

Cowling, M. (2013). *Management of seal tourism in New Zealand-Tourism and the New Zealand fur seal in the Bay of Plenty.* MSc thesis, Victoria University, Wellington.

Cowling, M., Kirkwood, R., Boren, L. J., Sutherland, D., & Scarpaci, C. (2015). The effects of vessel approaches on the New Zealand fur seal (*Arctocephalus forsteri*) in the Bay of Plenty, New Zealand. *Marine Mammal Science*, *31*(2), 501–519. https://doi.org/10.1111/mms.12171

Crawford, K., McDonald, R. A., & Bearhop, S. (2008). Applications of stable isotope techniques to the ecology of mammals. *Mammal Review*, *38*(1), 87–107.

Crawley, M. C., & Wilson, G. J. (1976). The natural history and behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). *Tuatara*, *22*(1), 1–29.

Cryer, M., Mace, P. M., & Sullivan, K. J. (2016). New Zealand's ecosystem approach to fisheries management. *Fisheries Oceanography*, *25*, 57–70. https://doi.org/10.1111/fog.12088

Davenport, S. R., & Bax, N. J. (2002). A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(3), 514–530. https://doi.org/10.1139/f02-031

Davis, B. T. (2014). *Effects of weaning age on body composition and growth of ex situ California sea lion (Zalophus californianus) pups.* Electronic Theses and Dissertations. 1334. University of Central Florida.

de Albernaz, T. L., Secchi, E. R., de Oliveira, L. R., & Botta, S. (2017). Ontogenetic and gender-related variation in the isotopic niche within and between three species of fur seals (genus *Arctocephalus*). *Hydrobiologia*, *787*(1), 123–139. https://doi.org/10.1007/s10750-016-2950-0

Dehnhardt, G. (2002). Sensory Systems. In A. R. Hoelzel (Ed.), *Marine Mammal Biology: An Evolutionary Approach* (pp. 116–135). Blackwell Publishing.

Dehnhardt, G., Mauck, B., & Bleckmann, H. (1998). Seal whiskers detect water movements. *Nature*, *394*(6), 235–236.

Dellinger, T., & Trillmich, F. (1988). Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable? *Canadian Journal of Zoology*, *66*, 1865–1870.

Department of Conservation. (2016). *Moutohorā (Whale Island) Wildlife Management Reserve ecological restoration plan 2014 - 2024*.

Derville, S., Torres, L. G., Newsome, S. D., Somes, C. J., Valenzuela, L. O., Vander Zanden, H. B., Baker, C. S., Bérubé, M., Busquets-Vass, G., Carlyon, K., Childerhouse, S. J., Constantine, R., Dunshea, G., Flores, P. A. C., Goldsworthy, S. D., Graham, B., Groch, K., Gröcke, D. R., Harcourt, R. G., … Carroll, E. L. (2023). Long-term stability in the circumpolar foraging range of a Southern Ocean predator between the eras of whaling and rapid climate change. *Proceedings of the National*

Academy of Sciences of the United States of America, *120*(10). https://doi.org/10.1073/pnas.2214035120

Dickie, G. S., & Dawson, S. M. (2003). Age, growth, and reproduction in New Zealand fur seals. *Marine Mammal Science*, *19*(1), 173–185.

Dix, B. (1993). A new record this century of a breeding colony in the North Island for the New Zealand fur seal *Arctocephalus forsteri*. *Journal of the Royal Society of New Zealand*, *23*(1), 1–4. https://doi.org/10.1080/03036758.1993.10721212

Douglas-Hamilton, I. (1973). On the ecology and behavior of the Lake Manyara elephants. *East African Wildlife Journal*, *11*, 401–403.

Drago, M., Cardona, L., Aguilar, A., Crespo, E. A., Ameghino, S., & García, N. (2010). Diet of lactating South American sea lions, as inferred from stable isotopes, influences pup growth. *Marine Mammal Science*, *26*(2), 309–323. https://doi.org/10.1111/j.1748-7692.2009.00321.x

Ducatez, S., Dalloyau, S., Richard, P., Guinet, C., & Cherel, Y. (2008). Stable isotopes document winter trophic ecology and maternal investment of adult female southern elephant seals (*Mirounga leonina*) breeding at the Kerguelen Islands. *Marine Biology*, *155*(4), 413–420. https://doi.org/10.1007/s00227-008-1039-3

Dunn, M., Hurst, R., Renwick, J., Francis, C., Devine, J., & McKenzie, A. (2009). New Zealand Aquatic Environment and Biodiversity Fish abundance and climate trends in New Zealand. *New Zealand Aquatic Environment and Biodiversity Report No. 31. 75 p.*

Dunton, K. H., Saupe, S. M., Golikov, A. N., Schell, D. M., & Schonberg, S. V. (1989). Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. *Marine Ecology Progress Series*, *56*, 89–97.

Durante, L. M., Smith, R. O., Kolodzey, S., McMullin, R. M., Salmond, N. H., Schlieman, C. D., O'Connell-Milne, S. A., Frew, R. D., Van Hale, R., & Wing, S. R. (2021). Oceanographic transport along frontal zones forms carbon, nitrogen, and oxygen isoscapes on the east coast of New Zealand: Implications for ecological studies. *Continental Shelf Research*, *216*(104368). https://doi.org/10.1016/j.csr.2021.104368

Dussex, N., Robertson, B. C., Salis, A. T., Kalinin, A., Best, H., & Gemmell, N. J. (2016). Low spatial genetic differentiation associated with rapid recolonization in the New Zealand fur seal *Arctocephalus forsteri*. *Journal of Heredity*, *107*(7), 581–592. https://doi.org/10.1093/jhered/esw056

Edwards, M. R., Cárdenas-Alayza, S., Adkesson, M. J., Daniels-Abdulahad, M., & Hirons, A. C. (2021). Peruvian Fur Seals as Archivists of El Niño Southern Oscillation Effects. *Frontiers in Marine Science*, *8*(651212). https://doi.org/10.3389/fmars.2021.651212

Ehleringer, J. R., & Rundel, P. W. (1989). Stable Isotopes: History, Units, and Instrumentation. In *Stable Isotopes in Ecological Research* (Vol. 68). Springer-Verlag.

Elorriaga-Verplancken, F. R., Juárez-Ruiz, A., Baleytó, M. A., Galván-Magaña, F., & Aguíñiga-García, S. (2016). Isotopic variation between adult female Guadalupe fur seals and their offspring: Implications for the use of neonates as proxies for maternal foraging. *Aquatic Mammals*, *42*(3), 268–276. https://doi.org/10.1578/AM.42.2.2016.268

Emami-Khoyi, A., Hartley, D. A., Paterson, A. M., Boren, L. J., Cruickshank, R. H., Ross, J. G., Murphy, E. C., & Else, T. A. (2016). Identifying prey items from New Zealand fur seal (*Arctocephalus forsteri*) faeces using massive parallel sequencing. *Conservation Genetics Resources*, *8*(3), 343–352. https://doi.org/10.1007/s12686-016-0560-9

Emami-Khoyi, A., Hartley, D. A., Paterson, A. M., Paterson, A. M., Boren, L. J., Ross, J. G., Murphy, E. C., & Else, T. A. (2016). Mitochondrial DNA structure and colony expansion dynamics of New Zealand fur seals (*Arctocephalus forsteri*) around Banks Peninsula. *New Zealand Journal of Zoology*, *43*(4), 322–335. https://doi.org/10.1080/03014223.2016.1179649

Espinasse, B., Pakhomov, E. A., Hunt, B. P. V., & Bury, S. J. (2019). Latitudinal gradient consistency in carbon and nitrogen stable isotopes of particulate organic matter in the Southern Ocean. *Marine Ecology Progress Series*, *631*, 19–30. https://doi.org/10.3354/meps13137

Falla, R. A. (1962). Exploitation of seals, whales and penguins in New Zealand. *Proceedings of the New Zealand Ecological Society*, *9*, 34–38.

Falla, R. A. (1965). Birds and mammals of the subantarctic islands. *Proceedings of the New Zealand Ecological Society*, *12*, 63–68.

Fea, N. I., Harcourt, R. G., & Lalas, C. (1999). Seasonal variation in the diet of New Zealand fur seals (*Arctocephalus forsteri*) at Otago Peninsula, New Zealand. *Wildlife Research*, *26*(2), 147–160. https://doi.org/10.1071/WR98024

Fisk, A. T., Tittlemier, S. A., Pranschke, J. C., & Norstrom, R. J. (2002). Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of Greenland sharks. *Ecology*, *83*(8), 2162–2172. https://doi.org/10.1890/0012-9658(2002)083[2162:UACASI]2.0.CO;2

Foo, D., Hindell, M., McMahon, C. R., & Goldsworthy, S. D. (2019). Identifying foraging habitats of adult female long-nosed fur seal *Arctocephalus forsteri* based on vibrissa stable isotopes. *Marine Ecology Progress Series*, *628*, 223–234. https://doi.org/10.3354/meps13113

Foster, J. B. (1966). The giraffe of Nairobi National Park: home range, sex ratios, the herd, and food. *East African Wildlife Journal*, *4*, 139–148.

Fowler, S. L., Costa, D. P., & Arnould, J. P. Y. (2007). Ontogeny of movements and foraging ranges in the Australian sea lion. *Marine Mammal Science*, *23*(3), 598–614. https://doi.org/10.1111/j.1748-7692.2007.00134.x

Frame, L. H., Malcolm, J. R., Frame, G. W., & Lawick, H. Van. (1979). Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967-1978. *Zeitschrift Fiir Tierpsychologie*, *50*, 225–249.

Franco-Trecu, V., Aurioles-Gamboa, D., & Inchausti, P. (2014). Individual trophic specialisation and niche segregation explain the contrasting population trends of two sympatric otariids. *Marine Biology*, *161*(3), 609–618. https://doi.org/10.1007/s00227-013-2363-9

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

Galbraith, D. (2022). *The New Zealand Fur Seal in Northland and Auckland – Recolonisation and Mortality. Wildlife Management Report: 340.* Otago University, Dunedin.

Gales, N. J., & Cheal, A. J. (1992). Estimating diet composition of the Australian sea-lion (*Neophoca cinerea*) from scat analysis: an unreliable technique. *Wildlife Research*, *19*, 447–456.

Galimberti, F., Sanvito, S., & Boitani, L. (2000). Marking of southern elephant seals with passive integrated transponders. *Marine Mammal Science*, *16*(2), 500–504. https://doi.org/10.1111/j.1748-7692.2000.tb00943.x

Gálvez, C., Pardo, M. A., & Elorriaga-Verplancken, F. R. (2020). Impacts of extreme ocean warming on the early development of a marine top predator: The Guadalupe fur seal. *Progress in Oceanography*, *180*(102220). https://doi.org/10.1016/j.pocean.2019.102220

Gartrell, B. D., Jolly, M. J., & Hunter, S. A. (2024). The risks and consequences of a high pathogenicity avian influenza outbreak in Aotearoa New Zealand. *New Zealand Veterinary Journal*, *72*(2), 63–65. https://doi.org/10.1080/00480169.2023.2294915

Gemmell, N. J., Allen, P. J., Goodman, S. J., & Reed, J. Z. (1997). Interspecific microsatellite markers for the study of pinniped populations. *Molecular Ecology*, *6*, 661–666.

Gentry, R. L., Costa, D. P., Croxall, J. P., David, J. H. M., Davis, R. W., Kooyman, G. L., Majluf, P., McCann, T. S., & Trillmich, F. (1986). Synthesis and Conclusions. In R. L. Gentry & G. L. Kooyman (Eds.), *Fur Seals: Maternal Strategies on Land and at Sea* (pp. 221–264). Princeton University Press.

Gentry, R. L., & Kooyman, G. L. (1986). Introduction. In R. L. Gentry & G. L. Kooyman (Eds.), *Fur Seals - Maternal Strategies on Land and at Sea* (pp. 3–27). Princeton University Press.

Gibbs, M., Leduc, D., Nodder, S. D., Kingston, A., Swales, A., Rowden, A. A., Mountjoy, J., Olsen, G., Ovenden, R., Brown, J., Bury, S., & Graham, B. (2020). Novel Application of a Compound-Specific Stable Isotope (CSSI) Tracking Technique Demonstrates Connectivity Between Terrestrial and Deep-Sea Ecosystems via Submarine Canyons. *Frontiers in Marine Science*, *7*(608). https://doi.org/10.3389/fmars.2020.00608

Gilkinson, A. K., Pearson, H. C., Weltz, F., & Davis, R. W. (2007). Photo-Identification of Sea Otters Using Nose Scars. *Journal of Wildlife Management*, *71*(6), 2045–2051. https://doi.org/10.2193/2006-410

Ginter, C. C., DeWitt, T. J., Fish, F. E., & Marshall, C. D. (2012). Fused traditional and geometric morphometrics demonstrate pinniped whisker diversity. *PLoS ONE*, *7*(4). https://doi.org/10.1371/journal.pone.0034481

Goldsworthy, S. D. (2006). Maternal strategies of the New Zealand fur seal: Evidence for interannual variability in provisioning and pup growth strategies. *Australian Journal of Zoology*, *54*(1), 31–44. https://doi.org/10.1071/ZO05041

Goldsworthy, S. D., & Page, B. (2007). A risk-assessment approach to evaluating the significance of seal bycatch in two Australian fisheries. *Biological Conservation*, *139*(3–4), 269–285. https://doi.org/10.1016/j.biocon.2007.07.010

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior.* The Belknap Press of Harvard University Press, Boston, Mass.

Gooday, O. J. (2016). *New Zealand fur seal (Arctocephalus forsteri) pup behaviour and an assessment of non-invasive population survey methods.* MSc thesis, University of Canterbury.

Gormley, A. M., Dawson, S. M., Slooten, E., & Bräger, S. (2005). Capture-recapture estimates of Hector’s dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science*, *21*(2), 204–216. https://doi.org/10.1111/j.1748-7692.2005.tb01224.x

Graham, B., & Bury, S. (2019). Marine isoscapes for trophic and animal movement studies in the southwest Pacific Ocean. *New Zealand Aquatic Environment and Biodiversity Report No. 218*.

Grant, R. A., & Goss, V. G. A. (2022). What can whiskers tell us about mammalian evolution, behaviour, and ecology? *Mammal Review*, *52*(1), 148–163. https://doi.org/10.1111/mam.12253

Guinet, C., Dubroca, L., Lea, M. A., Goldsworthy, S. D., Cherel, Y., Duhamel, G., Bonadonna, F., & Donnay, J. P. (2001). Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series*, *219*, 251–264.

Hall, A. A., Chilvers, B. L., Weir, J. S., & Boren, L. J. (2024). Earthquake impacts on a protected pinniped in New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *34*(1). https://doi.org/10.1002/aqc.4055

Hamer, D. J., & Goldsworthy, S. D. (2006). Seal-fishery operational interactions: Identifying the environmental and operational aspects of a trawl fishery that contribute to by-catch and mortality of Australian fur seals (*Arctocephalus pusillus doriferus*). *Biological Conservation*, *130*(4), 517–529. https://doi.org/10.1016/j.biocon.2006.01.014

Hammond, P. S., Mizroch, S. A., & Donovan, G. P. (1990). Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. *Report of the International Whaling Commission (Special Issue 12)*. International Whaling Commission.

Hansen, J. H., Hedeholm, R. B., Sünksen, K., Christensen, J. T., & Grønkjær, P. (2012). Spatial variability of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios in an Arctic marine food web. *Marine Ecology Progress Series*, *467*, 47–59. https://doi.org/10.3354/meps09945

Hanson, N., Jones, E. L., & Harris, R. N. (2018). Multi-decadal and ontogenetic trophic shifts inferred from stable isotope ratios of pinniped teeth. *Oikos*, *127*(1), 134–146. https://doi.org/10.1111/oik.04441

Hanson, N., Wurster, C. M., Bird, M. I., Reid, K., & Boyd, I. L. (2009). Intrinsic and extrinsic forcing in life histories: patterns of growth and stable isotopes in male Antarctic fur seal teeth. *Marine Ecology Progress Series*, *388*, 263–272. https://doi.org/10.2307/24873594

Harcourt, R. G. (2001). Advances in New Zealand mammalogy 1990–2000: Pinnipeds. *Journal of the Royal Society of New Zealand*, *31*(1), 135–160. https://doi.org/10.1080/03014223.2001.9517644

Harcourt, R. G., Bradshaw, C. J. A., & Davis, L. S. (2001). Summer foraging behaviour of a generalist predator, the New Zealand fur seal (*Arctocephalus forsteri*). *Wildlife Research*, *28*(6), 599–606. https://doi.org/10.1071/WR01045

Harcourt, R. G., Bradshaw, C. J. A., Dickson, K., & Davis, L. S. (2002). Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series*, *227*, 11–24.

Harcourt, R. G., & Davis, L. (1997). The use of satellite telemetry to determine fur seal foraging areas. In *Marine Mammal Research in the Southern Hemisphere Volume 1: Status, Ecology and Medicine* (Vol. 1, pp. 137–142).

Harcourt, R. G., Schulman, A. M., Davis, L. S., & Trillmich, F. (1995). Summer foraging by lactating female New Zealand fur seals (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. *Canadian Journal of Zoology*, *73*, 678–690.

Harting, A., Baker, J., & Becker, B. (2004). Non-metrical digital photo-identification system for the Hawaiian monk seal. *Marine Mammal Science*, *20*(4), 886–895. https://doi.org/10.1111/j.1748-7692.2004.tb01200.x

Haussmann, N. S., Rudolph, E. M., Kalwij, J. M., & McIntyre, T. (2013). Fur seal populations facilitate establishment of exotic vascular plants. *Biological Conservation*, *162*, 33–40. https://doi.org/10.1016/j.biocon.2013.03.024

Hawke, D. J. (1992). Salinity variability in shelf waters near Otago Peninsula, New Zealand, on a time scale of hours. *New Zealand Journal of Marine and Freshwater Research*, *26*(2), 167–173. https://doi.org/10.1080/00288330.1992.9516511

Hebert, C. E., Weseloh, D. V. C., Gauthier, L. T., Arts, M. T., & Letcher, R. J. (2009). Biochemical tracers reveal intra-specific differences in the food webs utilized by individual seabirds. *Oecologia*, *160*(1), 15–23. https://doi.org/10.1007/s00442-009-1285-1

Helm, R. C. (1984). Rate of digestion in three species of pinnipeds. *Canadian Journal of Zoology*, *62*, 1751–1756.

Hennen, D. (2006). Associations between the Alaska Steller sea lion decline and commercial fisheries. *Ecological Applications*, *16*(2), 704–717. https://doi.org/10.1890/1051-0761(2006)016[0704:ABTASS]2.0.CO;2

Herman, D. P., Burrows, D. G., Wade, P. R., Durban, J. W., Matkin, C. O., LeDuc, R. G., Barrett-Lennard, L. G., & Krahn, M. M. (2005). Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. *Marine Ecology Progress Series*, *302*, 275–291.

Hiby, A. R., & Lovell, P. (1990). Computer-aided matching of natural markings: a prototype system for grey seals. Paper SC/A88/ID. *Report of the International Whaling Commission Special Issue 12* (pp. 57–62).

Higdon, J. W., Bininda-Emonds, O. R. P., Beck, R. M. D., & Ferguson, S. H. (2007). Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evolutionary Biology*, *7*(1). https://doi.org/10.1186/1471-2148-7-216

Hirons, A. C., Schell, D. M., & Finney, B. P. (2001). Temporal records of $\delta^{13}C$ and $\delta^{15}N$ in North Pacific pinnipeds: Inferences regarding environmental change and diet. *Oecologia*, *129*(4), 591–601. https://doi.org/10.1007/s004420100756

Hirons, A. C., Schell, D. M., & St Aubin, D. J. (2001). Growth rates of vibrissae of harbor seals *Phoca vitulina* and Steller sea lions *Eumetopias jubatus*. *Canadian Journal of Zoology*, *79*(6), 1053–1061.

Hobbs, L., & Russell, P. (1979). *Report on the pinniped and sea otter tagging workshop, 18-19 January*. http://hdl.handle.net/1834/19894

Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, *120*, 314–326.

Hobson, K. A. (2005). Using stable isotopes to trace long-distance dispersal in birds and other taxa. In *Diversity and Distributions* (Vol. 11, Issue 2, pp. 157–164). https://doi.org/10.1111/j.1366-9516.2005.00149.x

Hobson, K. A., Barnett-Johnson, R., & Cerling, T. (2010). Using isoscapes to track animal migration. In *Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping* (pp. 273–298). Springer Netherlands. https://doi.org/10.1007/978-90-481-3354-3_13

Hobson, K. A., Piatt, J. F., & Pitocchelli, J. (1994). Using Stable Isotopes to Determine Seabird Trophic Relationships. In *Source: Journal of Animal Ecology* (Vol. 63, Issue 4).

Hobson, K. A., Schell, D. M., Renouf, D., & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 528–533.

Hoffman, J. I., & Forcada, J. (2012). Extreme natal philopatry in female Antarctic fur seals (*Arctocephalus gazella*). *Mammalian Biology*, *77*(1), 71–73. https://doi.org/10.1016/j.mambio.2011.09.002

Hohenlohe, P. A., Funk, W. C., & Rajora, O. P. (2021). Population genomics for wildlife conservation and management. *Molecular Ecology*, *30*(1), 62–82. https://doi.org/10.1111/mec.15720

Holborow, J. (1999). *The Diet of New Zealand Fur Seals (Arctocephalus forsteri) in Southern New Zealand.* MSc Thesis, University of Otago, Dunedin.

Horning, M., Andrews, R. D., Bishop, A. M., Boveng, P. L., Costa, D. P., Crocker, D. E., Haulena, M., Hindell, M., Hindle, A. G., Holser, R. R., Hooker, S. K., Hückstädt, L. A., Johnson, S., Lea, M. A., McDonald, B. I., McMahon, C. R., Robinson, P. W., Sattler, R. L., Shuert, C. R., … Womble, J. N. (2019). Best practice recommendations for the use of external telemetry devices on pinnipeds. *Animal Biotelemetry*, *7*(20). https://doi.org/10.1186/s40317-019-0182-6

Horning, M., Haulena, M., Tuomi, P. A., Mellish, J. A. E., Goertz, C. E., Woodie, K., Berngartt, R. K., Johnson, S., Shuert, C. R., Walker, K. A., Skinner, J. P., & Boveng, P. L. (2017). Best practice recommendations for the use of fully implanted telemetry devices in pinnipeds. *Animal Biotelemetry*, *5*(13). https://doi.org/10.1186/s40317-017-0128-9

Iijima, H. (2020). A Review of Wildlife Abundance Estimation Models: Comparison of Models for Correct Application. *Mammal Study*, *45*(3), 177–188. https://doi.org/10.3106/ms2019-0082

Iverson, S. J. (2009). Tracing aquatic food webs using fatty acids: From qualitative indicators to quantitative determination. In *Lipids in Aquatic Ecosystems* (Vol. 9780387893662, pp. 281–308). Springer New York. https://doi.org/10.1007/978-0-387-89366-2_12

Jabour, J. G., & Bradshaw, C. J. A. (2004). The “capacity to reason” in conservation biology and policy: The southern elephant seal branding controversy. *Journal for Nature Conservation*, *12*(1), 25–39. https://doi.org/10.1016/j.jnc.2004.04.001

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, S., & Wilson, R. P. (2002). The potential costs of flipper-bands to penguins. *Functional Ecology*, *16*(1), 141–148. https://doi.org/10.1046/j.0269-8463.2001.00606.x

Jeanniard-Du-Dot, T., Thomas, A. C., Cherel, Y., Trites, A. W., & Guinet, C. (2017). Combining hard-part and DNA analyses of scats with biologging and stable isotopes can reveal different diet compositions and feeding strategies within a fur seal population. *Marine Ecology Progress Series*, *584*, 1–16. https://doi.org/10.3354/meps12381

Jenkins, S. G., Partridge, S. T., Stephenson, T. R., Farley, S. D., & Robbins, C. T. (2001). Nitrogen and carbon isotope fractionation between mothers, neonates, and nursing offspring. *Oecologia*, *129*(3), 336–341. https://doi.org/10.1007/s004420100755

Jones, K. A., Baylis, A. M. M., Orben, R. A., Ratcliffe, N., Votier, S. C., Newton, J., & Staniland, I. J. (2020). Stable Isotope Values in South American Fur Seal Pup Whiskers as Proxies of Year-round Maternal Foraging Ecology. *Marine Biology*, *167*(10). https://doi.org/10.1007/s00227-020-03760-4

Jones, K. N., Currie, K. I., McGraw, C. M., & Hunter, K. A. (2013). The effect of coastal processes on phytoplankton biomass and primary production within the near-shore Subtropical Frontal Zone. *Estuarine, Coastal and Shelf Science*, *124*, 44–55. https://doi.org/10.1016/j.ecss.2013.03.003

Jusufovski, D., Saavedra, C., & Kuparinen, A. (2019). Competition between marine mammals and fisheries in contemporary harvested marine ecosystems. *Marine Ecology Progress Series*, *627*, 207–232. https://doi.org/10.3354/meps13068

Keegan, L. J., White, R. S. A., & Macinnis-Ng, C. (2022). Current knowledge and potential impacts of climate change on New Zealand's biological heritage. *New Zealand Journal of Ecology*, *46*(1), 1–24. https://doi.org/10.2307/48652113

Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, *78*(1), 1–27.

Kelly, M. J. (2001). Computer-Aided Photograph Matching in Studies Using Individual Identification: An Example from Serengeti Cheetahs. *Journal of Mammalogy*, *82*(2), 440–449.

Kernaléguen, L., Dorville, N., Ierodiaconou, D., Hoskins, A. J., Baylis, A. M. M., Hindell, M. A., Semmens, J., Abernathy, K., Marshall, G. J., Cherel, Y., & Arnould, J. P. Y. (2016). From video recordings to whisker stable isotopes: a critical evaluation of timescale in assessing individual foraging specialisation in Australian fur seals. *Oecologia*, *180*(3), 657–670. https://doi.org/10.2307/48718019

King, J. E. (1983). *Seals of the World*. British Museum (Natural History).

Kovacs, K. M., Aguilar, A., Aurioles, D., Burkanov, V., Campagna, C., Gales, N., Gelatt, T., Goldsworthy, S. D., Goodman, S. J., Hofmeyr, G. J. G., Härkönen, T., Lowry, L., Lydersen, C., Schipper, J., Sipilä, T., Southwell, C., Stuart, S., Thompson, D., & Trillmich, F. (2012). Global threats to pinnipeds. *Marine Mammal Science*, *28*(2), 414–436. https://doi.org/10.1111/j.1748-7692.2011.00479.x

Kurle, C. M., & McWhorter, J. K. (2017). Spatial and temporal variability within marine isoscapes: Implications for interpreting stable isotope data from marine systems. *Marine Ecology Progress Series*, *568*, 31–45. https://doi.org/10.3354/meps12045

Kurle, C. M., & Worthy, G. A. J. (2001). Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*) and their prey. *Oecologia*, *126*(2), 254–265. https://doi.org/10.1007/s004420000518

Lalas, C. (2008). Recolonisation of Otago, southern New Zealand, by fur seals and sea lions: unexpected patterns and consequences. *Clarkson, B.; Kurian, P.; Nachowitz, T.; Rennie, H. (Eds.), Proceedings of the Conser-Vision Conference, University of Waikato*.

Lalas, C., & Bradshaw, C. J. A. (2001). Folklore and chimerical numbers: Review of a millennium of interaction between fur seals and humans in the New Zealand region. *New Zealand Journal of Marine and Freshwater Research*, *35*(3), 477–497. https://doi.org/10.1080/00288330.2001.9517017

Lalas, C., & Harcourt, R. (1995). Pup production of the New Zealand fur seal on Otago Peninsula, New Zealand. *Journal of the Royal Society of New Zealand*, *25*(1), 81–88. https://doi.org/10.1080/03014223.1995.9517483

Lalas, C., & Murphy, B. (1998). Increase in the abundance of New Zealand fur seals at the Catlins, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, *28*(2), 287–294. https://doi.org/10.1080/03014223.1998.9517564

Latch, E. K., Dharmarajan, G., Glaubitz, J. C., & Rhodes, O. E. (2006). Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. *Conservation Genetics*, *7*(2), 295–302. https://doi.org/10.1007/s10592-005-9098-1

Lea, M. A., & Hindell, M. A. (1997). Pup growth and maternal care in New Zealand fur seals, *Arctocephalus forsteri*, at Maatsuyker Island, Tasmania. *Wildlife Research*, *24*(3), 307–318. https://doi.org/10.1071/WR96054

Lea, M. A., Hindell, M., Guinet, C., & Goldsworthy, S. D. (2002). Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. *Polar Biology*, *25*(4), 269–279. https://doi.org/10.1007/s00300-001-0339-6

Lee, S. (2022). Using citizen science to quantify juvenile kekeno/New Zealand fur seal (*Arctocephalus forsteri*) mortality in the Hauraki Gulf Marine Park. In *http://blog.shaunlee.co.nz/wp-content/uploads/2022/02/HGMP-kekeno-mortalities-2021-10.pdf*.

Leguia, M., Garcia-Glaessner, A., Muñoz-Saavedra, B., Juarez, D., Barrera, P., Calvo-Mac, C., Jara, J., Silva, W., Ploog, K., Amaro, Lady, Colchao-Claux, P., Johnson, C. K., Uhart, M. M., Nelson, M. I., & Lescano, J. (2023). Highly pathogenic avian influenza A (H5N1) in marine mammals and seabirds in Peru. *Nature Communications*, *14*(1). https://doi.org/10.1038/s41467-023-41182-0

Lento, G. M., Haddon, M., Chambers, G. K., & Baker, C. S. (1997). Genetic variation of southern hemisphere fur seals (*Arctocephalus* spp.): Investigation of population structure and species identity. *Journal of Heredity*, *88*, 202–208.

Lento, G. M., Mattlin, R. H., Chambers, G. K., & Baker, C. S. (1994). Geographic distribution of mitochondrial cytochrome b DNA haplotypes in New Zealand fur seals (*Arctocephalus forsteri*). *Canadian Journal of Zoology*, *72*, 293–299.

Ling, J. K. (1999). Exploitation of fur seals and sea lions from Australian, New Zealand and adjacent subantarctic islands during the eighteenth, nineteenth and twentieth centuries. *Australian Zoologist*, *31*(2), 323–350.

Littnan, C. L., & Arnould, J. P. Y. (2002). At-sea movements of female Australian fur seals *Arctocephalus pusillus doriferus*. *Australian Mammalogy*, *24*, 65–72.

Lowther, A. D., & Goldsworthy, S. D. (2011). Detecting alternate foraging ecotypes in Australian sea lion (*Neophoca cinerea*) colonies using stable isotope analysis. *Marine Mammal Science*, *27*(3), 567–586. https://doi.org/10.1111/j.1748-7692.2010.00425.x

Lowther, A. D., Harcourt, R. G., & Goldsworthy, S. D. (2013). Regional variation in trophic ecology of adult female Australian sea lions inferred from stable isotopes in whiskers. *Wildlife Research*, *40*(4), 303–311. https://doi.org/10.1071/WR12181

Lübcker, N., Whiteman, J. P., Newsome, S. D., Millar, R. P., & Nico De Bruyn, P. J. (2020). Can the carbon and nitrogen isotope values of offspring be used as a proxy for their mother's diet? Using foetal physiology to interpret bulk tissue and amino acid δ15N values. *Conservation Physiology*, *8*(1). https://doi.org/10.1093/conphys/coaa060

Makhado, A. B., Crawford, R. J. M., & Underhill, L. G. (2006). Impact of predation by Cape fur seals *Arctocephalus pusillus pusillus* on Cape gannets *Morus capensis* at Malgas Island, Western Cape, South Africa. *African Journal of Marine Science*, *28*(3–4), 681–687. https://doi.org/10.2989/18142320609504216

Mate, B., Mesecar, R., & Lagerquist, B. (2007). The evolution of satellite-monitored radio tags for large whales: One laboratory's experience. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *54*(3–4), 224–247. https://doi.org/10.1016/j.dsr2.2006.11.021

Mattlin, R. H. (1978a). *Population biology, thermoregulation and site preference of the New Zealand fur seal, Arctocephalus forsteri (Lesson, 1828), on the Open Bay Islands, New Zealand.* Ph. D. thesis. University of Canterbury.

Mattlin, R. H. (1978b). Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri*, Lesson). *New Zealand Journal of Ecology*, *1*, 138–144.

Mattlin, R. H. (1981). Pup growth of the New Zealand fur seal *Arctocephalus forsteri* on the Open Bay Islands, New Zealand. *Journal of the Zoological Society of London*, *193*, 305–314.

Mattlin, R. H., Gales, N. J., & Costa, D. P. (1998). Seasonal dive behaviour of lactating New Zealand fur seals (*Arctocephalus forsteri*). *Canadian Journal of Zoology*, *76*(2), 350–360.

McCafferty, D. J., Boyd, I. L., Walker, T. R., & Taylor, R. I. (1998). Foraging responses of Antarctic fur seals to changes in the marine environment. *Marine Ecology Progress Series*, *166*, 285–299. http://ingrid.

McConkey, S. D. (1999). Photographic identification of the New Zealand sea lion: A new technique. *New Zealand Journal of Marine and Freshwater Research*, *33*(1), 63–66. https://doi.org/10.1080/00288330.1999.9516857

McKenzie, J., Page, B., Shaughnessy, P. D., & Hindell, M. A. (2007). Age and reproductive maturity of New Zealand fur seals (*Arctocephalus forsteri*) in southern Australia. *Journal of Mammalogy, 88(3):639–648, 2007*, *88*(3), 639–648.

McMahon, C. R., Bradshaw, C. J. A., & Hays, G. (2006). Branding can be justified in vital conservation research. *Nature*, *439*, 392.

Meyer, S., Robertson, B. C., Chilvers, B. L., & Krkošek, M. (2015). Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocarctos hookeri*. *Marine Biology*, *162*(8), 1587–1596. https://doi.org/10.1007/s00227-015-2695-8

Meynier, L., Morel, P. C. H., Chilvers, B. L., Mackenzie, D. D. S., MacGibbon, A., & Duignan, P. J. (2008). Temporal and sex differences in the blubber fatty acid profiles of the New Zealand sea lion *Phocarctos hookeri*. *Marine Ecology Progress Series*, *366*, 271–279. https://doi.org/10.3354/meps07617

Miller, E. H. (1971). *Social and thermoregulatory behaviour of the New Zealand fur seal, Arctocephalus forsteri (Lesson, 1828).* MSc Thesis, University of Canterbury, Christchurch.

Miller, E. H. (1975a). A Comparative Study of Facial Expressions of Two Species of Pinnipeds. *Behaviour*, *53*(4), 268–284.

Miller, E. H. (1975b). Annual cycle of fur seals, *Arctocephalus forsteri* (Lesson), on the Open Bay Islands, New Zealand. *Pacific Science*, *29*(2), 139–152.

Minagawa, M., & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. *Geochimica et Cosmochimica Acta*, *48*, 1135–1140.

Morishita, J. (2008). What is the ecosystem approach for fisheries management? *Marine Policy*, *32*(1), 19–26. https://doi.org/10.1016/j.marpol.2007.04.004

Murdoch, R. C., Proctor, R., Jillett, J. B., & Zeldis, J. R. (1990). Evidence for an eddy over the continental shelf in the downstream lee of Otago Peninsula, New Zealand. *Estuarine, Coastal and Shelf Science*, *30*, 489–507.

Newsome, S. D., Bentall, G. B., Tinker, M. T., Oftedal, O. T., Ralls, K., Estes, J. A., & Fooel, M. L. (2010). Variation in δ^{13} C and δ^{15} N diet-vibrissae trophic discrimination factors in a wild population of California sea otters. *Ecological Applications*, *20*(6), 1744–1752. https://doi.org/10.1890/09-1502.1

Newsome, S. D., Clementz, M. T., & Koch, P. L. (2010). Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*, *26*(3), 509–572. https://doi.org/10.1111/j.1748-7692.2009.00354.x

Newsome, S. D., Koch, P. L., Etnier, M. A., & Aurioles-Gamboa, D. (2006). Using carbon and nitrogen isotope values to investigate maternal strategies in Northeast Pacific otariids. *Marine Mammal Science*, *22*(3), 556–572. https://doi.org/10.1111/j.1748-7692.2006.00043.x

Newsome, S. D., Martinez del Rio, C., Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, *5*(8), 429–436. https://doi.org/10.1890/060150.1

Newsome, S. D., Tinker, M. T., Monson, D. H., Oftedal, O. T., Ralls, K., Staedler, M. M., Fogel, M. L., & Estes, J. A. (2009). Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology*, *90*(4), 961–974.

Noè, S. (2013). *Spatial and temporal variation in foraging behaviour of New Zealand fur seals (Arctocephalus forsteri) using archival tissue.* MSc Thesis, University of Portsmouth.

Nyakatura, K., & Bininda-Emonds, O. R. P. (2012). Updating the evolutionary history of Carnivora (Mammalia): A new species-level supertree complete with divergence time estimates. *BMC Biology*, *10*(12). https://doi.org/10.1186/1741-7007-10-12

Ogilvy, C., Constantine, R., Bury, S. J., & Carroll, E. L. (2022). Diet variation in a critically endangered marine predator revealed with stable isotope analysis. *Royal Society Open Science*, *9*(8). https://doi.org/10.1098/rsos.220470

Ogilvy, C., Constantine, R., & Carroll, E. (2023). Spatial variation in isotope values of Hector's dolphins from the north coast of the South Island, New Zealand. *Marine Ecology Progress Series*, *711*, 61–75. https://doi.org/10.3354/meps14301

Olsen, E., Budgell, W. P., Head, E., Kleivane, L., Nøttestad, L., Prieto, R., Silva, M. A., Skov, H., Víkingsson, G. A., Waring, G., & Øien, N. (2009). First satellite-tracked long-distance movement of a sei whale (*Balaenoptera borealis*) in the North Atlantic. *Aquatic Mammals*, *35*(3), 313–318. https://doi.org/10.1578/AM.35.3.2009.313

Ono, K. A., Boness, D. J., & Oftedal, O. T. (1987). The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Behavioral Ecology and Sociobiology*, *21*(2), 109–118. https://doi.org/10.1007/BF02395438

Osterrieder, S. K., Kent, C. S., Anderson, C. J. R., Parnum, I. M., & Robinson, R. W. (2015). Whisker Spot Patterns: A Noninvasive Method of Individual Identification of Australian Sea Lions (*Neophoca cinerea*). *Journal of Mammalogy*, *96*(5), 988–997. https://doi.org/10.1093/jmammal/gyv102

Osterrieder, S. K., Parnum, I. M., Kent, C. P. S., & Robinson, R. W. (2017). Difficulties identifying Australian sea lions (*Neophoca cinerea*) in the wild using whisker spot patterns. *Australian Mammalogy*, *39*(1), 56–71. https://doi.org/10.1071/AM15051

Page, B., McKenzie, J., & Goldsworthy, S. D. (2005a). Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Marine Ecology Progress Series*, *293*, 283–302.

Page, B., McKenzie, J., & Goldsworthy, S. D. (2005b). Inter-sexual differences in New Zealand fur seal diving behaviour. *Marine Ecology Progress Series*, *304*, 249–264.

Page, B., McKenzie, J., Sumner, M. D., & Coyne, M. (2006). Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology Progress Series*, *323*, 263–279. https://doi.org/10.2307/24870629

Parrish, G. R., & Anderson, P. J. (1999). Lizard transfers from Matapia Island to Motuopao Island, Northland and observations on other fauna. *Tane*, *37*, 1–14.

Pavanato, H., Schattschneider, J., Childerhouse, S., & Briscoe, D. (2023). Assessment of New Zealand fur seal/kekeno bycatch by trawlers in the Cook Strait hoki fishery. *Department of Conservation. Cawthron Report No. 3854. 32 p.*

Pemberton, D., Brothers, N., & Copson, G. (1991). Predators on marine fish farms in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, *125*, 33–35. https://doi.org/10.26749/rstpp.125.33

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, *160*, 497–508.

Peterson, J. C. B. (1972). An identification system for zebra (*Equus burchelli*, Gray). *East African Wildlife Journal*, *10*, 59–63.

Petso, T., Jamisola, R. S., & Mpoeleng, D. (2022). Review on methods used for wildlife species and individual identification. *European Journal of Wildlife Research*, *68*(1). https://doi.org/10.1007/s10344-021-01549-4

Ramos, R., & González-Solís, J. (2012). Trace me if you can: The use of intrinsic biogeochemical markers in marine top predators. *Frontiers in Ecology and the Environment 10*(5), 258–266. https://doi.org/10.1890/110140

Ratcliffe, N., Adlard, S., Stowasser, G., & McGill, R. (2018). Dietary divergence is associated with increased intra-specific competition in a marine predator. *Scientific Reports*, *8*(1). https://doi.org/10.1038/s41598-018-25318-7

Rayment, W., Dawson, S., Slooten, E., Bräger, S., Fresne, S. Du, & Webster, T. (2009). Kernel density estimates of alongshore home range of Hector’s dolphins at Banks Peninsula, New Zealand. *Marine Mammal Science*, *25*(3), 537–556. https://doi.org/10.1111/j.1748-7692.2008.00271.x

Rea, L. D., Christ, A. M., Hayden, A. B., Stegall, V. K., Farley, S. D., Stricker, C. A., Mellish, J. A. E., Maniscalco, J. M., Waite, J. N., Burkanov, V. N., & Pitcher, K. W. (2015). Age-specific vibrissae growth rates: A tool for determining the timing of ecologically important events in Steller sea lions. *Marine Mammal Science*, *31*(3), 1213–1233. https://doi.org/10.1111/mms.12221

Read, A. J. (2008). The looming crisis: Interactions between marine mammals and fisheries. *Journal of Mammalogy*, *89*(3), 541–548. https://academic.oup.com/jmammal/article/89/3/541/859978

Reid, C. M., James, N. P., & Bone, Y. (2011). Carbonate sediments in a cool-water macroalgal environment, Kaikoura, New Zealand. *Sedimentology*, *58*(7), 1935–1952. https://doi.org/10.1111/j.1365-3091.2011.01246.x

Reinhold, S. L., Goldsworthy, S. D., Arnould, J. P. Y., Gillanders, B. M., Connell, S. D., & McIntosh, R. R. (2022). Tracing Seal Predation Back to the Source Colony of Their Penguin Prey: A Trace Element and Stable Isotope Analysis. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.813106

Reiter, J., Stinson, N. L., & Le Boeuf, B. J. (1978). Northern elephant seal development: the transition from weaning to nutritional independence. *Behavioral Ecolology and Sociobiology*, *3*, 337–367.

Riccialdelli, L., Newsome, S. D., Fogel, M. L., & Goodall, R. N. P. (2010). Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. *Marine Ecology Progress Series*, *418*, 235–248. https://doi.org/10.3354/meps08826

Richards, R. (1994). “The upland seal” of the Antipodes and Macquarie Islands: A historian’s perspective. *Journal of the Royal Society of New Zealand*, *24*(3), 289–295. https://doi.org/10.1080/03014223.1994.9517473

Richardson, K. C., & Gales, N. J. (1987). Functional morphology of the alimentary tract of the Australian sea lion, *Neophoca cinerea*. *Australian Journal of Zoology*, *35*, 219–245.

Riet-Sapriza, F. G., Duignan, P. J., Chilvers, B. L., Wilkinson, I. S., Lopez-Villalobos, N., Mackenzie, D. D. S., Macgibbon, A., Costa, D. P., Gales, N., & Swanson, B. J. (2012). Interannual and individual variation in milk composition of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Mammalogy*, *93*(4), 1006–1016. https://doi.org/10.1644/1

Roberts, J., & Hendriks, H. (2022). Potential climate change effects on New Zealand marine mammals: a review. *DOC Research and Development Series 366*.

Roberts, J., & Neale, D. (2016). Census & individual size of New Zealand fur seal/kekeno pups on the West Coast South Island from 1991 to 2016. *NIWA Client Report DOC16305*.

Robertson, B. C., & Chilvers, B. L. (2011). The population decline of the New Zealand sea lion *Phocarctos hookeri*: A review of possible causes. *Mammal Review*, *41*(4), 253–275. https://doi.org/10.1111/j.1365-2907.2011.00186.x

Robertson, B. C., Chilvers, B. L., Duignan, P. J., Wilkinson, I. S., & Gemmell, N. J. (2006). Dispersal of breeding, adult male *Phocarctos hookeri*: Implications for disease transmission, population management and species recovery. *Biological Conservation*, *127*(2), 227–236. https://doi.org/10.1016/j.biocon.2005.08.011

Robertson, B. C., & Gemmell, N. J. (2005). Microsatellite DNA markers for the study of population structure in the New Zealand fur seal *Arctocephalus forsteri*. *DOC Science Internal Series 196*. Dept. of Conservation.

Rodríguez, J. P., Fernández-Gracia, J., Thums, M., Hindell, M. A., Sequeira, A. M. M., Meekan, M. G., Costa, D. P., Guinet, C., Harcourt, R. G., McMahon, C. R., Muelbert, M., Duarte, C. M., & Eguíluz, V. M. (2017). Big data analyses reveal patterns and drivers of the movements of southern elephant seals. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-00165-0

Rogers, T. L., Fung, J., Slip, D., Steindler, L., & O'Connell, T. C. (2016). Calibrating the time span of longitudinal biomarkers in vertebrate tissues when fine-scale growth records are unavailable. *Ecosphere*, *7*(12). https://doi.org/10.1002/ecs2.1449

Rossi, S. P., Cox, S. P., Hammill, M. O., Den Heyer, C. E., Swain, D. P., Mosnier, A., & Benoît, H. P. (2021). Forecasting the response of a recovered pinniped population to sustainable harvest strategies that reduce their impact as predators. *ICES Journal of Marine Science*, *78*(5), 1804–1814. https://doi.org/10.1093/icesjms/fsa

Rubenstein, D. R., & Hobson, K. A. (2004). From birds to butterflies: Animal movement patterns and stable isotopes. *Trends in Ecology and Evolution*, *19*(5), 256–263. https://doi.org/10.1016/j.tree.2004.03.017

Salis, A. T., Easton, L. J., Robertson, B. C., Gemmell, N., Smith, I. W. G., Weisler, M. I., Waters, J. M., & Rawlence, N. J. (2016). Myth or relict: Does ancient DNA detect the enigmatic Upland seal? *Molecular Phylogenetics and Evolution*, *97*, 101–106. https://doi.org/10.1016/j.ympev.2015.12.012

Schaller, G. B. (1972). *The Serengeti lion*. The University of Chicago Press, Chicago, Illinois.

Scherer, R. D., Doll, A. C., Rea, L. D., Christ, A. M., Stricker, C. A., Witteveen, B., Kline, T. C., Kurle, C. M., & Wunder, M. B. (2015). Stable isotope values in pup vibrissae reveal geographic variation in diets of gestating Steller sea lions *Eumetopias jubatus*. *Marine Ecology Progress Series*, *527*, 261–274. https://doi.org/10.3354/meps11255

Schoeninger, M. J., & Deniro, M. J. (1984). Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta*, *48*, 625–639.

Schwarz, C. J., & Seber, G. A. F. (1999). Estimating Animal Abundance: Review III. *Statistical Science*, *14*(4), 427–456.

Shaughnessy, P. D. (1994). Tag-shedding from South African fur seals *Arctocephalus pusillus pusillus*. *South African Journal of Marine Science*, *14*(1), 89–94. https://doi.org/10.2989/025776194784287148

Shaughnessy, P. D., Gales, N. J., Dennis, T. E., & Goldsworthy, S. D. (1994). Distribution and abundance of New Zealand fur seals, *Arctocephalus forsteri*, in South Australia and Western Australia. *Wildlife Research*, *21*, 667–695.

Shaughnessy, P. D., & Goldsworthy, S. D. (2015). Scientific Correspondence: Long-nosed fur seal: A new vernacular name for the fur seal, *Arctocephalus forsteri*, in Australia. *Marine Mammal Science*, *31*(2), 830–832. https://doi.org/10.1111/mms.12203

Shaughnessy, P. D., & Goldsworthy, S. D. (2020). Dispersion of long-nosed fur seals (*Arctocephalus forsteri*) determined by tagging. *Australian Journal of Zoology*, *67*(3), 173–179. https://doi.org/10.1071/ZO20032

Shaughnessy, P. D., Goldsworthy, S. D., & Mackay, A. I. (2015). The long-nosed fur seal (*Arctocephalus forsteri*) in South Australia in 2013-14: Abundance, status and trends. *Australian Journal of Zoology*, *63*(2), 101–110. https://doi.org/10.1071/ZO14103

Sinclair, J. G., & Wilson, K.-J. (1994). A radio tracking study of the movements and foraging ecology of female New Zealand fur seals (*Arctocephalus forsteri*) at Cape Foulwind. *Lincoln University Wildlife Management Report 5*.

Slater, C., Preston, T., Weaver, L. T. (2001) Stable isotopes and the international system of units. *Rapid Communications in Mass Spectrometry, 15*: 1270–1273.

Slooten, E., Dawson, S. M., & Lad, F. (1992). Survival rates of photographically identified Hector's dolphins from 1984 to 1988. *Marine Mammal Science*, *8*, 327–343.

Smith, I. (1989). Maori impact on the marine megafauna: pre-European distributions of New Zealand sea mammals. In *Sutton, D.G. (Ed.) "Saying so doesn't make it so", papers in honour of B. Foss Leach. New Zealand Archaeological Association, Dunedin* (pp. 76–108).

Smith, I. (2002). *The New Zealand sealing industry: history, archaeology, and heritage management: Vol. ISBN 0–478–22250–5*. Department of Conservation.

Smith, I. (2005). Retreat and resilience: fur seals and human settlement in New Zealand. In *The Exploitation and Cultural Importance of Sea Mammals* (pp. 6–18). Oxbow Books.

Smith, R. I. L. (1988). Destruction of Antarctic Terrestrial Ecosystems by a Rapidly Increasing Fur Seal Population. *Biological Conservation*, *45*, 55–72.

Staniland, I. J. (2002). Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. *Marine Mammal Science*, *18*(1), 223–243. https://doi.org/10.1111/j.1748-7692.2002.tb01030.x

Staniland, I. J., Reid, K., & Boyd, I. L. (2004). Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella*. *Marine Ecology Progress Series*, *275*, 263–274.

Stanton, B. R. (1976). Circulation and hydrology off the west coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *10*(3), 445–467. https://doi.org/10.1080/00288330.1976.9515629

Stegall, V. K., Farley, S. D., Rea, L. D., Pitcher, K. W., Rye, R. O., Kester, C. L., Stricker, C. A., & Bern, C. R. (2008). Discrimination of carbon and nitrogen isotopes from milk to serum and vibrissae in Alaska Steller sea lions (*Eumetopias jubatus*). *Canadian Journal of Zoology*, *86*(1), 17–23. https://doi.org/10.1139/Z07-115

Stevens, C. L., O'Callaghan, J. M., Chiswell, S. M., & Hadfield, M. G. (2021). Physical oceanography of New Zealand/Aotearoa shelf seas–a review. *New Zealand Journal of Marine and Freshwater Research*, *55*(1), 6–45. https://doi.org/10.1080/00288330.2019.1588746

Stevick, P. T., Palsbøll, P. J., Smith, T. D., Bravington, M. V., & Hammond, P. S. (2001). Errors in identification using natural markings: Rates, sources, and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(9), 1861–1870. https://doi.org/10.1139/cjfas-58-9-1861

Stirling, I. (1971a). Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson) I. Annual cycle, postures and calls, and adult males during the breeding season. *Australian Journal of Zoology*, *19*, 243–266.

Stirling, I. (1971b). Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). II. Adult females and pups. *Australian Journal of Zoology*, *19*(3), 267–273.

Stoffers, P., Plÿger, W., & Walter, P. (1984). Geochemistry and mineralogy of continental margin sediments from Westland, New Zealand. *New Zealand Journal of Geology and Geophysics*, *27*(3), 351–365. https://doi.org/10.1080/00288306.1984.10422303

Stovall, W. R. (2016). *Population genetics of New Zealand fur seals (Arctocephalus forsteri): Genomic tools for research and management.* MSc Thesis. University of Otago, Dunedin.

Street, R. J. (1964). Feeding Habits of the New Zealand Fur Seal. *New Zealand Marine Department Fisheries Technical Report N. 9*.

Stricker, C. A., Christ, A. M., Wunder, M. B., Doll, A. C., Farley, S. D., Rea, L. D., Rosen, D. A. S., Scherer, R. D., & Tollit, D. J. (2015). Stable carbon and nitrogen isotope trophic enrichment factors for Steller sea lion vibrissae relative to milk and fish/invertebrate diets. *Marine Ecology Progress Series*, *523*, 255–266. https://doi.org/10.3354/meps11205

Taylor, R. H. (1982). New Zealand fur seals at the Bounty Islands. *New Zealand Journal of Marine and Freshwater Research*, *16*(1), 1–9. https://doi.org/10.1080/00288330.1982.9515942

Taylor, R. H. (1990). Records of subantarctic fur seals in New Zealand (note). *New Zealand Journal of Marine and Freshwater Research*, *24*(4), 499–502. https://doi.org/10.1080/00288330.1990.9516441

Taylor, R. H., Barton, K. J., Wilson, P. R., Thomas, B. W., & Karl, B. J. (1995). Population status and breeding of New Zealand fur seals (*Arctocephalus forsteri*) in the Nelson-Northern Marlborough region, 1991–94. *New Zealand Journal of Marine and Freshwater Research*, *29*(2), 223–234. https://doi.org/10.1080/00288330.1995.9516656

Thomas, B., Holland, J. D., & Minot, E. O. (2011). Wildlife tracking technology options and cost considerations. *Wildlife Research*, *38*(8), 653–663. https://doi.org/10.1071/WR10211

Thompson, D., Moss, S. E., & Lovell, P. (2003). Foraging behaviour of South American fur seals *Arctocephalus australis*: extracting fine scale foraging behaviour from satellite tracks. *Marine Ecology Progress Series*, *260*, 285–296.

Thompson, F. N., Abraham, E. R., & Berkenbusch, K. (2011). *Marine mammal bycatch in New Zealand trawl fisheries, 1995-96 to 2009-10*. www.dragonfly.co.nz

Thuo, D., Furlan, E., Broekhuis, F., Kamau, J., MacDonald, K., & Gleeson, D. M. (2019). Food from faeces: Evaluating the efficacy of scat DNA metabarcoding in dietary analyses. *PLoS ONE*, *14*(12). https://doi.org/10.1371/journal.pone.0225805

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences 365*(1550), 2163–2176). https://doi.org/10.1098/rstb.2010.0090

Towns, D. R., Bellingham, P. J., Mulder, C. P. H., & Lyver, P. O. (2012). A research strategy for biodiversity conservation on New Zealand's offshore islands. *New Zealand Journal of Ecology*, *36*(1), 1–20.

Uhart, M., Vanstreels, R. E. T., Nelson, M. I., Olivera, V., Campagna, J., Zavattieri, V., Lemey, P., Campagna, C., Falabella, V., & Rimondi, A. (2024). *Massive outbreak of Influenza A H5N1 in elephant seals at Península Valdés, Argentina: increased evidence for mammal-to-mammal transmission*. https://doi.org/10.1101/2024.05.31.596774

Ulloa, M., Fernández, A., Ariyama, N., Colom-Rivero, A., Rivera, C., Nuñez, P., Sanhueza, P., Johow, M., Araya, H., Torres, J. C., Gomez, P., Muñoz, G., Agüero, B., Alegría, R., Medina, R., Neira, V., & Sierra, E. (2023). Mass mortality event in South American sea lions (*Otaria flavescens*) correlated to highly pathogenic avian influenza (HPAI) H5N1 outbreak in Chile. *Veterinary Quarterly*, *43*(1), 1–10. https://doi.org/10.1080/01652176.2023.2265173

Voges, D., Carl, K., Klauer, G. J., Uhlig, R., Schilling, C., Behn, C., & Witte, H. (2012). Structural characterization of the whisker system of the rat. *IEEE Sensors Journal*, *12*(2), 332–339. https://doi.org/10.1109/JSEN.2011.2161464

Walker, K. A., Trites, A. W., Haulena, M., & Weary, D. M. (2012). A review of the effects of different marking and tagging techniques on marine mammals. *Wildlife Research*, *39*(1), 15–30. https://doi.org/10.1071/WR10177

Walters, A., Hindell, M., Goebel, M. E., Bester, M. N., Trathan, P. N., Oosthuizen, W. C., & Lea, M. A. (2020). Southern Ocean isoscapes derived from a wide-ranging circumpolar marine predator, the Antarctic fur seal. *Ecological Indicators*, *118: 106694*. https://doi.org/10.1016/j.ecolind.2020.106694

Walters, A., Lea, M. A., Van Den Hoff, J., Field, I. C., Virtue, P., Sokolov, S., Pinkerton, M. H., & Hindell, M. A. (2014). Spatially explicit estimates of prey consumption reveal a new krill predator in the

Southern Ocean. *PLoS ONE*, *9*(1: e86452. doi:10.1371/journal.pone.0086452). https://doi.org/10.1371/journal.pone.0086452

Watson, D. M., Beaven, B., & Bradshaw, C. J. A. (2015). Population trends of New Zealand fur seals in the Rakiura region based on long-term population surveys and traditional ecological knowledge. *New Zealand Journal of Marine and Freshwater Research*, *49*(1), 106–118. https://doi.org/10.1080/00288330.2014.953184

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution*, *17*(2), 76–83.

Wells, R. S. (2009). Identification Methods II. Pinnipeds. In B. Wursig, J. G. M. Thewisson, & K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals (Second Edition)* (pp. 593–599).

West, J. B., Bowen, G. J., Cerling, T. E., & Ehleringer, J. R. (2006). Stable isotopes as one of nature's ecological recorders. *Trends in Ecology and Evolution*, *21*(7), 408–414. https://doi.org/10.1016/j.tree.2006.04.002

Wilkinson, I. S., Chilvers, B. L., Duignan, P. J., & Pistorius, P. A. (2011). An evaluation of hot-iron branding as a permanent marking method for adult New Zealand sea lions, *Phocarctos hookeri*. *Wildlife Research*, *38*(1), 51–60. https://doi.org/10.1071/WR10077

Willis, T. J., Triossi, F., & Meynier, L. (2008). Diet of fur seals *Arctocephalus forsteri* at Tonga Island, Abel Tasman National Park. In *NIWA Project: DOC07401*.

Wilson, G. J. (1981). Distribution and abundance of the New Zealand fur seal, *Arctocephalus forsteri*. *Fisheries Research Division Occasional Publication No. 20* (pp. 1–39).

Wilson, R. P., & McMahon, C. R. (2006). Measuring devices on wild animals: What constitutes acceptable practice? *Frontiers in Ecology and the Environment 4*(3), 147–154 https://doi.org/10.1890/1540-9295(2006)004[0147:MDOWAW]2.0.CO;2

Wolf, J. B. W., Harrod, C., Brunner, S., Salazar, S., Trillmich, F., & Tautz, D. (2008). Tracing early stages of species differentiation: Ecological, morphological and genetic divergence of Galápagos sea lion populations. *BMC Evolutionary Biology*, *8*(1). https://doi.org/10.1186/1471-2148-8-150

Wursig, B., & Jefferson, T. A. (1990). *Methods of Photo-Identification for Small Cetaceans* (pp. 43–52). Report of the International Whaling Commission (Special Issue 12).

Wynen, L. P., Goldsworthy, S. D., Insley, S. J., Adams, M., Bickham, J. W., Francis, J., Gallo, J. P., Hoelzel, A. R., Majluf, P., White, R. W. G., & Slade, R. (2001). Phylogenetic relationships within the eared seals (Otariidae: Carnivora): Implications for the historical biogeography of the family. *Molecular Phylogenetics and Evolution*, *21*(2), 270–284. https://doi.org/10.1006/mpev.2001.1012

Yochem, P. K., Stewart, B. S., Mina, M., Zorin, A., Sadovov, V., & Yablokov, A. (1990). Non-metrical analyses of pelage patterns in demographic studies of harbor seals. *Report of the International Whaling Commission Special Issue 12* (pp. 87–90).

Yonezawa, T., Kohno, N., & Hasegawa, M. (2009). The monophyletic origin of sea lions and fur seals (Carnivora; Otariidae) in the Southern Hemisphere. *Gene*, *441*(1–2), 89–99. https://doi.org/10.1016/j.gene.2009.01.022

Zeppelin, T. K., & Orr, A. J. (2010). Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. *Marine Ecology Progress Series*, *409*, 241–253. https://doi.org/10.3354/meps08624

Zeppelin, T. K., Pelland, N., Sterling, J., Brost, B., Melin, S., Johnson, D., Lea, M. A., & Ream, R. (2019). Migratory strategies of juvenile northern fur seals (*Callorhinus ursinus*): bridging the gap between pups and adults. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-50230-z

Appendix 1

Data file for stranded New Zealand fur seal young-of-the-year

ID	Name	Date	Location	Latitude	Longitude	Body length (cm)	Vibrissa length (mm)	Vibrissa length - 10 mm subtracted from plucked samples	Vibrissa width at base (mm)	Vibrissa width at two-thirds (mm)	Vibrissa section	δ13C	δ15N	C%	N%	Sample weight	C/N ratio	Number of days from median pupping date	Estimated vibrissa length at birth	Age-class (green - Northland West; orange - Northland East; blue - Napier)
205A	UW1	16/09/2023	Northland West	35 34.932 S	173 24.068 E	88	116	106	1.11	0.69	Two thirds	-17.1	12.9	37.7	12.6	0.6	2.99	275	40	Pup
205B	UW1	16/09/2023	Northland West	35 34.932 S	173 24.068 E						Base	-17.1	10.3	34.6	11.6	0.6	2.99	275		
206A	UW2	16/09/2023	Northland West	35 46.196 S	173 34.371 E	87	155	145	1.16	0.52	Two thirds	-16.2	17.1	41.2	13.8	0.5	2.99	275	79	Pup
206B	UW2	16/09/2023	Northland West	35 46.196 S	173 34.371 E						Base	-15.5	13.9	38.3	12.7	0.4	3.02	275		
207A	UW3	17/09/2023	Northland West	35 55.389 S	173 42.951 E	85	125	115	1.19	0.67	Two thirds	-17.2	17.8	33.5	11.3	0.6	2.97	276	49	Pup
207B	UW3	17/09/2023	Northland West	35 55.389 S	173 42.951 E						Base	-17.1	10.7	40.1	13.8	0.8	2.89	276		
208A	UW4	17/09/2023	Northland West	35 58.153 S	173 45.468 E	100	160	150	1.37	0.65	Two thirds	-16.5	14	34.1	11.3	0.5	3.02	276	84	Non-pup
208B	UW4	17/09/2023	Northland West	35 58.153 S	173 45.468 E						Base	-16.4	13.3	45.9	15	0.3	3.06	276		
209A	UW5	17/09/2023	Northland West	35 53.787 S	173 41.568 E	83	149	139	1.43	0.62	Two thirds	-16.9	16.1	44.2	14.8	0.4	2.99	276	73	Pup
209B	UW5	17/09/2023	Northland West	35 53.787 S	173 41.568 E						Base	-17.7	10.4	50.7	17.1	0.4	2.96	276		
210A	UE1	9/09/2023	Northland East	35 48.981 S	174 33.589 E	82	114	104	1.06	0.48	Two thirds	-16.9	14.3	39.1	13.5	0.6	2.91	268	40	Pup
210B	UE1	9/09/2023	Northland East	35 48.981 S	174 33.589 E						Base	-18.6	8.3	40.2	13.6	0.5	2.96	268		
211A	UE2	9/09/2023	Northland East	35 47.107 S	174 33.092 E	84	157	147	1.17	0.6	Two thirds	-16.5	15.4	36.5	12.3	0.4	2.98	268	83	Pup
211B	UE2	9/09/2023	Northland East	35 47.107 S	174 33.092 E						Base	-17.1	10.5	37	12	0.4	3.07	268		
212A	UE3	10/09/2023	Northland East	35 57.992 S	174 28.207 E	89	136	126	1.42	0.7	Two thirds	-17.1	17.5	54.2	18.7	0.5	2.90	269	61	?
212B	UE3	10/09/2023	Northland East	35 57.992 S	174 28.207 E						Base	-16.1	NA	45.6	NA	0.8	NA	269		
213	UE4	10/09/2023	Northland East	35 58.945 S	174 28.652 E	114	260	250	1.39	0.64								269	185	Non-pup
214A	UE5	11/09/2023	Northland East	35 58.945 S	174 28.652 E	92	141	131	1.23	1.03	Two thirds	-16.7	15.8	41	13.9	0.5	2.95	270	66	Pup
214B	UE5	11/09/2023	Northland East	35 58.945 S	174 28.652 E						Base	-18.1	9.9	41.2	14.4	0.8	2.86	270		
215	UE6	11/09/2023	Northland East	35 57.193 S	174 27.931 E	98	205	195	1.4	0.64								270.0	130	Non-pup
216A	UE7	12/09/2023	Northland East	35 54.861 S	174 27.650 E	84	98	88	1.01	0.49	Two thirds	-16.9	16.8	32.5	10.9	0.6	2.97	271	23	Pup
216B	UE7	12/09/2023	Northland East	35 54.861 S	174 27.650 E						Base	-18.5	10.7	53.7	19	0.4	2.83	271		
217A	UE8	12/09/2023	Northland East	35 55.725 S	174 27.680 E	82	162	152	1.17	0.96	Two thirds	-16.8	NA	72.4	NA	0.5	NA	271	87	?
217B	UE8	12/09/2023	Northland East	35 55.725 S	174 27.680 E						Base	-18.7	NA	40.1	NA	0.8	NA	271		
218A	UE9	15/09/2023	Northland East	36 01.246S	174 30.040 E	92	150	150	1.02	0.68	Two thirds	-15.6	18.5	42.6	15	0.5	2.84	274	84	?
218B	UE9	15/09/2023	Northland East	36 01.246S	174 30.040 E						Base	-15.8	NA	45.4	NA	0.8	NA	274		
219A	UE10	15/09/2023	Northland East	36 00.881 S	174 29.807 E	90	127	117	1.11	0.54	Two thirds	-16.5	17.2	42.8	15.4	0.6	2.79	274	51	Pup
219B	UE10	15/09/2023	Northland East	36 00.881 S	174 29.807 E						Base	-18.2	11	43.9	15.6	0.6	2.81	274		
220A	UE11	15/09/2023	Northland East	36 00.150 S	174 29.574 E	87	131	121	1.27	0.77	Two thirds	-16.5	17.4	31.2	11.1	0.7	2.80	274	55	Pup
220B	UE11	15/09/2023	Northland East	36 00.150 S	174 29.574 E						Base	-17.9	11.2	27.9	9.9	0.8	2.82	274		
221	UE12	15/09/2023	Northland East	36 00.150 S	174 29.340 E	123	200	190	1.4	NA								274	124	Non-pup
222A	UE13	15/09/2023	Northland East	35 59.785 S	174 29.107 E	89	151	141	1.21	0.66	Two thirds	-16.8	15.1	38.1	13.8	0.6	2.76	274	75	Pup
222B	UE13	15/09/2023	Northland East	35 59.785 S	174 29.107 E						Base	-16	13.6	49.3	17.7	0.5	2.79	274		
223A	UW6	17/09/2023	Northland West	36 4.498 S	173 51.051 E	85	158	148	1.18	0.46	Two thirds	-16.8	15.8	28.1	9.8	0.5	2.86	276	82	Pup
223B	UW6	17/09/2023	Northland West	36 4.498 S	173 51.051 E						Base	-16.7	13.6	43.6	15.4	0.5	2.84	276		
224	UW7	17/09/2023	Northland West	36 3.598 S	173 50.268 E	102	216	206	1.43	NA								276.0	140	Non-pup
225	UW8	17/09/2023	Northland West	36 2.658 S	173 49.436 E	112	168	158	1.5	NA								276.0	92	Non-pup
226A	UW9	17/09/2023	Northland West	36 1.589 S	173 48.526 E	93	142	132	1.18	0.7	Two thirds	-17	17	42.4	15.2	0.7	2.80	276	66	Pup
226B	UW9	17/09/2023	Northland West	36 1.589 S	173 48.526 E						Base	-19.7	9.3	36.7	12.8	0.6	2.86	276		
227A	UW10	17/09/2023	Northland West	36 0.447 S	173 47.487 E	79	120	110	1.04	0.73	Two thirds	-16.1	16.4	42	15.2	0.6	2.77	276	44	Pup
227B	UW10	17/09/2023	Northland West	36 0.447 S	173 47.487 E						Base	-16.8	12.5	44.8	16.1	0	2.79	276		
228A	UW11	28/09/2023	Northland West	36 6.203 S	173 52.456 E	85	148	138	1.24	0.67	Two thirds	-16.7	17.2	48.2	17	0.5	2.84	287	69	Pup
228B	UW11	28/09/2023	Northland West	36 6.203 S	173 52.456 E						Base	-17.1	13.2	36.6	13	0.7	2.82	287		
229	UW12	28/09/2023	Northland West	36 7.780 S	173 53.724 E	116	222	212	1.38	NA								287.0	143	Non-pup
230	UW13	28/09/2023	Northland West	36 9.344 S	173 55.123 E	129	215	205	1.49	NA								287.0	136	Non-pup
231A	UE14	23/09/2023	Northland East	35 47.200 S	174 33.056 E	87	121	111	0.99	0.39	Two thirds	-17.2	14.1	35.1	12.4	0.5	2.83	282	43	Pup
231B	UE14	23/09/2023	Northland East	35 47.200 S	174 33.056 E						Base	-18.2	12.1	43.8	15.5	0.7	2.82	282		
232A	UW14	7/10/2023	Northland West	35 58.256 S	173 45.490 E	75	90	80	1.22	0.8	Two thirds	-16.7	16.7	42.7	15	0.5	2.85	296	9	?
232B	UW14	7/10/2023	Northland West	35 58.256 S	173 45.490 E						Base	-17.5	NA	46.4	NA	0.7	NA	296		
233A	UW15	7/10/2023	Northland West	35 58.959 S	173 46.070 E		122	112	1.4	0.65	Two thirds	-16.4	16.8	46.3	16.5	0.4	2.80	296	41	Pup
233B	UW15	7/10/2023	Northland West	35 58.959 S	173 46.070 E						Base	-16.7	12.2	29.6	10.5	0.7	2.82	296		
234A	UW16	7/10/2023	Northland West	35 59.845 S	173 46.861 E	81	127	117	1.15	0.75	Two thirds	-16.7	16.8	40	14	0.6	2.86	296	46	Pup
234B	UW16	7/10/2023	Northland West	35 59.845 S	173 46.861 E						Base	-16.8	12.1	38.8	13.6	0.5	2.86	296		
235A	UN1	7/09/2023	Napier	39 27.383 S	176 52.400 E		111	111	1.05	0.46	Two thirds	-16.2	17.1	44.7	15.8	0.5	2.83	266	47	Pup
235B	UN1	7/09/2023	Napier	39 27.383 S	176 52.400 E						Base	-17.2	12.7	26.1	8.9	0.5	2.93	266		
236A	UN2	8/09/2023	Napier	39 27.916 S	176 52.600 E		112	112	1.09	0.66	Two thirds	-16	17.4	52	18.2	0.4	2.85	267	48	Pup
236B	UN2	8/09/2023	Napier	39 27.916 S	176 52.600 E						Base	-16.4	14.2	32.8	11.6	0.5	2.83	267		
237A	UN3	8/09/2023	Napier	39 27.966 S	176 52.616 E		91	91	1.05	0.79	Two thirds	-16.6	17.4	39.9	14.1	0.7	2.83	267	27	Pup
237B	UN3	8/09/2023	Napier	39 27.966 S	176 52.616 E						Base	-18.1	11.2	52	18.3	0.5	2.84	267		
238A	UN4	8/09/2023	Napier	39 27.967 S	176 52.617 E		125	125	1.05	0.64	Two thirds	-16.6	16.5	44.6	15.8	0.5	2.82	267	61	Pup
238B	UN4	8/09/2023	Napier	39 27.967 S	176 52.617 E						Base	-17.5	12.2	41.8	15	0.7	2.79	267		
239A	UN5	8/09/2023	Napier	39 22.633 S	176 53.666 E		140	130	1	0.51	Two thirds	-18	9.4	40.6	14.3	0.6	2.83	267	66	?
239B	UN5	8/09/2023	Napier	39 22.633 S	176 53.666 E						Base	-17.7	11.7	46.7	16.6	0.6	2.82	267		
240A	UN6	11/09/2023	Napier	39 27.966 S	176 52.616 E		97	87	1.32	0.58	Two thirds	-15.9	15.9	31.1	10.7	0.5	2.90	270	22	Pup
240B	UN6	11/09/2023	Napier	39 27.966 S	176 52.616 E						Base	-18.5	10.8	43.4	15.4	0.7	2.83	270		
241A	UN7	1/10/2023	Napier	39 39.800 S	176 55.200 E		143	143	1.15	0.66	Two thirds	-16.6	14.4	34.3	11.8	0.4	2.90	290	73	Pup
241B	UN7	1/10/2023	Napier	39 39.800 S	176 55.200 E						Base	-18	10.3	35.1	12.3	0.6	2.86	290		