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Establishment of a stable isotope database for New Zealand fur seal breeding colonies using $\delta^{13}C$ and $\delta^{15}N$ in pup vibrissae

Diana Galbraith and B. Louise Chilvers

Wildbase, School of Veterinary Science, Massey University, Palmerston North, New Zealand

ABSTRACT
The New Zealand fur seal/kekeno (*Arctocephalus forsteri*, NZFS) is native to Aotearoa/New Zealand. Its original range included the entire coast of mainland New Zealand, and offshore and subantarctic islands. The NZFS has gradually recolonised much of its former range after being almost extirpated by hunting, however, little is known about species dispersal in the non-breeding season. Stable isotope analysis (SIA) can trace foraging ecology and migration in marine mammal species. Isotopic niche width can be described statistically and provides ecologically relevant information on diet and potentially foraging location. Otariid pup vibrissae (whiskers) can be used as proxies for maternal foraging as they provide a sequential record of nutrient intake derived from maternal milk. In this study, vibrissae from NZFS pups were collected from seven established breeding areas around the coast of New Zealand. A stable isotope database of $\delta^{13}C$ and $\delta^{15}N$ was established for each breeding colony, and isotopic niche widths estimated. Isotopic niche widths were largest at Open Bay Islands and Cape Foulwind. Results were discussed in light of previous oceanographic and NZFS diet and foraging studies. Colonies are not likely to be sufficiently isotopically distinct for pups to be identified to their colony of origin.

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Introduction

Little is known about the fine-scale dispersal of the New Zealand fur seal/kekeno (*Arctocephalus forsteri*, Lesson, 1828, family *Otariidae*, hereafter 'NZFS') around Aotearoa/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 and Wilson 1976). NZFS pup production is declining in some colonies (Roberts and Neale 2016), and increasing in others (Hall et al. 2025). Population decline could be due to either emigration or threats that

CONTACT B. Louise Chilvers b.l.chilvers@massey.ac.nz

vary by region. To assess whether threats differ by region, it is necessary to be able to distinguish between individuals from different areas.

The NZFS is native to New Zealand, and inhabits the rocky coast of New Zealand and its sub-Antarctic islands (Crawley and Wilson 1976), as well as southern and western Australia (Shaughnessy et al. 2015). It is classified as 'Least Concern' on the IUCN Red List (Chilvers and Goldsworthy 2015) and Increasing, Secure Overseas in the New Zealand Threat Classification Series (Baker et al. 2019). It is, however, susceptible to anthropogenic threats including fisheries bycatch (Lalas and Bradshaw 2001; Hamer and Goldsworthy 2006; Thompson et al. 2011; Abraham and Berkenbusch 2017; Abraham et al. 2021), aquaculture (Baker 2005), entanglement (Boren et al. 2006), disturbance (Cowling et al. 2015), tourism (Boren et al. 2002; Cowling 2013), and climate change (Roberts and Hendriks 2022). Having been almost extirpated by hunting (Smith 1989; Ling 1999), populations are recovering (Lalas and Bradshaw 2001), however, there have been no recent, comprehensive, New Zealand-wide surveys (Chilvers and Goldsworthy 2015). The latest estimate for the total New Zealand population is 131,338–168,269 based on pup production estimates, and 181,646–239,473 based on modelling (Hall et al. 2025). The NZFS is completely protected under the Marine Mammals Protection Act 1978 (Chilvers and Goldsworthy 2015).

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 (Lalas and Harcourt 1995; Taylor et al. 1995; Lalas and Murphy 1998; Boren 2005), 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.

Foraging behaviour in marine generalist predator species can vary markedly between individuals (Chilvers et al. 2005; Drago et al. 2010). Individual NZFSs are generalist predators (Harcourt et al. 2001, 2002; Emami-Khoyi et al. 2016). Previous research has shown that season, region, breeding or non-breeding site, and age/sex of NZFSs affect foraging behaviour and, therefore, diet (Boren 2010; Emami-Khoyi et al. 2016). Dietary studies on NZFSs in New Zealand (Street 1964; Carey 1991; Fea et al. 1999; Holborow 1999; Willis et al. 2008; Allum and Maddigan 2012; Emami-Khoyi et al. 2016) showed a range of species was consumed. Arrow squid (*Nototodarus sloanii*) and octopus (*Octopus maorum*) were the only species found in all studies (Boren 2010).

Foraging research on NZFSs in New Zealand has mostly been undertaken on lactating females, using VHF radio tracking (Sinclair and Wilson 1994; Mattlin et al. 1998; Boren 2005), satellite-linked transmitters (Harcourt and Davis 1997; Harcourt et al. 2002), or Time Depth Recorders (TDRs) (Harcourt et al. 1995, 2001, 2002; Mattlin et al. 1998). Dive behaviour varied among individuals, regions, seasons, and, in some cases, years (Sinclair and Wilson 1994; Mattlin et al. 1998; Harcourt et al. 2001, 2002; Boren 2005). For lactating female NZFSs in southern Australia, foraging trip distances and durations varied among individuals and colonies, reflecting a high level of plasticity in foraging and provisioning strategies (Baylis et al. 2012).

Biogeochemical markers, such as stable isotopes, can be used to trace feeding ecology and migration (Hobson 1999; Crawford et al. 2008; Hobson et al. 2010; Ramos and 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 and González-Solís 2012), provide indirect information on diet and foraging locations (Rubenstein and Hobson 2004), and can be used to determine an individual's area of origin (Hobson 1999; Webster et al. 2002). A database of isotopic values from multiple individuals in different areas is required to identify the area of origin of an individual (Rubenstein and 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). In otariids vibrissae grow continually and are retained for at least two years (Hirons et al. 2001). Vibrissa growth rates and retention times vary among species and age-class (Hirons et al. 2001; Rea et al. 2015; Jones et al. 2020). 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 et al. 2015; Chilvers 2017, 2021a).

In this study, samples from the proximal vibrissa of NZFS pups from seven established breeding areas in New Zealand were used to construct an isotopic database of $\delta^{13}C$ and $\delta^{15}N$ values for each area, and to calculate the isotopic niche width for each colony (Jackson et al. 2011).

Methods

Sampling

Vibrissa sampling was carried out between 25 January and 10 March 2023, which is 39–84 days after the assumed median pupping date for NZFS in New Zealand. Based on calculated vibrissa growth rates (Galbraith 2024) all sampled vibrissae would have been formed in the post-natal period. Vibrissae were taken from NZFS pups in seven areas: Open Bay Islands (Taumaka), 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 1). 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.

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 the Department of Conservation, and under Massey University Animal Ethics Permit AEC 22/60. A single vibrissa was collected from between 20 and 50 pups at each location.

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

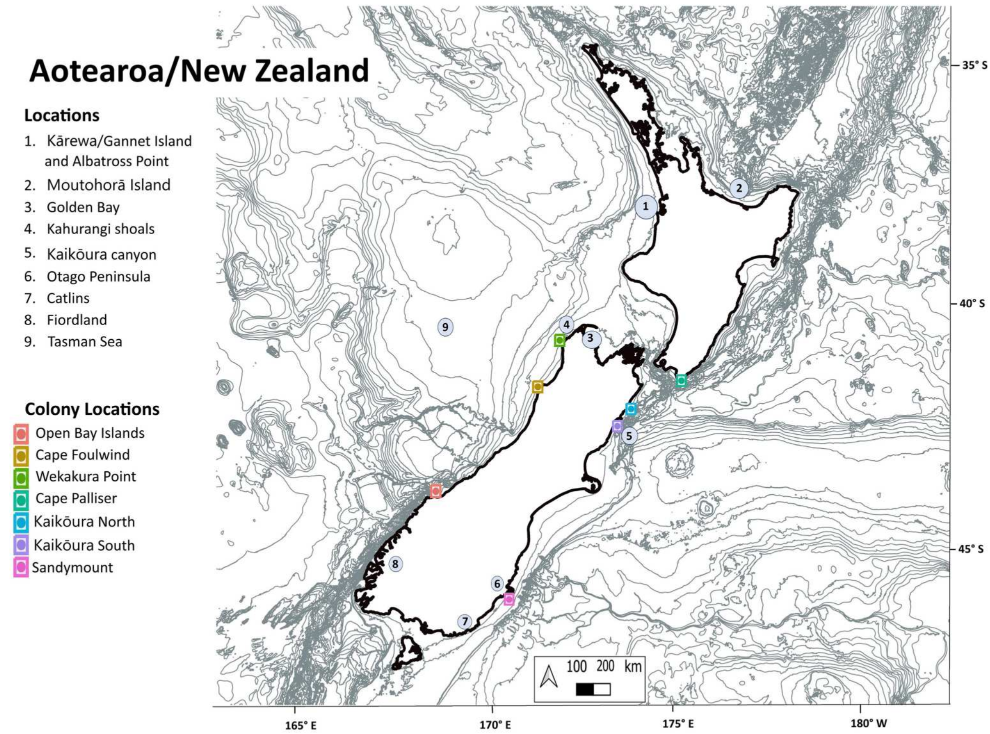

Figure 1. The locations of the seven established New Zealand fur seal breeding areas from which pup vibrissae were sampled, and locations of all places in New Zealand mentioned in the text. Bathymetric data from the National Institute of Water and Atmospheric Research.

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).

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.

Statistical analysis

Statistical analysis of the $\delta^{13}C$ and $\delta^{15}N$ results from the NZFS vibrissa samples was carried out in R 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 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 (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 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 parts per thousand squared (‰^{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).

Results

In total, 147 pup vibrissa samples were analysed from the seven breeding areas (Table 1, Figure 2). 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 1). 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 to 16.9 ‰.

Table 1. The number of New Zealand fur seal pup vibrissa samples at each location, and the mean, standard deviation, and range of $\delta^{13}C$ and $\delta^{15}N$ values (‰). Kaikōura North combines the results from Needles Point and Ōhau Point.

Location	Mean $\delta^{13}C$ ± sd	Range	Mean $\delta^{15}N$ ± sd	Range	*n*
Open Bay Islands	−17.0 ± 0.28	−17.7 to −16.5	15.0 ± 0.66	14.0 to 16.8	23
Cape Foulwind	−16.9 ± 0.31	−17.4 to −16.3	16.7 ± 0.82	14.8 to 18.1	20
Wekakura Point	−16.7 ± 0.18	−17.0 to −16.3	17.6 ± 0.48	16.6 to 18.5	20
Cape Palliser	−16.5 ± 0.23	−16.8 to −16.0	16.9 ± 0.24	16.3 to 17.3	20
Kaikōura North	−16.4 ± 0.19	−16.7 to −16.0	16.8 ± 0.48	15.6 to 17.4	24
Kaikōura South	−16.1 ± 0.20	−16.5 to −15.7	16.8 ± 0.53	15.4 to 17.8	20
Sandymount	−16.8 ± 0.16	−17.1 to −16.6	14.6 ± 0.42	14.1 to 15.7	20
Total samples	−16.6 ± 0.38	−18.1 to −16.0	16.3 ± 1.14	14 to 18.5	147

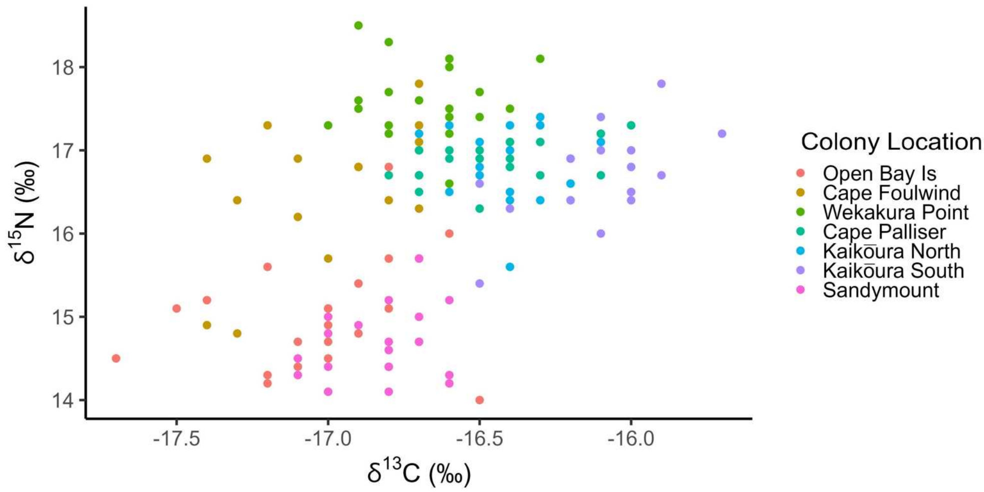

Figure 2. $\delta^{13}C$ and $\delta^{15}N$ values (‰) in the proximal vibrissa of New Zealand fur seal pups at seven breeding colonies around the coast of New Zealand. Colours represent breeding colonies.

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 3, Figure 4). Conversely, on the west coast $\delta^{13}C$ increased slightly from south to north, but $\delta^{15}N$ markedly increased from south to north. Previous studies have taken samples from Ōhau Point to be representative of the whole Kaikōura area, however, the present study showed

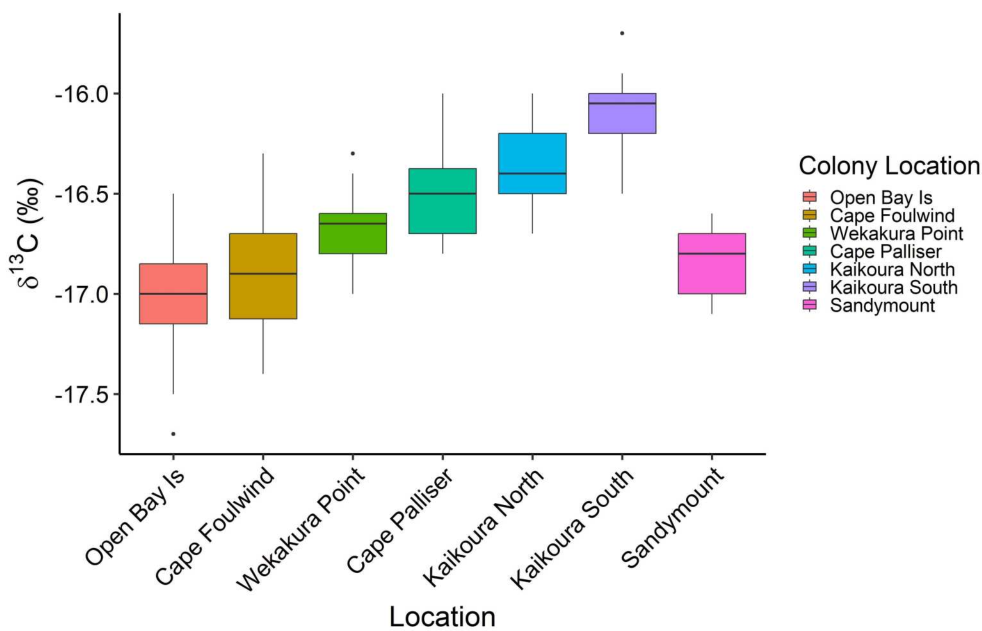

Figure 3. Boxplots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (‰) at seven established breeding colonies in New Zealand, showing medians, upper and lower quartiles and ranges. Colonies are ordered clockwise from southwest to southeast. Black dots are outliers.

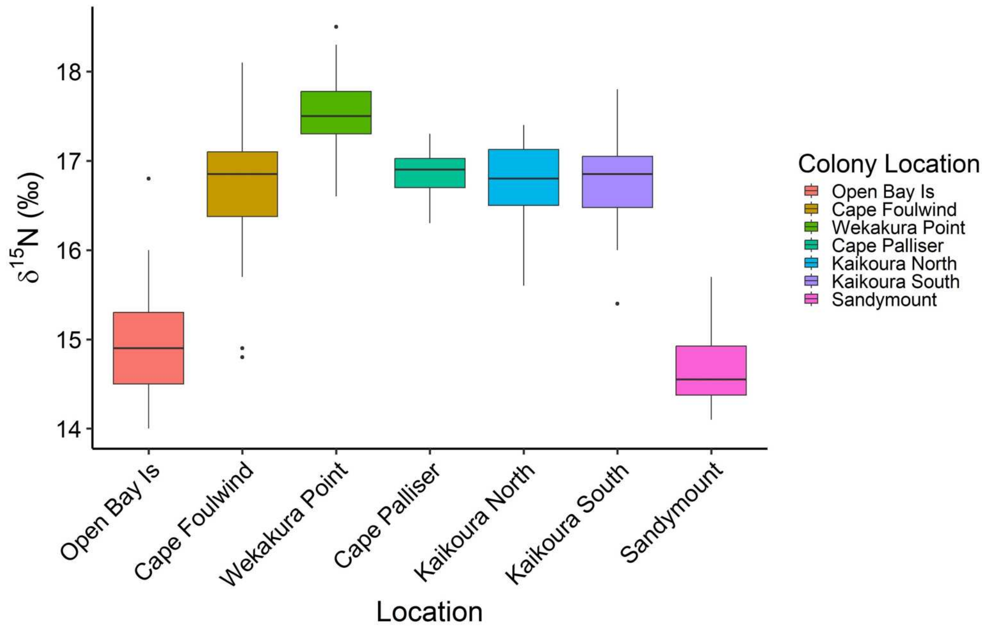

Figure 4. Boxplots of New Zealand fur seal pup vibrissa $\delta^{15}N$ (‰) at seven established breeding colonies in New Zealand, showing medians, upper and lower quartiles and ranges. Colonies are ordered clockwise from southwest to southeast. Black dots are outliers.

that samples from Kaikōura South had higher mean $\delta^{13}C$ values (−16.1 ‰) than Kaikōura North (−16.4 ‰), despite being only 40 km south of Ōhau Point (ANOVA: $F = 19.78$, $P < 0.0001$).

Mean $\delta^{13}C$ was higher at Kaikōura North than at Cape Foulwind (Table 1, Figure 3, 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 1, Figure 4), 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: $P = 0.05$). The carbon to nitrogen ratio (C:N) can be used as a control for keratin quality (Newsome et al. 2009). In this study the mean (± SD) C:N ratio was 2.93 ± 0.02.

Permutational MANOVA analysis at the seven breeding colonies showed that location had a significant effect on $\delta^{13}C$ and $\delta^{15}N$ ($F = 76.02$, $P < 0.001$, $R^2 = 0.77$). The colony pairs that consistently did not differ significantly were Open Bay Islands and Sandymount (700 km apart); Kaikōura North and Cape Palliser (132 km apart); and Kaikōura North and Kaikōura South (40 km apart) ($P > 0.05$). 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 2, Figure 3). It was not possible to identify pups to their colony of origin as colonies were not sufficiently isotopically distinct. The results of cluster analysis are not presented here, as the overlap in $\delta^{13}C$ and $\delta^{15}N$ values between colonies meant that individual colonies did not form separate clusters.

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

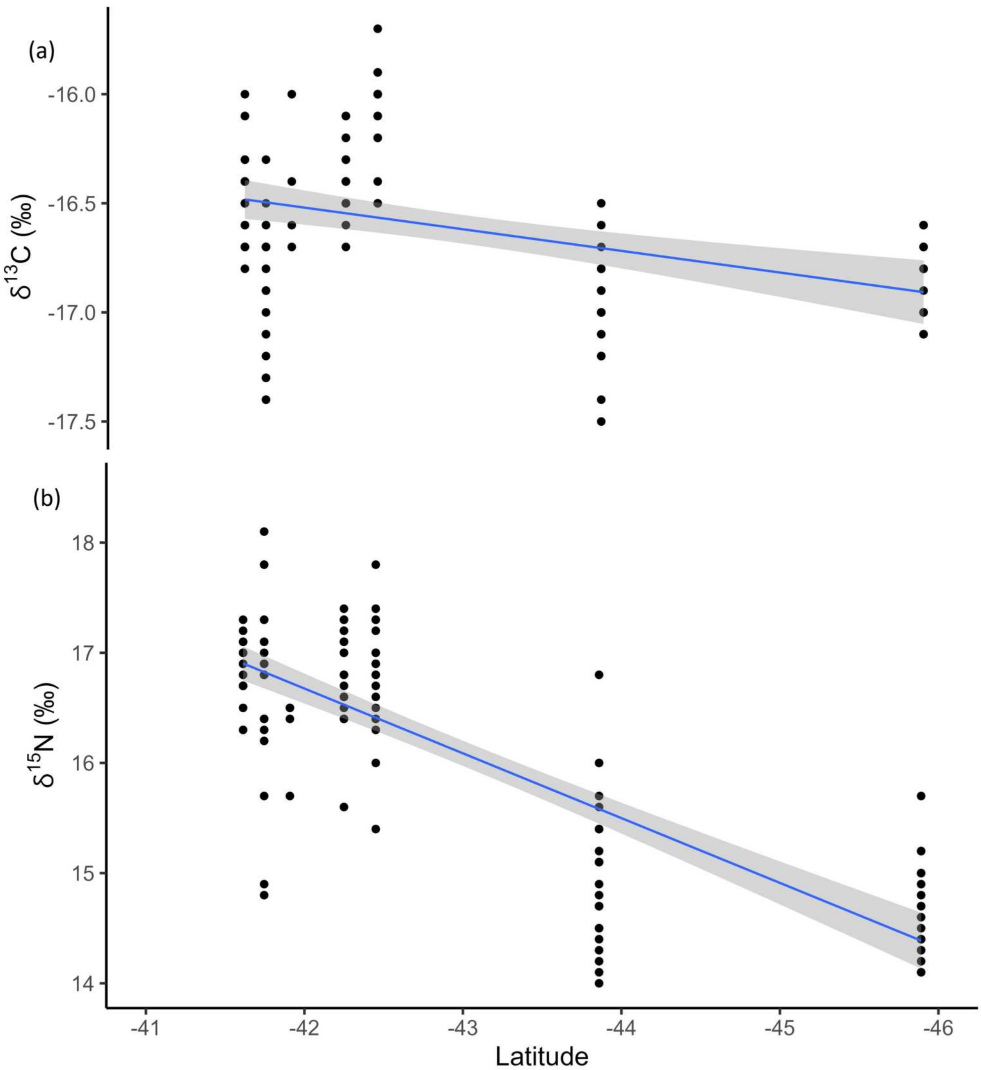

Figure 5. Scatter plots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (**a**) and $\delta^{15}N$ (**b**) values (‰) against latitude. Linear model regression line shown in blue and 95% confidence intervals in grey shading.

$\delta^{15}N$. Linear modelling showed that $\delta^{13}C$ values decreased with increasing latitude (t = 3.72, slope −0.07, $P < 0.001$, adjusted R-squared = 0.08), and increased with increasing longitude (t = 10.69, slope = 0.12, $P < 10^{-15}$, adjusted R-squared = 0.44) (Figure 5, Figure 6). $\delta^{15}N$ values also decreased with increasing latitude (t = 18.08, slope = −0.61, $P < 10^{-15}$, adjusted R-squared = 0.69), and increased with increasing longitude (t = 9.63, slope = 0.35, $P < 10^{-15}$, adjusted R-squared = 0.39) (Figure 5, Figure 6).

The isotopic niche size can be shown graphically (Figure 7, Figure 8) and also described quantitatively (Table 2) (Jackson et al. 2011). The standard ellipse area (SEA or SEA_B) represents the size of the isotopic niche. SIBER analysis of niche widths reaches an asymptote at a sample size of 30 (Jackson et al. 2011), while in the present study there were 20–24 samples per colony. The SEA_C (standard ellipse area corrected

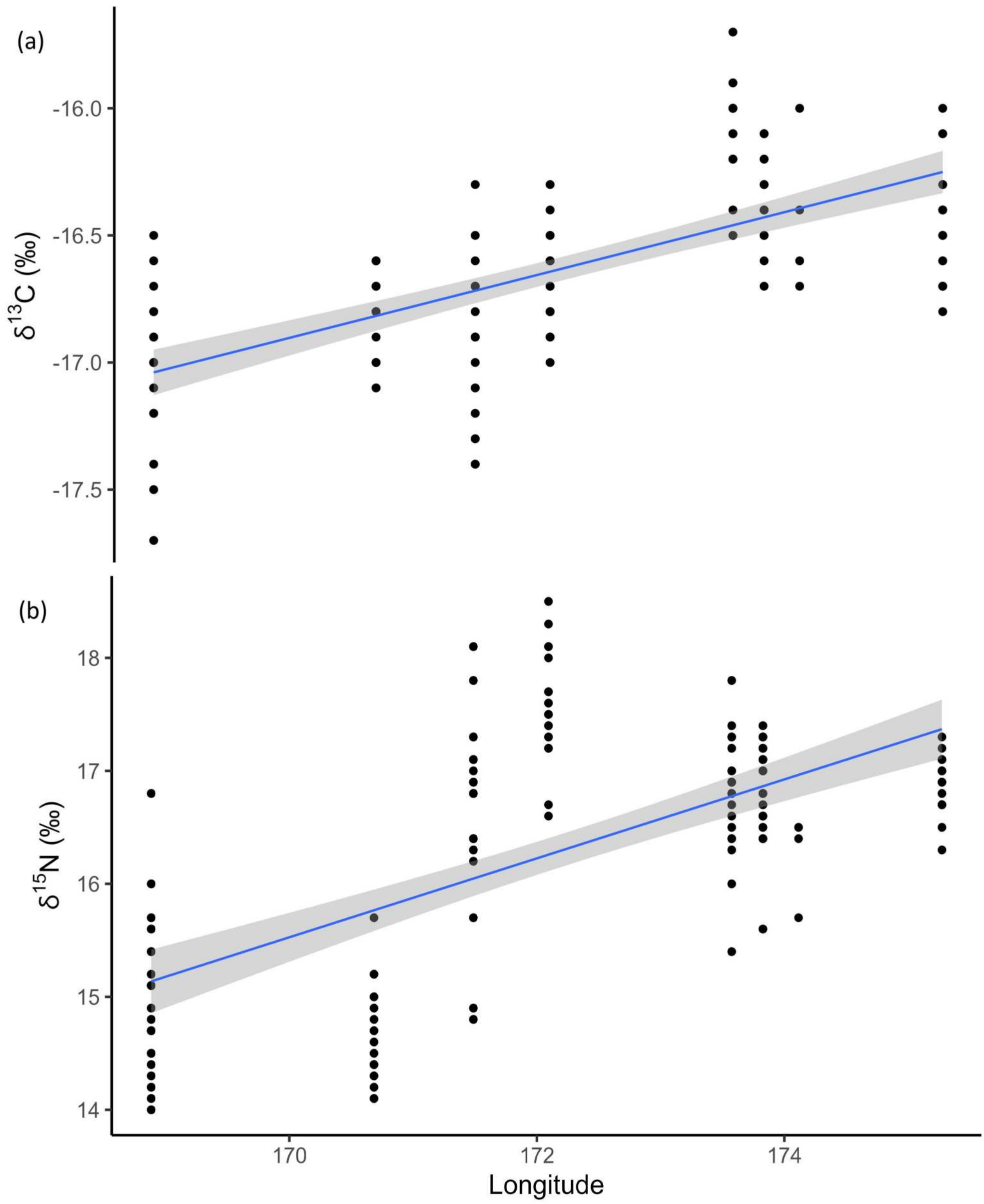

Figure 6. Scatter plots of New Zealand fur seal pup vibrissa $\delta^{13}C$ (**a**) and $\delta^{15}N$ values (**b**) against longitude. Linear model regression line shown in blue 95% confidence intervals in grey shading.

for sample size) was only 0.01–0.03 ‰^{2} greater than the 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 2). The SEA_C is corrected for sample size (Table 2). Cape Foulwind has the largest niche size ($SEA_C = 0.69$ ‰^{2}), with Open Bay Islands next largest ($SEA_C = 0.59$ ‰^{2}). Cape Palliser showed the smallest niche size ($SEA_C = 0.17$ ‰^{2}), with Sandymount next smallest ($SEA_C = 0.22$ ‰^{2}). Isotopic niche widths were compared between colonies, and the probability that the niche at one site is smaller than another site was estimated (Table 3).

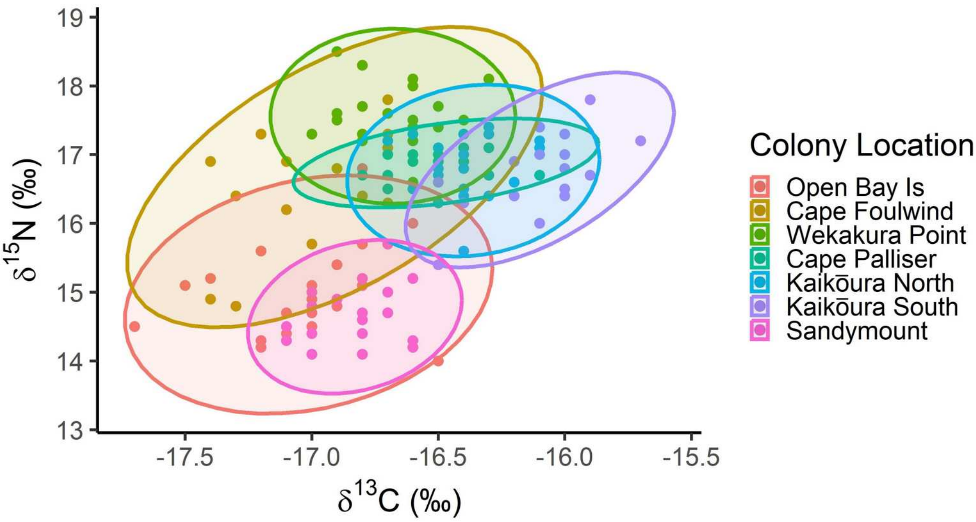

Figure 7. Bayesian ellipses at 95% confidence intervals for $\delta^{13}C$ and $\delta^{15}N$ (‰) in vibrissa samples taken from New Zealand fur seal pups at seven established breeding colonies around New Zealand. Each colour represents a different colony.

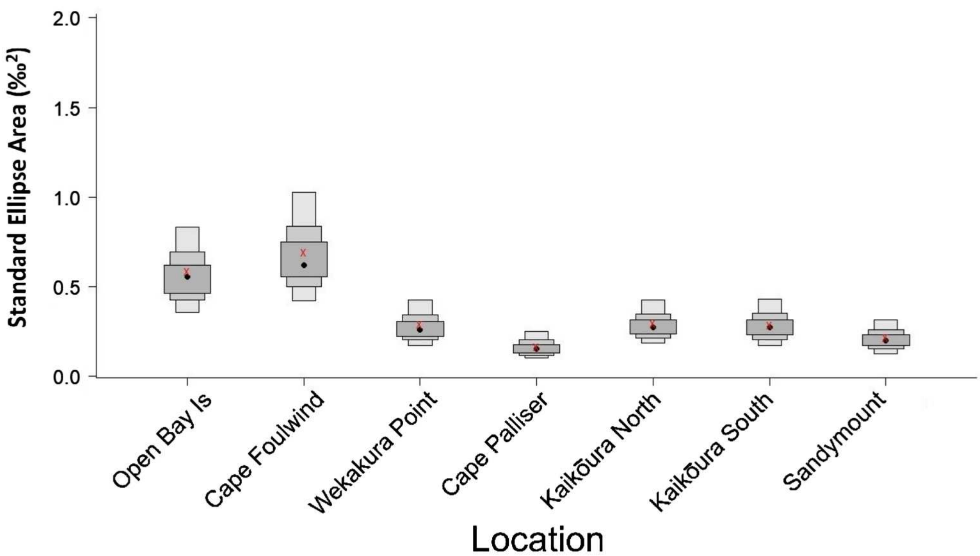

Figure 8. Standard ellipse areas (‰^{2}) of $\delta^{13}C$ and $\delta^{15}N$ values in New Zealand fur seal pup vibrissa sampled at seven established breeding colonies in New Zealand. Black dot represents the mode and red x represents the SEA_C (standard ellipse area corrected for sample size). Box edges from dark to light are 50%, 75% and 95% CI. Colonies are ordered clockwise from southwest to southeast.

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

Table 2. 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

Table 3. Ellipse areas (‰^{2}) for δ^{13}C and δ^{15}N values in vibrissae from New Zealand fur seal pups from seven established breeding areas, 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

reliably (Robertson and Gemmell 2005; Dussex et al. 2016), and both tagging and resighting rates have been too low to provide useful data (see: www.dragonfly.co.nz). This study developed a database 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 were calculated and compared, to indicate the diversity of foraging among lactating females at each colony (Jackson et al. 2011).

The relationships between species and marine habitats can be complex (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).

Stable isotope values

In the seven colonies sampled, the mean δ^{13}C was lowest at Open Bay Islands and highest at Kaikōura South (Table 1). Mean δ^{15}N values were lowest at Sandymount and highest at Wekakura Point. Permutational MANOVA and post hoc comparisons showed that the combined δ^{13}C and δ^{15}N values differed significantly between all colony pairs except Open Bay Islands and Sandymount; Kaikōura North and Cape Palliser; and Kaikōura

North and Kaikōura South. The similarities between Kaikōura and Cape Palliser were expected: it is approximately 132 km from Cape Palliser to Kaikōura North, and a further 40 km down the coast to Kaikōura South. However, Cape Foulwind was isotopically more similar to Kaikōura and Cape Palliser than to Wekakura Point, despite being only 100 km from Wekakura Point. The overlap between Open Bay Islands and Sandymount was also unexpected, given they are approximately 700 km apart and on opposite coasts. 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 and Bury 2019).

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 5, Figure 6). In this study, locations were selected for sampling largely for logistical reasons. To assess the effect of latitude and longitude it would be preferable to sample more colonies at more regularly spaced locations. Nevertheless, some trends in $\delta^{13}C$ and $\delta^{15}N$ values are consistent with other studies, particularly the decrease in $\delta^{13}C$ with increasing latitude (Graham and Bury 2019). On a finer scale, however, the trends were not consistent, with an increase in $\delta^{13}C$ from Wekakura Point to Kaikōura South (Table 1, Figure 3). $\delta^{13}C$ values at Cape Foulwind, on the west coast, were lower than at comparable latitudes on the east coast. 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 and McWhorter 2017). Marine coastal ecosystems are subject to more dynamic processes and variable isotopic inputs than oceanic ecosystems, and, therefore, tend to be more isotopically heterogenous (Graham and Bury 2019). In coastal and shelf environments isotope values can vary with depth, so it is important to know the depth range of prey species (Graham and Bury 2019). NZFSs forage on a wide range of prey (Emami-Khoyi et al. 2016), including vertically migrating species (Harcourt et al. 1995; Mattlin et al. 1998), from shallow, inshore waters out to the 200 m depth contour (Harcourt et al. 1995). In summer, lactating females tend to feed closer inshore and shallow dive patterns predominate (Sinclair and Wilson 1994; Harcourt et al. 2002).

Carbon to nitrogen ratios are a valuable proxy for tissue quality, however, this is less relevant in proteinaceous tissues such as keratin (Newsome et al. 2010). The theoretical atomic carbon to nitrogen ratio of keratin is approximately 3.0 (Newsome et al. 2010), consistent with the range of 2.81–3.15 in the present study. Carbon and nitrogen percentages are influenced by sample weight (C. Wood, pers. comm.), so the carbon to nitrogen ratios in the present study may have been more consistent if the sample weights had been more precise. Sample weight does not affect $\delta^{13}C$ and $\delta^{15}N$ values unless nitrogen is completely saturated (C. Wood, pers. comm.).

Effects of diet on stable isotope values

Like other otariids, NZFSs are 'central place foragers' (Baylis 2008), however, they are also generalised predators (Harcourt et al. 2002; Emami-Khoyi et al. 2016). 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 and Wilson 1976). 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. 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 1998). Colony-specific foraging areas have been noted in other fur seal species (Bonadonna et al. 2001; Staniland et al. 2004; Bailleul et al. 2005), and in NZFSs in Australia (Baylis et al. 2008, 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), however, there have been relatively few studies on NZFS foraging in New Zealand (Boren 2010). There have also been limited studies on NZFS diet at the present study locations, particularly in the summer, and no recent studies.

In earlier studies, squid have been more commonly found in the NZFS diet in summer (Street 1964; Fea et al. 1999; Harcourt et al. 2002), and octopus in winter (Street 1964). At Kaikōura, barracouta (*Thyrsites atun*), miscellaneous fish, and squid predominated (Street 1964), particularly lanternfish (*Symbolophorus* spp.) in autumn to winter (Carey 1991). Barracouta, octopus, and squid were the main species found at the Otago Peninsula (Street 1964). Cape Palliser and Kaikōura, both sampled in winter, had the greatest overlap of prey species (Emami-Khoyi et al. 2016), which is consistent with their similar isotopic values in the present study. There was, however, little overlap in species between summer and winter diets in Kaikōura, indicating seasonal variation (Emami-Khoyi et al. 2016). Conversely, at Cape Foulwind, of eight NZFSs sampled in the winter, seven had similar isotopic signatures to individuals sampled in the summer (L. Meynier, unpublished data). 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 1991). Anchovy was the major prey species from May, while ahuru consumption declined from April (Carey 1991).

The higher mean $\delta^{13}C$ value at Kaikōura South compared to Kaikōura North indicates that individuals from Kaikōura South may 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, and the colonies are only 40 km apart. The lack of data on diet and foraging of NZFSs in the study colonies, and the absence of baseline SIA values for prey species, limit the interpretation of these SIA results. DNA analysis of scats throughout the year and baseline SIA of prey would help to clarify NZFS diets.

Effects of oceanography and geography on stable isotope values

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 200 m contour is approximately five kilometres from shore at Cape Palliser, 12–25 km at Kaikōura North, and two km at Kaikōura South. 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 distribution of sediments also depends on longshore currents (Reid et al. 2011; Gibbs et al. 2020; Stevens et al. 2021). The overlap in δ^{13}C and δ^{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 δ^{13}C between Kaikōura North, and Kaikōura South could also indicate fine-scale differences in baseline δ^{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 approximately 700 km apart and on opposite coasts of the lower South Island. 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). At Cape Saunders, Otago Peninsula, the 200 m contour is between 14 and 24 km from the coast. Similarly, at Open Bay Islands, the 200 m contour is between 10 and 22 km from the colony. On the west coast of the 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). The subtropical front (STF) has enhanced temperature and salinity gradients (Durante et al. 2021) and flows northwards approximately 30 km offshore at the Otago Peninsula (Chiswell et al. 2015). Open Bay Islands is also subject to the STF, however, the current is weaker in the Tasman Sea (Stanton 1976). At both locations, the shallow dive pattern was consistent with NZFS feeding on pelagic, vertically migrating species such as arrow squid (Harcourt et al. 1995; Mattlin et al. 1998).

At Cape Foulwind the 200 m depth contour is around 52 km from shore, with Wekakura Point similar at 48 km. Female NZFSs at Cape Foulwind, tracked using radio-telemetry, foraged mostly in depths from 100 to 200 m, less than 30 km from shore in April, and in deeper water further offshore in July (Sinclair and Wilson 1994). 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 could 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 1), 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.

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 (*Cephalorhynchus hectori*) showed that δ^{13}C values were significantly higher in the eastern part and δ^{15}N values were higher in the west, however, median δ^{13}C and δ^{15}N values differed by less than 1 ‰ (Ogilvy et al. 2023). In the present study, mean δ^{13}C differed by less than 1 ‰ among colonies, and mean δ^{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 feeding mostly on demersal and benthopelagic fish species (Ogilvy et al. 2023), usually live in water less than 39 m deep (Bräger et al. 2003), have small home ranges of up to 50 km along the coast (Rayment et al. 2009), and show high levels of site fidelity (Rayment et al. 2009; Bräger and Bräger 2018). Deep water, such as the Kaikōura Canyon is a barrier to Hector's dolphin dispersal (Bräger and Bräger 2018). NZFSs are also generalist predators (Harcourt et al. 2001, 2002), with bulk faecal analysis identifying up to 46 species of fish and 18 species of cephalopod from a single colony (Emami-Khoyi et al. 2016), however, they may forage more widely than Hector's dolphins. At Open Bay Islands mean NZFS dive depth was 30 ± 37 m in summer and 54 ± 47 m in autumn, with a maximum recorded dive depth of 274 m in autumn (Mattlin et al. 1998). Lactating female NZFSs in Otago regularly foraged as far as the continental slope and shelf in summer, up to 78 km from the breeding colony, and into deeper water (>1000 m) in autumn, up to 178 km from the colony (Harcourt et al. 2002).

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 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, also 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 also higher at Kaikōura North than at Cape Foulwind (Table 1, Figure 3). Mean $\delta^{15}N$ at Wekakura Point was higher than at Cape Palliser, which is more consistent with other studies finding higher $\delta^{15}N$ values further west (Noè 2013).

Pinniped pup tissues can be used as proxies for maternal foraging (Ducatez et al. 2008; Lowther and Goldsworthy 2011; Cherel et al. 2015; Chilvers 2017, 2021b), however, ecological and physiological processes vary, so offspring isotopic profiles will be tissue- and species-specific (Jenkins et al. 2001). Therefore, while NZFS pup vibrissa $\delta^{13}C$ and $\delta^{15}N$ values are likely to be closely related to maternal $\delta^{13}C$ and $\delta^{15}N$ values, there will be some variation, which must be considered when drawing conclusions about maternal foraging from the present study.

Isotopic niche widths

The isotopic niche quantitatively represents the spread of $\delta^{13}C$ and $\delta^{15}N$ values in a group, and provides information about the ecological niche of an organism (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). $\delta^{13}C$ 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 et al. 2010).

Isotopic niche widths were largest, and most variable, at Cape Foulwind and Open Bay Islands, and smallest at Cape Palliser and Sandymount (Figure 7, Figure 8, Table 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. 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. Niche widths in other species, such as Magellanic penguins (*Spheniscus magellanicus*) and Māui dolphins (*Cephalorhynchus hectori maui*), have been shown to be inversely proportional to food availability (Ciancio et al. 2021; Ogilvy et al. 2022). Pup production at Wekakura Point has declined by 87% from its peak in the mid-1990s, while pup production at Cape Foulwind has declined by 81% over a similar period (Roberts and Neale 2016). The larger niche width at Cape Foulwind may indicate that lack of food availability is a greater driver for population decrease there than at Wekakura Point, however, further research would be needed to establish this. Likewise, while Sandymount and Open Bay Islands were not isotopically distinct, the isotopic niche width of Open Bay Islands was greater than that of Sandymount (Table 3). Pup production at Open Bay Islands has declined by 55% from its peak (Roberts and Neale 2016), while pup production at Sandymount has decreased by more than 80% in the past 20 years (P. Seddon, unpublished data). Pup production in Otago/Catlins was thought to have stabilised by 2011 (Lalas and MacDiarmid 2014), however, pup production at Sandymount has approximately halved since then (P. Seddon, unpublished data). There have been no recent population surveys of the greater Otago Peninsula, so there is no way of knowing whether pup production is declining in the rest of the area (Hall et al. 2025). Once again, it is not clear how declining pup production relates to isotopic niche width, and more research is needed to clarify this.

Study constraints and future research

NZFS demographic parameters and foraging ecology in New Zealand are not well 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 δ^{13}C and δ^{15}N values has not been studied in NZFSs and appears to be pair-specific in other pinnipeds (Lübcker et al. 2020). Pups were sampled at 39–84 days after the assumed median pupping date, so the δ^{13}C and δ^{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, δ^{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 δ^{15}N was at Wekakura Point, one of the first colonies sampled, and the lowest was at Sandymount, the last colony sampled. Analysing sequential sections along vibrissae sampled from multiple six-month-old pups at one or more colonies would show how $\delta^{13}C$ and $\delta^{15}N$ values vary in the first months of life.

This study was the first to create a database of $\delta^{13}C$ and $\delta^{15}N$ 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 (Ono et al. 1987; Fraser and Lalas 2004; Page et al. 2005) and the survival of high-level predators (Beauplet et al. 2005; Adame et al. 2020; Gálvez et al. 2020), and vulnerable coastal species are increasingly subject to the effects of climate change (Bond and Lavers 2014; Keegan et al. 2022; Roberts and Hendriks 2022). Ongoing measurement of $\delta^{13}C$ and $\delta^{15}N$ 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.

Conclusions

A database of $\delta^{13}C$ and $\delta^{15}N$ values of NZFS pup vibrissae from seven established breeding areas was compiled. The combined $\delta^{13}C$ and $\delta^{15}N$ values differed significantly among most of the sampled NZFS colonies in New Zealand, and the geographically closest colonies did not necessarily have the most similar $\delta^{13}C$ and $\delta^{15}N$ values. There was a trend for $\delta^{13}C$ and $\delta^{15}N$ values to decrease with increasing latitude and increase with increasing longitude, however, this was not consistent at a fine scale. There appear to be insufficient data on oceanography, baseline $\delta^{13}C$ and $\delta^{15}N$ values, and NZFS foraging and physiology, to draw firm conclusions about what NZFSs are feeding on. There is likely to be insufficient separation of $\delta^{13}C$ and $\delta^{15}N$ values among colonies to determine the colony of origin of stranded or bycaught individuals solely from SIA. Isotopic niche widths varied among colonies, being larger at two of the three west coast colonies. Other studies, on Magellanic penguins and Māui dolphins, have shown isotopic niche width to be inversely correlated to prey availability, however, assessing food stocks was outside the scope of the present study.

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ORCID

B. Louise Chilvers http://orcid.org/0000-0002-7657-4217

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