

Stable isotope analysis of New Zealand sea lion (*Phocarctos hookeri*) whiskers shows distinct regional ecological niches

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ABSTRACT

A region's isoscape (isotopic values within a marine ecosystem) can vary markedly, providing the ability to assess the foraging and migration behaviours of apex marine predators through stable isotope analysis of inert tissue such as whiskers. Additionally, these values can be used to determine the area of origin. The New Zealand sea lion (*Phocarctos hookeri*) breeds over 7 degrees of latitude from Otago Peninsula (45.8°S), South Island, New Zealand, to Campbell Island (52.5°S), a 750 km distance. For most of their range, there is incomplete description of their foraging ecology and diet.

We analysed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios from pup whiskers ($n = 160$) from the five main breeding areas, across three distinct regions for New Zealand sea lions. We investigated isotopic niches for each breeding area to give insight into foraging behaviours and determined whether isotopic values could be used to identify the place of origin of individuals. We found significant differences in isotopic values between the five breeding areas except Enderby and Dundas Islands, Auckland Islands. The differences between breeding areas are likely driven by a combination of prey abundance, distribution and consumption by the pups' mothers, underlying oceanographic variability, varying isotopic baselines, and potential impacts from human influences. Isotopic niche widths were greatest in the Auckland Islands region. This research highlights the value of stable isotope analysis to investigate regional scale variations of apex marine predators foraging and could provide insight into anthropogenic and environmental factors that could influence resource use.

1. Introduction

Understanding how animals travel and forage within their ecosystem is fundamental for a species' conservation and management (Staniland et al., 2004; Hennen, 2006; Elorriaga-Verplancken et al., 2016). For large marine apex predators that can travel large distances in any foraging trip or reside in remote locations, it is often challenging to collect data on diet or foraging behaviour. Instead, diet and foraging research may need to rely more on physical, biological, and chemical cues to indicate prey species consumed and foraging ecology. The traditional ways of understanding diet and foraging ecology are through direct observation, analysis of faeces or stomach contents, or tracking of individuals (Bolnick et al., 2003; Chilvers et al., 2005; Bowen and Iverson, 2013; Ingram et al., 2018). However, all of these techniques have limitations, particularly in the marine environment. Observations of individuals can be limited as marine species forage underwater, "out of sight" and often over large distances, analysis of faeces and stomach contents only shows diet over a short time scale (days to weeks) and

stomach content analysis often involves lethal sampling. Tracking data are often limited by the cost of instruments and the difficulty of capturing or applying instruments to marine species. Additionally, these methods can struggle to quantify changes in diet or foraging behaviour over time or across regions.

Intrinsic biogeochemical markers, such as stable isotopes, are increasingly being used to understand the foraging ecology of marine species (Bearhop et al., 2004; Newsome et al., 2010; Ramos and González-Solís, 2012; Chilvers, 2017, 2019). In the marine environment, analysis of stable isotopes from tissues of predators provides information on resource (trophic level, $\delta^{15}\text{N}$) and habitat ($\delta^{13}\text{C}$) use by individuals (Newsome et al., 2010). Stable isotope analysis from marine predators can be used to determine marine ecosystem productivity (Rounick and Winterbourn, 1986; Bowen and Iverson, 2013) and to identify differences between foraging ecotypes in individuals (e.g., pelagic and benthic foragers, Chilvers, 2019). It can also be used to define an individual's or population's ecological niche space and size. Isotopic niche is where axes represent relative proportions of isotopically distinct

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resources incorporated into an animal's tissue. Isotopic niche size can be described statistically and can provide ecologically relevant information at individual, population, and regional levels (Jackson et al., 2011).

Stable isotope analysis of different tissues reflects different time-scales (Crawford et al., 2008). For short-term information on diet, blood samples can be used to look at diet in timeframes of days to weeks (Hildebrand et al., 1996; Chilvers, 2021a), and muscle and blubber for weeks to months (Ogilvy et al., 2023). For investigation of long-term diet and foraging strategies, inert keratinised tissues (i.e., whiskers, claws, feathers, or hair) 'record' the stable isotope ratio an individual is consuming at the time of growth, and this record remains unchanged once the tissues are formed (Cherel et al., 2009). Samples taken from the base of a whisker represent the most recent tissue growth and, depending on whisker growth rate and how long individuals retain whiskers, these tissues can indicate diet and foraging behaviour for days and months, to an animal's entire life (Cherel et al., 2009; McHuron et al., 2016; Chilvers, 2019, 2021a).

There are many examples of stable isotope analysis indicating diet and foraging behaviour for adult female otariid pinniped species (fur seals and sea lions; e.g., Arnould et al., 2011, Staniland et al., 2004; Chilvers, 2017, 2019). However, given the risks involved in anaesthetising wildlife, along with the difficulties of collecting samples from wild adult female pinnipeds (because of their size, mobility, and for many species the remote location of their habitat), there are increasing numbers of studies that use pup whisker stable isotope values to investigate the trophic ecology of lactating females (e.g., Australian sea lions, *Neophoca cinerea*, Drago et al., 2010; Galapagos sea lions, *Zalophus wollebaeki*, Páez-Rosas and Aurióles-Gambo, 2010). Additionally, research on Australian and New Zealand (*Phocarctos hookeri*) sea lion species has used pup whisker stable isotope values to determine the foraging ecotype of their mothers (Lowther and Goldsworthy, 2011; Lowther et al., 2011, 2013; Chilvers, 2021b).

Here, we aimed to investigate the differences in the foraging ecology of adult female New Zealand sea lions between the species' five main breeding areas, in three breeding regions, using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis from pup whiskers from each breeding area. We used stable isotope analysis to investigate differences in isotopic niche width between breeding areas to reflect dietary differences and/or environmental differences in underlying isoscapes. Isotopic niche width is a measure of the variation in isotope composition among individuals in a population. It is a proxy for the trophic niche of a population in an area and can provide insight into the ecology of a species across regions. A large isotopic niche width indicates isotopic diversity of the diet while a small niche width indicates consistent feeding on a smaller diversity food source. Comparing isotope niches across regions or along a spatial or temporal gradient can provide insights into shifts in diet along gradients (Boucher et al., 2020).

In addition to understanding isotopic niche width between these breeding areas for New Zealand sea lions, stable isotope values are investigated to see if they can be used to determine animal origins. For many species, animals' origins can be determined using differences in DNA between populations or regions (Hamner et al., 2012; Phillips et al., 2011). However, for species where the population structure of the species is not defined enough for DNA to determine the area of origin (e.g., New Zealand fur seals, *Arctocephalus forsteri*, Robertson and Gemmell, 2005, New Zealand sea lions, Collins et al., 2014, 2017), stable isotope analysis is a technique that could be used to trace the origin or migration of wildlife, given that stable isotope signatures in animal tissues reflect those of local food webs (e.g., Peterson and Fry, 1987; Michener and Schell, 1994). A record of the isotope signature where the animals were born and what their mothers or they originally fed can be retained in keratinous tissues such as whiskers and analysed to determine the place of origin if there is a database of isotopic values for each of the regions or breeding colonies for the species (Galbraith and Chilvers, 2025).

The New Zealand sea lion is the least abundant species of sea lion in the world. They are classified as Endangered by IUCN (Chilvers, 2015)

and their pup production and total population have been in decline for over two decades (Chilvers, 2008; Meyer et al., 2015; Chilvers and Meyer, 2017; Chilvers and Dobbins, 2021). New Zealand sea lions used to breed throughout New Zealand but were reduced to breeding only on New Zealand's subantarctic islands due to over-harvesting (Childerhouse and Gales, 1998). It has only been in the last 30 years that breeding has returned to New Zealand's mainland, with females recolonising the Otago Peninsula, South Island and Stewart Island (Fig. 1; McConkey et al., 2002; Chilvers and Dobbins, 2021). Limited foraging studies, mainly of lactating females, have been undertaken in all regions where New Zealand sea lions breed (Chilvers et al., 2005, 2006, 2011; Chilvers and Wilkinson, 2009; Augé et al., 2011; Chilvers, 2018; Lea et al., 2023), however, isotope analysis has only been undertaken on individuals from Enderby Island, Auckland Islands and Stewart Island (Chilvers, 2017, 2019, 2021a, 2021b, 2023). Previous research using satellite tracking data and full whisker length stable isotopic values on female New Zealand sea lions from both Enderby and Stewart Islands has shown clear, consistent, individual foraging ecotypes and isotopic niches across an adult female's entire life (Chilvers and Wilkinson, 2009; Chilvers, 2018, 2019, 2023). These consistencies remain despite the known natural variation that had occurred in their environments, their changing age, and their reproductive status. Additionally, it has been shown that female foraging ecotypes can be identified through their pup's proximal whisker isotope values (Chilvers, 2021a, 2021b). Given these previous studies, this research utilises pup whiskers taken from the five main breeding areas across the three breeding regions of New Zealand sea lions to assess the differences in isotopic values as indicators of diet and foraging behaviour to investigate oceanographic and diet variability, varying isotopic baseline, and potential impacts from human influences. Additionally, the data will be used to assess if stable isotope values can be used to indicate the area of origin of individuals such as bycaught, stranded, or recolonising animals.

2. Material and methods

New Zealand sea lion pup whiskers ($n = 160$) were collected from the five main breeding areas of New Zealand sea lions during the austral summers of 2010 to 2013 (Table 1, Fig. 1). Mainland pups were two to three months of age when whiskers were collected. All of the subantarctic samples were collected when the pups were approximately one month of age.

The outermost whisker from either side of the pups' head was cut as close to the face as possible (a biopsy would have been needed to remove the root, and this was considered too invasive and not permitted) and stored individually in plastic bags until cleaned. Whiskers were cleaned for 5 min in distilled water, then in 96 % ethanol for 5 min, and a final clean and scraping in distilled water for an additional 5 min (Cherel et al., 2009; Chilvers, 2017). Each whisker was checked under a stereomicroscope for any remaining tissue or dirt and contaminants removed with a scalpel blade. All samples were then rinsed with distilled water and left to air-dry overnight. The proximal 5 mm of the whisker was cut from each pup whisker which was thought to represent ex utero whisker growth for all pups (Chilvers, 2021b). Each pup whisker section was weighed with a micro-balance, packed in tin foil capsules, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined using a Dumas elemental analyser (Europa Scientific ANCA-SL) interfaced to an isotope-ratio mass spectrometer (Europa Scientific 20–20 Stable Isotope Analyser). Results are presented in the conventional δ notation calculated as the relative variation of stable isotope ratios expressed as per mille (‰) relative to a laboratory standard for sucrose and urea (with the urea calibrated relative to atmospheric nitrogen) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Quality control samples were run between every 12 samples. The precision for the $\delta^{13}\text{C}$ measurements was 0.1 ‰ and 0.2 ‰ for $\delta^{15}\text{N}$.

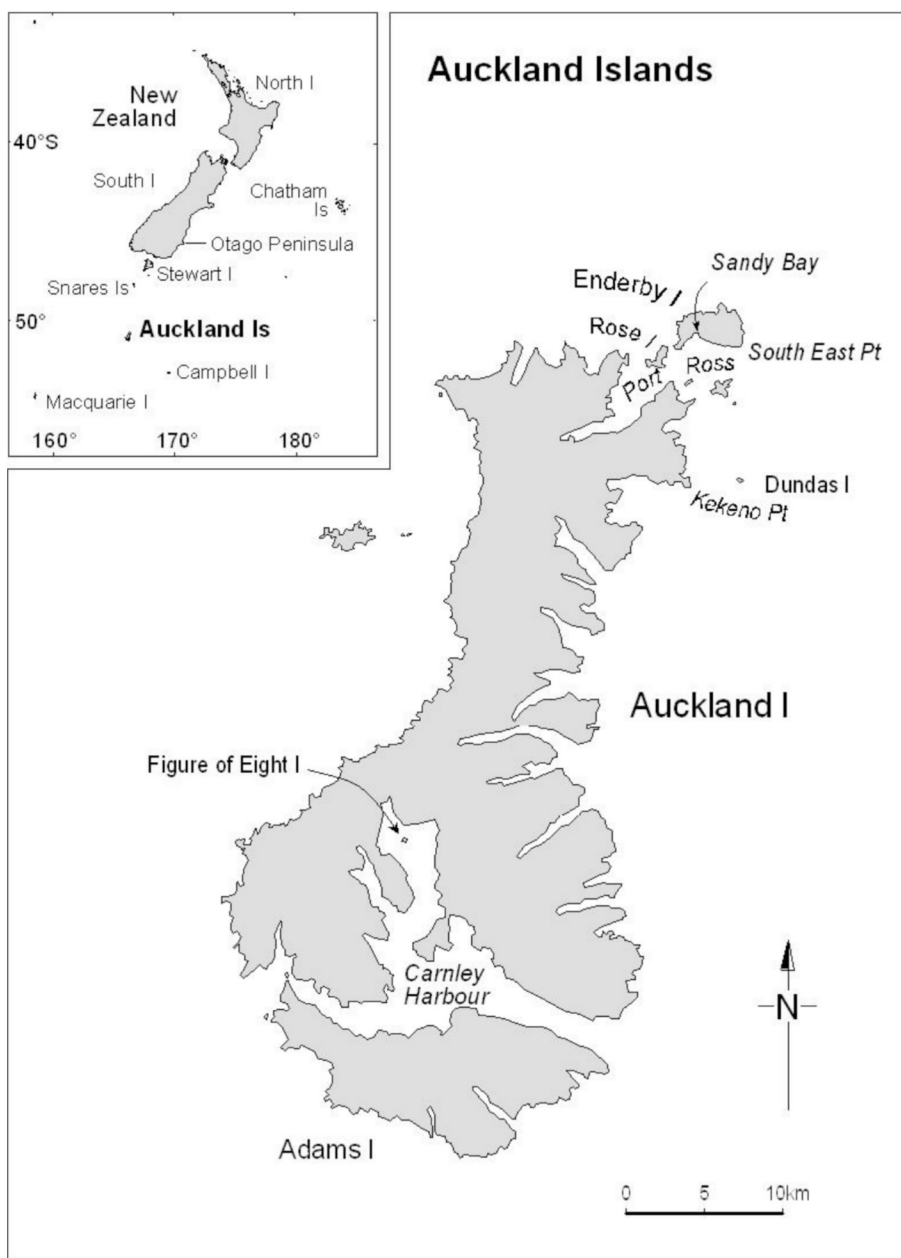


Fig. 1. Auckland Islands, showing the main breeding islands for New Zealand sea lions Enderby and Dundas Islands. Inset: New Zealand and its subantarctic area showing Otago Peninsula, Stewart (combined referred to as Mainland New Zealand) and Campbell Island.

Table 1

New Zealand sea lion whisker samples were collected from the five main breeding areas of New Zealand sea lions during the austral summers of 2010 to 2013.

Colony	2010	2011	2012	2013	Total
Mainland NZ					
Otago		2	5	5	12
Stewart Island			19	20	39
Auckland Islands					
Enderby Island	24	5			29
Dundas Island	40				40
Campbell Island	40				40
Total					160

2.1. Statistical analysis

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for New Zealand sea lion samples were statistically analysed in R Version 4.4.1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were plotted and visually examined for trends in the data. Both $\delta^{13}\text{C}$ ($p = 0.015$) and $\delta^{15}\text{N}$ ($p < 0.001$) failed the Levene’s test for homogeneity of variance so a permutational multivariate analysis of variance (PerMANOVA) was used including multi post-hoc testing (adonis2, package: ‘vegan’, method: ‘euclidian’, permutations = 999), to assess differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the pups’ whiskers according to breeding area. Separately to this multivariate analysis, t -tests were used to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values separately between regions. Analysis of variance (ANOVA) was carried out on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to compare between years at Otago, Stewart Island and Enderby Island. There was no significant difference between years at any location and all data passed the Levene’s test so for further analysis the data for all years were combined for each location. K-means cluster analysis based on Euclidian

distances was used to compare statistical groups to sampled breeding areas or regions. The gap statistic showed four clusters.

2.2. Isotopic niche width analysis

To compare the isotopic niche width of New Zealand sea lion pups from the different areas and regions, we used the stable isotope Bayesian ellipses (SIBER; v.2.1.6) package in R (Jackson et al., 2011). Bivariate ellipses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were plotted using 95 % credibility intervals. The isotopic niche width (SEA_B) of New Zealand sea lions was calculated using the default priors (Inverse Wishart and vague normal) and fitted using JAGS and compared between breeding areas and regions. SEA_C is the isotopic niche width corrected for sample size. Niche area is reported as $\%^2$. SIBER analysis assumes normal distribution of the data, however, in this case both $\delta^{13}\text{C}$ ($p < 0.0001$) and $\delta^{15}\text{N}$ ($p < 0.0001$) failed the Shapiro test for normality. However, when each breeding area was analysed individually, only $\delta^{13}\text{C}$ at Stewart Island ($p = 0.028$) failed the Shapiro test. Similarly, for each region, only $\delta^{13}\text{C}$ in the Mainland NZ region failed the Shapiro test ($p = 0.014$) as this is the region that contains Stewart Island.

3. Results

3.1. Stable isotope ratios of New Zealand Sea lion pup whiskers

In total 160 New Zealand sea lion pup whisker samples were included in the stable isotope analysis (Table 1). The samples had an overall mean ($\pm\text{SD}$) $\delta^{13}\text{C}$ value of -16.3 ± 0.70 ‰ (range: -17.9 to -15.2 ‰) and a mean $\delta^{15}\text{N}$ value of 14.6 ± 1.77 ‰ (range: 12.0 to 18.2 ‰; Table 2). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ distributions of the combined data set were not normally distributed (Shapiro test: $\delta^{13}\text{C}$ $p < 10^{-7}$; $\delta^{15}\text{N}$ $p < 10^{-7}$).

3.2. Spatial variation in isotope values

The combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of New Zealand sea lion pup whiskers were significantly different between breeding areas (PerMANOVA $F = 218$, $df = 4$, $p = 0.001$, Fig. 2). Post hoc tests showed each location was significantly different from every other ($p < 0.01$; Supplementary data Table 1) except Enderby and Dundas Islands. Similarly, all three regions were significantly different from each other ($p = 0.003$, Fig. 2).

Mean $\delta^{13}\text{C}$ values were significantly lower at the Auckland Islands than at the Mainland breeding region (Welch two-sample t -test $t = 28.03$, $p < 0.0001$) and significantly lower at Campbell Island than at Auckland Islands ($t = 21.05$, $p < 0.0001$) (Fig. 2). Mean $\delta^{15}\text{N}$ values were significantly lower at Auckland Islands than at the Mainland region ($t = 24.41$, $p < 0.0001$) and significantly lower at Campbell Island than at Auckland Islands ($t = 5.31$, $p < 0.0001$).

Table 2

New Zealand sea lion whisker samples included in stable isotope analysis. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) are provided for each breeding area.

Location	$\delta^{13}\text{C}$ Mean \pm SD (Range)	$\delta^{15}\text{N}$ Mean \pm SD (Range)	Total
Otago Peninsula	-15.7 ± 0.28 (-16.1 to -15.2)	17.6 ± 0.42 (17.0 to 18.2)	12
Stewart Island	-15.8 ± 0.26 (-16.3 to -15.3)	16.8 ± 0.45 (15.9 to 17.7)	39
Enderby Island	-15.9 ± 0.41 (-16.7 to -15.3)	13.9 ± 0.97 (12.1 to 15.6)	29
Dundas Island	-16.1 ± 0.38 (-16.7 to -15.2)	13.7 ± 0.73 (12.3 to 15.4)	40
Campbell Island	17.3 ± 0.25 (-17.9 to -16.6)	13.1 ± 0.59 (12.0 to 14.5)	40
Overall	-16.3 ± 0.70 (-17.9 to -15.2)	14.6 ± 1.77 (12.0 to 18.2)	160

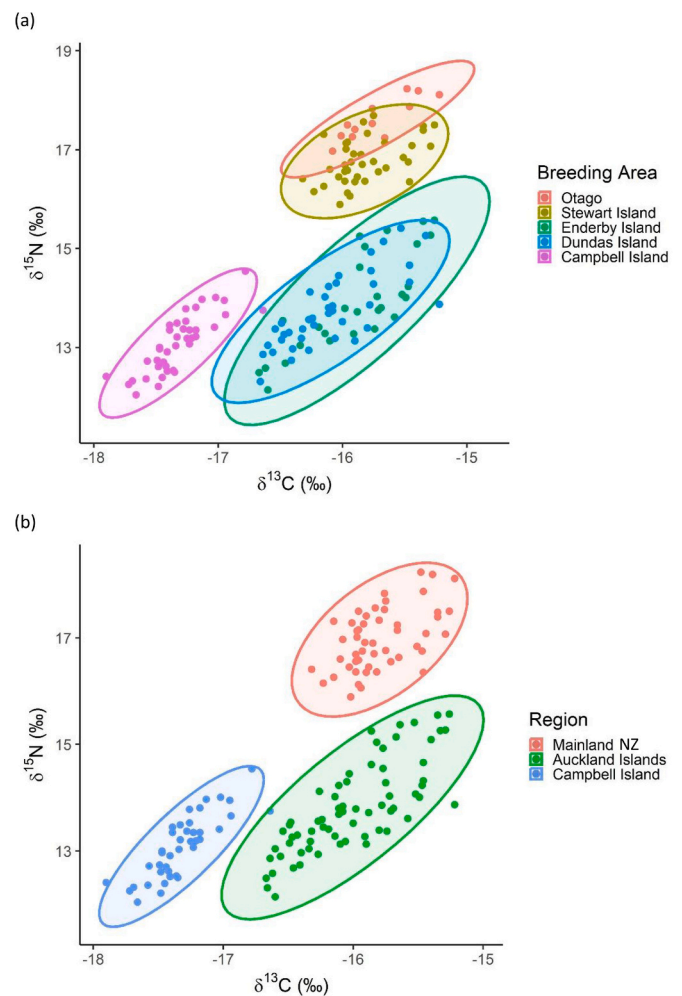


Fig. 2. Bayesian ellipses at 95 % credibility intervals for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) in whiskers of New Zealand sea lion pups at (a) five breeding areas in New Zealand and (b) the three breeding regions. Each colour represents a different area or region.

3.3. Isotopic niche width

The SIBER analysis of New Zealand sea lion pup whisker samples at the five areas indicated the 95 % C.I. ellipses largely overlapped at Enderby Island and Dundas Island, and partially overlapped at Otago and Stewart Island (Fig. 2). Among the regions, there was no overlap between the 95 % C.I. ellipses. Enderby Island had the largest isotopic niche width, followed by Dundas Island (Fig. 3, Table 3), while Otago had the smallest niche width, followed by Campbell Island.

3.4. Cluster analysis

All samples from Otago and Stewart Island are in the same cluster (Fig. 4). Two of the 40 samples from Campbell Island clustered with the Auckland Islands samples (Fig. 4). Of the 69 samples from the Auckland Islands, 38 were in one cluster and 31 in the other (Fig. 4).

4. Discussion

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the whiskers of New Zealand sea lion pups, showed that there is a statistically significant difference in isotope values from the five main breeding areas and across the three regions, except within the Auckland Islands (Dundas and Enderby Islands). This likely reflects a difference in isoscapes across this 750 km distance of

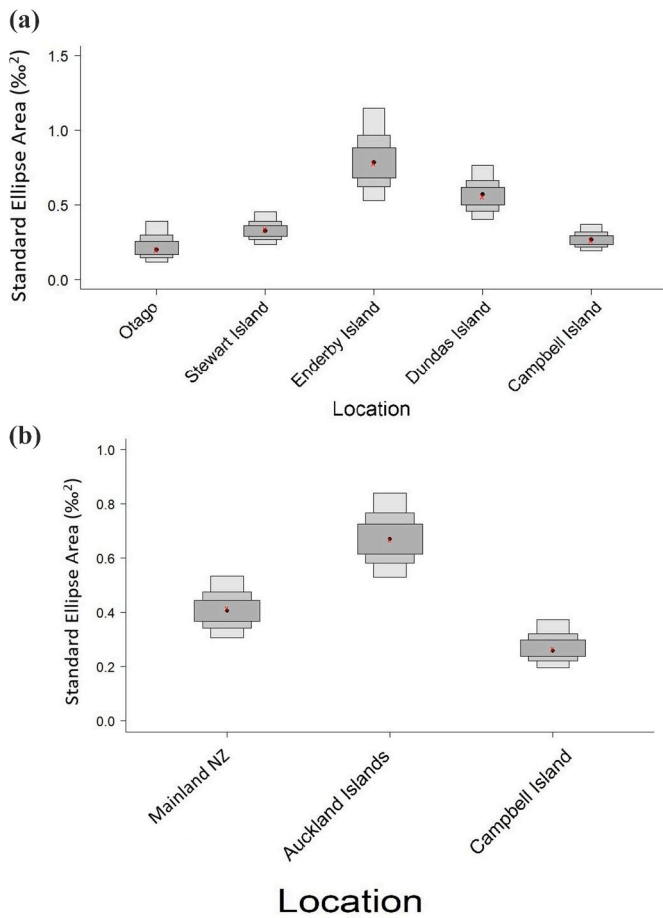


Fig. 3. Bayesian standard ellipse areas ($\%^{2}$) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in whiskers from New Zealand sea lion pups collected in five breeding areas (a) and three regions (b) of New Zealand and the subantarctic.

Table 3

Standard ellipse areas (SEA - $\%^{2}$) of each breeding area and region. ‘Probability’ is the probability that the ellipse area of the first location is smaller than the ellipse area of the second location in each combination.

Area 1	SEA	Area 2	SEA	Probability
Otago	0.19	Stewart Island	0.33	0.85
Otago	0.19	Enderby Island	0.76	1.00
Otago	0.19	Dundas Island	0.55	0.99
Otago	0.19	Campbell Island	0.26	0.71
Stewart Island	0.33	Enderby Island	0.76	0.99
Stewart Island	0.33	Dundas Island	0.55	0.99
Stewart Island	0.33	Campbell Island	0.26	0.19
Enderby Island	0.76	Dundas Island	0.55	0.08
Enderby Island	0.76	Campbell Island	0.26	0.00
Dundas Island	0.55	Campbell Island	0.26	0.00

Region 1	SEA	Region 2	SEA	Probability
Mainland	0.41	Auckland Islands	0.66	0.99
Mainland	0.41	Campbell Island	0.26	0.03
Auckland Islands	0.66	Campbell Island	0.26	0.00

latitude, and differences in foraging ecology between the breeding areas, which has also been shown in previous tracking and foraging ecology studies (Chilvers et al., 2005, 2006, 2011; Chilvers and Wilkinson, 2009; Augé et al., 2011; Chilvers, 2018; Lea et al., 2023). For Enderby and Stewart Islands, this has also been shown in stable isotope studies (Chilvers, 2017, 2019, 2021b, 2023). These differences are likely to be

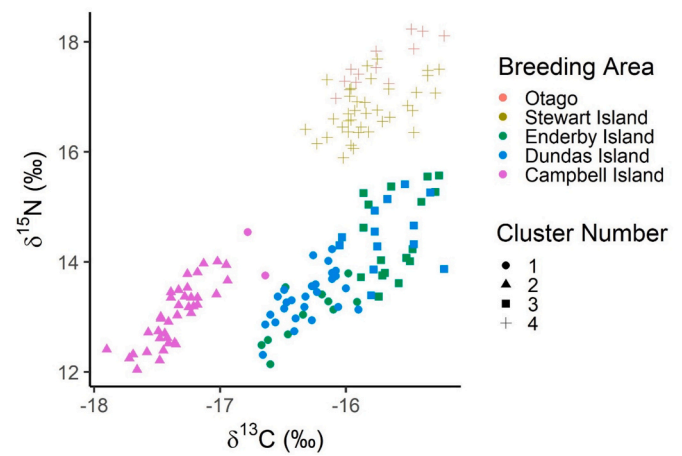


Fig. 4. Cluster analysis of scaled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from New Zealand sea lion pup whiskers at five main breeding colonies in New Zealand and the subantarctic. Cluster is colour and region is shape.

driven by differing prey availability and distribution and underlying oceanographic variability between the regions. This finding was expected. Both pinniped and cetacean species can exhibit stable isotope differences and inferred differences in foraging ecology due to the occupation of different habitats over large, oceans (Arnould et al., 2011) and small, kilometres (Ogilvy et al., 2023) scales. These differences can be used as baseline data, allowing stable isotope values to be tracked between breeding areas as ecosystem changes due to climate change or changing anthropogenic influences.

Along with the clear differences in isotope values, we also show only minimum isotopic niche space overlap between the five breeding areas and three regions. We did observe overlap of isotopic niche space within the two Auckland Island breeding areas and partial overlap between the Mainland, Otago and Stewart Island breeding areas. For both regions these overlaps may reflect common prey species and/or the movement of individuals between each of the two areas within the regions (Fig. 2). Movement and breeding area connectedness and shared foraging areas have previously been documented for both of these regions (Chilvers and Wilkinson, 2008; Chilvers et al., 2011; Chilvers and Dobbins, 2021).

Overall, there were only small ranges of stable isotope values recorded at any of the breeding areas which indicates and supports the hypothesis that female New Zealand sea lions have a restricted diversity of species in their diet (Augé et al., 2012; Meynier et al., 2009), and suggests it is unlikely that they migrate or move away from or between their breeding areas, except within their region (Chilvers and Wilkinson, 2008; Chilvers and Dobbins, 2021). This is also backed up within this study by the finding that no difference in stable isotope values was found in pup whiskers between years of sampling within breeding areas, indicating the consistency of diet and foraging behaviours for females at Otago, Stewart and Enderby Islands. Given that these small ranges in values have also been demonstrated across the entire length of the whisker for Enderby and Stewart Island females, it indicates that female New Zealand sea lion foraging behaviours and prey are unlikely to alter significantly during an individual’s lifetime (Chilvers, 2017, 2019, 2023). These results support the findings from the Auckland Islands that this restricted diet and set foraging behaviours make New Zealand sea lions vulnerable to changes within their environments, whether it be environmental change or anthropogenic impacts such as fisheries resource competition (Chilvers et al., 2006; Chilvers and Wilkinson, 2009; Robertson and Chilvers, 2011).

In the Southern Ocean, both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values vary with latitude and along an inshore/offshore gradient (Cherel and Hobson, 2007). $\delta^{15}\text{N}$ values increase with latitude i.e., isoscape $\delta^{15}\text{N}$ values are higher the further south in latitude. While $\delta^{13}\text{C}$ values are expected to decrease with latitude i.e., $\delta^{13}\text{C}$ values become larger negative numbers the

further south in latitude and the further offshore animals are foraging. Additionally, $\delta^{13}\text{C}$ values are higher in benthic prey and lower in pelagic prey (Rubenstein and Hobson, 2004). This pattern is matched in the New Zealand sea lion pup whiskers for $\delta^{13}\text{C}$ values with Stewart Island and Otago areas having the smallest mean values, however, Enderby and Dundas have equally low mean values (Fig. 2). $\delta^{15}\text{N}$ should be highest at Campbell Island however the reverse is seen with all three subantarctic breeding areas having the lowest $\delta^{15}\text{N}$ values (Fig. 2). This could indicate that the females from these breeding areas are foraging on lower trophic level prey with lower $\delta^{15}\text{N}$ levels. There is limited information on isotope values from the regions the females would be foraging in, however, as an indication, finfish from the Campbell Island Plateau, which are representative of the prey for the subantarctic breeding areas, had mean $\delta^{15}\text{N}$ values of 10.2 ± 0.28 ‰ and mean $\delta^{13}\text{C}$ values of -19.5 ± 0.18 ‰ (Meynier et al., 2008). Finfish species from Stewart Island, showed mean $\delta^{15}\text{N}$ values of 14.5 ± 0.09 ‰ and mean $\delta^{13}\text{C}$ values of -14.6 ± 0.26 ‰ (Chilvers, 2023). These relative values match what is seen in the pup whisker stable isotope values. Also, diet studies from Otago (Augé et al., 2012) and Enderby Island (Meynier et al., 2009, 2014) indicate that in the Otago breeding area, New Zealand sea lions are foraging on a range of fish species, many of which are at a higher trophic level than the prey species observed to be eaten by Auckland Island individuals.

4.1. SIBER analysis and niche width of New Zealand Sea lions

The concept of the isotopic niche is a useful tool for understanding a species or population's position within its environment, similar to understanding a population's ecological niche (Newsome et al., 2012). Isotopic niche width analysis can help investigate resource use, habitat specialisation and foraging ecology in marine mammals (e.g. Yurkowski et al., 2016; Ciancio et al., 2021). The width of the isotopic niche is estimated using the variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values (Jackson et al., 2011) and can indicate changes in prey distribution and availability across temporal and spatial gradients (Bearhop et al., 2004; Newsome et al., 2012; Boucher et al., 2020). For many marine species, large isotopic niche widths can indicate either prey diversity of individual foraging behaviour, or foraging specialisation with specialist foraging on differing or diverse prey species (Bearhop et al., 2004). A narrow isotopic niche width reflects a species or population with less diverse prey species foraged on and can be more vulnerable to changes within their environments, such as climate change or anthropogenic activities, which can impact their habitat and/or the availability of prey. Similar to overall stable isotope values, the SIBER analysis of New Zealand sea lion pup whiskers indicates that the results from each breeding area show relatively small isotopic niche spaces that are distinct between the breeding areas, with almost no overlap between regions (Fig. 2). Similar small isotopic niche spaces have been seen for New Zealand fur seals and Hector's dolphins, *Cephalorhynchus hectori* (Ogilvy et al., 2023; Galbraith and Chilvers, 2025).

The largest niche widths were seen for Enderby followed by Dundas Islands, while the smallest was seen for Otago (Fig. 3). The small niche spaces reported for Campbell Island and the mainland breeding areas likely reflect that females forage over a limited number of prey species. The two Auckland Island breeding areas show larger niche widths, and it is known from foraging studies that the females from this area are life-long benthic or mesopelagic specialists including diet specialisation (Chilvers and Wilkinson, 2009; Meynier et al., 2014; Chilvers, 2019). This individual specialisation would be shown by narrow isotopic niche width for each specialist, however, when there are multiple specialists within a single population this can present as a wider isotopic niche width, which is likely what is seen at the Auckland Islands. This result also, therefore, suggests that this specialisation and segregation of foraging areas and ecotypes is not being displayed in the other breeding areas. The foraging research from Stewart Island and Otago area supports this given no differences between females in foraging ecotypes

have been found (Augé et al., 2011; Chilvers, 2018). Not enough information is available on the foraging behaviour of sea lions at Campbell Island to know if this theory is supported or not in this region. Groups of specialised individuals are more vulnerable to location-specific environmental changes. This can be seen for New Zealand sea lions at the Auckland Islands as this is the population showing the most consistent and continuous decline in numbers, thought to be driven by the deaths of females in the deep-sea trawl fishery surrounding the Auckland Islands (Chilvers, 2008; Robertson and Chilvers, 2011; Meyer et al., 2015; Chilvers and Meyer, 2017).

4.2. Using stable isotope for identifying place of origin

The cluster analysis results clearly show distinct differences in stable isotope values between the three breeding regions of New Zealand sea lions (Fig. 4). This means that using stable isotope analysis of whisker, individuals bycaught, stranding or unmarked females that start breeding on the mainland could be traced to their birth breeding region (Campbell Island, Auckland Islands or Mainland regions) based on whisker stable isotope values. Given the genetic structure of New Zealand sea lions, individuals cannot be identified to breeding area or region by genetics (Collins et al., 2014, 2017). The ability to do this using stable isotope analysis is an important finding for this research. This result could be confirmed by testing known origin adult whiskers to confirm region matching and to understand the location along the whisker that would need sampling to be able to match the timeframe of the individual being a pup or by matching female / pup pairs and determining fractionation between them (Galbraith, 2024).

5. Conclusions - consequence for management

This research highlights the value of stable isotope analysis particularly in its ability to investigate regional scale variation of apex marine predators' foraging. Given the extremely limited information on the foraging behaviour and prey choice of New Zealand sea lions, particularly from Campbell Island (Lea et al., 2023), our study highlights the value of stable isotope research in being able to help identify the foraging ecology and diet of individuals and populations in extremely difficult to reach regions. It also allows the understanding of diet and foraging behaviour across differing gradients that are likely to have different biogeochemistry, climate, and anthropogenic pressures. The niche width analysis supports the foraging studies undertaken at the Auckland Islands, indicating the finding of two foraging ecotypes and their prey separation, also indicating that this separation of foraging behaviour does not occur at any of the other breeding areas. The small range of stable isotope values and the isotope niche widths seen at each of the breeding areas indicate the likely restricted range of prey that New Zealand sea lion females forage on. Species that forage on restricted numbers of prey species or have a high level of foraging specialisation, as seen at the Auckland Islands, are known to be more susceptible to environmental change and anthropogenic impacts in their habitats. This is certainly a factor that has been indicated in the continuous decline of New Zealand sea lions at the Auckland Islands (Chilvers and Meyer, 2017; Chilvers and Dobbins, 2021). In a paper analysing long-term changes in the structure of coastal marine food webs supporting remnant and recolonising populations of New Zealand sea lions within their New Zealand range, Wing et al. (2025) noted that the current position of New Zealand sea lions in their food web is consistent with populations experiencing a vastly changed resource landscape in both their recolonising and established breeding populations. Additionally, this research represents a catalogue of stable isotope values from across the New Zealand sea lion breeding range that can be used to monitor changes in New Zealand sea lion isotopic values and niche width across time as influences such as climate change and anthropogenic impacts change in each breeding area's ecosystem.

CRediT authorship contribution statement

B. Louise Chilvers: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Data curation, Conceptualization. **Diana Galbraith:** Writing – review & editing, Methodology.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2025.152121>.

Data availability

The datasets analysed during the current study are available from the corresponding author on reasonable request.

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