NRC Research Press

ARTICLE

Foraging diversity in lactating New Zealand sea lions: insights from qualitative and quantitative fatty acid analysis

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Abstract: Lactating New Zealand (NZ) sea lions (*Phocarctos hookeri*) exhibit different foraging patterns during their foraging trips, with benthic divers spending more energy at sea than mesopelagic conspecifics. We compared blubber fatty acids (FAs) of 14 benthic and 12 mesopelagic females captured at the Auckland Islands, NZ subantarctic, in late January 2000 using an analysis of similarities (ANOSIM). FA profiles between foraging types were significantly different (global $R = 0.30$, $p = 0.001$), suggesting a different use in prey resources. We then compared the diet predictions by quantitative FA signature analysis (QFASA) by using a prey FA library available in the region. Overall, diet predictions were significantly distinct between benthic and mesopelagic females (global $R = 0.17$, $p = 0.022$), although the diets consisted of the same prey but in different contributions. The results suggest benthic females do not compensate their higher foraging costs by feeding on prey with higher energy densities. Foraging areas of benthic females are not exploited by the trawling fishery; therefore, the benthic tactic might be a trade-off between a higher foraging cost and less resource competition.

Résumé : Les lionnes de mer de Nouvelle Zélande (NZ) lactantes utilisent des tactiques de chasse en mer différentes : les individus chassant sur le benthos dépensant plus d'énergie que les individus mesopélagiques. Nous avons comparé avec une ANOSIM les acides gras (AG) du lard de 14 lionnes de mer benthiques et 12 mesopélagiques capturées aux Iles Auckland (région subantarctique de la NZ) fin janvier 2000. Les profiles d'AG entre les comportements de chasse présentent des différences significatives (global $R = 0.30$, $p = 0.001$), probablement dues à une utilisation différente des ressources entre ces deux groupes. La composition du régime alimentaire a été estimée par l'analyse quantitative des profiles d'AG (QFASA), en utilisant un catalogue d'AG de proies venant de la même région. Les régimes alimentaires des deux types de chasse comprennent les mêmes espèces de proies mais avec des proportions significativement différentes (global $R = 0.17$, $p = 0.022$). Il semble donc que les femelles chassant sur le benthos ne compensent pas leurs dépenses énergétiques plus élevées en mer par des proies de qualité supérieure. Les zones de chasse des femelles benthiques ne sont pas exploitées par les pêcheries; ces individus pourraient chercher un compromis entre une dépense énergétique élevée et une compétition faible pour la ressource. [Traduit par la Rédaction]

Introduction

The distribution and abundance of prey are major drivers in the foraging behavior of individuals (Costa 1993). Lactating otariids display a "central place foraging" strategy during lactation because they are restrained in foraging range by the need to regularly nurse their pup on land (Orians and Pearson 1979). Thus, the ideal foraging areas are likely to be the nearest favourable environment with abundant and predictable prey that meet the seals' needs. If resources are limited or unpredictable in the foraging range of female otariids, individuals may develop resource partitioning to reduce intraspecific competition for food and maximize energy intake (Tinker et al. 2008; Villegas-Amtmann et al. 2008). Differential foraging strategies among lactating females has been shown for several otariid species, such as northern fur seals (*Callorhinus ursinus*) (Robson et al. 2004), Antarctic fur seals (*Arctocephalus gazella*) (Lea et al. 2002; Staniland and Boyd 2003), New Zealand (NZ) fur seals (*Arctocephalus forsteri*) (Baylis and Nichols 2009), Galapagos sea lions (*Zalophus wollebaeki*) (Villegas-Amtmann et al. 2008), Australian sea lions (*Neophoca cinerea*) (Baylis et al. 2009), and NZ sea

lions (*Phocarctos hookeri*) (Chilvers and Wilkinson 2009). These foraging strategies are reflected by a specialization in habitat use. Two ecotypes are generally described: individuals foraging in inshore–neritic waters versus individuals foraging in offshore–oceanic waters, suggesting partitioning in prey resources (Staniland and Boyd 2003; Robson et al. 2004; Villegas-Amtmann et al. 2008; Baylis et al. 2009). The diet among lactating otariids displaying foraging specialization was assessed for the three fur seal species (Staniland et al. 2007; Baylis and Nichols 2009; Zeppelin and Orr 2010) and for the Australian sea lion (Baylis et al. 2009). All studies showed differences in prey consumption. During the beginning of the lactation period (austral summer), lactating NZ sea lions from Enderby Island, Auckland Islands (50°41′S, 166°E; the second-largest breeding colony), exhibit different diving patterns in distinct foraging areas (Chilvers et al. 2006; Chilvers and Wilkinson 2009), but resource partitioning has not been assessed yet.

NZ sea lions have a restricted breeding range with 71% of the pups being born at the Auckland Islands in the NZ subantarctic region (Chilvers et al. 2007). They are classified as "vulnerable in decline" by the International Union of the Conservation for

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Fig. 1. Kernel home ranges (KHR) of satellite locations from 14 female New Zealand sea lions (summers, 2003 and 2004). (Figure from Chilvers and Wilkinson (2009), reproduced with permission of Mar. Ecol. Prog. Ser. **378**: 299–308, © 2009 Inter-Research.) The nine benthic divers are represented by dark-shaded KHR, with intensity of shade representing percentage of time spent in the area; shade scales range from black (95% of all satellite locations) to light gray (5% of all satellite locations). The five mesopelagic divers are represented by the light-shaded KHR, with shade intensity ranging from light gray (95% of all locations) to black (5% of all locations). Thick black lines represent the squid trawl fishery effort (50% and 95% kernel). Thin gray lines are the bathymetric contours. The area with white dots on black (lower left of panel) represents the Auckland Islands.
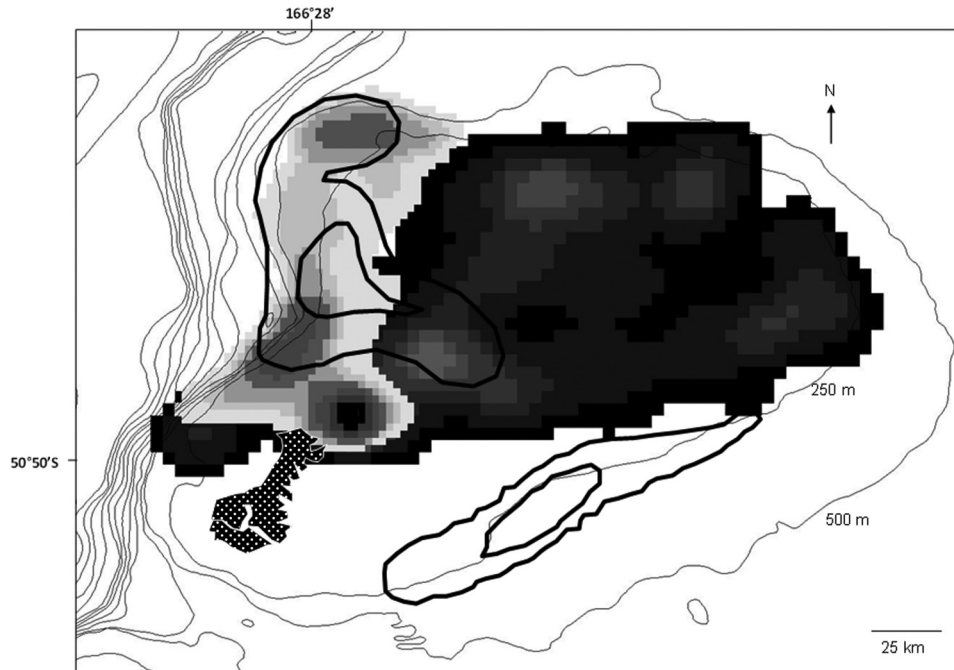
Nature (Gales 2008), with a 49% drop in pup production since 1998. Nutritional stress has been proposed to contribute to the decline of the population (Chilvers and Wilkinson 2009). Female NZ sea lions display the longest foraging trips and the deepest dives than any other otariid (Chilvers et al. 2005, 2006) and may not be able to compensate their high energy needs with appropriate food resource. Some females travel north–northeast from the breeding site and make consecutive dives at similar depths on the Auckland Islands seafloor shelf (called benthic divers), while others travel north–northwest from the breeding site and make most of their dives at deeper and variable depths at the edges of the shelf (called mesopelagic divers) (Chilvers and Wilkinson 2009; Fig. 1). To understand how each strategy succeeds in maximizing energy intake, it is critical to assess the diet of these two ecotypes.

Scat analysis is the most common method for estimating the diet of pinnipeds (Tollit et al. 2010). It is inexpensive, and scats can be easily collected without disturbance to the animals. However, it is not suitable for describing the diet of two groups of individuals that haul out at the same colony because scat collection generally cannot be attributed to a particular individual (exception when an enema is collected on a captured animal; e.g., Staniland et al. 2007). Other well-known limitations of scat analysis are the bias due to different digestion–retention rates and a diet picture limited to the last foraging bout (Tollit et al. 2010). Baylis and Nichols (2009) showed that scat analysis of NZ fur seals underestimated the diet contribution of oceanic prey foraged in waters distant from the colony; thus, the two distinct foraging zones highlighted by satellite-tracking were not detected in the scat samples. Owing to these limitations, biochemical methods such as fatty acid (FA) and stable isotope analyses are more and more used to complement dietary information provided by traditional methods (Tollit et al. 2010). FA analysis has been extensively applied to various species of pinnipeds to assess diet variation among groups of individuals (e.g., Grahl-Nielsen et al. 2005; Staniland and Pond 2005; Tucker et al. 2008). FAs undergo predictable biochemical change when deposited in the adipose tissue of a predator in positive energy balance (Budge et al. 2004; Iverson et al. 2004) and have the potential to reflect dietary intake over several weeks to months depending on the tissue turnover rate (Kirsch et al. 2000; Iverson et al. 2004; Cooper et al. 2005). Quantitative FA signature analysis (QFASA) goes a step further by quantifying the relative mass of prey in the diet of marine predators (Iverson et al. 2004). QFASA was used to estimate the diet of male and female NZ sea lions from bycatch in trawling boats during late summer and autumn 2000 to 2006, and predictions varied among years following prey availability (Meynier et al. 2010). There was, however, no investigation yet on the possible dietary variation among lactating females displaying different foraging strategies. In the present study, we investigated the variation in FA composition of the blubber of lactating NZ sea lions that were categorized benthic or mesopelagic divers from a previous diving study (Chilvers et al. 2006). We estimated the diet of each ecotype by QFASA. Results were discussed in terms of prey energy densities, prey availability, and feeding strategy.

Methods

Sample collection

Lactating NZ sea lions were captured at random at Sandy Bay, Enderby Island, Auckland Islands, in late January 2000 as part of a reproductive study (Childerhouse et al. 2010). The Sandy Bay colony is the second-largest breeding colony for NZ sea lions, with approximately 300 pups born per year (Chilvers et al. 2007). Females were anaesthetized following standard procedures detailed in previous studies (Costa and Gales 2000; Chilvers et al. 2005, 2006). Blubber was biopsied from females by scrubbing the posterior flank (dorsolateral lumbar region) with surgical disinfectant and making a 10 mm incision in the skin using a sterile scalpel. A core was sampled through the full depth of the blubber layer excluding the skin, wrapped in clean aluminium foil, transferred

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into a 2 mL cryogenic vial, and stored at –196 °C in liquid nitrogen. On return from the field, blubber samples were stored at –80 °C until analyzed.

Stratification of FAs, although weak, occurs in the blubber of NZ sea lions (Lambert et al. 2013). Inner blubber is believed to be more metabolically active than the outer blubber, reflecting recent dietary FA intake (Grahl-Nielsen et al. 2005). However, the full blubber core was analyzed in this study because it reflects the long-term integration of dietary FAs (Iverson et al. 2004). Blubber FAs are a combination of dietary FAs accumulated over weeks and FA metabolism within the tissue. A feeding experiment on captive juvenile harbour seals (*Phoca vitulina*), fed ad libitum, showed an FA turnover of 2 to 3 months (Nordstrom et al. 2008). In the wild and with the energetic cost of lactation, we would expect a faster FA turnover. Therefore, blubber FAs in our study are likely to represent the diet accumulated over a month at least, i.e., the diet ingested since parturition (mean pupping time the 26th of December; Chilvers et al. 2007).

Foraging–diving information

Lactating individuals sampled for blubber in 2000 were categorized benthic or mesopelagic divers from foraging–diving information collected on the same animals in subsequent years (Chilvers et al. 2006; Chilvers and Wilkinson 2009), as no foraging–diving study was conducted in 2000. Analysing blubber within the same year allows excluding the effect of the year factor on the variation of FA profiles and focusing the study on the effect of foraging strategies.

Lactating NZ sea lions captured in the summer 2000 were recaptured in the following summers. They were fitted with satellite-linked platform transmitting terminals (PTTs) and time–depth recorders (TDRs) during late January of 2003 and 2004 and with PTTs only during late January of 2001, 2002, and 2005. Results are presented by Chilvers and co-authors in previous publications (Chilvers et al. 2005, 2006; Chilvers and Wilkinson 2009). Chilvers (2008) found that lactating female NZ sea lions are returning to the same foraging location from one year to another; therefore, the diving pattern observed for a lactating female during a particular summer was assumed to be similar in the summer of 2000. Females exhibited different diving patterns depending on the foraging areas they exploited (Chilvers and Wilkinson 2009). Benthic divers displayed 85% of their dives between 100 and 200 m on the Auckland Islands shelf north–northeast of their breeding site. Mesopelagic divers displayed a wide range of dive depths with >30% of dives shallower than 50 m and >10% of dives deeper than 300 m, north–northwest of their breeding site near the continental slope (Fig. 1). For females with no TDRs, the foraging pattern was deduced from the foraging locations.

The foraging–diving information collected each summer was between late January and late February. This is at a later time period than the diet picture represented by blubber FAs collected in late January. However, lactating NZ sea lions display strong foraging site fidelity in consecutive trips (Chilvers et al. 2005), and we expected each female to exploit the same foraging area throughout the summer season.

Lipid analysis

Lipids from blubber were extracted following Folch et al. (1957). Briefly, lipids were extracted in a mixture of 8:4:3 chloroform–methanol–saline water (by volume) containing 0.01% butylated hydroxytoluene (BHT) as an antioxidant. FA methyl esters were prepared using 10% boron trifluoride in methanol and extracted into hexane. They were analyzed by gas chromatography using a polar capillary column coated with 50% cyanopropyl polysiloxane (0.25 μm film thickness; J&W DB-23, Folsom, California). More

details of the laboratory protocol were given in Meynier et al. (2010).

Blubber samples were stored for 7 years at –80 °C before being processed. A recent study evaluated the stability of blubber FAs over 4 to 6 years of storage at –20 °C and showed no notable difference in the mass percentages of 65 FAs after 6 years (Lind et al. 2012). Nonetheless, oxidation was minimized with blubber being wrapped in aluminium foil and put in a small cryogenic vial with minimum air.

Statistical analysis

FAs were expressed as a percent mass of total FAs. FA profiles of individual sea lions were compared by using the vegan package in R (Oksanen et al. 2013). Individual FAs were standardized before analysis by dividing the value of each FA in each sample by the standard deviation of that FA across all samples (Lane et al. 2011). Resemblance matrices were created by using Bray–Curtis similarity (Bray and Curtis 1957). Nonmetric multidimensional scaling nmds (function "metamds", 20 restarts) was used to visualize the degree of similarity among groups of individuals on a two-dimensional plot. Stress values range from 0 to 1 and indicate the degree of confidence in the analysis; values <0.2 are assumed to correctly represent the links between samples (e.g., Lane et al. 2011). The effect of foraging type on FA signatures was assessed by an analysis of similarities ANOSIM (maximum permutations = 999); ANOSIM produces a statistic R that ranges between –1 and 1 depending on whether the average rank similarity between FA signatures within a group was more similar than the average rank similarity between FA signatures from different groups. An R close to zero means a strong similarity, while an R close to –1 or 1 means a complete separation of the sampling groups. If ANOSIM was significant, a one-way similarity percentage analysis simper on Bray–Curtis similarity matrices was conducted to determine the FAs that contributed the most to the differences among foraging types. All statistical tests have α significance level of 0.05.

A body condition index (BCI) for each animal was calculated as the residual between the measured and predicted body mass from a mass–length regression based on the equation of Childerhouse et al. (2010). For instance, a positive BCI means that the animal was heavier than average for individuals of the same body length. Differences in BCI between foraging types were tested using a Mann–Whitney (M–W) test.

QFASA model[1]

The diets of individual sea lions were estimated using QFASA described by Iverson et al. (2004) and a prey FA library from the Auckland Islands region (Meynier et al. 2008). The model takes the mean FA profiles of each prey species in the prey library and estimates the mixture of prey FA profiles that comes the closest to match the FA profile of the predator's adipose tissue. The Kullback–Liebler (KL) distance was the mathematical distance minimized by the model. Then, the best mixture is weighted by the fat content of each prey species and translated into a diet estimate (percent mass). Lipid metabolism in the predator's adipose tissue is taken into account by calibration coefficients (CCs) determined from feeding experiments on captive animals (e.g., Iverson et al. 2004; Rosen and Tollit 2012). CCs are calculated from the ratio of a specific FA in the predator tissue over that in the prey obtained during feeding studies of captive animals with a constant diet and appear to vary to some degree with the diet and the predator species (Rosen and Tollit 2012). To date, there are none available for NZ sea lions, but a previous study comparing the outputs of the QFASA model with different CCs sets (from three different pinnipeds and different diets) found that CCs calculated from experiments on Steller sea lions (*Eumetopias jubatus*) fed on Pacific

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[1]The QFASA program is available on request by writing to the corresponding author.

Table 1. Mean (±SD) and range of energy densities (ED in kJ·g⁻¹ wet mass) of the common prey species of NZ sea lions collected from the Auckland Islands Rise region, New Zealand.

Species	Scientific name	Collection date	n	ED (kJ·g⁻¹)	Range
Hoki	*Macruronus novaezelandiae*	Dec. 2005	11	7.1±1.0	6.0–8.3
Javelin (rattails)	*Lepidorhynchus denticulatus*	Dec. 2005	10	6.7±0.8	5.3–7.8
Red cod	*Pseudophycis bachus*	Apr. 2006	5	7.3±0.5	6.9–7.5
Opalfish	*Hemerocoetes* spp.	Apr. 2006	10	8.5±1.9	5.2–10.6
Arrow squid	*Nototodarus sloani*	Mar. 2004	10	6.3±0.6	5.3–7.0
Octopus	*Enteroctopus zealandicus*	Apr. 2006	6	3.8±0.4	3.2–4.4
Scampi	*Metanephrops challengeri*	Jan. 2007	6	3.8±0.6	3.1–4.4

Note: Table modified from Meynier et al. (2008), reproduced with permission of N.Z. J. Mar. Freshw. Res. **42**: 425–437, © 2008 Taylor and Francis Group; http://www.tandf.co.uk/journals/.

herring (*Clupea pallasii*) were the "best of fit" CCs for NZ sea lions (Meynier et al. 2010). QFASA outputs with these CCs appeared to give reliable results when compared with the variation of prey availability in the foraging area. Another QFASA parameter tested in this previous study was the prey individual variability in FA signatures, which performed better (KL distance significantly lower) than using mean FA signatures of prey species (Meynier et al. 2010). Similarly in the present study, accounting for prey individual variability gave better results (mean ± SD KL of 4.4 ± 1.2) than with mean prey (mean ± SD KL of 6.2 ± 1.9; Wilkinson signed rank test: $p < 0.001$) and was the only scenario presented here for simplicity.

Differences in diet estimates among foraging types were tested with an ANOSIM based on a Bray–Curtis similarity matrix and 999 permutations. Estimated percentages by mass of prey were not transformed prior to the Bray–Curtis similarity matrix to keep a strong influence of the dominant species (Clarke et al. 2006). A biplot was created using nmds to visualize the variation in diet estimates among foraging types and the correlation with prey. simper analysis determined the prey that contributed the most to the differences when ANOSIM was significant (see previous section for more details).

Prey FA library and energy density

The energy content and FA profiles of the common marine species found in the Auckland Islands region have been determined in a previous study in an attempt to build a reference prey library for QFASA estimations (Meynier et al. 2008). Fresh specimens of hoki (*Macruronus novaezelandiae*), rattails (Macrouridae), southern arrow squid (*Nototodarus sloanii*), scampi (*Metanephrops challengeri*), opalfish (*Hemerocoetes* spp.), red cod (*Pseudophycis bachus*), giant octopus (*Enteroctopus zealandicus*), and spiny dogfish (*Squalus acanthias*) were collected around the Auckland Islands from December to April between 2004 and 2008, aboard commercial fishing and research vessels. The specimens analyzed for FAs and energy densities were all collected after 2000, the year of blubber collection. The year is not considered an important factor of intraspecific variation in energy and lipid content (Anthony et al. 2000); therefore, we assumed that the FAs and energy contents of collected specimens would be representative of that available to sea lions in the year 2000. Energy densities are displayed in Table 1 to facilitate the assessment of energy intake optimization for the two foraging strategies.

Results

FA composition and variation

Blubber samples were analyzed from 26 lactating NZ sea lions captured in January 2000 (12 mesopelagic versus 14 benthic divers). Although 38 FAs were originally identified, only 28 FAs were used, ranging from 14:0 to 22:6n-3 (Table 2). The 10 FAs removed were either short-chain FAs (<14 carbons), known to come primarily from endogenous biosynthesis (Iverson et al. 2004), or FAs for which the identification was not certain. Together the FAs in greatest concentration were 14:0, 16:0, 16:1n-7, 18:1n-9, 18:1n-7, 20:1n-9, and 22:6n-3, which accounted for approximately 83% of

Table 2. Fatty acid (FA) composition from 26 biopsied lactating New Zealand sea lions per foraging type in mean percent mass ± SD.

| FA	FA composition (mean % mass ± SD)		
	Total ($n = 26$)	Mesopelagic divers ($n = 12$)	Benthic divers ($n = 14$)
SFA	**22.9±3.1**	**22.2±1.9**	**23.8±3.7**
14:0	6.6±1.5	6.0±0.9	7.2±1.7
15:0*	0.5±0.1	0.5±0.1	0.5±0.1
16:0	13.3±1.9	13.1±0.9	13.6±2.5
17:0	0.4±0.1	0.4±0.1	0.4±0.0
18:0	2.1±0.4	2.2±0.4	2.1±0.4
MUFA	**58.8±2.9**	**60.9±2.4**	**57.1±2.2**
14:1*	0.7±0.2	0.6±0.2	0.7±0.2
15:1*	0.2±0.1	0.2±0.0	0.2±0.0
16:1n-7	8.9±1.5	8.3±1.4	9.5±1.6
18:1n-9	33.0±2.7	35.0±2.0	31.4±2.2
18:1n-7	4.3±0.4	4.4±0.3	4.1±0.4
18:1n-5*	0.4±0.1	0.4±0.1	0.5±0.1
20:1n-11	1.7±0.2	1.7±0.2	1.7±0.3
20:1n-9	7.9±1.6	8.6±1.6	7.4±1.6
22:1n-11	1.5±0.4	1.5±0.2	1.6±0.5
22:1n-9	0.2±0.1	0.3±0.1	0.2±0.1
PUFA	**18.3±2.2**	**16.9±1.2**	**19.1±2.2**
16:3n-4	0.1±0.0	0.1±0.0	0.2±0.0
18:2n-6	1.9±0.3	1.8±0.3	1.2±0.2
18:3	0.9±0.1	0.8±0.1	0.9±0.1
20:2n-6	0.4±0.1	0.3±0.0	0.4±0.1
20:3n-6	0.1±0.0	0.1±0.0	0.1±0.0
20:3n-3	0.2±0.0	0.6±0.1	0.7±0.2
20:4n-6*	0.6±0.2	0.2±0.0	0.2±0.0
20:5n-3	1.9±0.5	1.5±0.2	2.2±0.3
21:5n-3	0.2±0.1	0.2±0.1	0.2±01
22:4n-6	0.1±0.0	0.1±0.0	0.1±0.0
22:5n-6	0.2±0.0	0.2±0.0	0.2±0.1
22:5n-3	2.7±0.4	2.5±0.3	2.8±0.5
22:6n-3	9.1±1.3	8.7±0.9	9.2±1.4

Note: All blubber samples were collected in late January 2000. SFA, saturated FAs; MUFA, monounsaturated FAs; and PUFA, polyunsaturated FAs.
*FAs were deleted for quantitative fatty acid signature analysis.

the total FAs in the blubber (Table 2). Monounsaturated FAs accounted for more than half of the total mass. Saturated FAs ranked second in importance with approximately 23%, and polyunsaturated FAs were the least represented group with approximately 18% (Table 2).

An ANOSIM showed a significant difference in FA signatures of lactating sea lions by foraging type (global $R = 0.30$, $p = 0.001$; Fig. 2). According to the simper analysis, the FAs contributing the most to the variation were 20:5n-3, 16:3n-4 (being more concentrated in the blubber of benthic divers), and monounsaturated 18:1n-9 and 18:1n-7 (more concentrated in the blubber of mesopelagic divers; Table 2). BCIs were significantly different between foraging types (M–W test on eight mesopelagic and 13 benthic; $W = 91$ or $Z = -2.701$, $p = 0.007$). Mesopelagic divers (median BCI of

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Fig. 2. Nonmetric multidimensional scaling (NMDS) plot (stress = 0.19) of the fatty acid signatures of lactating NZ sea lions by foraging type (ANOSIM global $R = 0.30$, $p = 0.001$). Circles represent the mesopelagic individuals, while triangles represent the benthic ones.
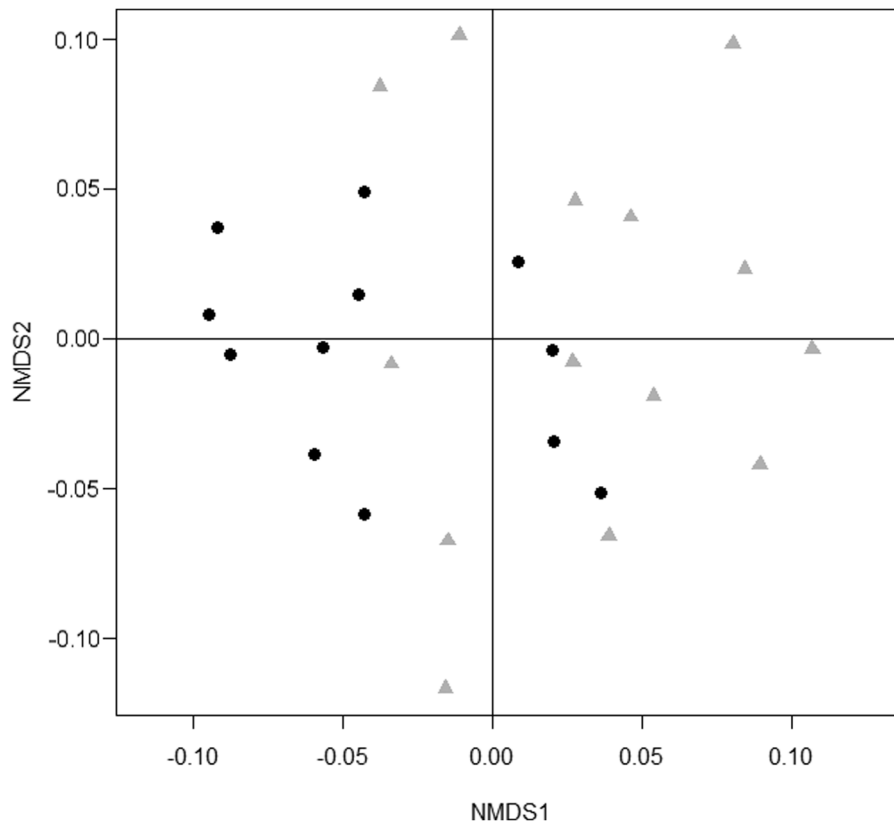
9 kg) were in better body condition than benthic divers (median BCI of –2 kg).

Diet estimates and variation using QFASA

Overall, rattails, hoki, red cod, arrow squid, and scampi were considered prey in more than half the samples (Table 3). Hoki and rattails were dominant in both diving profiles with a median mass of over 10% each. The variability among individuals was high, however, as indicated by large SD values. Opalfish and octopus were considered minor prey (occurrence <50% and median percent mass of 0), and spiny dogfish was absent from the diet estimates.

Although the ANOSIM using QFASA outputs revealed significant differences in the diet of mesopelagic and benthic divers, the separation between groups was weaker than with FA profiles (global $R = 0.17$, $p = 0.022$). An nmds biplot revealed positive correlations between 8 out of 12 mesopelagic females and the prey species rattails, hoki, and red cod (acute angles between species and sample vectors to the origin; Fig. 3). The high distance between opalfish and octopus and the origin of the plot showed their low occurrence in diet predictions by QFASA. Scampi and arrow squid were positively correlated with 9 out of 14 benthic females and four mesopelagic females. The main prey responsible for the dissimilarities were scampi (simper: dissimilarity contribution of 28%), rattails, and red cod (simper: dissimilarity contribution for each prey of 20%). Arrow squid and hoki made up approximately 10% of the dissimilarity each.

Discussion

Resource partitioning between foraging ecotypes

The generalization of foraging studies using geographic data loggers on animals highlighted the large intraspecies diversity in habitat utilization that was largely underestimated before (Bolnick

et al. 2003). Otariid populations must no longer be seen as homogeneous units as reflected by an increasing body of literature on the foraging diversity of males and females (e.g., Kirkwood et al. 2006; Staniland and Robinson 2008) or among age groups within the same population (Fowler et al. 2007; Spence-Bailey et al. 2007). Foraging specialization also occurs at a narrower scale, e.g., among lactating otariids from the same colony (Villegas-Amtmann et al. 2008; Baylis and Nichols 2009; Baylis et al. 2009; Chilvers and Wilkinson 2009). Lactating NZ sea lions are no exception and display distinct ecotypes (benthic versus mesopelagic) depending on the area of the Auckland Islands shelf exploited (Chilvers and Wilkinson 2009). The present study showed significant differences between FA profiles of both ecotypes, suggesting a different use in food resources among lactating NZ sea lions (Fig. 2). This is consistent with preliminary stable isotope results from whiskers of lactating NZ sea lions, which showed clearly distinct carbon and nitrogen ratios between mesopelagic and benthic ecotypes (B.L. Chilvers, unpublished data).

The analysis of blubber FAs is considered a useful tool to determine resource partitioning among individual groups (e.g., Grahl-Nielsen et al. 2005; Staniland and Pond 2005; Tucker et al. 2008). However, FA concentrations in the blubber originate from biosynthesis as well as dietary intake, and rates of FA metabolization can vary according to the nutritional status of the animal (Kirsch et al. 2000). Although benthic individuals were significantly leaner than the mesopelagic ones (BCI of –2 versus 9 kg), all had a stable body mass during a 1-month interval at the beginning of the lactation period (individuals captured twice with mass measurements between January and February) (Chilvers et al. 2006). Thus, we believe that lactating sea lions were depositing dietary FAs at the time of blubber sampling (end of January) and that variation in FA profiles came mostly from a differential diet between the groups. The most important differences were 20:5n-3, 16:3n-4 (more concentrated in benthic individuals), and 18:1n-9 (more concentrated in mesopelagic

Table 3. Predicted proportions (mean and median % mass) of prey species by quantitative fatty acid signature analysis of blubber collected in late January 2000 from (*i*) 12 lactating New Zealand sea lions with a mesopelagic diving profile and (*ii*) 14 lactating NZ sea lions with a benthic diving profile.

Prey	*O*	*%O*	Mean	SD	Median	25th percentile	75th percentile
Mesopelagic							
Arrow squid	7	58	6	7	2	0	11
Hoki	12	100	20	9	19	14	25
Rattails	12	100	35	11	32	29	40
Red cod	11	92	24	16	22	13	37
Opalfish	5	42	2	6	0	0	1
Octopus	0	0	0	0	0	0	0
Scampi	6	50	13	17	1	0	35
Benthic							
Arrow squid	14	100	15	5	14	13	17
Hoki	13	93	16	8	16	12	20
Rattails	14	100	19	11	15	12	26
Red cod	12	86	14	15	6	1	27
Opalfish	3	21	3	7	0	0	<1
Octopus	3	21	6	14	0	0	<1
Scampi	10	71	27	25	27	1	49

Note: *O* is occurrence (number of individuals for which the prey has a percentage mass > 0); SD is standard deviation. Values between the 25th and the 75th percentiles represent the interquartile range within which 50% of the data is distributed.

Fig. 3. Nonmetric multidimensional scaling (NMDS) biplot (stress = 0.09) of the QFASA predictions of lactating NZ sea lions by foraging type (ANOSIM global *R* = 0.17, *p* = 0.022). Circles represent the mesopelagic individuals, while triangles represent the benthic ones.
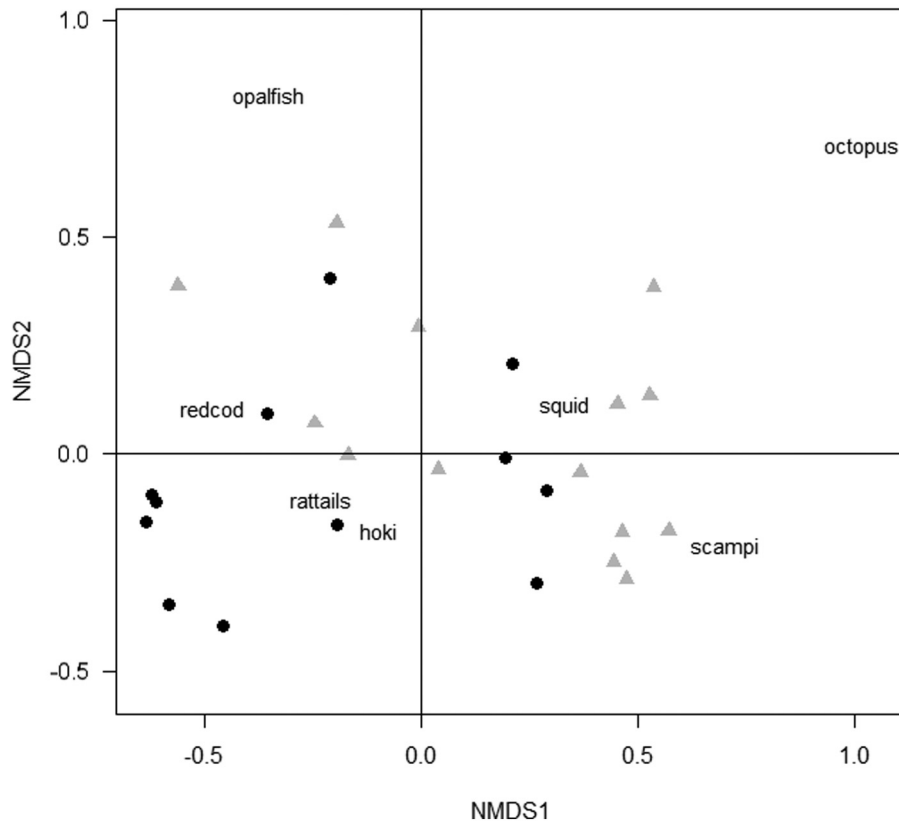
females). The FA 20:5n-3 is found in higher concentrations in scampi and arrow squid than in fish, while 18:1n-9 is in high levels in hoki and rattails (Meynier et al. 2008). Consistently, QFASA predicted more scampi and squid in the diet of benthic divers and more hoki and rattails in the diet of mesopelagic divers, although there was an overlap in the diet estimations of some individuals with different strategies (Fig. 3).

Mesopelagic females concentrate their at-sea movements in waters above the western slope of the Auckland Islands shelf with dives at variable depths (Chilvers and Wilkinson 2009; Fig. 1). This foraging pattern matches the distribution of hoki and rattails, which dominate the demersal fish assemblages at the upper and midslope of the Auckland Islands' shelf (Jacob et al. 1998), and is consistent with QFASA estimates for most mesopelagic animals. Benthic females feed predominantly over the shelf, with most of their dives at depths between 100 and 200 m on the benthos. Consistently, scampi, a benthic crustacean, was estimated in high percentages in the diet of benthic animals compared with meso-

pelagic conspecifics. Red cod and arrow squid, the other two prey estimated by QFASA, are distributed in both continental and oceanic waters depending on maturity (Ministry of Primary Industries 2013). Hence, it is hard to interpret their differential diet contributions in terms of feeding ecology between the two diving strategies. However, the QFASA predictions have to be taken cautiously, because lipid biosynthesis plays a role in blubber FA signatures and may not be well represented by the CCs calculated from feeding experiments. Indeed, CCs vary with the animal taxon or species and the diet they are fed (Iverson et al. 2004; Nordstrom et al. 2008; Rosen and Tollit 2012). The CC set chosen for this study (Steller sea lions fed on pacific herring; Rosen and Tollit 2012) gave the best goodness of fit for NZ sea lions among the CC sets available and gave diet predictions that were consistent with the trends of prey availability in the ecosystem (Meynier et al. 2010). There is no measure of how close these CCs are from the true metabolism of NZ sea lions, especially lactating females with higher energetic needs than the rest of the population. Thus, we recommend for future applications of our results that the relative importance of prey between the two foraging strategies is used and not the absolute percentages by mass predicted by QFASA.

Foraging strategy and energy intake

Benthic divers spend more time at sea, dive more frequently, and travel for greater distances than mesopelagic divers do (Chilvers and Wilkinson 2009). These individual foraging traits are believed to persist through the year and across years (Chilvers et al. 2005, 2013; Chilvers 2008). Benthic females also have a lower body condition (BCI of −2 versus 9 kg). The tenet behind the optimal foraging theory is that predators should maximize their energy gain while foraging, i.e., individuals that expend more energy foraging should be compensated by higher quality, more numerous, or more predictable prey (Orians and Pearson 1979). Therefore, we would have expected benthic divers to ingest more energy per dive than their conspecifics to sustain higher foraging costs. The Antarctic fur seals in South Georgia followed this prediction, with seals travelling long distances targeting more energy-dense prey than seals displaying short foraging trips (Staniland et al. 2007). In contrast, the present results suggested that the diet of benthic divers did not consist of a larger proportion of high-energy-dense prey compared with the diet of mesopelagic divers. Energy densities were similar among the main prey of NZ sea lions, ranging from 5 to 8 kJ·g^{-1}, except for scampi, which displayed lower energy values (3.1 to 4.4 kJ·g^{-1}; Table 1). The higher foraging efforts made by benthic divers do not seem to be compensated by greater energy income from individual prey. On the contrary, scampi has lower energy values than the rest of the prey available to sea lions. We hypothesized that benthic females must be more efficient during each dive by having a higher success rate in catching prey than the mesopelagic strategy. Benthic species are believed to be more predictable because of a more stable environment than the water column, while pelagic prey tend to be more influenced by oceanographic perturbations (Thums et al. 2011). Variable dives displayed by mesopelagic divers may reflect searching for prey in the water column, not actual foraging. When the patch of prey is located, however, it would be highly profitable to the predator (Boyd 1996).

The appearance of two foraging strategies in lactating NZ sea lions could originate from the limited choice of profitable resources lactating sea lions have around the Auckland Islands. The northwest slope of the Auckland Islands' shelf, probably the nearest area to the colony with favourable feeding grounds, is exploited not only by NZ sea lions but also by the southern arrow squid fishery, one of the most profitable fisheries in the NZ exclusive economic zone (Ministry of Primary Industries 2013; Fig. 1). The benthic tactic displayed by some lactating NZ sea lions might be a trade-off between longer foraging trips and less resource competition. Diversity in foraging among individuals of the same species is considered a sign of limited ecosystem productivity (Tinker et al. 2008). This strengthens a previous hypothesis found

in the literature that the Auckland Islands, historically the southernmost limit of NZ sea lions' range, is a marginal environment for this species (Costa and Gales 2000; Chilvers et al. 2005; Augé et al. 2011). Any reduction of prey availability at the slope of the Auckland Islands' shelf is likely to be detrimental to the reproductive success of this vulnerable species.

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