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Vibrissae growth rates and foraging and migration patterns for juvenile male northern fur seals (*Callorhinus ursinus*) from St. Paul Island, Alaska determined with stable isotope analysis

Christina Susan Kelleher

A Thesis submitted in partial satisfaction of the requirements for the degree Master of Science

in

Biology

by

Christina Susan Kelleher

Committee in charge:

Professor Carolyn Kurle, Chair
Professor Lin Chao
Professor Jonathan Shurin

2016

The Thesis of Christina Susan Kelleher is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2016

DEDICATION

To my loved ones

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ABSTRACT OF THE THESIS

Vibrissae growth rates and foraging and migration patterns for juvenile male northern fur seals (*Callorhinus ursinus*) from St. Paul Island, Alaska determined with stable isotope analysis

by

Christina Susan Kelleher

Master of Science in Biology

University of California, San Diego, 2016

Professor Carolyn Kurle, Chair

The causes of recent declines of the population of northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska are unknown. Estimations of northern fur seal migratory patterns could lead to understanding the reasons for their decline. A method used to reconstruct marine vertebrate foraging and movement patterns is stable isotope analysis of animal tissues. I analyzed the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values at intervals along entire vibrissae collected from 8, known age (2, 3, and 4 year-old), juvenile male northern fur seals from St. Paul Island, Alaska. I determined vibrissae growth rates to match stable isotope patterns to specific time periods in the animals' lives. I also analyzed the δ^{13}C and δ^{15}N values of the segments from the longest and shorter vibrissae from the same individuals (n=3) to determine if equivalent data were reflected in both sizes, saving resources. The mean vibrissae growth rate (±SD) per month for juvenile males of all ages was 3.2 ± 1.1 mm/month. When separated by age category, the average vibrissae growth rate per month for the first year of life (3.6 ± 0.9 mm/month) was faster than 1-4 year-olds (3.0 ± 1.1 mm/month). I found annual oscillations in the δ^{13}C and δ^{15}N values, indicating that juvenile male fur seals are traveling south during the non-breeding season and returning every year to the Pribilof Islands. The δ^{13}C oscillations seem to provide a more accurate representation of variations in foraging location over time than the δ^{15}N values. Shorter vibrissae matched the isotopic values of the longest vibrissae indicating full analysis of the longest whisker is unnecessary.

INTRODUCTION

Northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska (Figure 1), have been declining for over 55 years, for a variety of reasons, the most recent of which are unknown (Towell et al. 2006; Testa 2013; Towell et al. 2014). The population dropped by 60% from 1958 until 1980 (Testa 2013), largely due to commercial and scientific harvesting, then there was a period of population stability until 1998 when numbers continued to steadily decline (Towell et al. 2006; Testa 2013; Towell et al. 2014). As over half of the world's northern fur seal population resides on the Pribilof Islands during the breeding season, it is especially important to understand potential reasons for their failure to recover.

Northern fur seals spend approximately 5 months (mid-June to mid-November) based on land during the breeding season, and the rest of their year is spent in the open ocean (Gentry 1998; Testa 2013). During this pelagic, winter migration phase, the southern boundary of the northern fur seal range extends across the Pacific Ocean, between southern California and the Okhotsk Sea and Honshu Island, Japan, whereas the northern boundary is to the Bering Sea and the North Pacific Ocean (Kajimura 1984; Perez and Bigg 1986; Ragen and Dayton 1990; Goebel et al. 1991; Kiyota et al. 1992; Ragen et al. 1995; Loughlin et al. 1999; Baba et al. 2000; Robson et al. 2004). Year round, they feed primarily on fish and squid (Sinclair et al. 1994; Antonelis et al. 1997; Kurle and Worthy 2001 and 2002; Sterling et al. 2014), and during the breeding season, adult males fast on average 73 to 86% of their time on land (Gentry 1998) whereas juvenile males and adult females alternate between fasting on land and foraging (Loughlin et al. 1986; Baker et al. 1994). While there are various potential threats to this species, including lack of prey availability, predation, bycatch by fishing gear, and environmental change, the specific causes of recent population declines are unknown (Hanna 1922; Bychkov 1967; Gentry and Johnson 1980; Fowler 1987; National Marine Fisheries Service 1993; Lea et al. 2009; Testa 2013). The non-breeding season migration patterns of juvenile fur seals are relatively unknown (Kurle and Worthy 2002; Sterling and Ream 2004), so studying their winter migration patterns is essential to understanding the continued population decline and for developing successful conservation strategies for their recovery.

A tool widely used to study migration patterns and foraging ecology of marine animals is the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analysis of their tissues (Newsome et al. 2010). Predictable variations in the δ^{13}C and δ^{15}N values from predator tissues that reflect ingested prey and the underlying isotopic signatures of particular regions allow for their application in predicting animal trophic level and habitat use (Hobson 1999). Other methods exist to research the foraging and migration patterns of marine mammals, including observation, tagging, and stomach and fecal content analyses, however, stable isotope analysis is a minimally invasive, cost and time effective way to study cryptic vertebrates that spend the majority of their lives in the ocean.

Tissues that are especially useful for providing long-term isotopic records of individuals are those that grow continuously, but become biologically inert after each growth phase such as hair, teeth, bone, and vibrissae (whiskers). For example, layers of bone growth can be removed and isotopically analyzed, allowing for temporal reconstructions of ontogenetic shifts in habitat use and foraging patterns for cryptic marine vertebrates such as sea turtles (Turner Tomaszewicz et al. 2015). Otariids, such as northern fur seals, unlike phocids, grow their whiskers continuously throughout their lives, storing isotope data from when they are developing in utero to the date of whisker collection (Hirons et al. 2001; Rea et al. 2015). The stable isotope values from vibrissae collected from otariids have been shown to provide insights into ecological questions related to seasonal and annual variations in their diets and migration at finer time scales than those provided by annual growth layers in teeth and bone (Sherer et al. 2015; Kernaleguen et al. 2012). This works best when whiskers are cut, individual segments analyzed separately, and vibrissae growth rates are known (Hirons et al. 2001; Rea et al. 2015; Sherer et al. 2015).

Average vibrissae growth rates for adult male Antarctic fur seals have been determined (3.9 ± 0.2 mm/month) (Cherel et al. 2009), as well as Steller sea lions (4.4 ± 1.5 mm/month) (Rea et al. 2015) but there is a high potential for variation in growth rates among species and age-groups. For example, whisker growth rate is faster in younger animals than adults (Hirons et al. 2001; Rea et al. 2015). Therefore estimating species and age-group specific whisker growth rates may be important for the best interpretation of stable isotope data from vibrissae.

I determined the vibrissae growth rates for subadult male northern fur seals to best match the stable isotope values from specific portions of their whiskers with proper estimates of the time periods each portion represented. Previous studies demonstrate repetitive oscillations in the $\delta^{13}C$ values from sequentially sampled otariid and phocid vibrissae that reflect seasonal patterns in animal migration (Hirons et al. 2001; Cherel et al. 2009; Kernaelguen et al. 2012; Rea et al. 2015) and these can be used to determine timing of whisker growth. These oscillations are assumed to represent a seasonal pattern of migration depicting annual trends and can be used to correlate time and whisker length (Hirons et al. 2001; Cherel et al. 2009; Kernaelguen et al. 2012; Rea et al. 2015). Hirons et al. (2001) used the annual oscillations of $\delta^{13}C$ values observed from Steller sea lion vibrissae to estimate their whisker growth rates and found that they matched the rates estimated by injecting animals with enriched ^{13}C and ^{15}N glycine as a marker, providing further evidence that $\delta^{13}C$ oscillations occur annually. I used these techniques to establish vibrissae growth rates for juvenile male northern fur seals. I then analyzed the stable isotope data from whiskers collected from juvenile male northern fur seals to estimate their migration patterns by comparing their isotope values with previously published values from primary producers from various known fur seal migration regions.

Finally, in previous studies, the longest pinniped whisker is often targeted for stable isotope analysis. It was thought that, since longer whiskers contain more segments, they may reflect isotopic data over a longer time-scale than shorter whiskers, and may also have a greater chance of being intact (Rea et al. 2015). If shorter whiskers contain the same amount of data as longer whiskers, then significant time and resources could be conserved by analyzing segments from a shorter whisker.

To determine which length is best for the most comprehensive representation of the temporal record of a fur seal's stable isotope values, I also compared the $\delta^{13}C$ and $\delta^{15}N$ values along the lengths of both the longest whisker and a shorter whisker from individual animals.

To better understand the use of vibrissae in isotopic analysis and fur seal movement and trophic patterns, my study used stable isotope analysis of juvenile male northern fur seal whiskers to demonstrate a) their whisker growth rates for several age classes, b) estimations of their migration routes and foraging ecology, and c) the potential for differences in analysis of short vs. long vibrissae.

MATERIALS AND METHODS

Whisker Acquisition

Scientists from NOAA's National Marine Mammal Laboratory collected whiskers of multiple lengths from juvenile male northern fur seals aged two (n=3), three (n=3), and four years (n=1), from the Polovina haul-out on August 1, 2014 and from one, four year-old male at the Lukanin haul-out on August 4, 2014 on St. Paul Island, Alaska (Figure 1). All animals were sacrificed as part of the annual juvenile fur seal harvest. Body lengths (cm) were recorded and teeth collected from each animal to verify age via counting tooth cementum annuli. All samples were frozen in Whirl-pac plastic specimen bags until laboratory analysis. I thawed each sample and removed the cheek tissue surrounding the whiskers in order to keep the root of each vibrissa intact to maintain the longest growth record (Rea et al. 2015). I used the longest whisker for stable isotope analysis from all eight animals and, to compare isotope values along whiskers of different lengths, I also analyzed a shorter whisker which appeared to be unbroken at the distal tip for three individuals.

Whisker Processing and Stable Isotope Analysis

To remove all lipids and other contaminants, I placed the whiskers in individual test tubes, covered them with petroleum ether, and sonicated them in a 60°C water bath for 5 minutes, then rinsed them with ultrapure water and sonicated them for another 5 minutes. After cleaning, I only handled whiskers with gloves or forceps to prevent contamination. I measured the length of each vibrissa using a digital caliper, then, starting at the proximal end, I cut each whisker into 1 or 2 mm segments using either a 1 mm or 2 mm metal biopsy punch. I packaged segments into 5 X 9 mm tin capsules and samples weighed between 0.5 and 1.0 mg. The size of the segment cut (1 or 2 mm) varied depending upon the amount of material needed to equal at least 0.5 mg for an adequate sample weight for isotopic analysis. The amount of segments included in a sample also varied depending upon the thickness of the whisker and ranged from 0.5 mm near the thicker proximal end to 13 mm at the distal end. All isotope ratios were measured at the Stable Isotope Laboratory at the University of California, Santa Cruz with a Carlo Erba 1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer. I reported the stable carbon and nitrogen isotope values from the samples using conventional delta (δ) notation (expressed as δ^{13}C and δ^{15}N, respectively, in parts per thousand, ‰) as the relative differences between the isotope ratios for samples and the international measurement standards which are Vienna Peedee belemnite for C and atmospheric N_2 for N. The laboratory estimated analytical error (SD) for δ^{13}C and δ^{15}N at ±0.04‰ and ±0.1‰, respectively. The stable carbon (δ^{13}C) and stable nitrogen (δ^{15}N) values were calculated as:

$$\delta X\,(‰) = (R_{Sample} - R_{Standard} / R_{Standard}) \times 1000$$

where R_{Sample} is the ratio of heavy/light isotope composition in the tissue being studied, and $R_{Standard}$ is the ratio of heavy/light isotope composition of the corresponding standard.

Whisker Growth Rates

I graphed δ^{13}C isotope values vs. whisker length (mm) for each whisker from the known-age juveniles to determine regular isotopic oscillation patterns that appear to occur on an annual basis (Figures 2 A-C and Appendix Figures 4 A-H). Following published protocols from other studies examining isotopic patterns in otariid whiskers (Hirons et al. 2001; Cherel et al. 2009; Kernaleguen et al. 2012; Rea et al. 2015), I assumed that oscillations occurred annually because a) northern fur seals and other otariids follow predictable seasonal migration patterns, with animals returning to the same location on the Pribilof Islands each breeding season (Gentry 1998; Cherel et al. 2009; Rea et al. 2015) and b) the number of oscillations matched the numbers of years of age for each individual plus one with the final year marking their return to the Pribilof Islands just before they were sampled. In addition, Hirons et al. (2001) found that whisker growth rate estimates obtained using natural, annual oscillations in the δ^{13}C values observed in Steller sea lion (*Eumetopias jubatus*) vibrissae matched those from vibrissae marked with ^{15}N or ^{13}C enriched glycine. I used the δ^{13}C values, rather than the δ^{15}N values, because they most reflect geographical patterns in marine systems (Kurle et al. 2011) and so were expected to exhibit the clearest oscillations (Rea et al. 2015).

The first δ^{13}C value at the proximal end of the whisker represented the most recent growth. Therefore the time period assigned to this value was the month previous to whisker collection (assigned as July 2014 as whiskers were collected

August 1, 2014), reflecting time spent foraging in the Eastern Bering Sea near St. Paul Island. Following Rea et al. (2015), I measured the distance of one full oscillation of $\delta^{13}C$ values (Figures 2 A-C and Appendix Figures 4 A-H), starting from the root at the proximal end, and calculated that as an annual growth rate. I then divided the annual growth rate by 12 to estimate the monthly growth rate. For young of the year whisker growth rates, I divided the whisker length from in utero to 1 year of age by 15, in order to account for the three months of growth in utero. The ages of all animals from which a whisker was collected were known, so the $\delta^{13}C$ oscillations were matched to known years in one-year increments. The number of minima in the $\delta^{13}C$ oscillations was the same as or one greater than the animal age, providing further evidence that these $\delta^{13}C$ oscillations occur annually. In this way, I could estimate seasonal and annual variations in foraging locations for juvenile fur seals over multiple years. As very young animals are thought to exhibit faster whisker growth than older animals (Hirons et al. 2001; Rea et al. 2015), I separated growth rates between the young of the year old animals and the older juveniles (1-4 year-olds). All means are reported with ±SD.

To determine if whiskers of different lengths reflected similar stable isotope values and thus similar time periods, I compared the $\delta^{13}C$ and $\delta^{15}N$ values from segments cut from a short and the longest whisker from a subset (n=3) of animals. The use of shorter whiskers, and thus the isotopic analysis of fewer segments, saves resources, so could be valuable for future studies. Finally, I estimated juvenile fur seal migration patterns by referencing known location data from tagged seals and by comparing the δ^{13}C and δ^{15}N values from the whisker segments to known isotope values from primary producers from various locations in the Bering Sea and North Pacific.

RESULTS

Whisker growth rates

The range of longest whisker lengths was 90 mm (2 year-old) to 165 mm (4 year-old) and the mean growth rate (±SD) for the eight longest vibrissae from the subadult juvenile males was 3.2 ± 1.1 mm/month (Appendix, Table 1). The growth rates exhibited large variability among individuals within and among age groups. The mean growth rates for each year were 3.6 ± 0.9 mm/month (young of the year), 3.2 ± 1.0 mm/month (1-2 year-olds), 2.5 ± 1.1 mm/month (2-3 year-olds), and 3.4 ± 1.1 mm/month (3-4 year-olds) (Appendix, Table 1). The young of the year individuals (age 0 to 1 year) had faster growth rates (3.6 ± 0.9 mm/month) than the older ages combined (1 to 4 year-olds, 3.0 ± 1.1 mm/month).

The number of minima in the graphed δ^{13}C isotope data were either equal to or one greater than the animal age (there sometimes existed a minimum value for whisker lengths representing 0-1 year-old data, but not always) (see Figures 2 A-C and Appendix, Figures 4 A-H). All δ^{13}C and δ^{15}N isotope values for each vibrissal segment and the length of each segment are provided in the Appendix, Table 3, and graphs of all the δ^{13}C and δ^{15}N values vs. whisker lengths are in the Appendix, Figures 4 A-H and 5 A-H.

Comparison of isotope values between short and long vibrissae

The δ^{13}C and δ^{15}N values of segments taken from the longest and shorter vibrissae of each animal were nearly identical, but were condensed into smaller segments (Figures 3 A-C). One set of whiskers varied on the distal end because the longer whisker appeared to be broken at the tip. The mean (±SD) difference in length between the shorter and longest whiskers was 20.16 ± 2.29 mm (T3 = 19.52 mm, T11 = 17.73 mm, and T7 = 23.23 mm). Average whisker growth rates ± SD for the shorter whiskers (Appendix, Table 2) were 2.0 ± 0.7 mm/month (0-4 year-olds), being slightly less than those for the longest whiskers as expected. Separating the whisker growth rates by age categories shows that as age increases, whisker growth decreases, as they did with the longest growth rates. Young of the year animals had the fastest growth rates (2.5 ± 0.3 mm/month), then 1-2 year-olds (2.0 ± 0.7 mm/month), then 2-3 year-olds (1.5 ± 0.7 mm/month), and 3-4 year-olds had the slowest growth rates (1.25) (n = 1, so no standard deviation).

Estimations of movement patterns and foraging ecology

The δ^{13}C stable isotope values from juvenile male northern fur seal whisker segments ranged from -19.3 to -16.4‰ and the mean δ^{13}C values were slightly higher (-17.7 ± 0.6‰) during the non-breeding season (mid-November to mid-June) than in the breeding season (mid-June to mid-November) (-18.1 ± 0.5‰; t=-7.99, df = 520, $p \ll 0.0001$). This indicates that juvenile males moved out of the eastern Bering Sea near the Pribilof Islands during the non-breeding seasons and the cyclical nature of the isotope data indicate that they did so each year (Appendix, Figures 4 A-H). The δ^{15}N values ranged from 9.8 to 20.1‰, were highly variable and, not as clearly cyclical as the δ^{13}C data. The mean δ^{15}N values were not significantly different between the breeding and non-breeding seasons. Any variation in δ^{15}N values could reflect changes in trophic position as juvenile males transit between their non-breeding and breeding season foraging areas, or they could reflect nitrogen processing differences at the base of the food webs in the locations they are inhabiting.

Accounting for a nitrogen isotope discrimination factor of 4.0 to 5.0‰ (Kurle 2002), the range of δ^{15}N values observed in the whiskers indicates that juvenile males could be eating a wide variety of potential prey in the Bering Sea and North Pacific including arrowtooth flounder (*Atheresthes stomias*), atka mackerel (*Pleurogrammus monopterygius*), eulachon (*Thleichthys pacificus*), Pacific cod (*Gadus marocephalus*), Pacific herring (*Clupea pallasii pallasii*), Pacific sand lance (*Ammodytes hexapterus*), salmon (*Oncorhynchus* spp.), squid (*Gonatopsis borealis and Berryteuthis magister*), walleye Pollock (*Theragra chalcogramma*), and Yellow Irish lord (*Hemilepidotus jordani*) (Kurle and Worthy 2002, Kurle et al. 2011).

DISCUSSION

My research determined the growth rates of vibrissae from juvenile male northern fur seals and their variation with age. My results support previous research (Hirons et al. 2001; Rea et al. 2015) indicating that younger animals have faster growth rates than older individuals as I showed that young of the year fur seals had faster whisker growth rates than older juveniles and age was inversely correlated with growth rates. These growth rates allowed for the temporal assignment of the isotope data measured along the lengths of the whiskers so as to better understand migration and foraging patterns of juvenile male fur seals over time.

I also observed annual oscillations in the δ^{13}C values along the lengths of the whiskers that reflected the same number of years as the age of each animal. This supports the hypothesis that isotopic data collected from a whisker can be used to reconstruct movement and dietary patterns from the entire life of a juvenile fur seal. I also found that isotope data obtained from shorter and longest whiskers from the same individual represent the same time periods, and temporal data are not lost by analyzing shorter whiskers. Using the δ^{13}C isotopic data, I found that juvenile males likely leave the Bering Sea in the direct vicinity of the Pribilof Islands and migrate south during the non-breeding season, returning each breeding season to the Pribilof Islands.

I found that the average whisker growth rates of all eight animals (3.2 ± 1.1 mm/month) (0-4 year-olds), are similar to those of adult Antarctic fur seals, which were 3.9 mm/month (Cherel et al. 2009), and to those of adult Stellar sea lions, which were 4.4 ± 1.5 mm/month (Rea et al. 2015). Young of the year animals have a faster growth rate (3.6 ± 0.9 mm/month) than 1-4 year-olds (3.0 ± 1.1 mm/month) and standard deviations were reduced when separating whisker growth rates by age category. Rea et al. (2015) also found this in Steller sea lions, and presented their whisker growth rates by age category, with adults growing more slowly (4.4 ± 1.5 mm/month), subadults faster (6.1 ± 1.0 mm/month), and young of the year the fastest and with the greatest standard deviation (8.7 ± 2.8 mm/month). They found a correlation between body mass increase and increased whisker growth rates, which could explain why younger animals have larger whisker growth rates (Rea et al. 2015). Similarly, Hirons et al. (2001) found a higher growth rate in juvenile Steller sea lions than in adults. While whisker growth rates are similar for different otariid species, my results underscore the potential for considerable variability, thus supporting the utility of species and age-group specific estimates of growth rates. I recommend that when applying temporal estimations to whiskers in the absence of individualized growth rates from $\delta^{13}C$ isotope oscillations, species-specific and age-specific growth rates should be applied, especially with younger animals.

To estimate growth rates, I matched whisker length with a period of time using graphed annual $\delta^{13}C$ isotope oscillations. This method is often used to determine average whisker growth rates of otariids (Merrick et al. 1997; Hirons et al. 2001; Cherel et al. 2009; Kernaleuguen et al. 2012; Rea et al. 2015), and therefore, when available, it is more accurate than applying a general average growth rate because it gives individualized temporal estimations. While there are physiological effects that can drive stable isotopic values in marine mammals (Newsome et al. 2010), these likely do not account for the cyclic δ^{13}C isotope values for a variety of reasons. First, I found that the number of minima in δ^{13}C isotope values per animal is either equal to or one greater than the animal age, depending on whether or not there is a minimum in the variable young of the year data. Second, In Hirons et al. (2001), by analyzing captive and wild animals, it was found that isotope oscillations in Steller sea lion whiskers were caused by changes in diet and geography, rather than by endogenous rhythms. Hirons et al. (2001) also found that growth rates estimated using annual oscillations matched those using enriched ^{13}C and ^{15}N glycine injections. Finally, δ^{13}C values of primary producers in the northern hemisphere are higher in lower latitudes, which could be caused by decreasing dissolved CO_2 concentration with increasing temperatures (Rau et al. 1989; Goericke and Fry 1994; Schell et al. 1998; Burton and Koch 1999). These oceanographic patterns fit with data indicating that juvenile male northern fur seals move between southern and more northern latitude waters between non-breeding and breeding seasons (see below), therefore it follows that these geographic changes in δ^{13}C values are causing the δ^{13}C oscillations in the whiskers. I compared the stable δ^{13}C and δ^{15}N isotope data of the longest vibrissae with that of a shorter, intact vibrissae of the same animal (n=3). The isotope data from segments along a shorter vibrissa matched those of the longest vibrissa plucked from the same cheek, but in a condensed form. Therefore a shorter whisker can be used for isotopic analysis rather than the longest, saving time and resources. This indicates that the differences in whisker lengths is not due to the tip of the whisker being broken, as previously assumed, but rather different growth rates and resultant lengths among whiskers.

After determining the correct methodology for applying temporal estimations to whisker length, I used the isotopic data to estimate migration patterns for juvenile male northern fur seals from the Pribilof Islands. Previously published stable δ^{13}C and δ^{15}N isotope data from fur seals, primary producers, and potential prey items from Alaskan waters and the Pacific Ocean, along with tagging location data of northern fur seals from the Pribilof Islands (Wu et al. 1997; Shell et al. 1998; Wu et al. 1999; Kurle and Worthy 2001; Kurle and Worthy 2002; Sterling and Ream 2004; Kurle et al. 2011; Sherer et al. 2015; Kurle and McWhorter 2015) informed my estimations.

Juvenile male northern fur seals from the Pribilof Islands tagged during the breeding season, remained in the Bering Sea but traveled significant distances (up to 680 km) from the Pribilof Islands during foraging trips, returning every 8.74 to 29.81 days (Sterling and Ream 2004). Adult male and female northern fur seals from the Pribilof Islands migrate south during the non-breeding season, with females traveling farther south to the Gulf of Alaska and California current than males who remain largely in the Bering Sea and northern North Pacific (Kajimura 1984; Perez and Bigg 1986; Ragen and Dayton 1990; Goebel et al. 1991; Kiyota et al. 1992; Ragen et al. 1995; Loughlin et al. 1999; Baba et al. 2000; Kurle and Worthy 2002; Robson et al. 2004; Sterling et al. 2014).

The stable δ^{13}C isotope data of primary producers and prey demonstrate decreasing δ^{13}C stable isotope values with increasing latitude in the Northern hemisphere (Wu et al. 1997; Schell et al. 1998; Wu et al. 1999; Kurle and McWhorter 2015) which follows the trend I observed of lower δ^{13}C values from whisker segments that reflect isotope values incorporated during the breeding season, when animals are further north near the Pribilof Islands in the eastern Bering Sea, vs. in the non-breeding season when they are likely moving further south. Therefore my data support that juvenile male northern fur seals from St. Paul Island, Alaska leave the Pribilof Islands and travel south during the non-breeding season to the North Pacific Ocean, and return every year during the breeding season.

The δ^{13}C data from the first year of life was variable among individual fur seals (Appendix, Figures 4 A-H) and did not match that of 1-4 year-old animals. Tagging data from Baker et al. (2007) showed post weaning northern fur seal pups from the Pribilof Islands had variable migration patterns in the non-breeding season, as many traveled south to the North Pacific Ocean during the non-breeding season, some traveled north, and some stayed in the Bering Sea. These values from the whisker segments grown during the earliest months of life reflect ingestion of their mother's milk which introduces a potentially complicating factor (Polischuk et al. 2001). Temporal patterns in the δ^{15}N values along the lengths of juvenile male whiskers were less clear than those from the δ^{13}C data. In general, I observed a minimum or near minimum in the δ^{15}N values from the whisker segments that corresponded with time spent around the Pribilof Islands at around July of each year (Appendix, Figures 5 A-H). Higher δ^{15}N values appear to correspond to non-breeding season months, when juveniles have likely migrated away from the Pribilof Islands and head further south. As mentioned previously, these patterns are not as clear as they are for the δ^{13}C data, but they match geographic patterns demonstrated in the δ^{15}N values from zooplankton in the Bering Sea and North Pacific (Schell et al. 1998), and particulate organic matter from the Bering Sea and nearshore Canada (Wu et al. 1997 and 1999; Smith et al. 2002).

These patterns in the δ^{15}N values likely reflect a combination of differential nitrogen cycling processes that dominate in each region and potential prey switching that may occur throughout the course of the juveniles' lives. Foraging on particular prey may not follow predictable, seasonal patterns, but this follows what one would expect from a generalist predator that encounters a wide variety of prey from multiple trophic levels and utilizes waters dominated by different nitrogen cycling regimes (Kurle et al. 2011).

Previous work (Kurle and Worthy 2002) demonstrated that the δ^{15}N values from multiple tissues collected from juvenile male northern fur seals on St. Paul Island and spanning a temporal continuum of ~one year ranged from 14.9 ± 0.2‰ (fur, incorporating stable isotopes from prey during the July - November molt) to 15.1 ± 0.2‰ (muscle, late fall to tissue collection in late July) to 17.0 ± 0.1‰ (brain, spring to tissue collection in late July), to 16.2 ± 0.1‰ (liver, June/July). The range of these data from 14.9 to 17.0‰ was much less than what I observed in the range of δ^{15}N values from whiskers in this study (9.8 to 20.1‰). The stable isotope values within soft tissues such as brain, muscle, and liver reflect an amalgamation of isotope values from prey sources that are incorporated over longer periods of time that cannot be separated into fine scale intervals. One is effectively analyzing an average of stable isotope values incorporated for sometimes months up to the time of tissue collection (Kurle 2009). The use of isotope analysis with whisker segments allows for a much more fine scale separation of data into discreet time periods over which to investigate individual and population-level foraging and migration patterns that are impossible to obtain with analysis of other tissues.

Finally, in stable isotope data from Steller sea lion pup whiskers, Rea et al. (2015) found a minimum δ^{15}N value either prior to or immediately following birth which they postulated could be used as a temporal marker for parturition. I also observed a minimum δ^{15}N value within all in utero to 1 year-old whisker data, which could indicate birth. It is possible that this δ^{15}N minimum occurs because of the dietary shift from gestation to nursing when a pup is born. Human fetuses developing in utero have higher δ^{15}N values than their mothers (de Luca et al. 2012) because they are essentially growing via amino acid transfer and metabolic restructuring from mother to fetus which leads to isotopic discrimination and ^{15}N enrichment (Doronin et al. 2012). The δ^{15}N values in the fetus may drop as growth slows considerably as parturition nears, then increase again after birth as young gain nutrients via their mothers' milk. Individuals that fed exclusively on mothers' milk have even higher δ^{15}N values (Fuller et al. 2006) than those from fetuses, which could explain the δ^{15}N minima observed in juvenile male northern fur seal whisker data (0-1 year-old) that may indicate parturition.

In conclusion, I examined the δ^{13}C and δ^{15}N values from entire vibrissae from two, three, and four year-old subadult male northern fur seals collected on St. Paul Island, Alaska to estimate year-round habitat use of these animals and to better understand the applications of stable isotope analysis to vibrissae. I matched whisker length to specific years for each animal using annual graphed δ^{13}C isotope data. I recommend that this method be used to obtain growth rates rather than applying a standard average growth rate when possible as it is more accurate. I presented average growth rates for subadult males and found much faster growth rates for 0-1 year-old animals than for 1-4 year-old animals. I recommend that in the absence of individualized growth rates, age-specific growth rates should be used to apply temporal estimates to whiskers. I determined that a shorter whisker that is intact can be used for stable isotope analysis rather than the longest whisker, saving time and resources. Finally, I estimated that juvenile male northern fur seals from St. Paul Island, Alaska (excluding 0-1 year-olds) are migrating south to the Northern Pacific Ocean, out of the Pribilof Islands during the non-breeding season each year, and returning every year for the breeding season.

FIGURES

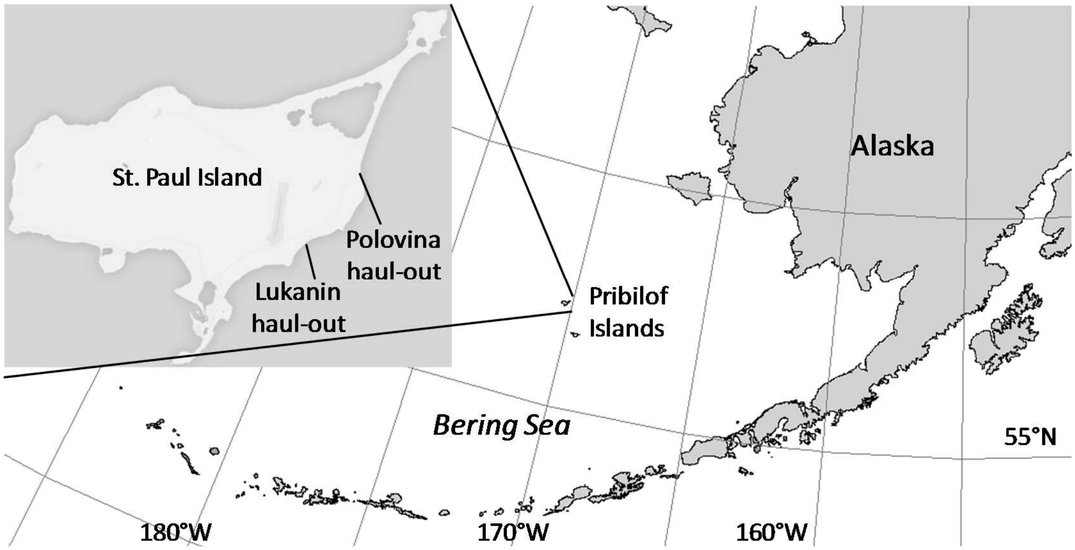
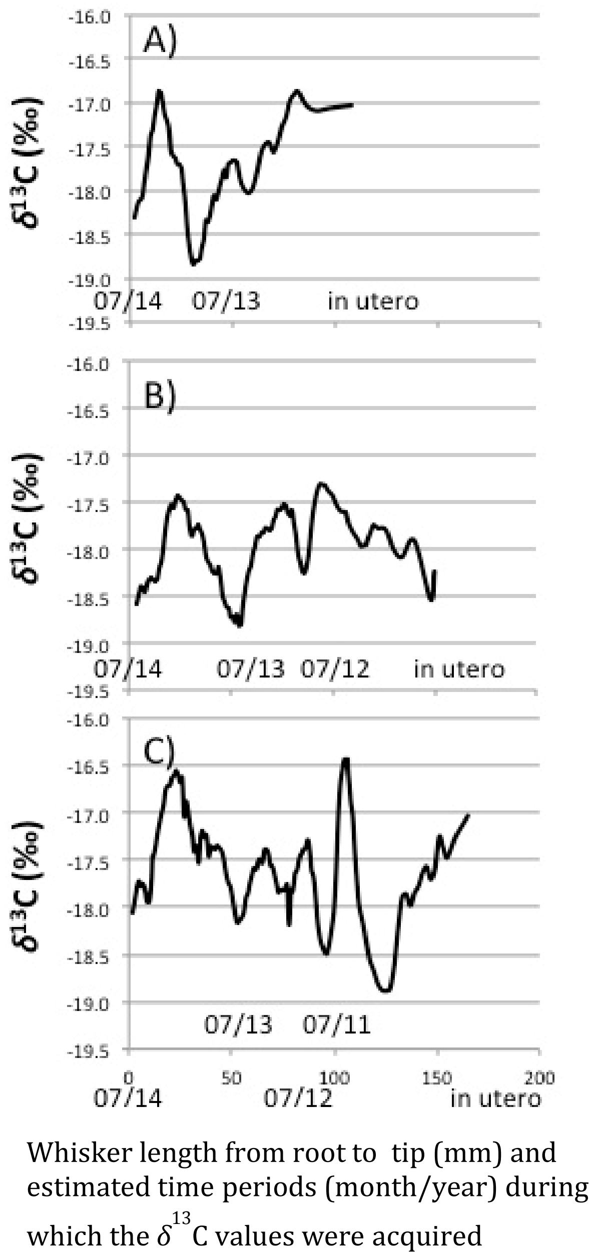
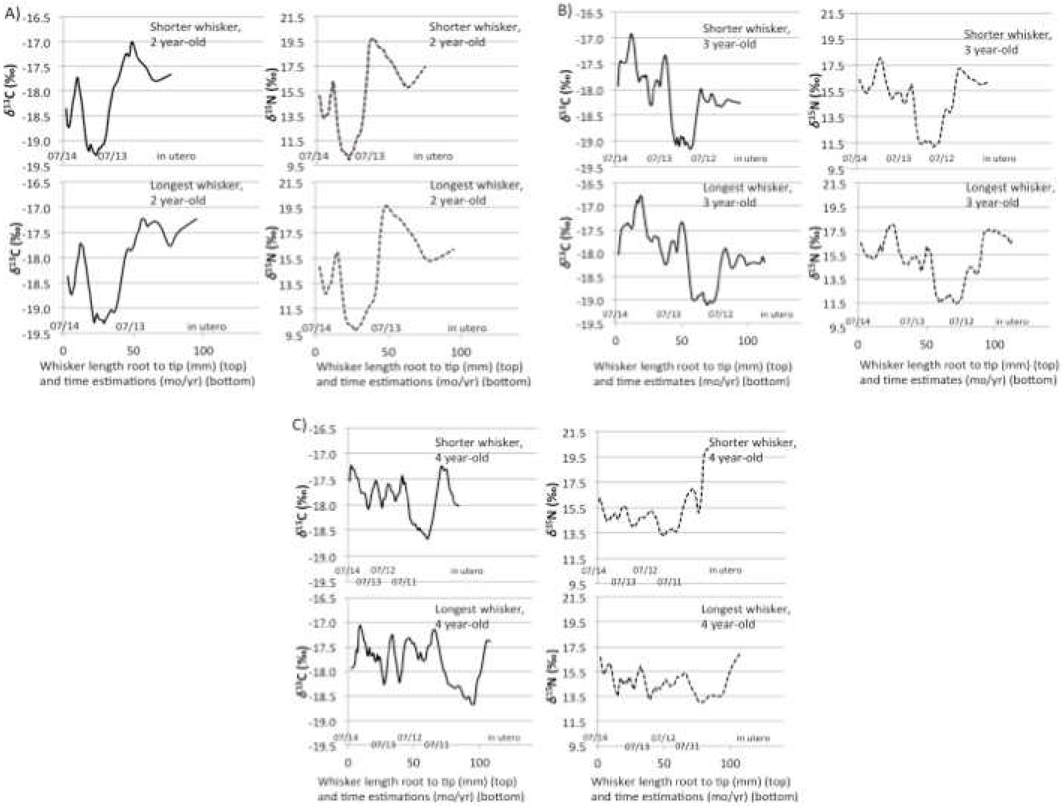


Figure 1. Study site where vibrissae from northern fur seal juvenile males were collected at Polovina and Lukanin haul-outs on St. Paul Island, Alaska.

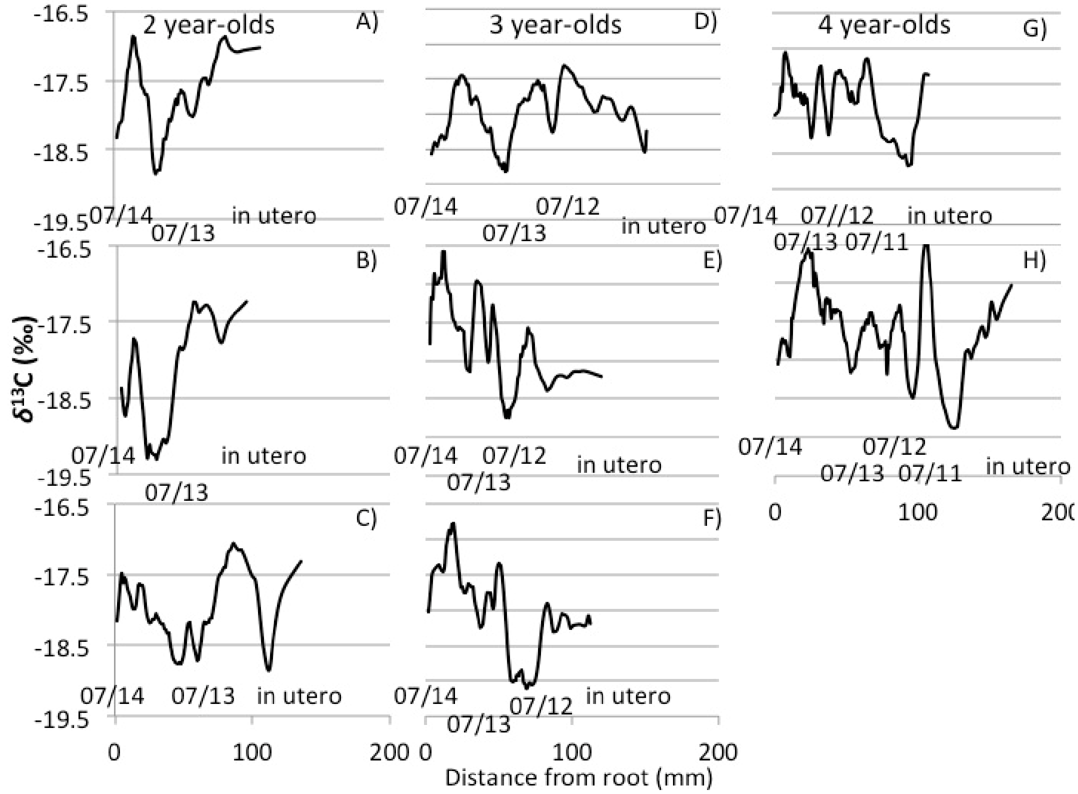


Figures 2A-C. The $\delta^{13}C$ values along the length of whiskers taken from juvenile, male northern fur seals that reflect time periods ranging from approximately July 2014 (the minima at 0), just before sample collection, to in utero (the minima from the segment furthest from the root of the whisker) for a A) two year-old (animal T17), B) three year-old (animal T6), and C) four year-old (animal T32), respectively. The numbers of $\delta^{13}C$ minima are one greater than the age of the animal as the final minima reflects their return to the Pribilof Islands just before the whisker was sampled and each minima is labeled with the estimated date during which the isotope values were acquired.

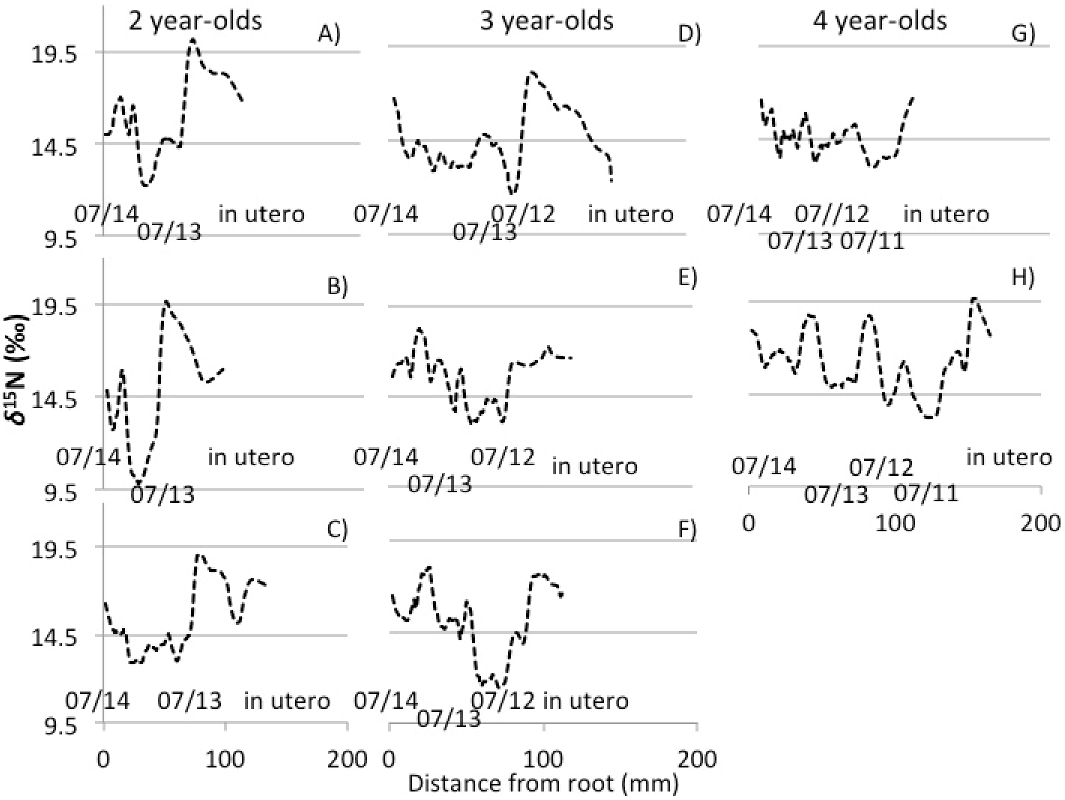


Figures 3 A-C. The δ^{13}C (left) and δ^{15}N (right) values along the lengths of whiskers from the same individual juvenile male northern fur seals demonstrated very similar patterns regardless of total whisker length (shorter vs. longest) for a A) two year-old (T3), B) 3 year-old (T11), and C) 4 year-old (T7). The mean difference in whisker length was 20.2 ± SD 2.3 mm.

APPENDIX



Figures 4 A-H. The $\delta^{13}C$ values along the lengths of whiskers with time estimations (month/year) for all 2 year-olds (left), 3 year-olds (center), and 4 year-olds (right) show that the number of oscillations are the same as the animal age. A) animal T17, B) animal T3, C) animal T5, D) animal T6, E) animal T15, F) animal T11, G) animal T7, H) animal T32



Figures 5 A-H. The δ^{15}N values along the lengths of whiskers with time estimations (month/year) for all 2 year-olds (left), 3 year-olds (center), and 4 year-olds (right) show no significant pattern. A) animal T17, B) animal T3, C) animal T5, D) animal T6, E) animal T15, F) animal T11, G) animal T7, H) animal T32

Table 1. Mean growth rates, standard deviation (SD), and range of growth rates by age category for the longest vibrissa of each animal

Age Group	Mean (mm/mo)	SD (mm)	Range (mm/mo)	Sample Size
YOY	3.61	0.91	2.61 - 5.83	8
1-2	3.16	1.01	1.83 - 5.50	8
2-3	2.53	1.13	1.00 - 4.33	5
3-4	3.38	1.13	2.25 - 4.50	2
1-4	2.98	1.11	1.00 - 5.50	8
All Ages	3.21	1.09	1.00 - 5.83	8

Table 2. Mean growth rates, standard deviation (SD), and range of growth rates by age category for the shorter vibrissa of each animal

Age Group	Mean (mm/mo)	SD (mm)	Range (mm/mo)	Sample Size
YOY	2.46	0.31	2.13 – 2.87	3
1-2	2.00	0.71	1.00 – 2.50	3
2-3	1.54	0.71	0.5 – 2.25	2
3-4	1.25	N/A	N/A	1
1-4	1.72	0.71	0.5 – 2.67	3
All Ages	1.97	0.70	0.5 – 3.92	3

Table 3. Raw data of stable δ^{13}C and δ^{15}N isotope values given for each vibrissae segment with segment length for the longest vibrissa of each animal, Continued

Animal T3 (2 year-old)

Whisker length (mm)	δ13C	δ15N
0-3	-18.38	14.82
3-5	-18.68	13.52
5-6	-18.74	12.89
6-7	-18.63	12.72
7-8	-18.54	12.86
8-9	-18.25	13.26
9-10	-18.08	13.45
10-11	-17.95	13.70
11-12	-17.72	14.59
12-13	-17.74	15.22
13-14	-17.80	15.90
14-15	-17.98	15.94
15-16	-18.13	15.25
16-17	-18.33	14.30
17-18	-18.54	13.14
18-19	-18.71	12.01
19-20	-18.95	11.17
20-21	-19.15	10.66
21-22	-19.30	10.35
22-23	-19.19	10.27
23-24	-19.12	10.13
24-25	-19.21	10.14
25-27	-19.24	9.80
27-28	-19.25	9.93
28-29	-19.31	10.02
29-30	-19.24	10.10
30-32	-19.14	10.51
32-34	-19.04	11.07
34-36	-19.09	11.53
36-38	-18.95	11.96
38-40	-18.65	12.30
40-42	-18.29	13.68
42-44	-17.98	17.00
44-46	-17.83	19.00
46-48	-17.87	19.63

Table 3, Continued

50-52	-17.56	19.13
52-54	-17.45	18.85
54-56	-17.24	18.76
56-58	-17.25	18.53
58-60	-17.38	18.33
60-62	-17.33	17.96
62-66	-17.28	17.43
66-70	-17.41	16.69
70-76	-17.77	15.42
76-82	-17.49	15.38
82-90	-17.23	16.18

Animal T5 (2 year-old)

Whisker length (mm)	δ13C	δ15N
0-2	-18.15	16.22
2-4	-17.62	15.57
4-5	-17.48	15.39
5-6	-17.62	15.03
6-7	-17.55	14.96
7-8	-17.59	14.82
8-9	-17.69	14.67
9-10	-17.75	14.68
10-11	-17.81	14.55
11-12	-17.90	14.56
12-13	-17.99	14.52
13-14	-18.00	14.48
14-15	-17.96	14.59
15-16	-17.82	14.62
16-17	-17.65	14.78
17-18	-17.64	14.66
18-19	-17.65	14.30
19-20	-17.66	13.78
20-21	-17.76	13.21
21-22	-17.93	12.92
22-23	-18.07	12.92
24-25	-18.19	12.96
25-26	-18.18	12.97

Table 3, Continued

26-27	-18.14	13.04
27-28	-18.14	12.92
28-29	-18.14	12.99
29-30	-18.06	12.93
30-31	-18.09	12.94
31-32	-18.14	13.04
32-33	-18.17	13.23
33-34	-18.20	13.41
34-35	-18.19	13.57
35-36	-18.27	13.67
36-37	-18.28	13.87
37-38	-18.33	13.88
38-39	-18.32	13.92
39-40	-18.46	13.81
40-41	-18.57	13.76
41-42	-18.67	13.71
42-43	-18.70	13.62
43-44	-18.75	13.70
44-46	-18.77	13.69
46-47	-18.74	13.90
47-48	-18.76	13.96
48-50	-18.62	13.96
half of 50-52	-18.30	14.42
52-53	-18.19	14.51
53-54	-18.18	14.51
54-55	-18.26	14.11
55-57	-18.48	13.60
57-59	-18.64	13.22
59-60	-18.72	13.00
60-61	-18.70	13.02
61-62	-18.54	13.22
62-63	-18.42	13.48
63-64	-18.25	13.70
64-65	-18.17	14.05
65-66	-18.20	14.16
66-67	-18.18	14.20
67-68	-18.17	14.25
68-69	-18.13	14.34

Table 3, Continued

70-71	-18.05	14.42
72-73	-17.81	15.57
73-74	-17.66	16.69
74-75	-17.55	17.77
75-76	-17.52	18.42
76-77	-17.49	18.99
77-78	-17.45	19.03
78-79	-17.41	19.08
79-80	-17.40	19.00
80-82	-17.19	18.87
82-84	-17.14	18.55
84-86	-17.06	18.32
86-88	-17.11	18.17
88-90	-17.16	18.12
90-92	-17.16	18.18
92-94	-17.23	18.10
94-96	-17.33	18.04
96-98	-17.45	17.84
98-100	-17.53	17.62
100-102	-17.58	17.21
102-104	-17.83	16.25
104-108	-18.55	15.22
108-112	-18.85	15.29
112-116	-18.29	16.72
116-122	-17.74	17.61
122-135.17	-17.31	17.20

Animal T17 (2 year-old)

Whisker length (mm)	δ13C	δ15N
0-2	-18.32	14.99
2-4	-18.14	14.98
4-6	-18.07	15.21
6-7	-17.91	15.34
7-8	-17.75	15.91
8-9	-17.60	16.27

Table 3, Continued

9-10	-17.37	16.59
10-11	-17.30	16.78
11-12	-17.14	16.87
12-13	-17.02	16.99
13-14	-16.86	16.88
14-15	-16.89	16.57
15-16	-17.00	16.05
16-17	-17.14	15.80
17-18	-17.20	15.42
18-19	-17.30	15.17
19-20	-17.55	14.98
20-21	-17.60	15.50
21-22	-17.64	16.10
22-23	-17.70	16.55
23-24	-17.70	16.34
24-25	-17.75	15.79
25-26	-17.93	15.15
26-27	-18.13	14.28
27-28	-18.43	13.50
28-29	-18.63	12.95
29-30	-18.78	12.49
30-31	-18.84	12.30
31-32	-18.80	12.23
32-33	-18.80	12.22
33-34	-18.78	12.23
34-35	-18.66	12.25
35-36	-18.56	12.33
36-37	-18.34	12.46
37-38	-18.35	12.63
38-39	-18.30	12.82
39-40	-18.16	13.08
40-41	-18.06	13.66
41-42	-18.09	13.85
42-43	-18.03	13.96
43-44	-17.93	14.30
44-45	-17.84	14.39
45-46	-17.77	14.67
46-47	-17.85	14.76

Table 3, Continued

47-48	-17.70	14.76
48-49	-17.69	14.75
49-50	-17.65	14.91
50-51	-17.65	14.73
51-52	-17.69	14.73
52-54	-17.90	14.59
54-56	-18.00	14.55
56-58	-18.03	14.32
58-60	-17.97	14.37
60-62	-17.79	15.72
62-64	-17.57	17.41
64-66	-17.47	19.15
66-68	-17.46	19.93
68-70	-17.56	20.15
70-72	-17.46	19.80
72-74	-17.28	19.51
74-76	-17.17	19.00
76-78	-16.98	18.69
78-80	-16.91	18.53
80-82	-16.87	18.48
82-86	-17.03	18.30
86-91	-17.09	18.32
91-97	-17.06	18.15
97-108	-17.03	16.85

Animal T6 (3 year-old)

Whisker length (mm)	δ13C	δ15N
0-4	-18.58	16.67
4-6	-18.40	16.15
6-7	-18.42	15.87
7-8	-18.46	15.07
8-9	-18.38	14.70
9-10	-18.33	14.26
10-11	-18.30	14.00
11-12	-18.32	13.83
12-13	-18.35	13.66

Table 3, Continued

13-14	-18.33	13.51
14-15	-18.20	13.47
15-16	-18.14	13.55
16-17	-18.00	13.82
17-18	-17.81	14.23
18-19	-17.66	14.34
19-20	-17.58	14.44
20-21	-17.53	14.26
21-22	-17.57	14.28
22-23	-17.47	14.27
23-24	-17.44	14.15
24-25	-17.44	14.13
25-26	-17.47	13.88
26-27	-17.50	13.72
27-28	-17.58	13.40
28-29	-17.59	13.14
29-30	-17.77	12.85
30-31	-17.86	12.84
31-32	-17.79	13.16
32-33	-17.79	13.31
33-34	-17.75	13.49
34-35	-17.80	13.77
35-36	-17.84	13.81
36-37	-17.95	13.72
37-38	-18.08	13.39
38-39	-18.14	13.20
39-40	-18.16	13.08
40-41	-18.23	13.03
41-42	-18.25	13.06
42-43	-18.25	13.27
43-44	-18.19	13.35
44-45	-18.32	13.21
45-46	-18.49	13.14
46-47	-18.56	13.02
47-48	-18.62	13.07
48-49	-18.62	13.07
49-50	-18.72	13.09
50-51	-18.72	13.11

Table 3, Continued

51-52	-18.78	13.21
52-53	-18.70	13.19
53-54	-18.82	13.04
54-55	-18.80	13.09
55-56	-18.60	13.44
56-57	-18.45	13.70
57-58	-18.32	13.78
58-59	-18.23	14.10
59-60	-18.18	14.31
60-61	-18.05	14.52
61-62	-17.97	14.69
62-63	-17.87	14.83
63-64	-17.87	14.81
64-65	-17.83	14.75
65-66	-17.82	14.69
66-67	-17.77	14.69
67-68	-17.79	14.62
68-69	-17.81	14.38
69-70	-17.78	14.20
70-71	-17.70	14.24
71-72	-17.66	14.34
72-73	-17.58	14.29
73-74	-17.59	14.10
74-75	-17.57	13.97
75-76	-17.52	13.81
76-77	-17.55	13.59
77-78	-17.62	13.24
78-79	-17.65	12.87
79-80	-17.59	12.74
80-81	-17.72	12.04
81-82	-17.85	11.86
82-83	-18.03	11.57
83-84	-18.14	11.60
84-86	-18.26	11.93
86-88	-18.08	12.96
88-90	-17.67	14.91
90-92	-17.42	16.71
92-94	-17.31	17.84

Table 3, Continued

94-96	-17.33	18.12
96-98	-17.39	18.08
98-100	-17.44	17.84
100-102	-17.54	17.51
102-104	-17.60	17.42
104-106	-17.61	17.21
106-108	-17.74	16.93
108-110	-17.83	16.54
110-112	-17.89	16.43
112-114	-17.97	16.12
114-116	-17.95	16.26
116-118	-17.85	16.31
118-120	-17.74	16.34
120-122	-17.77	16.14
122-126	-17.80	16.03
126-130	-18.01	15.58
130-134	-18.09	14.82
134-140	-17.91	14.09
142-148	-18.54	13.58
148-149.86	-18.24	12.33

Animal T11 (3 year-old)

Whisker length (mm)	δ13C	δ15N
0-2	-18.03	16.48
2-4	-17.52	15.79
4-5	-17.45	15.59
6-7	-17.40	15.31
7-8	-17.38	15.20
8-9	-17.35	15.33
9-10	-17.41	15.21
10-11	-17.44	15.16
11-12	-17.47	15.16
12-13	-17.38	15.36
13-14	-17.11	15.66
14-15	-16.99	15.96

Table 3, Continued

15-16	-16.88	16.27
16-17	-16.93	15.78
17-18	-16.79	16.10
18-19	-16.78	16.82
19-20	-16.94	17.03
20-21	-17.15	17.68
21-22	-17.35	17.60
22-23	-17.52	17.93
23-24	-17.68	17.90
24-25	-17.68	18.05
25-26	-17.75	18.00
26-27	-17.76	17.44
27-28	-17.71	16.76
28-29	-17.63	16.20
29-30	-17.65	15.60
30-31	-17.68	15.53
31-32	-17.66	15.10
32-33	-17.83	14.81
33-34	-17.95	14.81
35-36	-18.14	14.68
36-37	-18.25	14.92
37-38	-18.24	15.06
38-39	-18.19	15.24
40-41	-17.87	15.15
41-42	-17.75	15.35
42-43	-17.76	15.18
43-44	-17.76	15.15
44-45	-17.87	14.71
45-46	-17.99	14.13
46-47	-17.87	14.55
47-48	-17.53	14.89
48-49	-17.40	15.32
49-50	-17.34	16.17
50-51	-17.37	15.87
51-52	-17.50	15.86
52-53	-17.70	15.58
53-54	-17.99	14.51
54-55	-18.26	13.70

Table 3, Continued

55-56	-18.60	12.67
56-57	-18.82	12.12
57-58	-18.99	11.99
58-59	-19.01	11.55
59-60	-19.00	11.60
60-61	-18.98	11.78
61-62	-18.92	11.74
62-63	-18.92	11.87
63-64	-18.89	11.93
64-65	-18.86	12.02
65-66	-18.85	11.94
66-67	-19.03	12.17
67-68	-19.03	12.00
68-69	-19.11	11.85
69-71	-19.02	11.44
71-73	-19.06	11.56
73-75	-18.97	11.75
75-77	-18.72	12.68
77-79	-18.30	13.81
79-81	-18.02	14.41
81-83	-17.91	14.45
83-85	-18.06	14.14
85-87	-18.31	13.89
87-89	-18.31	14.76
89-91	-18.19	16.57
91-93	-18.05	17.51
93-95	-18.06	17.55
95-97	-18.11	17.63
97-99	-18.26	17.46
99-101	-18.22	17.60
101-105	-18.20	17.14
105-109	-18.22	17.00
109-111	-18.08	16.45
115-112.5	-18.19	16.64

Table 3, Continued

Animal T15 (3 year-old)

Whisker length (mm)	δ13C	δ15N
0-3	-17.78	15.55
3-4	-17.17	15.91
4-5	-17.20	16.03
5-6	-16.87	16.25
6-7	-17.00	16.34
7-8	-16.99	16.34
8-9	-16.99	16.36
9-10	-16.92	16.50
10-11	-16.93	16.65
11-12	-16.58	16.63
12-13	-16.58	16.39
13-14	-16.87	15.93
14-15	-17.02	15.56
15-16	-17.10	16.07
16-17	-17.13	17.13
17-18	-17.34	17.50
18-19	-17.47	17.99
19-20	-17.50	18.20
20-21	-17.56	18.22
21-22	-17.60	18.10
22-23	-17.57	18.04
23-24	-17.59	17.81
24-25	-17.61	17.18
25-26	-17.63	16.52
26-27	-17.88	15.86
27-28	-18.09	15.31
28-29	-18.13	15.42
29-30	-18.15	15.86
31-32	-17.64	16.51
32-33	-17.33	16.49
33-34	-17.02	16.48
34-35	-16.96	16.36
35-36	-16.99	16.14
36-37	-17.00	15.99
37-38	-17.04	15.74
38-39	-17.18	15.30

Table 3, Continued

39-40	-17.35	14.94
40-41	-17.66	14.59
41-42	-17.88	13.94
42-43	-18.02	13.79
43-44	-17.99	13.67
44-45	-17.52	14.75
45-46	-17.27	15.55
46-47	-17.41	15.77
47-48	-17.55	16.02
48-49	-17.70	15.61
49-50	-18.00	14.69
50-51	-18.21	14.18
51-52	-18.50	13.66
52-53	-18.53	13.38
53-54	-18.68	13.12
54-55	-18.74	12.92
55-56	-18.65	13.13
56-57	-18.75	13.13
57-58	-18.63	13.09
58-59	-18.61	13.28
59-60	-18.56	13.25
60-61	-18.51	13.63
61-62	-18.40	13.57
62-63	-18.22	13.80
63-64	-18.17	14.05
64-65	-17.92	14.35
65-66	-17.95	14.25
66-67	-17.81	14.33
67-68	-17.83	14.22
68-69	-17.76	14.21
69-70	-17.58	14.32
70-71	-17.63	14.22
71-73	-17.68	13.65
73-75	-18.03	13.07
75-77	-18.13	13.54
77-79	-18.23	15.15
79-81	-18.30	16.26
81-83	-18.39	16.39
83-85	-18.36	16.37

Table 3, Continued

85-89	-18.22	16.22
89-93	-18.19	16.20
93-97	-18.22	16.39
97-101	-18.15	16.62
101-105	-18.14	17.24
105-109	-18.14	16.74
109-120	-18.21	16.62

Animal T7 (4 year-old)

Whisker length (mm)	δ13C	δ15N
0-2	-17.95	16.64
2-4	-17.91	15.28
4-5	-17.84	15.34
5-6	-17.56	15.62
6-7	-17.61	15.92
7-8	-17.14	16.02
8-9	-17.06	16.13
9-10	-17.14	15.78
10-11	-17.24	15.11
11-12	-17.38	14.55
12-13	-17.42	14.04
13-14	-17.60	13.75
14-15	-17.69	13.56
15-16	-17.52	14.57
16-17	-17.67	14.97
17-18	-17.67	14.72
18-19	-17.63	14.47
19-20	-17.78	14.66
20-21	-17.80	14.62
21-22	-17.66	14.56
22-23	-17.78	15.00
23-24	-17.72	15.04
24-25	-17.93	14.53
25-26	-18.10	14.33
26-27	-18.27	14.07

Table 3, Continued

27-28	-18.19	14.49
28-29	-17.99	15.04
30-31	-17.52	15.62
31-32	-17.36	15.92
32-33	-17.27	15.55
33-34	-17.26	15.42
34-35	-17.55	14.80
35-36	-17.74	14.35
36-37	-17.90	13.84
37-38	-18.11	13.35
38-39	-18.23	13.26
39-40	-18.10	13.56
40-41	-17.93	13.71
41-42	-17.63	14.16
42-43	-17.46	14.20
43-44	-17.35	13.99
44-45	-17.35	14.22
45-46	-17.32	14.19
46-47	-17.33	14.11
47-48	-17.39	14.31
48-49	-17.43	14.49
49-50	-17.42	14.65
50-51	-17.49	14.84
51-52	-17.57	14.67
52-53	-17.72	14.48
53-54	-17.76	14.33
54-55	-17.62	14.39
55-56	-17.69	14.35
56-57	-17.79	14.47
57-58	-17.78	14.60
58-59	-17.77	14.94
59-60	-17.58	15.02
60-61	-17.48	15.04
61-62	-17.45	15.11
62-63	-17.43	15.15
63-64	-17.21	15.21
64-66	-17.15	15.37
66-68	-17.37	14.90
68-70	-17.66	14.34

Table 3, Continued

70-72	-17.93	13.96
72-74	-18.06	13.54
74-76	-18.26	13.08
76-78	-18.28	13.02
78-80	-18.33	13.10
80-82	-18.33	13.34
82-84	-18.29	13.52
84-86	-18.37	13.58
86-88	-18.52	13.52
88-90	-18.56	13.54
90-92	-18.53	13.48
92-94	-18.67	13.63
94-96	-18.65	14.20
96-98	-18.22	14.98
98-101	-17.99	15.85
101-105	-17.38	16.61
105-108	-17.38	17.00

Animal T32 (4 year-old)

Whisker length (mm)	δ13C	δ15N
0-2	-18.07	17.93
2-4	-17.79	17.80
4-5	-17.72	17.72
5-6	-17.78	17.38
6-7	-17.75	17.03
7-8	-17.82	16.61
8-9	-17.94	16.22
9-10	-17.95	15.99
10-11	-17.71	15.95
11-11.5	-17.46	16.12
11.5-12	-17.46	16.12
12-13	-17.36	16.21
13-14	-17.22	16.40
14-15	-17.11	16.50
15-16	-17.01	16.64
16-17	-16.92	16.67
17-18	-16.76	16.84

Table 3, Continued

18-19	-16.72	16.87
19-20	-16.72	16.85
20-21	-16.63	16.87
21-22	-16.61	16.74
22-23	-16.56	16.73
23-24	-16.59	16.68
24-25	-16.68	16.53
25-26	-16.62	16.52
26-27	-17.04	16.29
27-28	-16.88	16.35
28-29	-16.99	16.22
29-30	-17.13	15.90
30-31	-17.24	15.72
31-32	-17.41	15.63
32-33	-17.35	16.00
33-34	-17.53	16.25
34-35	-17.24	16.96
35-36	-17.20	17.52
36-37	-17.27	18.09
37-38	-17.22	18.34
38-39	-17.46	18.53
39-40	-17.35	18.79
40-41	-17.35	18.74
41-42	-17.39	18.71
42-43	-17.34	18.72
43-44	-17.36	18.70
44-45	-17.39	18.61
45-46	-17.47	18.32
46-47	-17.59	17.66
47-48	-17.71	17.13
48-49	-17.74	16.49
49-50	-17.83	16.20
50-51	-17.96	15.68
51-52	-18.09	15.28
52-53	-18.17	15.09
53-54	-18.13	14.90
54-55	-18.11	14.98
55-56	-18.07	14.90
56-57	-17.90	14.91

Table 3, Continued

57-58	-17.85	15.00
58-59	-17.75	14.97
59-60	-17.66	15.05
60-61	-17.58	15.02
61-62	-17.61	14.99
62-63	-17.52	14.90
63-64	-17.49	15.00
64-65	-17.53	15.15
65-66	-17.39	15.18
66-67	-17.38	15.20
67-68	-17.44	15.33
68-69	-17.56	15.31
69-70	-17.56	15.28
70-71	-17.65	15.20
71-72	-17.75	15.07
72-73	-17.84	15.36
73-74	-17.82	15.89
74-75	-17.81	16.43
75-76	-17.81	17.02
76-77	-17.76	17.50
77-78	-18.19	18.08
78-79	-17.81	18.40
79-80	-17.84	18.64
80-81	-17.63	18.71
81-82	-17.62	18.77
82-83	-17.49	18.71
83-84	-17.46	18.49
84-85	-17.38	18.27
85-86	-17.38	17.99
86-87	-17.29	17.48
87-88	-17.39	16.83
88-89	-17.62	16.09
89-90	-17.65	15.62
90-91	-17.90	14.87
91-92	-18.16	14.46
92-93	-18.31	14.08
93-94	-18.40	13.92
95-96	-18.49	14.01
96-97	-18.44	14.20

Table 3, Continued

97-98	-18.32	14.44
98-99	-18.18	14.48
99-100	-17.99	14.71
100-101	-17.58	15.07
101-102	-17.04	15.32
102-103	-16.70	15.81
103-104	-16.55	15.93
104-105	-16.43	16.09
105-106	-16.44	16.24
106-107	-16.63	16.23
107-108	-16.89	15.87
108-109	-17.05	15.63
109-110	-17.41	15.15
110-111	-17.72	14.79
111-112	-17.97	14.42
112-113	-18.08	14.32
113-114	-18.17	14.13
115-117	-18.53	13.65
117-119	-18.66	13.35
119-121	-18.80	13.22
121-123	-18.87	13.22
123-125	-18.88	13.25
125-127	-18.87	13.21
127-129	-18.64	13.56
129-131	-18.23	14.49
131-133	-17.89	15.57
133-135	-17.86	15.99
135-137	-17.98	16.01
137-139	-17.85	16.46
139-141	-17.77	16.70
141-143	-17.63	16.85
143-145	-17.57	16.49
145-147	-17.71	15.69
147-149	-17.59	16.41
149-151	-17.25	18.47
151-153	-17.37	19.67
153-155	-17.47	19.65
155-159	-17.26	18.86
159-165	-17.03	17.68

Table 4. Longest whisker length (mm) and body size (cm) of each animal

Animal ID and age	Longest whisker length (mm)	Body size (cm)
T3 (2 yo)	90.0	114.0
T5 (2 yo)	135.17	108.5
T17 (2yo)	108.0	112.5
T6 (3 yo)	149.86	115.0
T11 (3 yo)	112.5	118.5
T15 (3 yo)	120.0	112.0
T7 (4 yo)	108.0	125.5
T32 (4 yo)	165.0	119.0

REFERENCES

Antonelis GA, Sinclair EH, Ream RR, Robson BW (1997) Inter- island variation in the diet of female northern fur seals (Callorhinus ursinus) in the Bering Sea. J Zool (Lond) **242**:435–451

Baba N, Boltnev AI, and Stus AI (2000) Winter migration of female northern fur seals *Callorhinus ursinus* from the Commander Islands. Bull. Natl. Res. Inst. Far Seas Fish, **37**: 39–44

Baker JD, Fowler CW, and Antonelis GA (1994) Mass change in fasting immature male northern fur seals. Can. J. Zool. **72**(2): 326–329

Baker JD (2007) Post-weaning migration of northern fur seal *Callorhinus ursinus* pups from the Pribilof Islands, Alaska. Mar. Ecol. Prog. Ser. **341**: 243–255

Ben-David M, Flaherty EA (2012) Stable isotopes in mammalian research: a beginner's guide. J Mammal **93**: 312−328

Burton RK, Koch PL (1999) Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. Oecologia **119**:578–585

Bychkov VA (1967) On killer whale attacks on fur seals off Tyuleniy Island. Zoological Zhurnal **46**: 149-150

Call KA, and Ream RR (2012) Prey selection of subadult male northern fur seals *(Callorhinus ursinus)* and evidence of dietary niche overlap with adult females during the breeding season. Mar. Mammal Sci. **28**(1): 1-15

Cherel, Y., L. Kernaléguen, P. Richard, and C. Guinet. (2009) Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals. Biology Letters **5**: 830-832

de Luca A, Boisseau N, Tea I, Louvet I, Robins RJ, Forhan A, Charles MA, Hankard R. (2011) δ^{15}N and δ^{13}C in hair from newborn infants and their mothers: a cohort study. Pediatr Res. **71**(5): 598-604

Doronin YK, Bednik DY, Ivanov AA, Golichenkova PD, and Kalistratova EN. (2012) Maternal-fetal interaction: an insight through the stable isotope fractionation prism. British Journal of Medicine and Medical Research. **2**:701-714

Fowler CW (1987) Marine debris and northern fur seals: a case study. Marine Pollution Bulletin **18**: 326-335

Gentry RL, and Johnson JH (1980) Predation by sea lions on northern fur seal neonates. Mammalia **45**: 423-430

Gentry R.L. (1998) Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, N.J.

Goebel M.E., Bengtson, J.L., Delong, R.L., Gentry, R.L., and Loughlin, T.R. (1991) Diving patterns and foraging locations of female northern fur seals. Fish. Bull. (Wash., D.C.), **89**(2): 171– 179

Goericke R, Fry B (1994) Variations of marine plankton δ13C with latitude, temperature, and dissolved CO2 in the world ocean. Global Biogeochem Cycles **8**:85–90

Hanna GD (1992) What becomes of the fur seals. Science **60**: 505-507

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

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

Kajimura, H. (1984) Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the Eastern North Pacific Ocean and Eastern Bering Sea. NOAA Tech. Rep. NMFS-SSRF No. 779

Kernaléguen L., B. Cazelles, J.P.Y. Arnould, P. Richard, C. Guinet, and Y. Cherel. (2012) Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. PLoS ONE **7**(3): e32916

Kiyota, M., Baba, N., Loughlin, T.R., and Antonelis, G.A. (1992) Characteristics of winter migration of female Pribilof fur seals. *In* XV Symposium on Polar Biology, Tokyo, Japan, 1992. National Institute of Polar Research, Tokyo. p. 75. [Abstract.]

Kurle CM, Worthy GAJ (2001) Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (Callorhinus ursinus) and their prey. Oecologia **126**: 254–265

Kurle CM. (2002) Stable-isotope ratios of blood componenets from captive northern fur seals (*Callorhinus ursinus*) and their diet: applications for studying the foraging ecology of wild otariids. Canadian Journal of Zoology. **80**:902-909

Kurle CM, Worthy GAJ (2002) Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal Callorhinus ursinus: implications for dietary and migratory reconstructions. Mar Ecol Prog Ser **236**: 289–300

Kurle CM. (2009) Interpreting temporal variation in omnivore foraging ecology via stable isotope modelling. Functional Ecology **23**: 733-744

Kurle CM, Sinclair EH, Edwards AE, Gudmundson CJ (2011) Temporal and spatial variation in the δ13C and δ15N values of fish and squid from Alaskan waters. Mar Biol **158**: 2389−2404

Kurle CM, and McWhorter J. (2015) Spatial and temporal variation within fine-scale, δ^{13}C and δ^{15}N isoscapes of the Southern California Bight: Applications for reconstructing foraging ecology and migration patterns of marine vertebrates. 21st Biennial Society for Marine Mammalogy Conference on the biology of Marine mammals, 13-18 Dec 2015 San Francisco, CA [Abstract]

Lea MA, Johnson D, Ream R, Sterling J, Melin S, Gelatt T. (2009) Extreme weather events influence dispersal of naïve northern fur seals. Biol. Lett. **5**: 252-257

Loughlin, T. R., J. L. Bengtson, and R. L. Merrick. (1987) Characteristics of feeding trips of female northern fur seals. *Canadian Journal of Zoology* **65**: art2079–2084

Loughlin EM (1986) Prediction of Surface Saturation Zones in Natural Catchments by Topographic Analysis. Water Resources Research **22**(5): 794-804

Loughlin, T.R., Baba, N., and Robson, B.W. (1999) Use of a surface-current model and satellite telemetry to assess marine mammal movements in the Bering Sea. *In* Dynamics of the Bering Sea. *Edited by* T.R. Loughlin and K. Ohtani. University of Alaska Sea Grant, Fairbanks. pp. 615–630

Merrick RL, Chumbley MK, Byrd GV. (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Can. J. Fish. Aquat. Sci. **54**: 1342-1348

National Marine Fisheries Service (1993) Final Conservation Plan for the northern fur seal (*Callorhinus ursinus*). Prepared by the National Marine Mammal Laboratory/Alaska Fisheries Science Center, Seattle, Washington, and the

Office of Protected Resources/National Marine Fisheries Service, Silver Spring, Maryland

Newsome, S. D., M.T. Clementz, and P.L. Koch. (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Marine Mammal Science **26**(3): 509–572

Perez, M.A., and Bigg, M.A. (1986) Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fish. Bull. (Wash., D.C.), **84**: 957–971

Polischuk SC, Hobson, KA, Ramsay, MA. (2001) Use of stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Canadian Journal of Zoology. **79**:499-511

Ragen, T.J., and Dayton, P.K. (1990) Migration of northern fur seal (*Callorhinus ursinus*) pups in the Bering Sea. Rep. No. MMS 90-0058, Scripps Institution of Oceanography, University of California San Diego, La Jolla

Ragen, T.J., Antonelis, G.A., and Kiyota, M. (1995) Early migration of northern fur seal pups from St. Paul Island, Alaska. J. Mammal. **76**(4): 1137–1148

Rau GH, Takahashi T, Des Marais DJ (1989) Latitudinal variations in plankton δ13C: implication for CO2 and productivity in past oceans. Nature **341**:516–518

Rea LD, Christ AM, Hayden AB, Stegall VK, Farley S, Stricker C, Mellish J, Maniscalco J, Waite J, Burkanov V (2015) Age-specific vibrissae growth rates: a tool for determining the timing of ecologically important events in Steller sea lions. Mar Mamm Sci (in press)

Robson, B.W., Goebel, M.E., Baker, J.D., Ream, R.R., Loughlin, T.R., Francis, R.C., Antonelis, G.A., and Costa, D.P. (2004) Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). Can. J. Zool. **82**(1): 20–29

Schell D, Barnett B, Vinette K (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi, and Beaufort Seas. Mar Ecol Prog Ser **162**:11–23

Sherer RD, Doll AC, Rea LD, Christ AM, Stricker CA, Witteveen B, Kline TC, Kurle CM, Wunder MB (2015) Stable isotope values in pup vibrissae reveal geographic variation in diets of gestating Steller sea lions *Eumetopias jubatus.* Mar Ecol Prog Ser **527**: 261-274

Sinclair EH, Loughlin TR, Pearcy W (1994) Prey selection by northern fur seals (Callorhinus ursinus) in the eastern Bering Sea. Fish Bull **92**:144–156

Smith SL, Menrichs SM, Taekeun Rho (2002) Stable C and N isotopic composition of sinking particles and zooplankton over the southeastern Bering Sea shelf. Deep-Sea Research II **49**: 6031-6050

Sterling JT and Ream RR (2004) At-sea behavior of juvenile male northern fur seals (*Callorhinus ursinus).* Can. J. Zool. **82**: 1621-1637

Sterling, J. T. , A. M. Springer, S. J. Iverson, S. P. Johnson, N. A. Pelland, D. S. Johnson, M.-A. Lea, and N. A. Bond. (2014) The sun, moon, wind, and biological imperative–shaping contrasting wintertime migration and foraging strategies of adult male and female northern fur seals (*Callorhinus ursinus*). *PloS ONE* **9**: e93068

Testa JW (2013) Fur Seal Investigations (2012) U.S. DEPARTMENT OF COMMERCE National Oceanic and Atmospheric Administration National Marine Fisheries Service□Alaska Fisheries Science Center

Towell, R. G., Ream, R. R. & York, A. E. (2006) Decline in northern fur seal (Callorhinus ursinus) pup production on the Pribilof Islands. Mar. Mamm. Sci. **22**, 486–491

Towell, R. G. , R. R. Ream, J. Bengston, and J. Sterling. (2014) *2014 northern fur seal pup production and adult male counts on the Pribilof Islands, Alaska. F/AKC3:RT*. Alaska Fisheries Science Centre, National Marine Mammal Laboratory, Seattle, Washington, USA.

Turner Tomaszewicz CN, Seminoff JA, Avens L, Goshe LR, Peckham SH, Rguez-Baron JM, Bickerman K, Kurle CM (2015) Age and residency duration of loggerhead turtles at a North Pacific bycatch hotspot using skeletochronology. Biological Conservation **186**: 134-142

Wu JP, Calvert SE, Wong CS (1997) Nitrogen isotope variations in the subarctic northeast Pacific: relationships to nitrate utilization and trophic structure. Deep-Sea Research **44**(2): 287-314

Wu JP, Calvert SE, Wong CS (1999) Carbon and Nitrogen Isotope Ratios in Sedimenting Particulate Organic Matter at an Upwelling Site off Vancouver Island. Estuarine, Coastal and Shelf Science **48**: 193-203