Springer

Dear Author:

Please find attached the pdf file of your contribution, which can be viewed using the Acrobat Reader, version 3.0 or higher. We would kindly like to draw your attention to the fact that copyright law is also valid for electronic products. This means especially that:

- You may not alter the pdf file, as changes to the published contribution are prohibited by copyright law.

- You may print the file and distribute it amongst your colleagues in the scientific community for scientific and/or personal use.

- You may make an article published by Springer-Verlag available on your personal home page provided the source of the published article is cited and Springer-Verlag is mentioned as copyright holder. You are requested to create a link to the published article in LINK, Springer's internet service. The link must be accompanied by the following text: The original publication is available on LINK **http://link.springer.de.** Please use the appropriate URL and/or DOI for the article in LINK. Articles disseminated via LINK are indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks and consortia.

- You are not allowed to make the pdf file accessible to the general public, e.g. your institute/your company is not allowed to place this file on its homepage.

Yours sincerely,

Springer-Verlag Berlin Heidelberg

Oecologia (2001) 126:254–265
DOI 10.1007/s004420000518

Carolyn M. Kurle · Graham A.J. Worthy

Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*) and their prey

Received: 14 March 2000 / Accepted: 21 August 2000 / Published online: 19 October 2000

Abstract We investigated the feeding ecology and foraging location of migrating and nursing northern fur seal (*Callorhinus ursinus*) adult females and migrating juvenile males from the Pribilof Islands, Alaska, using carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis of fur seal skin and whole potential prey. Post-parturient and lactating females had mean $\delta^{15}N$ values significantly (0.8‰) higher than pregnant, migratory females, and $\delta^{13}C$ values that were not significantly different. Two opportunistically collected, migrating, nulliparous females had mean $\delta^{13}C$ values 1.1‰ lower than migrating, pregnant females, and $\delta^{15}N$ values that were not different. Pregnant, migratory females had mean $\delta^{13}C$ values significantly (~1.5‰) higher than migratory juvenile males, and mean $\delta^{15}N$ values significantly (~0.6–1.6‰) higher than migratory juvenile males. The exception was one group of juvenile males from St. Paul Island with mean $\delta^{15}N$ values that were not significantly different from migrating females. The mean $\delta^{15}N$ values of pregnant females indicate they were feeding at a higher trophic level than juvenile males during migration. The higher mean $\delta^{13}C$ values for pregnant females suggest they were feeding coastally during the spring migration, while juvenile males and nulliparous females were feeding offshore. The higher $\delta^{15}N$ values for post-parturient, lactating females over migrating, pregnant females point to either a trophic shift in diet over time, or a more likely ^{15}N-enrichment due to negative nitrogen balance caused by the nutritional stress of lactation and the feeding/fasting regime experienced by females. Similar mean $\delta^{13}C$ values for migrating and breeding-season females indicate that both groups were feeding in coastal, on-shelf domains during their respective time periods. Similar mean $\delta^{15}N$ values for nulliparous and pregnant females indicate they were feeding at similar trophic levels despite indications of feeding in separate ecosystems during migration. Using a $\delta^{15}N$ shift of 2–3‰ per trophic level, we made general inferences about the trophic levels at which northern fur seals were feeding. The interpretation of our $\delta^{15}N$ data indicates that migrating pregnant females, lactating females and the majority of migrating juvenile males consumed prey with mean $\delta^{15}N$ values between 14.2‰ and 15.2‰, 15.1‰ and 16.1‰, and 13.6‰ and 14.6‰, respectively. Probable fur seal prey was analyzed as well. Walleye pollock showed progressive ^{15}N and ^{13}C-enrichments with age. Mean $\delta^{15}N$ and $\delta^{13}C$ values of 3- to 4-year-old fish were ~6.0‰ and 1.1‰ higher, respectively, than values for 0-age pollock. Atka mackerel also showed isotopic enrichment with age. The $\delta^{15}N$ and $\delta^{13}C$ values of large fish were 0.8‰ and 0.3‰ higher, respectively, than values for smaller fish.

Keywords Stable isotopes · Northern fur seals · Feeding ecology · Foraging · Migration

C.M. Kurle (✉)
National Marine Mammal Laboratory,
Alaska Fisheries Science Center,
National Marine Fisheries Service, 7600 Sand Point Way NE,
Seattle, WA 98115, USA
e-mail: Carolyn.Kurle@NOAA.gov
Fax: +1-206-5266615

G.A.J. Worthy
Physiological Ecology and Bioenergetics Laboratory,
Texas A&M University at Galveston, 5001 Avenue U, Suite 105,
Galveston, TX 77551, USA

Introduction

Adult female northern fur seals (*Callorhinus ursinus*) from the Pribilof Islands, Alaska, migrate over the course of a year, spending November through June at sea in the Gulf of Alaska and Pacific Ocean, and the remainder of the year primarily on and around St. Paul or St. George Islands in the eastern Bering Sea (Kajimura 1985; Bigg 1990). They arrive on the islands during late June/early July to pup and breed, and remain through late October and early November to wean their pups. They then travel south, typically migrating as far as southern California (Kajimura 1985; Bigg 1990). Juvenile males are thought to spend much of the year off-

shore in the eastern North Pacific, occasionally moving into coastal areas between the Bering Sea and California. The majority of fur seals return to the Pribilof Islands region by July, reaching a maximum density during mid-August after the majority of adult females have copulated (Bigg 1986, 1990; Gentry 1998).

Studies on the migratory pathway and the feeding ecology of northern fur seals indicate that prey consumed during migration are different from those consumed during the breeding season near the Pribilof Islands (Kajimura 1984, 1985; Perez and Bigg 1986). However, dietary data for migratory northern fur seals are difficult to obtain because they feed underwater, fecal material is not available, and it is illegal to kill animals in order to examine their stomach contents. Because northern fur seals haul-out on land during their breeding season, tissue samples can readily be collected for use in stable carbon and nitrogen isotope analysis. This method can be used to estimate trophic position, relative consumption of different prey species, and feeding location.

The study of pinniped food habits has traditionally been accomplished through the examination of fecal matter and stomach contents (e.g., Treacy and Crawford 1981; Antonelis et al. 1984, 1990; Perez and Bigg 1986; Sinclair et al. 1994; Burns et al. 1998). Such studies indicate that fur seals in the eastern Bering Sea eat primarily juvenile walleye pollock (*Theragra chalcogramma*) and, to a lesser degree, gonatid squid and other fish (Perez and Bigg 1986; Sinclair et al. 1994; Antonelis et al. 1997). Both stomach-content and scat analyses provide a picture of an animal's most recent meals, but do not illustrate long-term feeding habits. Use of carbon and nitrogen stable isotopes can be used to estimate assimilation of food resources over long periods.

The progressive ^{13}C and ^{15}N isotopic enrichment in tissues while moving to higher trophic levels allows for analysis of food web ecology, provided that the basal or source composition of the isotopes is known (e.g., DeNiro and Epstein 1978, 1981; see Kurle 1998). For instance, isotopic composition of marine predator tissues is determined initially by the isotopic composition of the baseline phyto- and zooplankton sources (McConnaughey and McRoy 1979; Minagawa and Wada 1984). Consumer tissue usually contains higher ratios of heavy to light carbon and nitrogen isotopes than prey tissues due to isotopic fractionation (McConnaughey and McRoy 1979; Minagawa and Wada 1984; Ambrose and DeNiro 1986; Owens 1987; Schimel 1993; Michener and Schell 1994; Gannes et al. 1997). The accepted step-wise enrichments of ^{15}N and ^{13}C in marine food webs between prey and predator attributed to dietary fractionation are ~3–5‰ and ~0.0–1.1‰ per trophic level, respectively (Rau et al. 1983; Minagawa and Wada 1984; Wada et al. 1987, 1991; Fry 1988; Hobson and Welch 1992; Hobson et al. 1994; France and Peters 1997).

Conclusions about certain prey in an animal's diet are most straightforward when examining differences in nitrogen and carbon isotope ratios of prey items such as C_3 versus C_4 and crassulacean acid metabolism (CAM) plants (Ambrose and DeNiro 1986), terrestrial versus marine prey (Hildebrand et al. 1996), and animal versus plant material (Ramsay and Hobson 1991). When using stable isotopes to assess diets of animals feeding at or near the top of a trophic web on several different prey items, many of which may have similar isotopic signatures, clear distinctions about diet are more difficult to determine. However, it may be possible to infer the general trophic level at which animals are feeding by applying ^{15}N (and, to an extent, ^{13}C) step-wise enrichment values to measured isotopic ratios in animal tissue. Carbon is a fairly weak indicator of trophic level, especially in marine vertebrate consumers (Rau et al. 1983; Wada et al. 1987; Fry 1988; Hobson and Welch 1992; Hobson 1993; Hobson et al. 1994; Kelly 2000; C.M. Kurle, unpublished work), but carbon isotopic signatures in marine food webs can be used to determine from which marine domain an animal is obtaining its prey (McConnaughey and McRoy 1979; Rau et al. 1983; Hobson and Welch 1992; Hobson 1993; Burton and Koch 1999). For example, $\delta^{13}C$ values are typically higher in near-shore or benthic food webs than in offshore food webs (McConnaughey and McRoy 1979; Hobson 1993; France 1995), higher in middle latitudes than high latitudes (Rau et al. 1982; Dunton et al. 1989; Saupe et al. 1989; Hobson et al. 1997; Burton and Koch 1999), and usually lower in riverine than marine systems (Hobson 1990; Mizutani et al. 1990).

Turnover of stable isotopes varies with the metabolic activity of the tissue sampled, and changes in diet can take anywhere from a few days to many weeks to appear in an animal's tissue (Tieszen et al. 1983; Hobson and Clark 1992a; Hobson 1993). Due to sampling constraints, our study analyzed northern fur seal skin. There is very little information on isotopic turnover rates for mammalian tissues, and none exists for fur seal skin. However, coupling fractional rates of protein synthesis in mammal tissues (summarized in Welle 1999) with known carbon isotope turnover rates in gerbils (Tieszen et al. 1983), we estimated the time in which dietary information becomes incorporated into fur seal skin. There is not a direct correlation between protein and isotopic turnover rates (S. Welle, personal communication), but there is a strong relationship so that combining the two can be useful in estimating isotopic turnover. Welle (1999) summarized fractional rates of tissue protein synthesis for skin from dogs as 13% day^{-1}. This indicates that the overall weighted average of protein half-lives of skin from dogs is 7–8 days. The rate for skeletal muscle is 8% day^{-1}, which gives an average half-life of 12–13 days. Protein synthesis rates summarized for other mammals place skin values between rates for liver and muscle. Tieszen et al. (1983) found carbon turnover half-life rates for liver and muscle of 6.4 and 27.6 days, respectively. Because protein synthesis rates for skin place it between liver and muscle, carbon turnover half-life rates for skin should be between 6.4 and 27.6 days. Isotopic analysis of a tissue indicates an integration of diet

over 2–3 half-lives (Hobson 1993), so $\delta^{13}C$ and $\delta^{15}N$ values from skin samples taken in July/August likely reflect nutrients consumed in the late spring/early summer, indicating feeding ecology for fur seals in late migration to the Pribilof Islands (Bigg 1990). Samples collected in November should reflect feeding ecology during the breeding season in the eastern/central Bering Sea.

A further complicating factor when interpreting isotopic data operates when an animal is nutritionally stressed (Hobson and Clark 1992b; Hobson et al. 1993; Hobson and Schell 1998; Doucett et al. 1999; Kelly 2000). Fasting can cause an animal to be in negative nitrogen balance, causing its nitrogen pool available for amino acid synthesis to become enriched in ^{15}N. When an animal is fasting and/or kept on a low-protein diet, nitrogen balance is maintained through nitrogen recycling which is thought to occur when urea is hydrolyzed in the colon by microflora (Houpt and Houpt 1968; Waterlow et al. 1978; Jackson 1998). The urea derived nitrogen is largely retained within the nitrogen metabolic pool and used for amino acid synthesis (Houpt 1963; Houpt and Houpt 1971; Waterlow et al. 1978; Forrester et al. 1994; Gannes et al. 1997; Jackson 1998). Nitrogen recycling has been demonstrated in several fasting species and is characterized by a decrease in overall urea nitrogen output (Wolfe et al. 1982; Motil et al. 1990; Nordøy et al. 1990; Ramsay et al. 1991; Castellini and Rea 1992; Kirby 1992; Adams and Costa 1993; Rodrigues et al. 1998).

This leads to the question of which isotope is preferentially recycled, ^{14}N or ^{15}N. Steele and Daniel (1978) demonstrated that urine produced from cattle had consistently lower $\delta^{15}N$ values relative to their diets. Cattle fed relatively low protein silage or cake feeds (Perry et al. 1999) produced urine that was more depleted in ^{15}N relative to their diet than cattle given hay, a feed with a higher protein percentage. Further, $\delta^{15}N$ values for urine were 1–2‰ less in the 6 h before and during feeding than the 18 h following feeding. When in the "fasting" stage of a 24-hour feeding cycle, and when the cattle were fed lower amounts of protein, the animals appear to preferentially excrete ^{14}N in the urea. Thus, it appears that animals undergoing nitrogen recycling preferentially return ^{15}N to their nitrogen pool, thereby enriching their tissues in ^{15}N by utilizing the more ^{15}N-rich nitrogen source for amino acid synthesis (Minagawa and Wada 1984; Sutoh et al. 1987; Kelly 2000). Therefore, ^{15}N-enrichment in tissues of fasting animals complicates interpretation of their $\delta^{15}N$ values. Nutritional stress has been found to have no enrichment effect on ^{13}C in lipid extracted animal tissues (Teeri and Schoeller 1979; Hobson et al. 1993).

The primary objective of this study was to use and assess the viability of stable isotope analysis to estimate diet variation in a migratory, high-level predator in an oceanic system. Specifically, we tested for differences in trophic level between pregnant, migrating female fur seals and lactating, post-parturient females on the Pribilof Islands by comparing stable isotope ratios in skin samples from live fur seals. We examined differences in feeding ecology for fur seals migrating to and hauling out on St. George and St. Paul Islands and between migrating juvenile males (age ~3 years), adult, pregnant females, and two nulliparous females. Finally, we compared isotopic signatures of typical fur seal prey species with each other and with those of fur seal skin tissues to provide information on trophic level and predator/prey interactions in the eastern Bering Sea and Gulf of Alaska.

Methods

Sample collection

The study areas were located on the Pribilof Islands in the eastern Bering Sea in Alaska (Fig. 1). Tissue samples were obtained from live female fur seals on land using a hand-held 70-pound (32 kg), Barnett Trident II pistol crossbow with a 4×15 mm biopsy dart. Darts struck the animals, bounced out, and were retrieved by a tether attaching the dart to the crossbow (adapted from Gemmell and Majluf 1997). A tissue plug containing hair, skin, and a trace of fat was extracted from the dart. Female northern fur seals restrict their movements to a small number of sites throughout a rookery (Gentry 1998). Hence, repeated sampling of the same individual within one time period was avoided by targeting animals in different sections of the rookery over a period of several days.

Female fur seals were selected for sampling based upon several factors: (1) accessibility, (2) physical condition, (3) reproductive status (pregnant or recently post-parturient females, as indicated by pup proximity and pup age, were sought during early July; females with pups were chosen for August and November to maintain consistency), and (4) proximity to other animals. Tissue samples were frozen within 1–2 h and kept frozen until preparation and analysis. All tissue samples from juvenile male fur seals were collected from animals killed in the Aleut subsistence harvest. Samples from two nulliparous females were collected opportunistically from animals accidentally killed in the subsistence harvest. Tissue samples were frozen within 2–3 h of the animal's death.

Relevant prey samples were collected opportunistically in the Bering Sea. A total of 88 fur seal prey items from eight species of fishes and squid were collected in trawls by National Marine Fisheries Service (NMFS) research cruises in the Bering Sea during summer of 1997. Prey items were frozen whole upon collection until they were processed for analysis. Age of individual walleye pollock was estimated based on length (Incze et al. 1988; Sinclair et al. 1994).

Sample preparation and analysis

Sub-samples of skin tissue for both female and male fur seals were dissected from hair and fat. All tissues were washed with distilled water. Whole prey items were homogenized with tissue grinders. Samples were freeze-dried for 24 h and all lipids were removed using petroleum ether (as recommended by Dobush et al. 1985; R. Doucett, personal communication; J. Neary, personal communication) in a Soxhlet extractor for 24 h. Samples were then oven-dried at 60°C for 24 h to remove any remaining solvent. Small sub-samples of skin were cut with a scalpel; prey items were ground to a powder by hand.

For approximately two-thirds of the samples, 1.5–1.9 mg were sealed into 5×9 mm tin capsules and analyzed using a Carlo Erba NA 1500 CHN combustion analyzer interfaced to a Finnigan Delta C mass spectrometer at the Stable Isotope/Soil Biology Laboratory, University of Georgia Institute of Ecology. For the remaining samples, 8–15 mg were flame-sealed into pre-combusted

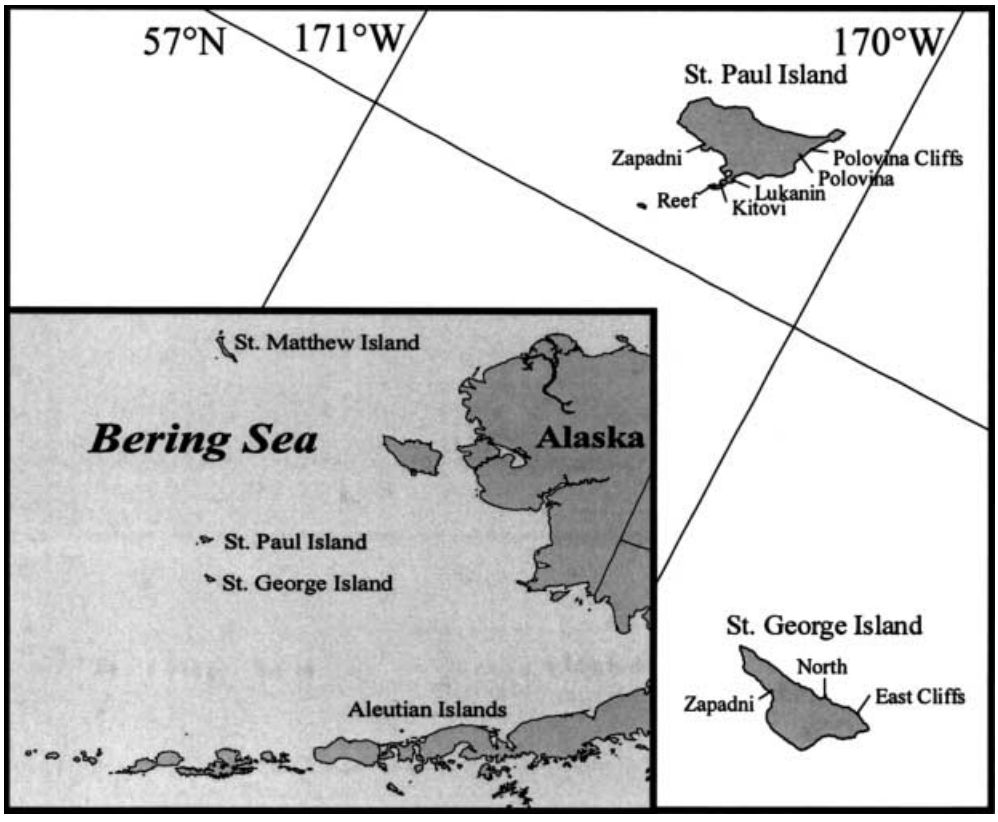

Fig. 1 Study areas shown by *sampling sites* for female and male tissue collection on St. Paul and St. George Islands in the Bering Sea

quartz tubes with 1.25 g of pre-combusted cupric oxide and 2.5 g of pre-combusted copper (Fiedler and Proksch 1975). Following the Dumas technique, they were then combusted in a muffle furnace at 850°C for 2 h and 650°C for 2 h. The gases of interest were removed by cryogenic distillation, and isotopic composition determined with a Finnegan Mat 252 mass spectrometer for carbon and a Nuclide 360 RMS mass spectrometer for nitrogen (Fiedler and Proksch 1975; Boutton 1991; Lajtha and Michener 1994). The average precision for the Dumas method is 0.10‰ (Boutton 1991), and the average precision for the in-line method for this data was 0.08‰ for nitrogen and 0.08‰ for carbon.

The natural isotopic abundance of ^{13}C or ^{15}N in a sample is expressed in delta notation, which is calculated using the equation:

$$\delta X(\Omega) = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000 \quad (1)$$

where δX is the parts-per-thousand (or "per mil") difference in isotopic composition between the sample and the standard, and R_{sample} and R_{standard} are the heavy-to-light isotope ratios of the sample and standard, respectively (i.e., $^{15}N/^{14}N$ and $^{13}C/^{12}C$) (DeNiro and Epstein 1981; Galimov 1985; Owens 1987; Ehleringer and Rundel 1989; Boutton 1991).

Statistical treatment of isotope ratio data

All data (except for the two nulliparous females) were judged to be sampled from parent distributions that were normal (Shapiro and Wilkes *W*-test for normality, SAS System for Windows v6.12, SAS Institute, Cary, N.C., 1989–1996). Analysis of variance (ANOVA) tests were used to determine equality of samples collected from females in November at different rookeries on St. Paul Island, and of samples collected from juvenile males at different haul-out sites on St. Paul Island. ANOVA tests were also performed to determine equality of isotopic signatures between different age classes of walleye pollock. Tukey-Kramer multiple comparison tests were used to sort the means for skin samples collected from juvenile males from different haul-out sites on St. Paul Island, and to sort the means for the different age classes of pollock. Unpaired *t*-tests were used to determine differences in stable nitrogen and carbon isotope ratios in female northern fur seal skin samples over time, between female and male northern fur seal skin samples, between juvenile male skin samples collected from two haul-out sites on St. George Island and between grouped haul-out sites on St. Paul Island, for animals between islands, and for differences in certain prey age classes (StatView for Windows, Abacus Concepts, Berkeley, Calif., 1992–1996). Significance was tested at the α=0.05 level.

Results

Northern fur seal tissue collection sites are shown in Fig. 1. All northern fur seal samples were collected from animals on St. Paul and St. George Islands during early July, late August, and mid-November 1997. July and August samples from females on St. George Island were collected on North ($\delta^{15}N$ n=24; $\delta^{13}C$ n=27) and East Cliffs ($\delta^{15}N$ n=22; $\delta^{13}C$ n=23) rookeries. There were no significant differences for mean $\delta^{15}N$ or $\delta^{13}C$ values between rookeries (P=0.135 and 0.494, respectively; *t*-tests), so all data were pooled as representative of St. George Island during their respective time periods. All November samples (n=3) from females on St. George Island were collected from North rookery. Sample size for females on St. George Island in November was very low, largely due to adverse weather. This small sample size may have affected some results. July and August samples from females on St. Paul Island were collected from Reef rookery

Table 1 Mean (±SE) $\delta^{15}N$ and $\delta^{13}C$ values for skin of northern fur seal females and juvenile males collected in summer and fall 1997 from the Pribilof Islands

Location	Time period	Sex	$\delta^{15}N$		$\delta^{13}C$	
			n	‰	*n*	‰
St. Paul Island, AK	July/August	Female	46	17.3±0.1	50	–16.0±0.0
St. George Island, AK	July/August	Female	46	17.3±0.1	50	–16.0±0.0
St. Paul Island, AK (Zapadni, Morjovi, Lukanin haul-outs)	July/August	Male	20	16.5±0.2	20	–17.5±0.1
St. Paul Island, AK (Gorbatch haul-out)	July/August	Male	5	15.6±0.2	5	–17.6±0.2
St. Paul Island, AK (Polovina haul-out)	July/August	Male	11	17.4±0.3	11	–17.3±0.1
St. Paul Island, AK (all haul-outs)	July/August	Male	See above	See above	36	–17.4±0.1
St. George Island, AK	July/August	Male	28	16.7±0.1	27	–17.4±0.1
St. Paul Island, AK	November	Female	15	18.1±0.2	15	–16.1±0.1
St. George Island, AK	November	Female	3	18.1±0.1	3	–16.3±0.2
St. Paul Island, AK	July/August	Nulliparous female	2	17.4±0.3	2	–17.1±0.2

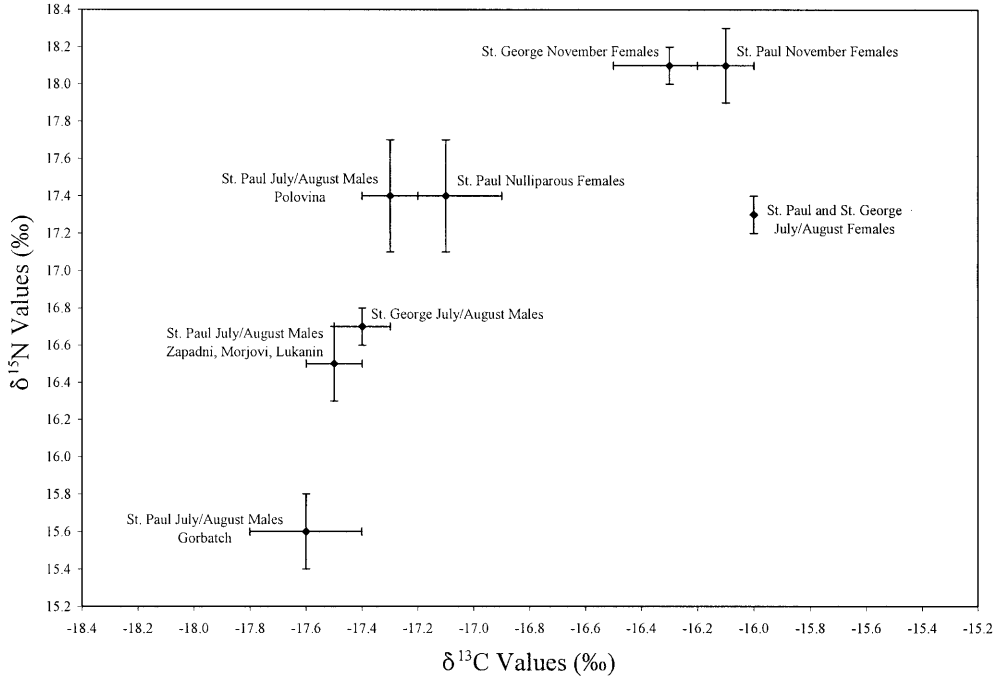

Fig. 2 Mean (±SE) stable carbon and nitrogen isotope ratios in skin tissue from northern fur seal females and juvenile males over time from St. Paul and St. George Islands in Alaska. Nulliparous females included for comparison

($\delta^{15}N$ *n*=46; $\delta^{13}C$ *n*=50); samples from summer nulliparous females were collected from haul-outs near Reef rookery (*n*=2); and November samples were collected from Kitovi (*n*=5), Polovina Cliffs (*n*=8), and Reef (*n*=2) rookeries. There were no significant differences in $\delta^{15}N$ or $\delta^{13}C$ between the three rookeries (*P*=0.082 and 0.813, respectively; ANOVA) on St. Paul Island in November, so these samples were pooled. There were no differences in mean isotopic values between July and August samples for the females on St. Paul or St. George Island ($\delta^{15}N$ *P*=0.259, $\delta^{13}C$ *P*=0.489 and $\delta^{15}N$ *P*=0.749, $\delta^{13}C$ *P*=0.844, respectively; *t*-tests), so these data were pooled for comparison with November values.

Mean isotope values for skin collected from females and juvenile males on St. Paul and St. George Islands are presented in Table 1 and Fig. 2. The mean $\delta^{15}N$ values for skin samples collected from adult female fur seals in November from St. Paul and St. George Islands (18.1‰ for both) were greater than the July/August samples (17.3‰ for both) on both islands (*P*<0.001 and *P*=0.021, respectively; *t*-tests). There were no significant differences (*P*=0.235 for St. Paul Island; *P*=0.109 for St. George Island; *t*-tests) in mean $\delta^{13}C$ values for skin from females on both islands in July/August (–16.0‰ for both) and November (St. Paul=–16.1‰; St. George= –16.3‰). There were no significant differences in mean $\delta^{15}N$ and $\delta^{13}C$ values between islands for skin samples from female fur seals taken in July/August (*P*=0.890 and *P*=0.636, respectively; *t*-tests) or November (*P*=0.981 and *P*=0.268, respectively; *t*-tests).

Skin from juvenile male fur seals was sampled from mid-July to early August from different juvenile male

Table 2 Mean (±SE) $\delta^{15}N$ and $\delta^{13}C$ values and mean standard lengths and weights for whole prey items separated by size and age class and collected in summer 1997 from the Bering Sea

Species	Mean Weight (g)	Mean Length (cm)[a]	Estimated age (years) or size class	*n*	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Walleye pollock	0.24	3.16	0[b]	10	10.8±0.1	–19.1±0.1
Walleye pollock	30.19	14.58	1–2[b]	10	12.7±0.2	–18.3±0.1
Walleye pollock	132.86	24.36	2–3[b]	5	15.2±0.2	–18.1±0.5
Walleye pollock	280.56	29.90	3–4[c]	4	16.3±0.3	–18.0±0.2
Eulachon	69.54	19.24	Medium	10	14.0±0.2	–18.4±0.1
Pacific sand lance	72.12	24.19	Large	10	9.0±0.0	–18.6±0.1
Pacific herring	135.64	23.20	Small	5	15.3±0.2	–19.3±0.5
Pacific herring	276.63	28.86	Medium	8	13.5±0.1	–17.6±0.1
Atka mackerel	199.45	23.82	Small	5	9.9±0.2	–18.5±0.1
Atka mackerel	1046.83	39.80	Large	5	10.7±0.3	–18.2±0.4
Chum salmon	1645.83	46.00	Medium	1	10.5	–19.2
Squid (*Gonatopsis borealis*)	22.4	7.7	Small	3	11.1±0.2	–18.4±0.5
Squid (*Berryteuthis magister*)	6.5	5.4	Small	3	11.4±0.2	–18.1±0.2
Squid (*B. magister*)	34.9	10.0	Medium	9	11.4±0.2	–18.3±0.2

[a] Standard length for fish; dorsal mantle length for squid
[b] Sinclair et al. (1994)
[c] Incze et al. (1988)

haul-out sites on both islands. Samples from St. Paul Island were collected from sites near Zapadni (*n*=10), Polovina (*n*=11), Reef (*n*=5), Lukanin (*n*=3), and Morjovi (*n*=7) rookeries, and on St. George Island from sites near Zapadni (*n*=16) and North (*n*=11) rookeries. We observed no significant differences in mean $\delta^{13}C$ values between the five haul-out sites on St. Paul Island (P=0.724; ANOVA), or $\delta^{15}N$ and $\delta^{13}C$ values between the two haul-out sites on St. George Island (P=0.437 and P=0.067, respectively; *t*-tests), so they were grouped as representative of their respective islands. There were significant differences in mean $\delta^{15}N$ values between haul-outs on St. Paul Island (P=0.001; ANOVA). When the means were sorted, Polovina and Reef were significantly different from each other (P<0.05; Tukey-Kramer), while the remaining haul-outs were not different (p>0.05; Tukey-Kramer). Zapadni, Lukanin, and Morjovi were grouped together (hereafter referred to as ZLM), while Polovina and Reef were kept separate. Mean $\delta^{15}N$ values from juvenile males sampled from Reef were significantly lower than values from the ZLM group (P=0.014; *t*-test) and the Polovina group (P<0.001; *t*-test). Mean $\delta^{15}N$ values from juvenile males sampled from Polovina were significantly higher than values from the ZLM group (P=0.004; *t*-test).

Mean $\delta^{15}N$ values were not different between skin sampled from juvenile males on St. George Island and from juvenile males in the ZLM group on St. Paul Island (P=0.517; *t*-test). The mean $\delta^{15}N$ values from skin sampled from juvenile males at Reef were lower than those sampled on St. George Island (P=0.001; *t*-test), and the mean $\delta^{15}N$ values from Polovina were higher than those sampled on St. George Island (P=0.003; *t*-test). There was no difference in mean $\delta^{13}C$ values between skin sampled from juvenile males on St. George or St. Paul Islands (P=0.358; *t*-test).

Mean $\delta^{13}C$ values were higher for skin samples from females (~1.4‰ greater) than for skin from juvenile males (all P<0.001; *t*-tests) on both islands. On St. George Island, mean $\delta^{15}N$ values were higher for skin samples from females over those from juvenile males (P<0.001; *t*-test). On St. Paul Island, mean $\delta^{15}N$ values were higher for skin samples collected from females over those collected from juvenile males from Reef and the ZLM haul-outs (P<0.001 for Reef; P=0.003 for ZLM group; *t*-tests). There was no difference in mean $\delta^{15}N$ values for skin samples collected from St. Paul Island females and those collected from juvenile males sampled from Polovina haul-out (P=0.396; *t*-test).

Mean isotope values for prey are presented in Table 2. Mean $\delta^{15}N$ values ranged from 9.0‰ for Pacific sand lance (*Ammodytes hexapterus*) to 16.3‰ for age 4+ year old walleye pollock. Mean $\delta^{13}C$ values ranged from –19.3‰ for small-sized Pacific herring (*Clupea pallasii*) to –17.6‰ for medium-sized Pacific herring. Mean $\delta^{15}N$ and $\delta^{13}C$ values increased with age for walleye pollock, ranging from 10.8‰ and –19.1‰ in age 0 fish, to 16.3‰ and –18.0‰ in age 4+ years pollock. There were significant differences in mean $\delta^{15}N$ and $\delta^{13}C$ values between all pollock age classes (P<0.001; ANOVA). When the means were sorted, $\delta^{15}N$ values were different for all age classes (P<0.05; Tukey-Kramer), and $\delta^{13}C$ values for age 0 pollock were significantly different from all other age classes (P<0.05; Tukey-Kramer). Atka mackerel (*Pleurogrammus monopterygius*) exhibited a more subtle isotopic shift with age, with mean $\delta^{15}N$ and $\delta^{13}C$ values ~0.8‰ and ~0.3‰ higher, respectively, in large fish over small fish. The increase in Atka mackerel mean $\delta^{15}N$ values was significant (P=0.049; *t*-test) with age, but not in mean $\delta^{13}C$ values (P=0.365; *t*-test). Mean $\delta^{15}N$ values from Pacific herring showed an opposite trend, with values ~1.8‰ higher in small fish over medium fish. Mean $\delta^{13}C$ values were ~1.7‰ higher in medium over small Pacific herring.

Mean $\delta^{15}N$ values from juvenile walleye pollock (up to 20 cm in standard length, SL) and squid had some sig-

nificant differences, but did not exhibit differences large enough to indicate they were feeding at distinctly different trophic levels. Age 0 pollock had significantly lower (P=0.03; Fisher's PLSD) mean $\delta^{15}N$ values than medium *Berryteuthis magister* by ~0.5‰. Age 1 year pollock had significantly higher (P<0.05; Fisher's PLSD) mean $\delta^{15}N$ values than all of the squid by ~1.3‰ to ~1.7‰.

Discussion

Samples collected from females in July/August reflect diet during the migration period along the southeastern Alaskan coast, in the Gulf of Alaska, and near the eastern Aleutians (April/May), and those taken in November reflect breeding season conditions in the Eastern Bering Sea (summer). Mean $\delta^{15}N$ values from skin sampled from females were not different between St. Paul and St. George Islands for their respective time periods. This indicates that females on each island were feeding at the same trophic levels regardless of their island destination during migration or island of origin during the breeding period. Mean $\delta^{15}N$ values were ~0.8‰ higher for skin samples taken from females in November than those taken in July/August. Several explanations could account for the increase in $\delta^{15}N$ values. The difference in nitrogen ratios could indicate that females migrating through the Gulf of Alaska in the spring could be choosing prey a fraction of a trophic level lower than those in the Bering Sea in the summer. However, the determination of a trophic level difference over time for animals who migrate great distances is complicated because isotope ratios vary among primary producers in marine ecosystems over geographic, seasonal and yearly time scales (Wada and Hattori 1976; Altabet and McCarthy 1985; Goering et al. 1990; Altabet and Francois 1994; Schell et al. 1998; Kline 1999), including between the Gulf of Alaska and the Bering Sea. These differences are carried up through a food web, and have implications for the isotopic enrichment of predators that are feeding while migrating across bodies of water that contain zooplankton and prey with demonstrated differences in $\delta^{15}N$ and $\delta^{13}C$ values.

For example, isotopic signatures of herbivorous copepods collected in late summer/early fall from 1985 to 1994 (coincident with fur seal breeding season) in the Eastern Bering Sea have higher $\delta^{15}N$ (9.8‰±0.2 SE) (Schell et al. 1998) values than those collected in May and June 1995 (coincident with fur seal migration) in the Gulf of Alaska (7.0‰±0.7 SD) (Kline 1999). In addition, small squid collected in the summer/early fall 1997 from the Bering Sea in this study have higher mean $\delta^{15}N$ values (11.1‰±0.2 to 11.4‰±0.2 SE; Table 2) than comparably sized squid collected in the late spring/early summers of 1992 and 1994 in the Gulf of Alaska (9.6‰±0.5) (Hobson et al. 1997). However, large size (3+ year-old; 15.2‰±0.2 to 16.3‰±0.3) and 0-age (10.8‰±0.1) pollock from the summer/early fall 1997 in the Bering Sea in this study have $\delta^{15}N$ values that are not different from pollock of the same size classes collected in the late spring/early summers of 1992 and 1994 in the Gulf of Alaska (15.7‰±0.7 and 10.9‰±0.2, respectively) (Hobson et al. 1997). The comparison of isotopic data from the squid and copepods over the different geographic areas during different seasons indicates there may have been a small increase in prey $\delta^{15}N$ values, but not necessarily an increase in the seals' trophic level, once the females started feeding in the Bering Sea. The pollock values do not support this, but the possibility should not be ignored. Finally, it must be noted that the isotopic data from other studies were collected over different years and may be inapplicable for this study.

Physiological processes can also complicate interpretation of isotopic data. The most plausible explanation for the higher mean $\delta^{15}N$ values seen in females sampled in November over those in June/July reflects the different reproductive conditions for the seals between the two time periods. The early group was pregnant, the later group was post-parturient and lactating. Lactation is the most energetically expensive part of reproduction for female mammals (e.g., Millar 1977; Gittleman and Thompson 1988), and pinnipeds have an added burden in that many fast for some period of time during lactation (e.g., Fedak and Anderson 1982; Bowen et al. 1992; Oftedal 1993; Boyd 1998). Female fur seals utilize stored energy reserves to support their metabolic overhead in addition to their lactation costs during their perinatal fast (Bonner 1968; Costa and Gentry 1986; Costa and Trillmich 1988; Trillmich 1996; Arnould 1997). The perinatal fast occurs between parturition and departure on their first feeding bout and lasts ~7 days for northern fur seals. During this time, females lose ~9 kg in mass, with only 13–14% of that mass being gained by their pups (Costa and Gentry 1986). In addition, lactating females undergo a repeated fasting/feeding regime of 1–3 days ashore fasting and suckling their pup, followed by 6–10 days feeding (Costa and Gentry 1986). This puts repeated fasting stress on the lactating female throughout the 4- to 5-month breeding season. As mentioned previously, negative nitrogen balance caused by nutritional stress can cause an animal's tissues to become ^{15}N-enriched (see Introduction), complicating the trophic interpretation of the mean $\delta^{15}N$ values from lactating females.

Skin from two nulliparous females that were sampled in July/August on St. Paul Island had $\delta^{15}N$ values (17.4‰ ±0.3) that were within range of the pregnant females sampled in July/August and appear slightly lower than lactating females sampled in November on St. Paul Island. The sample size was too small for statistical comparison, but the results suggest that pregnancy alone (as opposed to the feeding/fasting regime exhibited during lactation) may not have a dramatic ^{15}N enrichment affect on female skin tissue, and that nulliparous and pregnant females were feeding at a comparable trophic level during their spring time migrations. However, there are data from humans indicating that urea salvage occurs during early pregnancy (Forrester et al. 1994) which could lead

to a ^{15}N-enrichment in pregnant females that is not related to diet. Further sample collection from confirmed nulliparous females in the future could clarify these comparisons.

The mean $\delta^{15}N$ values for skin sampled from juvenile males on St. George Island were the same for those sampled from juvenile males on St. Paul Island from the ZLM haul-out group. Thus, these juvenile males were feeding at the same trophic level during their migration regardless of their destination island. Mean $\delta^{15}N$ values were ~0.9‰ higher for juvenile males sampled from Polovina haul-out, and ~0.9‰ lower for juvenile males sampled from Reef haul-out than both the St. George Island males and the ZLM group from St. Paul Island. Juvenile males migrating to Reef appear to be feeding at a slightly lower trophic level than those migrating to ZLM, and an even lower trophic level than those migrating to Polovina. The 5 haul-out sites are evenly spaced around St. Paul Island (Fig. 1), and there appears to be no geographic indicator to explain why these juvenile males would be feeding on trophically different prey in correlation with their haul-out site. The mean $\delta^{15}N$ values are dramatically different (~1.8‰) between Polovina and Reef which are geographically separated on St. Paul Island. Perhaps the males migrating to each of those haul-out sites traveled through distinct areas, thereby ingesting prey with significantly different trophic values during their spring migration.

The mean $\delta^{15}N$ values for skin sampled from all females in July/August on St. George and St. Paul Islands were ~0.8‰ higher than those for juvenile males collected from the ZLM and St. George Island haul-outs, and ~1.7‰ higher than those for males collected from Reef haul-out at the same time. This indicates that migrating females were possibly feeding at a slightly higher trophic level than migrating juvenile males. Pregnancy may also have contributed to the higher $\delta^{15}N$ values (Forrester et al. 1994). The 11 juvenile males sampled from Polovina haul-out on St. Paul Island were the exception. Their mean $\delta^{15}N$ values were not different from the females sampled on St. Paul Island, further suggesting that juvenile males migrating to specific haul-out sites on a particular island are not feeding at uniform trophic levels.

Skin sampled from females on each island exhibited no differences in mean $\delta^{13}C$ values over time. $\delta^{13}C$ values are weakly affected by trophic levels, and can be used as an indication of habitat usage (Wada et al. 1987; Schell et al. 1989a, 1989b; France and Peters 1997). Available data suggest three possible migration pathways for adult females, two of which place them coastally in the Gulf of Alaska and eastern Aleutians, and one which places them in the North Pacific/Southern Bering Sea near the eastern Aleutians during the late spring/early summer (Bigg 1990). One of the pathways suggests that females migrate north along the coast from California, Oregon and Washington, to the Gulf of Alaska, where they continue on a coastal path to the eastern Aleutians and up to the Pribilof Islands. A second pathway suggests offshore migration north to the Gulf of Alaska, and then a coastal route west to the eastern Aleutians and up to the Pribilofs, while a third suggests a completely offshore route from California, northwest to the Aleutians and up to the Pribilofs. Our $\delta^{13}C$ data suggests that females are feeding in similar domains both during migration and during the breeding season. Specifically, they appear to be feeding on-shelf (coastally) and not offshore. This suggests that females follow a migratory route that places them in coastal waters off the Gulf of Alaska in the spring, where they continue moving coastally westward to the Aleutians and then up to the Pribilof Islands. While on the Pribilofs during the breeding season, the $\delta^{13}C$ values suggest that they continue feeding onshelf.

Skin sampled from the two nulliparous females and the juvenile males from both islands had lower mean $\delta^{13}C$ values (–17.1±0.2) than those of the pregnant females (Fig. 2), but were not different from each other. Bigg (1990) estimated that the majority of 3-year-old males remain offshore in the eastern North Pacific and Gulf of Alaska between January and May, and are rarely in coastal regions. He also suggested that very young (1- to 2-year-old) females also follow an offshore migration pattern, remaining with the juvenile males in the offshore eastern North Pacific and Gulf of Alaska during the late spring/early summer, but that older (3–4 year-old) nonpregnant females follow the same coastal route as mature, pregnant females. The nulliparous females in this study were 3 and 4 years of age (based on growth line analysis of upper canine teeth), and their carbon isotope data suggests that they were not migrating with the older females. Instead, they were feeding in a similar location to the juvenile males, and that both juvenile males and nulliparous females were migrating offshore, contrasting with the pregnant females who were migrating in coastal waters. The mean $\delta^{13}C$ values for the three groups are consistent with $\delta^{13}C$ patterns for coastal versus offshore isotopic patterns (Hobson 1993; France 1995). There were no differences in mean $\delta^{13}C$ values between islands for migrating juvenile males, migrating pregnant females and lactating females. This suggests that, for each group, there was no difference in habitat usage regardless of the island of destination or island of origin.

As mentioned previously, the accepted step-wise enrichment of ^{15}N between prey and predator is ~3–5‰ (see Introduction). However, this ^{15}N trophic enrichment is based primarily on analysis of muscle tissue (e.g., Minagawa and Wada 1984; Fry 1988; Hobson et al. 1994). In this study, the sampling constraints imposed by darting live females precluded collecting muscle tissue, and skin tissue was used instead. Phocid seal skin (n=9) was reported to have a mean $\delta^{15}N$ value that was 2.3‰ higher than its prey (Hobson et al. 1996). While phocid seals are not the same family as northern fur seals, the 2–3‰ change in $\delta^{15}N$ per trophic level is indicative of pinniped skin trophic enrichment values.

The use of stable isotopes to delineate exact prey for northern fur seals is impractical since the prey exhibit overlap in their $\delta^{15}N$ signatures. However, isotopic trends or shifts over seasons and longer time scales can be observed. In addition, the ^{15}N-enrichment of 2–3‰ between diet and pinniped skin allows for general inferences about the trophic level at which northern fur seal females and juvenile males were feeding during their 1997 migration and what prey that trophic level may have encompassed. The mean $\delta^{15}N$ value for the majority of juvenile males observed in this study was ~16.6‰, which suggests they were feeding on prey with mean $\delta^{15}N$ values between 13.6‰ and 14.6‰. Published $\delta^{15}N$ values for prey taken near the Alaska Peninsula and Kodiak Island in unknown seasons of 1994 and 1996 indicate that the diet of most migrating juvenile males may have included adult sizes of the following: herring (species unknown) (14.3‰±0.1 to 14.7‰±0.1), sole (species unknown) (14.1‰±0.3 to 14.4‰±0.3), walleye pollock (14.2‰±0.3), and squid (species unknown) (13.8‰±0.6) (Hirons et al. 1998). Juvenile males sampled from Polovina haul-out on St. Paul Island had a higher mean $\delta^{15}N$ value (17.4‰) and were feeding at a slightly higher trophic level. Their prey may have had mean $\delta^{15}N$ values between 14.4‰ and 15.4‰, which included the same prey as the ZLM and St. George Island males, with the addition of adult capelin (*Mallotus villosus*) (15.5‰±0.2) and the possible exception of the squid (Hirons et al. 1998). The juvenile males sampled near Reef Rookery had a lower mean $\delta^{15}N$ value (15.6‰), indicating they were feeding at a lower trophic level than the majority of juvenile males. Their prey may have had mean $\delta^{15}N$ values between 12.6‰ and 13.6‰, which included squid, adult walleye pollock (13.2‰±0.2) from around Kodiak Island, and juvenile capelin (12.6‰±0.2) (Hirons et al. 1998). Mean $\delta^{15}N$ for migratory adult females was ~17.2‰, which suggests prey values between 14.2‰ and 15.2‰, encompassing similar prey to that of the juvenile males sampled near Polovina (Hirons et al. 1998).

Stepwise ^{15}N trophic enrichment can also be applied to the females sampled in November to estimate their trophic position in the Bering Sea during their time on the Pribilof Islands. The prey analyzed in this study were collected from the Bering Sea in the summer of 1997, so it is appropriate to compare their isotope values with the $\delta^{15}N$ values of the lactating females. The mean $\delta^{15}N$ value for skin samples collected in November from females on both islands was 18.1‰, which indicates females may have been feeding on prey with $\delta^{15}N$ values of 15.1‰ to 16.1‰. That includes 2- to 4-year-old walleye pollock (15.2‰±0.2 to 16.3‰±0.3) and small Pacific herring (15.3‰±0.2). These numbers do not include small juvenile walleye pollock (age 0–1 year) and squid with values of around 11‰, which are known primary prey items based on scat and stomach contents analysis (Sinclair et al. 1994; Antonelis et al. 1997).

There are several possible reasons for these discrepancies. The diet of the female northern fur seals feeding from the Pribilof Islands may not have been composed primarily of juvenile pollock and squid as indicated by studies using stomach content and scat analyses. The previously addressed caveats (see Introduction) of these methods may be contributing to a misclassification of their diet. Additionally, the diet may have changed over time to include a higher proportion of older pollock and less squid and juvenile pollock. The most plausible explanation is that the previously mentioned ^{15}N-enrichment caused by fasting during lactation inflated the $\delta^{15}N$ values of skin collected from lactating females, thereby confusing the isotopic comparisons between prey and predator. This probable enrichment of ^{15}N could be large enough to skew trophic predictions in the absence of information regarding isotopic fractionation dynamics of physiological processes other than those induced by diet.

Mean $\delta^{15}N$ values for prey show that walleye pollock feed at different trophic levels depending on their age. The oldest pollock (3–4 year-old) occupied the highest trophic position (mean $\delta^{15}N$=16.3‰), with the younger age groups showing progressively lower values. Age 2–3 year and age 3–4 year pollock are feeding at over-lapping trophic levels shown by the difference in their $\delta^{15}N$ values being less than 3‰. Our results support stomach content studies that show adult pollock feed mostly on juvenile pollock and, to a lesser extent, on other juvenile fish (Incze et al. 1988). In contrast, juvenile pollock feed almost exclusively on zooplankton (Incze et al. 1988). The trend for $\delta^{13}C$ is similar. The difference in mean $\delta^{15}N$ values between the age 0 and the age 3–4 pollock is ~6‰ suggesting a separation of two trophic levels between these age groups. The difference in mean $\delta^{13}C$ values between these same age groups (~1.1‰) indicates a separation of at least one trophic level.

Atka mackerel also showed a prey shift with age. Orlov (1997) compared diets of Atka mackerel under 33 cm and greater than 33.5 cm, and found that the frequency of occurrence of copepods was greater for small mackerel, and the occurrence of small fishes was substantially greater for the larger mackerel. Our results support those of Orlov (1997). In addition, the overlap in trophic level indicated by Orlov (1997) is also shown, because the difference in $\delta^{15}N$ values does not approach the step-wise enrichment of ~3‰ that would suggest trophic segregation. The trophic enrichment of larger fishes over smaller fishes is also suggested by the slight difference in their $\delta^{13}C$ values.

Grosse and Hay (1988) reported that juvenile and adult Pacific herring eat small zooplankton: primarily copepods for juvenile herring and larger zooplankton, such as euphausids and decapod larvae, for adult herring. These differences would not indicate a dramatic trophic shift. Indeed, although the greater $\delta^{15}N$ ($P<0.001$; *t*-test) in small-sized Pacific herring than in larger herring is counter intuitive, the difference is not large enough to segregate them trophically. The smaller herring may have been feeding on prey more enriched in ^{15}N than the

older fish were. The $\delta^{13}C$ for Pacific herring shows an opposite trend, with a significant (P=0.002; t-test) enrichment of ~1.7‰ in medium-sized over the smaller herring. This suggests that the medium-sized herring may have fed more in coastal and/or mid-latitude waters than the smaller herring (Hobson 1993; France 1995; Burton and Koch 1999). There were no differences in $\delta^{15}N$ and $\delta^{13}C$ values (all P>0.05; ANOVA) between the small and medium-sized squid of both species.

The vertical trophic structure suggested by $\delta^{15}N$ in prey species is different from that suggested by $\delta^{13}C$. As mentioned previously, carbon enrichment could be influenced by origin of prey and their feeding locations. Nitrogen may be a stronger indicator of trophic level in the prey organisms than it is for fur seals, because of the influence that lactation has on ^{15}N enrichment in the seals. $\delta^{13}C$ values can be used to differentiate between oceanic and coastal and/or benthic feeders and may also be an indicator of trophic level, but this aspect deserves further study. Analysis of prey collected off the coasts of California, Oregon, Washington, British Columbia, and in the Gulf of Alaska from the same time period as fur seal migration would strengthen the prey trophic structure analysis and provide a better idea of migration versus breeding diet for fur seals. Finally, other methods such as fatty acid analysis of prey/predator tissues may help provide a clearer picture of fur seal diet than isotope analysis.

In summary, mean $\delta^{15}N$ values indicate that migrating females may be feeding at a slightly lower trophic level than lactating/breeding season females. However, lactation had a strong influence on the ^{15}N-enrichment seen in the breeding season females over the migrating females, confounding the trophic interpretation. Mean $\delta^{15}N$ values also indicate that females are feeding at a slightly higher trophic level than juvenile males during their respective migrations. Mean $\delta^{13}C$ values indicate that pregnant females spent the late stage of their migration in coastal waters, while nulliparous and juvenile males spent the spring stage of their migration in offshore waters. Mean $\delta^{15}N$ values from prey analyzed in this study indicated trophic shifts with age for pollock and Atka mackerel, and provided insight into the type of prey eaten by breeding-season females. Isotopic values of prey from other studies provided data on the feeding ecology of migrating juvenile males and females.

Acknowledgements All northern fur seal samples were collected under National Marine Fisheries Service (NMFS) permit number 837. We thank J. Baker, T. Loughlin, T. Spraker, and R. Towell who assisted with tissue collection. We thank the people at the Alaska Fisheries Science Center who collected prey items on the summer 1997 FOCI and RACE Division cruises in the Bering Sea. Primary funding was provided by the National Marine Mammal Laboratory (NMML), and the material is based in part upon work supported by the Texas Advanced Research Program under grant number 010298-015B. We thank J. Baker, G. Duker, M. Krahn, J. Lee, T. Loughlin, K. McFadden, P. Ressler, B. Robson, J. Sease, K. Winemiller, and two anonymous reviewers for their comments on improving this manuscript.

References

Adams SH, Costa DP (1993) Water conservation and protein metabolism in northern elephant seal pups during the postweaning fast. J Comp Physiol B 163:367–373

Altabet MA, Francois R (1994) Sedimentary nitrogen isotopic ratio as a recorder for surface ocean nitrate utilization. Global Biogeochem Cycles 8:103–116

Altabet MA, McCarthy JJ (1985) Temporal and spatial variations in the natural abundance of ^{15}N in PON from a warm-core ring. Deep Sea Res A 32:755–772

Ambrose SH, DeNiro MJ (1986) The isotopic ecology of East African mammals. Oecologia 69:395–406

Antonelis GA, Fiscus CH, DeLong RL (1984) Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978–79. Fish Bull 82:67–76

Antonelis GA, Stewart BS, Perryman WF (1990) Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). Can J Zool 68:150–158

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

Arnould JPY (1997) Lactation and the cost of pup-rearing in Antarctic fur seals. Mar Mammal Sci 13:516–526

Bigg MA (1986) Arrival of northern fur seals, *Callorhinus ursinus*, on St. Paul Island, Alaska. Fish Bull 84:383–394

Bigg MA (1990) Migration of northern fur seals (*Callorhinus ursinus*) off western North America (Canadian Technical Report of Fisheries and Aquatic Science 1764). Pacific Biological Station, Nanaimo, British Columbia

Bonner WN (1968) The fur seal of South Georgia. Sci Rep Br Antarct Surv 56:1–81

Boutton TW (1991) Stable carbon isotope ratios of natural materials: I. Sample preparation and mass spectrometric analysis. In: Coleman DC, Fry B (eds) Carbon isotope techniques. Academic Press, San Diego, pp 155–171

Bowen DW, Oftedal OT, Boness DJ (1992) Mass and energy trasfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). Physiol Zool 65:844–866

Boyd IL (1998) Time and energy constraints in pinniped lactation. Am Nat 152:717–728

Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biol 19:272–282

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

Castellini MA, Rea LD (1992) The biochemistry of natural fasting at its limits. Experientia 48:575–582

Costa DP, Gentry RL (1986) Free-ranging energetics of northern fur seals. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey, pp 79–101

Costa DP, Trillmich F (1988) Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galápagos fur seals (*Arctocephalus galapagoensis*). Physiol Zool 61:160–169

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Dobush GR, Ankney CD, Krementz DG (1985) The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. Can J Zool 63:1917–1920

Doucett RR, Booth RK, Power G, McKinley RS (1999) Effects of spawning migration on the nutritional status of anadromous

Atlantic salmon (*Salmo salar*): insights from stable isotope analysis. Can J Fish Aquat Sci 56:2172–2180
Dunton KH, Saupe SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. Mar Ecol Prog Ser 56:89–97
Ehleringer JR, Rundel PW (1989) Stable isotopes: History, units, and instrumentation. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. Springer, Berlin Heidelberg New York, pp 1–15
Fedak MA, Anderson SA (1982) The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). J Zool Lond 198:473–479
Fiedler R, Proksch G (1975) The determination of nitrogen-15 by emission and mass spectrometry in biochemical analysis: a review. Anal Chim Acta 78:1–62
Forrester T, Badaloo AV, Chandrasekar P, Jackson AA (1994) Urea production and salvage during pregnancy in normal Jamaican women. Am J Clin Nutr 60:341–6
France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar Ecol Prog Ser 124:307–312
France RL, Peters RH (1997) Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs. Can J Fish Aquat Sci 54:1255–1258
Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol Oceanogr 33:1182–1190
Galimov EM (1985) The biological fractionation of isotopes. Academic Press, Orlando
Gannes LZ, O'Brien DM, Martínez del Rio C (1997) Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology 78:1271–1276
Gemmell NJ, Majluf P (1997) Projectile biopsy sampling of fur seals. Mar Mammal Sci 13:512–516
Gentry RL (1998) Behavior and ecology of the northern fur seal. Princeton University Press, Princeton
Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction. Am Zool 28:863–875
Goering J, Alexander V, Haubenstock N (1990) Seasonal variability of stable carbon and nitrogen isotopic ratios of organisms in a North Pacific bay. Estuarine Coastal Shelf Sci 30:239–260
Grosse DJ, Hay DE (1988) Pacific herring, *Clupea harengus pallasi*, in the northeast Pacific and Bering Sea. In: Wilimovsky NJ, Incze LS, Westrheim SJ (eds) Species synopses: life histories of selected fish and shellfish of the Northeast Pacific and Bering Sea. Washington Sea Grant Program and Fisheries Research Institute, University of Washington, Seattle, pp 35–54
Hildebrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C (1996) Use of stable isotopes to determine diets of living and extinct bears. Can J Zool 74:2080–2088
Hirons AC, Schell DM, Springer AM (1998) Isotope ratios in Steller sea lions, northern fur seals, and harbor seals of the Bering Sea and western Gulf of Alaska: trophic implications. In: Schell DM (ed) Testing conceptual models of marine mammal trophic dynamics using carbon and nitrogen stable isotope ratios (OCS Study MMS98–0031). U.S. Dept. of Interior, Minerals Management Service, Anchorage, pp 31–54
Hobson KA (1990) Stable isotope analysis of marbled murrelets: Evidence for fresh-water feeding and determination of trophic level. Condor 92:896–903
Hobson KA (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable isotope models. Mar Ecol Prog Ser 95:7–18
Hobson KA, Clark RG (1992a) Assessing avian diets using stable isotopes. I. Turnover of ^{13}C in tissues. Condor 94:181–188
Hobson KA, Clark RG (1992b) Assessing avian diets using stable isotopes. II. Factors influencing diet-tissue fractionation. Condor 94:189–197
Hobson KA, Schell DM (1998) Stable carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*). Can J Fish Aquat Sci 55:2601–2607
Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol Prog Ser 84:9–18
Hobson KA, Alisaukas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95:388–394
Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786–798
Hobson KA, Schell DM, Renouf D, Noseworthy E (1996) Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can J Fish Aquat Sci 53: 528–533
Hobson KA, Sease JL, Merrick RL, Piatt JF (1997) Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. Mar Mammal Sci 13:114–132
Houpt TR (1963) Urea utilization by rabbits fed a low-protein ration. Am J Physiol 205:1144–1150
Houpt TR, Houpt KA (1968) Transfer of urea nitrogen across the rumen wall. Am J Physiol 214:1296–1303
Houpt TR, Houpt KA (1971) Nitrogen conservation by ponies fed a low-protein ration. Am J Vet Res 32:579–588
Incze LS, Macgill Hynde C, Kim S, Strickland R (1988) Walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea. In: Wilimovsky NJ, Incze LS, Westrheim SJ (eds) species synopses: life histories of selected fish and shellfish of the Northeast Pacific and Bering Sea. Washington Sea Grant Program and Fisheries Research Institute, University of Washington, Seattle, pp 55–69
Jackson AA (1998) Salvage of urea-nitrogen in the large bowel: functional significance in metabolic control and adaptation. Biochem Soc Trans 26:231–6
Kajimura H (1984) Opportunistic feeding by the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea (NOAA Technical Report NMFS SSRF-779). US Department of Commerce, Washington, DC
Kajimura H (1985) Opportunistic feeding by the northern fur seal (*Callorhinus ursinus*). In: Beddington JR, Beverton RJH, Lavigne DM (eds) Marine mammals and fisheries. Allen and Unwin, London, pp 300–318
Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78:1–27
Kirby VL (1992) The regulation of fuel homeostasis in young northern elephant seals. PhD Thesis, University of California, Santa Cruz
Kline TC (1999) Temporal and spatial variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in pelagic biota of Prince William Sound, Alaska. Can J Fish Aquat Sci 56 (Suppl. 1):94–117
Kurle CM (1998) Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*). MS Thesis, Texas A&M University, College Station
Lajtha K, Michener RH (1994) Introduction. In: Lajtha K, Michener RH (eds) Stable isotopes in ecology and environmental science. Blackwell, Oxford, pp xi-xix
McConnaughey T, McRoy CP (1979) Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar Biol 53:257–262
Michener RH, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: Lajtha K, Michener RH (eds) Stable isotopes in ecology and environmental science. Blackwell, Oxford, pp 138–157
Millar JS (1977) Adaptive feature of mammalian reproduction. Evolution 31:370–386
Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140
Mizutani H, Fukuda M, Kabaya Y, Wada E (1990) Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk 107:400–403

Motil KJ, Montandon CM, Thotathuchery M, Garza C (1990) Dietary protein and nitrogen balance in lactating and nonlactating women. Am J Clin Nutr 51:378–84

Nordøy ES, Ingebretsen OC, Blix AS (1990) Depressed metabolism and low protein catabolism in fasting grey seal pups. Acta Physiol Scand 139:361–369

Oftedal OT (1993) The adaptation of milk secretion to the constraints of fasting in bears, seals, and baleen whales. J Dairy Sci 76:3234–3246

Orlov AM (1997) Mesopelagic fishes as prey of Atka mackerel (*Pleurogrammus monopterygius*, Hexagrammidae, Scorpaeniformes) off the Northern Kuril Islands. In: Forage fishes in marine ecosystems. Proceedings of the International Symposium on the role of forage fishes in marine ecosystems (Alaska Sea Grant College Program Report 97–01). University of Alaska, Fairbanks, pp 323–335

Owens NJP (1987) Natural variations in ^{15}N in the marine environment. Adv Mar Biol 24:389–451

Perez MA, Bigg MA (1986) Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fish Bull 84:957–971

Perry TW, Cullison AE, Lowrey RS (1999) Feeds and feeding. Prentice Hall, Upper Saddler River

Ramsay MA, Hobson KA (1991) Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. Oecologia 86:598–600

Ramsay MA, Nelson RA, Stirling I (1991) Seasonal changes in the ratio of serum urea to creatinine in feeding and fasting polar bears. Can J Zool 69:298–302

Rau GH, Sweeney RE, Kaplan IR (1982) Plankton ^{13}C:^{12}C ratio changes with latitude: differences between northern and southern oceans. Deep Sea Res 29:1035–1039

Rau GH, Mearns AJ, Young DR, Olson RJ, Schafer HA, Kaplan IR (1983) Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. Ecology 64:1314–1318

Rodrigues E, Rubens R, Bacila M (1998) Ureogenesis in Antarctic birds – blood levels of nitrogen compounds and liver and kidney arginase in penguins. Antarct Rec 42:111–119

Saupe SM, Schell DM, Griffiths WB (1989) Carbon-isotope ratio gradients in western arctic zooplankton. Mar Biol 103:427–432

Schell DM, Saupe SM, Haubenstock N (1989a) Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}C$ techniques. Mar Biol 103:433–443

Schell DM, Saupe SM, Haubenstock N (1989b) Natural isotope abundances in bowhead whale (*Balaena mysticetus*) baleen: markers of aging and habitat usage. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. Springer, Berlin Heidelberg New York, pp 260–269

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

Schimel DS (1993) Theory and application of tracers. Academic Press, San Diego

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

Steele KW, Daniel RM (1978) Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. J Agric Sci 90:7–9

Sutoh M, Koyama T, Yoneyama T (1987) Variations of natural ^{15}N abundances in the tissues and digesta of domestic animals. Radioisotopes 36:74–77

Teeri JA, Schoeller DA (1979) $\delta^{13}C$ values of an herbivore and the ratio of C_3 to C_4 plant carbon in its diet. Oecologia 39:197–200

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. Oecologia 57:32–37

Treacy SD, Crawford TW (1981) Retrieval of otoliths and statoliths from gastrointestinal contents and scats of marine mammals. J Wildl Manage 45:990–993

Trillmich F (1996) Parental investment in pinnipeds. Adv Stud Behav 25:533–577

Wada E, Hattori A (1976) Natural abundance of ^{15}N in particulate organic matter in the North Pacific Oecan. Geochim Cosmochim Acta 40:249–251

Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. Deep Sea Res 34:829–841

Wada E, Mizutani H, Minagawa M (1991) The use of stable isotopes for food web analysis. Crit Rev Food Sci Nutr 30:361–371

Waterlow JC, Garlick PJ, Millward DJ (1978) Protein turnover in mammalian tissues and in the whole body. North-Holland, Amsterdam

Welle S (1999) Human protein metabolism. Springer, Berlin Heidelberg New York

Wolfe RR, Nelson RA, Stein TP, Rogers L, Wolfe MH (1982) Urea nitrogen re-utilization in hibernating bears. Fed Proc 41:1623