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Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis

Larissa-A. Dehn · Gay G. Sheffield · Erich H. Follmann · Lawrence K. Duffy · Dana L. Thomas · Todd M. O'Hara

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Abstract Feeding habits of ringed (*Phoca hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*) and ribbon (*Phoca fasciata*) seals and walrus (*Odobenus rosmarus*) were studied using stomach contents and stable carbon and nitrogen isotopes. Bearded seals fed benthically, primarily crustaceans and mollusks. Both zooplankton and fish were significant prey for ringed seals, while fish was principal spotted seal prey. Few gastric contents were available from ribbon seals. $\delta^{15}N$ was positively correlated with age in ribbon seals and $\delta^{13}C$ was positively correlated with age in ringed and ribbon seals. $\delta^{15}N$ was highest in spotted seals, in agreement with their fish-dominated diet. $\delta^{15}N$ was not different between Alaskan-harvested ringed and bearded seals, while $\delta^{15}N$ was lowest in ribbon seals and walrus. Carbon-13 was most enriched in bearded seals and walrus reflecting benthic ecosystem use. Canadian ringed seals were depleted in ^{13}C compared to Alaskan pinnipeds, likely because of Beaufort Sea versus Chukchi and Bering seas influence.

L.-A. Dehn (✉) · E. H. Follmann · L. K. Duffy · T. M. O'Hara
Institute of Arctic Biology, University of Alaska Fairbanks,
Fairbanks, AK 99775-7000, USA
e-mail: ftld@uaf.edu

G. G. Sheffield
Alaska Department of Fish and Game, Fairbanks,
Division of Wildlife Conservation,
Fairbanks, AK 99701-1599, USA

D. L. Thomas
Department of Mathematics and Statistics,
University of Alaska Fairbanks,
Fairbanks, AK 99775-6660, USA

T. M. O'Hara
Department of Wildlife Management,
North Slope Borough, Barrow, AK 99723, USA

Introduction

Distribution, movement and feeding ecology of ringed (*Phoca hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*) and ribbon (*Phoca fasciata*) seals are strongly associated with Arctic sea ice (Braham et al. 1984). They are commonly referred to as ice or pagophilic seals, but are adapted to different niches within the sea ice environment, and only some overlap occurs among species (Burns 1970; Simpkins et al. 2003). These seals are important prey to higher trophic level organisms, including Arctic fox (*Alopex lagopus*), polar bear (*Ursus maritimus*), humans and some walrus (*Odobenus rosmarus*) (Smith 1976; Lowry and Fay 1984; Hammill and Smith 1991; Derocher et al. 2002). Ice seals have significant nutritional and cultural importance to the Native coastal population of Alaska and other Arctic areas. Trophic relationships are of key importance to the understanding, management and conservation of free-ranging marine mammals. Nutritional status of marine mammals is a factor that can limit reproductive output and thus population growth.

In the past, analysis of stomach contents has been used extensively to determine feeding ecology of pagophilic seals (Frost and Lowry 1980; Lowry et al. 1980a, b; Bradstreet and Finley 1983; Finley and Evans 1983; Smith 1987). Recently, it was suggested that analysis of stomach contents or scats of marine mammals is strongly biased and overestimates prey with chitinous structures (e.g., crustaceans, cephalopod beaks) and fish otoliths that resist digestion or are retained in the stomach, and underestimates soft prey such as snails and mussels that are digested within hours (Murie and Lavigne 1986; Gales and Cheal 1992; Bowen 2000; Sheffield et al. 2001). Secondary ingestion of prey, such as digestive tract contents of ingested fish, could also lead to biased prey assessments (Santos et al. 2001). It is therefore difficult to accurately assess the importance of prey species, prey preference or dietary shifts as stomach contents only present a single point in time and empty stomachs yield no prey-based information. The use of other methods has been suggested by Sheffield et al. (2001) to identify diet, and a combination of classic methods with chemical feeding ecology has proven powerful in dietary reconstructions (Hobson et al. 1997; Burns et al. 1998).

Stable isotopes of carbon and nitrogen have become increasingly important in trophic ecology studies. They occur naturally and nitrogen isotope ratios become enriched in consumer tissues as trophic level increases due to selective incorporation of the heavier isotope (^{15}N) in tissues (DeNiro and Epstein 1981). Thus, nitrogen isotope analysis is helpful in establishing trophic level and predator-prey relationships (Kelly 2000). However, turnover rates and tissue- and species-specific enrichment factors are poorly understood and make evaluation of stable isotope ratios difficult (Gannes et al. 1997; Adams and Sterner 2000; McCutchan et al. 2003). Further, biological variables, e.g., age, body condition, gestation, lactation, water stress, body protein catabolism and urea recycling can have substantial impact on stable isotope ratios and their interpretation (Hobson et al. 1993; Hobson et al. 1997; Fernandez-Mosquera et al. 2001).

Stable carbon isotopes may enrich in consumer tissues to a minor degree and are therefore less useful in the determination of trophic position or predator-prey relationships (Tieszen et al. 1983; France 1995a). However, species differences in δ^{13}C can provide insights on spatial habitat use and carbon sources (France 1995b, Smith et al. 1996; Schell et al. 1998; Burton and Koch 1999).

Feeding ecology of ice seals in the Alaskan Arctic has been determined almost solely via stomach contents analysis, and few data are available on stable isotopes in ice seals. However, stable isotope analysis provides a cost effective and potentially minimally invasive (via biopsy sampling) alternative to monitor trophic level and possibly nutritional status of free-ranging ice seals. In addition, stable isotopes have become important tools for ecotoxicological studies to assess contaminant transfer and magnification (Fisk et al. 2001; Hobson et al. 2002; Dehn et al. 2006a). Interpretation of baseline stable carbon and nitrogen isotope ratios and their natural variability can be more conclusive when prey composition and seal age are known. Simultaneous examination of stomach contents and stable isotope ratios promises the most success with dietary reconstructions.

The objectives of this study are threefold and aim to (1) evaluate and compare feeding ecology of Arctic phocids harvested in Alaska and Canada using stomach contents and stable isotope analysis, (2) provide baseline data for stable isotopes in muscle of apparently healthy pinnipeds and typically ingested prey and (3) discuss isotope ratios in muscle and prey composition in stomachs with regard to age.

Materials and methods

Sample collection

All marine mammal samples were obtained during Native subsistence harvests and thus most seals were acquired in nearshore areas. Basic morphometrics, e.g., body length, blubber thickness and sex were recorded. Seals were grossly examined for lesions and parasites. Lumbar muscle samples and stomachs were collected from ringed and bearded seals in Barrow, Alaska mainly during the summer period from 1996 to 2003. Ringed seal samples also were collected in Holman, NWT, Canada during summer, 2001. Tissues of spotted seals were collected in Little Diomede and Shishmaref, Alaska primarily during summer and fall in 2000–2001 and 2003. Ribbon seal samples were acquired in Little Diomede, Alaska, during summer 2003. Walrus muscle was obtained opportunistically in Barrow and Little Diomede during summer 1998 and 2003 and serves mainly as a comparison to bearded seal muscle. Figure 1 shows communities where samples were collected, and Table 1 summarizes sample sizes. Muscle tissue was sub-sampled under clean conditions with titanium or ceramic blades on a Teflon covered surface, following the sampling protocol for contaminants by Becker et al. (1999) and stored at –20°C in acid-washed vials or whirlpacks$^{\mathrm{TM}}$ until analysis. Several potential prey species were collected or donated by subsistence hunters in Barrow and the Alaskan Bering Strait region. Marine mammal samples were collected and analyzed under Permit Nos. 782–1399, 358–1585 and 932-1489-03.

Stomach contents analysis

Stomachs of ringed and bearded seals were collected by tying off cardiac and pyloric sphincters to avoid spillage, placed into a bag and frozen at –20°C until analysis in Fairbanks. Stomachs obtained from spotted and ribbon seals near Little Diomede and Shishmaref were archived and analyzed by the Alaska Department of Fish and Game (ADF& G) in Fairbanks.

Stomach contents were weighed to the nearest gram for ringed seals and with a chatillon scale (0.1 pound increments) for bearded seals and sequentially washed through three sieves with mesh sizes 3.96, 1.4 and 0.5 mm. Spotted and ribbon seal stomach contents were sequentially washed through sieves with mesh sizes 1.0 and 0.5 mm. Standard reference keys (Rathbun 1929; Akimushkin 1965; Keen and Coan 1974; Butler 1980; Frost and Lowry 1980; Frost 1981; Härkönen 1986; Kathman et al. 1986; Foster 1991; Jensen 1995; Harvey et al. 2000) were used for the identification of fish otoliths and invertebrate prey to the lowest possible taxonomic level. Identifiable prey were sorted, counted and weighed to the nearest milligram. Due to digestive biases on diagnostic tissues of varying endurance (e.g., overestimation of chitinous prey versus under-representation of soft prey, such as echiurid worms and polychaetes) a ranking of prey by weight or numerical frequency of prey in the stomach was not determined and only the frequency of occurrence of prey species i (FO_i method) was noted for all seals. FO_i is defined as the percentage of stomachs that contained one or more individuals of the prey species i:

$$\mathrm{FO}_i = (p_i/p_t) \times 100,$$

where p_i is the number of stomachs with the prey species i and p_t is the number of stomachs with digesta (Hjelset et al. 1999). Nematodes in the stomach and cestodes migrating from the duodenum to the stomach after death were found in all seals, in particular bearded seals on a regular basis and were considered normal (Lauckner 1985). They were not analyzed as a food item and hence not included in p_t.

Stable isotopes

Lumbar muscle of pinnipeds and total body homogenates of potential prey were freeze-dried and ground into a fine powder. For each sample, 0.2–0.4 mg of tissue was weighed into a 4.75 × 4 mm tin capsule and folded into a cube. Samples were analyzed for both stable carbon and nitrogen ratios at the University of Alaska Fairbanks (UAF) using a Finnigan MAT Delta$^{\mathrm{Plus}}$XL Isotope Ratio Mass Spectrometer (IRMS) directly coupled to a Costech Elemental Analyzer (ESC 4010). Samples were flash combusted at 1,020°C, followed by on-line chromatographic separation of sample N_2 and CO_2 with He as carrier gas. Samples analyzed for $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were standardized against atmospheric N_2 and PeeDee Belemnite limestone, respectively. Enrichment of a particular isotope was reported using the following notation and equation:

$$\delta R = \left(\left(R_{\mathrm{sample}}/R_{\mathrm{standard}}\right) - 1\right) \times 1{,}000,$$

where the differential notation (δR) represents the relative difference between isotopic ratios of the sample and standard gases (i.e., $^{13}C/^{12}C$, $^{15}N/^{14}N$). A laboratory-working standard (Peptone No. P-7750) was analyzed every 10 samples during analysis, and tin capsule blanks were run every 20 samples. Calibrations were made with the use of stable isotope reference materials provided by the National Institute of Standards and Technology (NIST). External instrument reproducibility for both carbon and nitrogen isotope analysis was ±0.2‰.

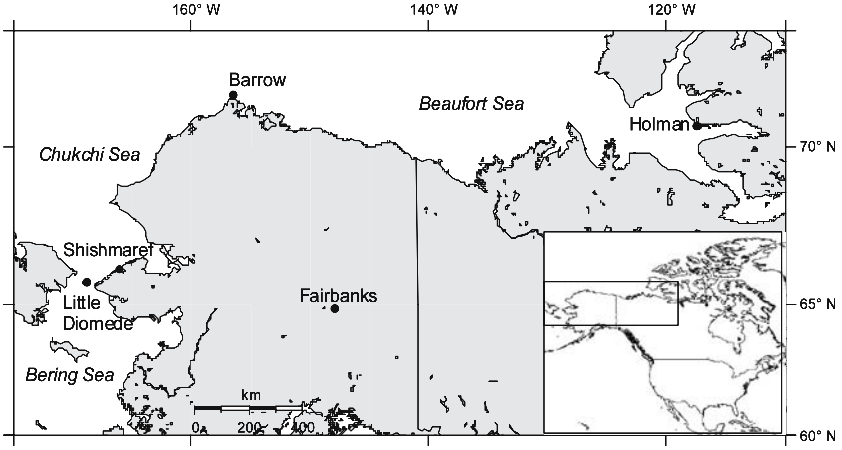

Fig. 1 Alaskan and Canadian communities where samples of subsistence-harvested Arctic pinnipeds were collected. Fairbanks serves as a point of reference

Table 1 Pinniped samples collected in Alaskan and Canadian villages, 1996–2003

Species	Sampling date	Sampling location	Number of samples collected				
			Males	Females	Unknown sex	Muscle	Stomach
Ringed seal	1996–2003	Barrow, AK, USA	49	30	3	82	50
Ringed seal	2001	Holman, Canada	12	13	–	25	25
Bearded seal	1998–2003	Barrow, AK, USA	17	33	5	55	37
Spotted seal	2000–2003	Little Diomede, Shishmaref, AK, USA	49	23	7	79	43
Ribbon seal	2003	Little Diomede, AK, USA	15	21	4	40	37
Walrus	1998–2003	Barrow, Little Diomede, AK, USA	3	1	2	6	–

Aging

Jaws and claws were collected from seals after 1997 and stored at –20°C until analysis. Ringed seals harvested in 1996 and 1997 were aged using the keratin layers of claws, which represent a minimum age estimate for the animals (Benjaminsen 1973). Two canines or canine and postcanine (if only one canine was available) were extracted from upper or lower jaw (depending on availability), submerged in a hot water bath for 30 min to avoid damage to the structure of the cementum, and stored in paper envelopes (Matson 1981). All teeth were shipped to Matson's Laboratory, Milltown, MT, USA for slide preparation. Teeth were prepared in 14 µm sections, placed on glass slides and stained with Giemsa histological stain suitable for cementum analysis. Age was estimated by counting annual growth layers in the cementum of teeth by two independent readers at UAF. Preparation and evaluation of teeth were done doubly blind by randomly assigning an identification number to each tooth with two teeth analyzed per animal. Animal identification and matching teeth were revealed only after all ages were estimated in duplicate. One growth layer per year of age was assumed for all seals (Benjaminsen 1973; Stewart et al. 1996). Maximum variation in age estimates was ±1 year for seals younger than 15 years and ±5 years in animals older than 15.

Statistical analysis

The response variables in the data set (age, δ^{15}N and δ^{13}C) were ranked prior to analysis to reduce the risk of violations of normality and homogeneity of variance assumptions. Variables were analyzed for sex and location differences using the Mann–Whitney test within a seal species. If no significant differences were detected for each variable, sexes and localities were pooled. A residual analysis was conducted to determine possible violations of assumptions. Spearman rank correlation was calculated within a species to determine correlations between age and stable isotope ratios. LOESS non-parametric smoothing was used on non-ranked raw data to estimate suitable functions between two variables and compare regression surfaces between species. The Kruskal–Wallis test followed by Tukey's multiple comparison procedure was used to compare variable means between seal species. For statistical analysis of stomach contents, indicator variables were established for each seal species based on presence and absence of prey items (0 = absent, 1 = present). These indicator variables were analyzed using logistic regression with interaction term (forward selection) with age and sex (indicator variable) as independent variables for each species. The odds-ratio (OR) is a term used in logistic regression and assesses the strength of an association. An OR of 1 indicates no association of variables, while an OR greater than 1 suggests that the "event" (i.e., presence of prey) is more likely to occur in one group than the other, e.g., male versus female. All statistical analyses were performed using SAS (Version 8) with $\alpha = 0.05$. SigmaPlot (Version 7.0) was used for graphic presentation of data. Results are reported as mean ± standard deviation (SD) unless otherwise noted.

Results

Stomach contents analysis

Table 2 presents frequency of occurrence (FO_i) of prey in stomachs of bearded, ringed and spotted seals harvested in Alaska. FO_i of prey was calculated for all stomachs containing digesta. For ringed seals, 50 stomachs were analyzed and 11 were empty or contained only bile, blood or parasites. Of 37 bearded seal stomachs, one was empty and contained only parasites. For spotted seals 43 stomachs were analyzed and 5 contained no food. All 25 stomachs of ringed seals harvested in Holman, Canada were

Table 2 Frequency of occurrence (FO_i) of prey species identified from bearded, ringed and spotted seal stomachs collected in Alaska, 1996-2001

Species	FO_i[%]
Bearded seals[a]	
Teleost Fish	
Eelpout (*Lycodes* spp.)	58.3
Cod (Gadidae)	41.7
Sculpin (Cottidae)	38.9
Rainbow Smelt (*Osmerus mordax*)	22.2
Flatfish (Pleuronectidae)	11.1
All Fish	*80.6*
Crustacea	
Sculptured Shrimp (*Sclerocrangon boreas*)	83.3
Northern Shrimp (*Pandalus* spp.)	63.9
Amphipoda	63.9
Spider Crab (*Hyas coarctatus*)	58.3
Hermit Crab (Paguridae)	30.6
Isopoda (*Saduria* spp.)	13.9
Other crustaceans	19.4
All crustacea	*97.2*
Mollusca	
Octopus (*Octopus* spp.)	69.4
Greenland Cockle (*Serripes groenlandicus*)	50.0
Whelk (*Buccinum* spp.)	38.9
Softshell Mussle (*Mya* spp.)	11.1
Whelk (*Neptunea* spp.)	8.3
All Mollusca	*83.3*
Marine Worms	
Echiura	61.1
Priapulida	16.7
Polychaeta	2.8
Echinoderma	
Sea Cucumber (Holothuroidea)	36.1
Other[b]	13.9
Ringed seals[c]	
Teleost Fish	
Cod (Gadidae)	46.2
Pacific Sand Lance (*Ammodytes hexapterus*)	20.5
Sculpin (Cottidae)	5.1
Eelpout (*Lycodes* spp.)	5.1
Unidentified fish	7.7
All Fish	*61.5*
Crustacea	
Euphausiacea (*Thysanoessa* spp.)	53.8
Mysidacea (*Mysis* spp. and *Neomysis* spp.)	46.2
Zooplankton (Euphausiacea and Mysidacea)	*64.1*
Amphipoda	38.5
Northern Shrimp (*Pandalus* spp.)	30.8
Sculptured Shrimp (*Sclerocrangon boreas*)	5.1
Isopoda (*Saduria* spp.)	5.1
All crustacea	*89.7*
Marine Worms	
Echiura	5.1
Cephalopoda	
Octopus (*Octopus* spp.)	2.6
Squid	2.6
Other[d]	10.3
Spotted seals[e]	
Teleost Fish	
Pacific Herring (*Clupea pallasii*)	52.6
Arctic Cod (*Boreogadus saida*)	42.1
Saffron Cod (*Eleginus gracilis*)	34.2
All Cod (Gadidae)	*47.4*
Rainbow Smelt (*Osmerus mordax*)	23.7
Capelin (*Mallotus villosus*)	15.8
Pacific Sand Lance (*Ammodytes hexapterus*)	13.2
Flatfish (Pleuronectidae)	10.5
Prickleback (Stichaeidae)	5.3
Sculpin (Cottidae)	2.6
Snailfish (Liparidae)	2.6
Unidentified fish	15.8
All Fish	*100.0*
Crustacea	
Amphipoda	26.3
Northern Crangon (*Crangon alaskensis*)	13.2
Tanner Crabs (Chionocetes)	2.6
Other crustacea	13.2
All crustacea	*44.7*
Mollusca	
Squid	2.6
Clams	5.3

[a] 37 stomachs analyzed, 1 stomach empty

[b] Includes Porifera, Echinoidea, Hemichordata, Sipuncula

[c] 50 stomachs analyzed, 11 stomachs empty

[d] Includes Feather, *Sclerocrangon* spp., Bryozoa, Hemichordata

[e] 43 Stomachs analyzed, 5 stomachs empty

empty. Of 37 stomachs collected from ribbon seals only two contained prey. The small sample size did not allow for further statistical analysis. Arctic cod (*Boreogadus saida*) otoliths were identified from both ribbon seal stomachs containing digesta (a 3-year-old male and a 2-year-old female). Additionally, the male contained one twospine crangon (*Crangon communis*) and the female had fragments of yellowleg pandalid (*Pandalus tridens*) in the stomach.

The frequency of fish was 62% in stomachs of ringed seals containing prey (Table 2). Of all fish identified, gadids like Arctic cod and saffron cod (*Eleginus gracilis*) were identified most often, followed by Pacific sand lance (*Ammodytes hexapterus*). Zooplankton in stomachs of ringed seals occurred at a frequency of 64%. Both euphausids and mysids were consumed in similar proportions, as were amphipods and pandalid shrimp. All other prey were present in less than 10% of stomachs with contents.

Prey diversity in bearded seal stomachs was higher than in ringed and spotted seals with more than 20 different species consumed representing more than 10 animal phyla (Table 2). Prey was ingested intact in most cases though only feet of ingested clams and snails were present and only abdomens of predominately gravid female spider crabs (*Hyas coarctatus*) were identified from stomach contents. Crustaceans were found in 97% of stomachs. Of the prey species consumed, sculptured shrimp (*Sclerocrangon boreas*) was present most often. The frequency of fish in bearded seal stomachs was 81%, with eelpout (*Lycodes* spp.) making up the majority of teleost prey. Other prey identified in more than 50% of the stomachs consisted of northern shrimp (*Pandalus* spp.), amphipods, spider crabs, octopus, Greenland cockle (*Serripes groenlandicus*) and echiurid worms.

Fishes were identified in all spotted seal stomachs containing prey (Table 2). Most frequently found was Pacific herring (*Clupea pallasii*), followed by gadid fish and rainbow smelt (*Osmerus mordax*). Capelin (*Mallotus villosus*), sand lance and flatfish were found in more than 10% of the stomachs, while other teleosts (e.g., sculpin) were present in less than 10%. Invertebrate prey was mainly comprised of crustaceans with amphipods making up the largest proportion. Mollusks occurred in less than 10% of the stomachs.

Generally, there was no statistical difference in the frequency of prey types consumed by males and females for either bearded or spotted seals. However, bearded seal males were 6 times more likely to contain smelt (OR = 6.06, $P = 0.04$) and 7.5 times more likely to contain sea cucumber than females (OR = 7.52, $P = 0.01$). In ringed seals, male stomachs were about 16 times more likely to contain zooplankton than females (OR = 15.87, $P = 0.0004$). This relationship was also significant when mysids and euphausids were analyzed separately ($P = 0.007$ and 0.002 for euphausids and mysids, respectively). Similarly, stomachs of female ringed seals were more likely to contain fish than those of males (OR = 5.42, $P = 0.04$). Sex was not significant when teleost species were analyzed separately.

Older bearded seals were less likely to consume whelks (*Buccinum* spp.) (OR = 0.87, $P = 0.049$). No other age effects were noted in bearded seal diets. In spotted seals, presence of capelin and flatfish increased with increasing age ($P = 0.003$, OR = 1.90 and $P = 0.005$, OR = 1.41, for capelin and flatfish, respectively). In ringed seals only the consumption of gadid fish was related to age ($P = 0.01$, OR = 1.22), while zooplankton ingestion was age independent.

Stable isotopes

Age and isotope composition of spotted seals harvested near Shishmaref and Little Diomede were not statistically different ($P = 0.09$, 0.25 and 0.68 for age, δ^{15}N and δ^{13}C, respectively). Therefore these data were pooled to increase sample size and power. Ringed seals harvested in Holman were significantly more depleted in ^{13}C than ringed seals from Barrow ($P < 0.0001$). Stable nitrogen isotope ratios and age were higher in Canadian ringed seals ($P = 0.01$ for both δ^{15}N and age) than in animals sampled in Barrow and therefore seals from Alaska and Canada were analyzed separately. Generally, there were no sex differences within species in age composition, stable carbon or stable nitrogen isotope ratios. However, female ringed seals harvested in Barrow had higher stable nitrogen isotope ratios than males harvested in Barrow ($P = 0.02$) and they were analyzed separately for this variable. Male and female ringed seals from Holman as well as bearded, ribbon and spotted seal sexes were pooled.

Spearman rank test showed no significant correlation between variables (age, δ^{15}N and δ^{13}C) in spotted seals and ringed seals harvested in Holman. Age was positively correlated with δ^{15}N in ribbon seals ($P = 0.004$), and was positively correlated with δ^{13}C in ringed seals from Barrow ($P = 0.0006$) and ribbon seals ($P = 0.009$). Age was negatively correlated with δ^{15}N in bearded seals ($P = 0.03$).

Mean ratios of stable carbon and nitrogen isotopes in seals, walrus and some prey species (analyzed in this study and compiled from literature) are given in Table 3. Kruskal–Wallis testing showed significant differences in stable carbon and nitrogen isotope ratios between seal species ($P < 0.0001$ for δ^{15}N and δ^{13}C). Figure 2 illustrates δ^{15}N versus δ^{13}C in pinnipeds analyzed. Stable nitrogen isotope ratios were significantly higher in spotted seals and ringed seals from Holman than walrus, bearded and ribbon seals and ringed seals harvested in Barrow. δ^{15}N was not statistically different in bearded seals and ringed seals from Barrow and was lowest in walrus and ribbon seals. Carbon-13 was significantly more enriched in bearded seals and walrus than the other species, while ringed seals from Holman were most depleted in ^{13}C. No difference in δ^{13}C was detected between ringed seals from Barrow, spotted seals and ribbon seals.

Discussion

Ringed seals

Stomach contents analysis

Analysis of ringed seal stomachs showed Arctic cod prevalence increased with age and could be related to hunting experience or habitat when foraging. This finding agrees with observations by Lowry et al.

Table 3 Stable carbon and nitrogen isotope ratios in Arctic phocids and selected prey species

Species	Sampling location	*n*	δ^{15}N(‰)	δ^{13}C(‰)	Reference
Pinnipeds:					
Ringed seal (*Phoca hispida*)	Barrow, AK, USA	82	16.9 ± 0.6	–18.5 ± 0.8	This study, includes data from Hoekstra et al. (2002)
	Holman, Canada	25	17.2 ± 0.7	–20.4 ± 0.4	This study
	Thuhle, Greenland	100	17.0 ± 0.1	–19.4 ± 0.1	Hobson et al. (2002)
	Canadian Arctic	9	17.3 ± 1.1	–17.3 ± 0.7	Hobson and Welch (1992)
	Canadian Arctic	8	13.9 ± 1.4	–19.7 ± 0.9	Muir et al. (1995)
Bearded Seal (*Erignathus barbatus*)	Barrow, AK, USA	55	16.8 ± 0.9	–17.1 ± 0.5	This study, includes data from Hoekstra et al. (2002)
	Canadian Arctic	5	16.8 ± 0.1	–16.6 ± 0.3	Hobson et al. (2002)
Spotted Seal (*Phoca largha*)	Little Diomede, Shishmaref, AK, USA	79	17.8 ± 1.0	–18.5 ± 0.9	This study
Ribbon Seal (*Phoca fasciata*)	Little Diomede, AK, USA	40	16.0 ± 1.2	–18.7 ± 0.1	This study
Harbor Seal (*Phoca vitulina*)	Copper River Delta, AK, USA	9	18.6 ± 0.3	–17.6 ± 0.2	Hobson et al. (1997)
Walrus (*Odobenus rosmarus*)	Barrow, Little Diomede, AK, USA	6	13.5 ± 1.0	–16.9 ± 0.2	This study
	Canadian Arctic	6	12.5 ± 0.6	–17.8 ± 0.3	Hobson and Welch (1992)
	Canadian Arctic, Akulivik	9	10.9 ± 0.5	–17.3 ± 0.5	Muir et al. (1995)
	Canadian Arctic, Inukjuak	12	11.7 ± 0.7	–18.7 ± 0.8	Muir et al. (1995)
Teleost Fish:					
Arctic Cod (*Boreogadus saida*)	Barrow, AK, USA	24	15.5 ± 1.0	–20.9 ± 0.4	This study, includes data from Hoekstra et al. (2002)
	Canadian Arctic	26	15.2 ± 0.7	–18.9 ± 1.0	Hobson and Welch (1992)
	Newfoundland	10	13.7 ± 0.4	–18.8 ± 1.0	Lawson and Hobson (2000)
Saffron Cod (*Eleginus gracilis*)	Barrow, AK, USA	1	14.2	–22.0	This study
Capelin (*Mallotus villosus*)	Newfoundland	11	12.2 ± 0.8	–21.4 ± 0.5	Ostrom et al. (1993)
	Gulf of Alaska	13	12.4 ± 0.1	–	Hobson et al. (1997)
Pacific Herring (*Clupea pallasii*)	Bering Strait	3	13.8 ± 0.9	–20.7 ± 1.7	This study
	Washington	2	14.5 ± 0.3	–	Hobson et al. (1997)
Walleye Pollock (*Theragra chalcogramma*)	Bering Strait	6	14.2 ± 2.0	–20.4 ± 2.5	This study
	Gulf of Alaska	24	10.9 ± 0.2	–	Hobson et al. (1997)
Pacific Sand Lance (*Ammodytes hexapterus*)	Barrow, AK, USA	1	14.6	–22.5	This study
	Gulf of Alaska	8	11.9 ± 0.1	–	Hobson et al. (1997)
Fourhorn sculpin (*Myoxocephalus quadricornis*)	Canadian Arctic	1	15.2	–18.1	Hobson and Welch (1992)
Rainbow Smelt (*Osmerus mordax*)	Barrow, AK, USA	10	14.8 ± 1.0	–21.2 ± 0.8	This study
Flounder (*Hippoglossoides* spp.)	Barrow, AK, USA	3	12.6 ± 0.0	–19.7 ± 0.1	Hoekstra et al. (2002)
Snailfish (*Liparis* spp.)	Canadian Arctic	4	15.0 ± 0.4	–17.4 ± 0.5	Hobson and Welch (1992)
Crustacea:					
Zooplankton (unsorted)	Kaktovik, AK, USA	21	10.4 ± 1.2	–24.9 ± 0.7	This study
	Barrow, AK, USA	13	9.9 ± 0.8	–20.3 ± 0.6	This study
	Holman, Canada	10	10.4 ± 0.5	–24.4 ± 0.6	Hoekstra et al. (2002)
Copepoda	Canadian Arctic	6	9.2 ± 0.5	–20.4 ± 0.4	Hobson and Welch (1992)
	East Chukchi	54/63	10.5 ± 0.2[a]	–21.8 ± 0.1[a]	Schell et al. (1998)
Euphausiacea	East Chukchi	33/38	9.7 ± 0.3[a]	–20.2 ± 0.2[a]	Schell et al. (1998)
	Gulf of Alaska	9	11.2 ± 0.5	–	Hobson et al. (1997)
Amphipoda (unsorted)	Bering Strait	40	7.9 ± 0.8	–19.9 ± 0.7	This study
Parathemisto libellula	Canadian Arctic	6	11.7 ± 0.7	–20.3 ± 0.4	Hobson and Welch (1992)
Onisimus glacialis	Canadian Arctic	4	11.4 ± 0.5	–18.2 ± 1.1	Hobson and Welch (1992)
Isopoda (*Saduria sabini*)	Barrow, AK, USA	4	13.7 ± 0.5	–17.0 ± 0.5	This study
Isopoda (*Saduria entomon*)	Barrow, AK, USA	3	14.3 ± 0.9	–20.7 ± 0.5	This study
Spider crab (*Hyas coarctatus*)	Bering Strait	2	13.4 ± 0.1	–18.4 ± 0.1	This study
Sculptured Shrimp (*Sclerocrangon boreas*)	Barrow, AK, USA	1	16.1	–19.8	This study
Northern Shrimp (*Pandalus borealis*)	Newfoundland	10	11.3 ± 0.2	–17.9 ± 0.3	Lawson and Hobson (2000)
Mollusca:					
Greenland Cockle (*Serripes groenlandicus*)	Bering Strait	1	8.0	–19.2	This study
	Canadian Arctic	7	8.9 ± 0.8	–18.7 ± 0.4	Hobson and Welch (1992)

Table 3 continued

Species	Sampling location	*n*	δ^{15}N(‰)	δ^{13}C(‰)	Reference
Whelk (*Buccinum* spp.)	Canadian Arctic	5	12.6 ± 0.7	na	Hobson and Welch (1992)
Softshell Mussel (*Mya truncata*)	Canadian Arctic	7	9.5 ± 0.7	–19.0 ± 0.4	Hobson and Welch (1992)
Octopus (*Octopus* spp.)	Bering Strait	1	9.9	–20.0	This study
Squid	Bering Strait	3	13.6 ± 1.2	–19.9 ± 1.3	This study
Squid-small	Gulf of Alaska	4	9.6 ± 0.5	–	Hobson et al. (1997)
Squid-large	Gulf of Alaska	1	16.7	–	Hobson et al. (1997)
Arctic Squid (*Gonatus fabricii*)	Newfoundland	10	12.3 ± 0.7	–18.5 ± 0.4	Lawson and Hobson (2000)
Squid-large (*Illex illecebrosus*)	Newfoundland	2	15.1	–20.0	Ostrom et al. (1993)
Squid-small (*Illex illecebrosus*)	Newfoundland	4	9.3 ± 0.1	–19.1 ± 0.4	Ostrom et al. (1993)
Echinoderma:					
Sea Cucumber (Holothuroidea)	Canadian Arctic	3	9.5 ± 0.5	–19.7 ± 1.2	Hobson and Welch (1992)
Urochordata:					
Tunicata	Barrow, AK, USA	2	11.3 ± 1.0	–23.3 ± 0.9	This study
Marine Worms:					
Priapulida	Barrow, AK, USA	1	15.5	–17.2	This study
Echiura	Barrow, AK, USA	1	9.6	–19.7	This study
Polychaeta	Bering Strait	3	10.3 ± 2.6	–19.5 ± 1.9	This study

Values are given as mean ± standard deviation unless otherwise noted (*n*: sample size)

[a]Standard error

(1980a) that ringed seal pups consume less gadids than adults, and Bradstreet and Finley (1983) noted a decline in the presence of crustaceans in stomachs with age in ringed seals. However, age was not a significant variable for consumption of zooplankton, crustaceans or invertebrate prey in general in this study. This could be related to the use of the FO_i method, as it tends to overestimate the importance of less commonly or unintentionally ingested prey (Hjelset et al. 1999). It is possible that seals preying on schooling fish, such as Arctic cod, will also ingest krill and amphipods as fish schools feed on zooplankton patches (Lowry and Frost 1981; Hop et al. 1997). Hence a decline in the importance of crustaceans with age cannot be ruled out, as the relationship of numerical frequency of krill with age was not determined. It is possible that ingestion of zooplankton is necessary nutritionally for these seals. Very little is known about nutritional quality of most marine forage or nutritional requirements of seals. Geraci (1975) reported high levels of thiaminase, an enzyme that breaks down thiamine (Vitamin B_1), in herring, smelt and capelin. As a result, captive and wild seal populations sustained exclusively on these fish can suffer from thiamine deficiency. Inclusion of krill in the diet, even in adult animals, could serve to fulfill a dietary requirement.

Analysis of stomach contents in this study showed significant differences in prey composition between male and female ringed seals harvested in Barrow. This difference in prey composition between sexes was also detected by means of stable isotope analysis. δ^{15}N was higher in females than males and stomach contents analysis showed that females were more likely to eat fish, while males consumed more zooplankton. Lowry et al. (1980a) reported that female ringed seals from the Bering Sea ate more fish and less shrimp than did males, but differences were minimal and similar differences in prey selection could not be found in other Arctic regions. Possible explanations for the differences in foods ingested by male and female ringed seals could include spatial segregation of sexes and associated differential use of resources. Fedoseev (2000) described segregation of ice-associated seals by age and sex outside the breeding period. Differences in foraging strategy and prey selection between sexes have been indicated for northern elephant seals (*Mirounga angustirostris*) and northern fur seals (*Callorhinus ursinus*) (Hobson et al. 1997; Le Boeuf et al. 2000). Das et al. (2003) showed that female harbor porpoise (*Phocoena phocoena*) were enriched in ^{15}N over males and suggested higher consumption or feeding on larger prey by pregnant or lactating animals.

Several circumpolar studies have noted that ringed seals prey only on a few key taxa, and Arctic cod and a variety of crustaceans were found as important food items (Lowry et al. 1980a; Bradstreet and Finley 1983; Smith 1987). Results of this study also show that krill and fishes (in particular Gadidae) make up the majority of ringed seal diet and are consumed in similar frequencies. Lowry et al. (1978) noted that amphipods had a high frequency (69%) in ringed seal stomachs taken near Barrow, but comprised only 4.6% of the total combined volume. Similarly, frequency of amphipods in this study was 39%, but biomass consumed was

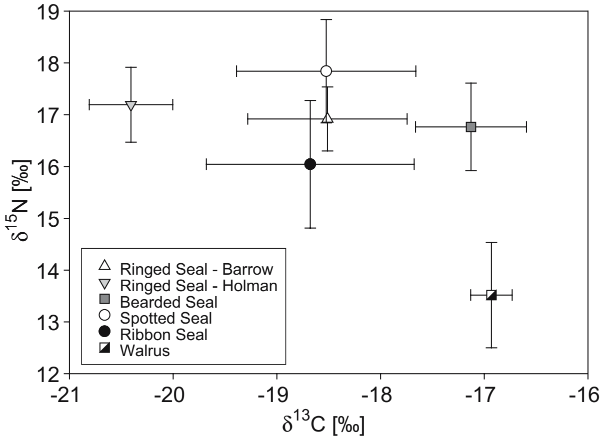

Fig. 2 δ^{13}C versus δ^{15}N of ringed seals harvested in Alaska and Canada, and bearded, ribbon and spotted seals, 1996–2003 and walrus 1998 and 2003 from Alaska. *Symbols* present the mean values and *error bars* show the standard deviations (± 1 SD)

negligible. Amphipods have been reported as a major food item for ringed seals from Svalbard and the Canadian Arctic (Bradstreet and Finley 1983; Smith 1987; Weslawski et al. 1994). Based on stable nitrogen isotope ratios in ringed seals from Barrow and Holman, and assuming an enrichment factor of 2.4‰ for δ^{15}N in seal muscle (Hobson et al. 1996), it is highly improbable that amphipods make up a large proportion of their diet in either region (Table 3). However, large variation in prey availability by region may confound a large-scale geographical comparison.

Ringed seals

Stable isotopes

Stable nitrogen isotopes varied over the range of one trophic level in ringed seals from both Barrow (15.6–18.0‰) and Holman (14.6–18.0‰). This likely reflects the consumption of different trophic level prey, e.g., either krill or Arctic cod. Stable nitrogen isotope ratios in assumed prey of ringed seals range from 9.9 ± 0.8 to 15.5 ± 1.0‰ for zooplankton and Arctic cod, respectively (Table 3), reflecting the upper, but not lower ranges of δ^{15}N found in ringed seals (2.4‰ enrichment factor after Hobson et al. 1996). This suggests minor significance of a zooplankton-exclusive diet, but points to a krill and gadid mix for these seals.

While the gastric prevalence of Arctic cod was positively correlated with age, δ^{15}N showed no age dependence. Several young animals (< 1 year) and one fetus displayed elevated ^{15}N values. Similar nitrogen-15 enrichment has been observed in northern fur seal pups and suckling harbor porpoises, and it was suggested that milk has isotope signatures comparable to other maternal tissues (Hobson et al. 1997; Das et al. 2003). Trophic enrichment could therefore occur in nursing pups or in fetuses during gestation compared to their mothers. Roth and Hobson (2000) theorized that high rate of protein synthesis and catabolism in tissues of juveniles causes excretion of predominantly light nitrogen while the heavier isotope is incorporated and magnified in tissues.

A positive correlation of carbon isotope ratios with age was shown for ringed seals from Barrow, but not for ringed seals from the Canadian Arctic (Fig. 3). In both locations a similar relationship was noticeable after a LOESS non-parametric smoothing. However, the positive relationship observed in seals harvested in Barrow was most likely driven by some young-of-the-year (YOY) and one fetus [highlighted as black triangles (▲) in Fig. 3] that are depleted in ^{13}C compared to the majority of seals. Body fat is usually depleted in ^{13}C due to selective fractionation (DeNiro and Epstein 1977) and the ratios for the fetus and YOY suggest mobilization and transfer of carbon from maternal lipid stores to fetal development and milk production (Jenkins et al. 2001; Polischuk et al. 2001; Dehn et al. 2006b).

Carbon isotope signatures in ringed seals from Holman were significantly depleted compared to the other seals. Schell et al. (1998) reported more depleted carbon-13 values in the Beaufort Sea versus continental shelf waters of the Bering and Chukchi seas and a similar pattern can be detected in baleen and muscle of bowhead whales (*Balaena mysticetus*) migrating between these two regions (Schell et al. 1989; Hoekstra

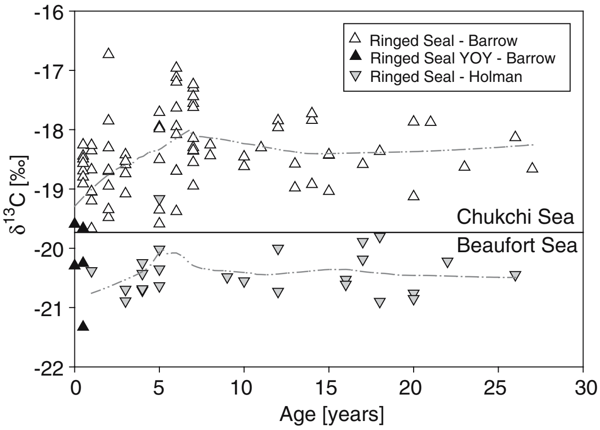

Fig. 3 δ^{13}C in muscle versus age based on cementum analysis of teeth of ringed seals harvested in Barrow, AK, USA, 1996–2003 and Holman, Canada, 2001. Four YOY and one fetus harvested in Barrow are highlighted as *black triangles.* A LOESS nonparametric smoothing (*dashed lines*) was employed to estimate and compare regression surfaces for ringed seals from both locations

et al. 2002). Figure 3 illustrates that δ^{13}C in ringed seals from the Canadian Arctic can clearly be distinguished from ringed seals harvested in Barrow. Since many phocid seals migrate (Lowry et al. 1998) and ringed seals of the Canadian Arctic are known to move toward the Chukchi and Bering seas (Smith 1987; Harwood and Smith 2003), it is possible that some of the ringed seals harvested in the Barrow area had migrated or dispersed from the Beaufort Sea and hence show the characteristic low carbon-13 signature. Geographically, Point Barrow is the point of separation for Beaufort and Chukchi seas (Fig. 1) and seals from either area and with either carbon signature are common and taken by subsistence hunters.

Bearded seals

Stomach contents analysis

Stomachs of bearded seals examined in this study contained a wide variety of benthic and epibenthic prey and these seals can be characterized as generalists. Some aspects of bearded seal diet were similar to those previously reported, but others were markedly different. Antonelis et al. (1994) noted high frequencies of fish in bearded seals sampled in the Bering Sea in spring; the most common teleost species consumed was capelin. Finley and Evans (1983) also found large occurrences of fish in bearded seal stomachs from the Canadian Arctic with gadids being most common. In contrast, Lowry et al. (1980b) did not consider fish important prey for bearded seals based on volumetric measurements, even though frequency of fish ranged from 78 to 82%. However, volume of fish would be severely underestimated when only otoliths or bones are present. Frequency of fish found in stomachs of seals from the Barrow area in this study was similar to occurrences reported by Lowry et al. (1980b), but the most common species consumed was eelpout followed by gadids.

Large regional differences in consumption of clams are seen in bearded seal diets. While frequencies of Greenland cockle in this study are high and are in agreement with prevalence of cockle reported by Lowry et al. (1980b) in the Bering Sea, others only documented infrequent occurrences of less than 10% in the Canadian Arctic and Svalbard (Finley and Evans 1983; Hjelset et al. 1999) to absence in diet in the Okhotsk Sea (Pikharev 1941).

Frequency of octopus and echiurid worms in stomachs also varied among locations. Finley and Evans (1983) noted a high frequency of occurrence of octopus in bearded seal stomachs from the Canadian Arctic, but amounts consumed were minimal, while echiurid worms were not found. They concluded that neither octopus nor marine worms were important prey. Antonelis et al. (1994) and Hjelset et al. (1999) came to the same conclusion for bearded seals harvested in the Bering Sea and Svalbard, respectively. Lowry et al. (1980b) found no cephalopods, and echiurids were of minor importance. In contrast, this study showed high frequencies of octopus and echiurids in the diet of bearded seals harvested near Barrow and is in accordance with studies in the Sea of Okhotsk (Pikharev 1941).

The high frequency of occurrence of crustacean prey is in agreement with previous studies, though some regional differences are notable in species composition (Pikharev 1941; Lowry et al. 1980b; Finley and Evans 1983; Antonelis et al. 1994; Hjelset et al. 1999). Sea cucumber was reported as a minor food item in bearded seal stomachs analyzed from the Canadian Arctic and Okhotsk Sea (Pikharev 1941; Finley and Evans 1983), but was fairly common in seals in this study. These variations in bearded seal diet are likely area specific and reflect the local distribution of available prey in the Arctic. However, there are some deviations in prey composition reported from the Bering and Chukchi seas (Lowry et al. 1980b; Antonelis et al. 1994) compared to seals collected in this study from the Chukchi Sea. This could reflect changes in prey distribution or abundance over the past 10–20 years, although even small seasonal or regional differences in prey availability between studies make a temporal comparison difficult.

Bearded seal versus walrus

Stable isotopes

Stable nitrogen isotope ratios in bearded seal muscle range widely (15.2–18.8‰), and reflect the diverse feeding habits of these seals. Similarly, isotopic signatures of potential prey consumed by bearded seals vary considerably and some scavenging species, e.g., sculptured shrimp, can occupy equally high trophic levels as teleosts (Table 3). This makes it difficult to discern the importance of any particular prey species to bearded seals by means of stable isotope analysis and demonstrates the greatest limitation of this technique when potential prey species are numerous and cover a range of trophic levels.

The low nitrogen isotope ratios in walrus muscle indicate the reliance on lower trophic level prey. The significance of clams to walrus diet has been emphasized by a variety of reports (Lowry et al. 1980b; Fay

1982; Fay et al. 1984) and is further supported by the δ^{15}N findings of this study. Fish are generally not present in walrus stomachs and frequency of octopus is negligible (Fay et al. 1984). While seal-eating walrus have been described, they do not represent the norm of the population (Lowry and Fay 1984). Based on nitrogen isotope ratios obtained it is not likely that walrus included in this study had consumed other pinnipeds in the recent past.

Values of δ^{13}C in bearded seals show a large distribution, while carbon isotope ratios of walrus have a smaller range (–18.7 to –15.8 and –17.3 to –16.8‰ in bearded seals and walrus, respectively). The more enriched carbon isotope signatures in bearded seals and walrus compared to ringed, ribbon and spotted seals (Fig. 2) are likely due to benthic feeding habits (France 1995b), as confirmed by analyses of stomach contents. Enrichment of ^{13}C has also been described for benthic feeding gray whales (*Eschrichtius robustus*) (Dehn et al. 2006b). The larger δ^{13}C range in bearded seals could be related to migration routes between Beaufort and Chukchi Seas as discussed for ringed seals, but could also be associated with opportunistic feeding on both benthos and plankton. In contrast, walruses are specialists and rely almost exclusively on benthic prey. However, sample size for walrus muscle was small and could account for the smaller variation in their isotope ratios. Based on these results it is unlikely that walrus and bearded seal have a large overlap in prey utilization, but it is possible that competition between these two pinnipeds is the driving force for a dietary change in bearded seals as suggested by Lowry et al. (1980b).

Ribbon seals

Stable isotopes

Very little is known about ribbon seal biology due to their remote distribution in the pack ice (Braham et al. 1984; Simpkins et al. 2003). Ribbon seals sampled for this study were harvested during their annual molt. During this time they generally do not forage (Shustov 1965; Frost and Lowry 1980) and only two ribbon seal stomachs contained food. Prey in both stomachs was comprised of diagnostic hard parts, i.e., Arctic cod otoliths, indicating advanced digestion (Sheffield et al. 2001; Christiansen et al. 2005) and consequently a break in feeding activity for more than 10 h. Analysis of stable carbon and nitrogen isotopes can provide some additional insights in the assessment of ribbon seal diet. δ^{15}N was positively correlated with age, suggesting that trophic level increases with increasing age of ribbon seals (Fig. 4). A change from low to high trophic level prey is in accordance with available studies suggesting that ribbon seal pups and juveniles feed mainly on small crustaceans and that the importance of fish and nektobenthos, e.g., cephalopods and pollock (*Theragra chalcogramma*) increases with age (Shustov 1965; Frost and Lowry 1980; Fedoseev 2000). Adult ribbon and spotted seals have similar nitrogen isotope ratios. Stable nitrogen isotopes in typical prey of adult ribbon seals range from 13.6 ± 1.2‰ in cephalopods to 14.2 ± 2.0 and 15.5 ± 1.0‰ for pollock and Arctic cod, respectively (Table 3). δ^{15}N in small crustaceans ranges from 9.9 ± 0.8 to 11.7 ± 0.7‰, for zooplankton (euphausids and copepods) and hyperiid amphipods (*Parathemisto libellula*), respectively (Table 3). Assuming a seal feeding exclusively on small crustaceans and further assuming an enrichment factor of 2.4‰ (Hobson et al. 1996), a muscle δ^{15}N value of approximately 13‰ can be expected while a seal preying on gadids would approximate 18‰. These extremes reflect the ranges of δ^{15}N found in ribbon seals. The high values of δ^{15}N in YOY (Fig. 4) are in agreement with enrichment of nitrogen-15 in pups and juveniles due to an increased demand of nitrogen for protein synthesis during growth or mobilization of maternal nitrogen to the offspring as described above (Hobson et al. 1997; Roth and Hobson 2000).

δ^{13}C is positively correlated with age in ribbon seals such that YOY are depleted in ^{13}C compared to adult seals and as discussed for ringed seals this likely indicates maternal carbon transfer and mobilization. Mean δ^{13}C in ribbon seals is similar to pelagic feeding ringed and spotted seals and is significantly lower than in

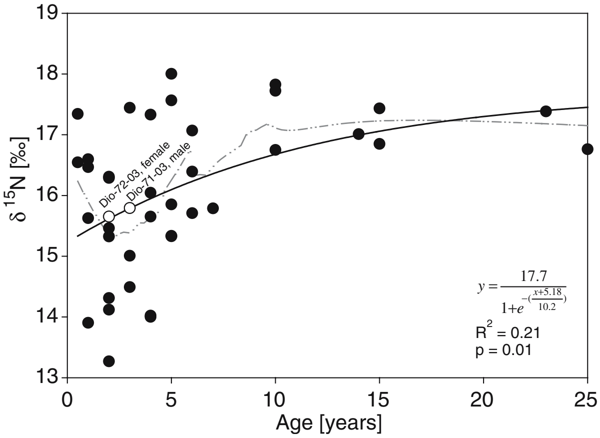

Fig. 4 δ^{15}N in muscle versus age based on cementum analysis of teeth of ribbon seals harvested near Little Diomede, 2003. A sigmoid function was fitted to the data set and a LOESS nonparametric smoothing (*dashed line*) was employed to estimate the regression surface. Gastric contents were present in two seals, highlighted as *open circles*

benthic feeding bearded seals. This is in agreement with pelagic feeding behavior of ribbon seals during the ice-free months (Burns 1970).

Spotted seals

Stomach contents analysis

Only in the past 20 years have spotted seals been differentiated from their close relative, the harbor seal (*Phoca vitulina*) (Burns et al. 1984). Feeding habits of spotted and harbor seals are similar and schooling fish, such as pollock, herring, smelt and salmonids dominate their diets (Bukhtiyarov et al. 1984; Iverson et al. 1997; Orr et al. 2004). The high frequency of fish in spotted seal diet reported herein is in accordance with studies conducted in the Alaskan and Russian Arctic and the Sea of Okhotsk (Bukhtiyarov et al. 1984; Sobolevskii 1996). The most common species present in spotted seal stomachs analyzed in this study was herring followed by gadids. Bukhtiyarov et al. (1984) noted that herring and smelt are minor foods for spotted seals in spring, but increase in prevalence during summer and fall. In late spring and early summer, spotted seals in the Sea of Okhotsk consumed mostly walleye pollock, followed by herring (Kato 1982). Pacific herring are abundant in coastal waters during spawning in summer and migrate offshore to their wintering grounds after spawning (Lassuy 1989). Hence spotted seals likely are responding to seasonal availability of forage fish. However, salmonids have been described as an important component of the diet in summer during spawning (Sobolevskii 1996; Lowry et al. 2000) but were not identified from stomachs of spotted seals in this study.

Kato (1982) and Bukhtiyarov et al. (1984) reported high frequencies of crustacean prey in younger spotted seals, while fish and cephalopods made up the majority of the adult diet. However, no age-related differences were found in the consumption of invertebrate prey in this study. This could be associated with the abundance of spawning herring that would make this species seasonally accessible and easy prey for spotted seal pups. However, age was a significant factor in the prevalence of flatfish and capelin in older seals. Bukhtiyarov et al. (1984) reported that older seals are more likely to feed on benthic organisms. Benthic prey may only be available to adults due to restrictions in diving performance of juveniles, as has been suggested for harbor seal pups (Jørgensen et al. 2001). This could explain the presence of flatfish or other benthic prey in adult spotted seals and relative absence in pups.

Spotted seals

Stable isotopes

Nitrogen isotope ratios of spotted seals demonstrate feeding on a higher trophic level than other pinnipeds in this study and results are comparable to stable isotope ratios reported for harbor seal muscle (Hobson et al. 1997). A higher trophic level (based on δ^{15}N) for spotted seals compared to other ice-associated seals is in accordance with stomach contents findings as fish occurs at a high frequency in their diet. Though there is some indication that nitrogen isotope ratios increase in seals younger than 5 years, the relationship of δ^{15}N with age was not significant. Kato (1982) and Bukhtiyarov et al. (1984) reported a change from low to high trophic level prey and suggested that spotted seal pups feed mainly on crustaceans and that the importance of fish increases with age. However, analysis of stomach contents in this study did not show any age effects for invertebrate prey. Considering that stable isotopes in muscle tissue show a signature that reflects feeding habits over about one month (Tieszen et al. 1983) it is possible that younger seals were feeding on a lower trophic level earlier in the year and switched their diet to take advantage of the abundant spawning herring in early summer. Hence the importance of invertebrates to immature seals was not detectable by means of stomach contents and stable isotope analysis.

Carbon isotope ratios of spotted seal muscle were not statistically different from δ^{13}C in ringed and ribbon seals harvested in Alaska. This suggests that these species rely on the planktonic food web rather than the benthic ecosystem as seen for bearded seals and walrus. However, stable carbon isotope ratios were not correlated with age in spotted seals as described for Alaskan ringed and ribbon seals. Lowry et al. (1998) showed long-distance migration of spotted seals equipped with satellite transmitters in the Chukchi Sea during the open-water season. Seals migrating between the Beaufort and Chukchi seas could therefore have different carbon isotope ratios. This possible movement and cyclical foraging of spotted seals in offshore areas and coastal haul-out sites as demonstrated by Lowry et al. (1998) or feeding in freshwater versus saltwater habitats could also result in highly variable carbon signatures (Smith et al. 1996; Hobson et al. 1997).

Conclusion

In conclusion, dietary habits of pinnipeds analyzed in this study are markedly different. Bearded seals and walruses relied heavily on the benthic food chain, and ringed, ribbon and spotted seals foraged mainly pelagically. Stable nitrogen and carbon isotope analysis are in agreement with most dietary compositions based on stomach contents. However, the interpretation of stable isotope ratios in pinnipeds (in particular bearded seals) consuming prey with different nitrogen contents and from a wide range of trophic levels can be challenging and sometimes inconclusive. This study documented that age is an important factor when reconstructing pinniped diets and accounts for much of the variability found in stable carbon and nitrogen isotope ratios. We recommend the use of traditional methods, e.g., stomach contents or scat analysis, in combination with chemical feeding ecology to assess dietary habits most accurately when direct observation of feeding behavior is not possible.

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