Trophic ecology of bowhead whales (*Balaena mysticetus*) compared with that of other arctic marine biota as interpreted from carbon-, nitrogen-, and sulfur-isotope signatures

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Abstract: In this study, stable carbon (δ^{13}C), nitrogen (δ^{15}N), and sulfur (δ^{34}S) isotope ratios were measured in muscle tissue from the Bering–Chukchi–Beaufort Sea population of bowhead whales (*Balaena mysticetus*; $n = 84$) and various marine biota between 1997 and 2000. In previous investigations, stable carbon and nitrogen isotope ratios in baleen from this population have been used to elucidate age, migratory behaviour, and feeding ecology. However, information on δ^{13}C, δ^{15}N, and δ^{34}S isotope patterns in bowhead whale muscle tissue and variability within the Bering Sea population is limited. Stable sulfur isotope values did not vary with δ^{13}C enrichment for three consecutive seasons ($n = 53$) and this suggests that habitat selection by bowhead whales was consistent over the sampling period. We found that in contrast to other studies, seasonal differences (spring versus fall) in δ^{13}C values were not associated with seasonal changes in δ^{15}N values, suggesting either that bowhead whales maintain a consistently lower trophic position relative to other marine mammals or that stable carbon and nitrogen isotope fractionation is tissue-dependent and (or) isotope-dependent within this species. Seasonal fluctuation in δ^{13}C values was consistent for all age classes of bowhead whales and suggests that the Bering and Beaufort seas are both important regions for feeding.

Résumé : Nous avons mesuré les rapports entre les isotopes stables de carbone (δ^{13}C), d'azote (δ^{15}N) et de soufre (δ^{34}S) dans les tissus musculaires de baleines boréales (*Balaena mysticetus*; $n = 84$) de la population des mers de Béring, de la Tchoukotka et de Beaufort et d'autres organismes marins entre 1997 et 2000. Au cours d'études antérieures, le rapport entre le carbone et l'azote stables du lard chez cette population a permis de déterminer l'âge, le comportement à la migration et l'écologie alimentaire des baleines. Cependant, les détails connus sur les tendances de δ^{13}C, δ^{15}N et δ^{34}S dans les tissus musculaires de cette baleine et sur la variabilité au sein de la population de la mer de Béring sont limités. Les valeurs des isotopes stables de soufre n'ont pas changé malgré l'enrichissement important en δ^{13}C durant trois saisons consécutives ($n = 53$), ce qui semble indiquer que le choix de l'habitat chez cette baleine a été constant pendant toute la période d'échantillonnage. Contrairement aux résultats obtenus au cours d'autres études, les variations saisonnières (printemps versus automne) de δ^{13}C n'étaient pas associées à des variations saisonnières de δ^{15}N, ce qui indique que les baleines boréales occupent toujours une position trophique inférieure à celle des autres mammifères marins ou que le fractionnement des isotopes stables de carbone et d'azote est fonction du tissu et (ou) de la nature de l'isotope. Les fluctuations saisonnières des valeurs de δ^{13}C sont les mêmes chez toutes les classes d'âge de baleines boréales et indiquent que les mers de Béring et de Beaufort sont des aires d'alimentation importantes.

[Traduit par la Rédaction]

Introduction

The bowhead whale (*Balaena mysticetus*) is an endangered cetacean of cultural and nutritional importance to the Native peoples of northern Alaska, Chukotka (eastern Russia), and Canada. The bowhead whale is the only mysticete that occupies seasonally ice-covered seas in the Arctic throughout the year. The Bering–Chukchi–Beaufort Sea stock migrates annually between the eastern Beaufort Sea in the summer and northern Bering Sea in the winter (Moore and Reeves 1993). As the quality and quantity of prey can affect population growth and health, it is important to understand

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the trophic dynamics of the bowhead whale relative to other species (Lowry 1993).

Stable isotopes of carbon, nitrogen, and sulfur have been previously used as tracers for trophic interactions in the marine environment and serve as a powerful tool for quantifying migratory patterns of biota (Schell et al. 1989; Hesslein et al. 1991; Hobson 1999; Kelly 2000). This approach is based on the notion that stable-isotope ratios in prey are transferred to higher trophic level organisms. These isotope ratios can vary spatially, owing to differences in biogeochemical processes within the environment (Hobson 1999; Kelly 2000).

In general, ^{15}N is enriched relative to ^{14}N via dietary uptake at approximately 3–5‰ per trophic level. This fractionation between biological compartments allows for the identification of trophic position in an ecological context (Kelly 2000). While enrichment of ^{13}C also occurs as trophic level increases (0.2–1‰), measurement of $^{13}C/^{12}C$ in biological systems can help elucidate trophic interactions and energetic dynamics by quantifying the relative contributions of marine versus terrestrial carbon sources (France and Peters 1997).

Sulfur-isotope analysis ($^{34}S/^{32}S$) is also useful for clarifying feeding habits and food-web structure. Stable sulfur isotope ratios do not change significantly with increasing trophic level (Peterson and Fry 1987). However, in regions with different anthropogenic or geological signatures, $\delta^{34}S$ signatures can be used to identify the relative importance of marine and freshwater sulfur sources (Petersen et al. 1986; Peterson and Fry 1987) and to differentiate migration patterns of various fish species (Hesslein et al. 1991).

Habitat selection by the bowhead whale is believed to change with season (Moore et al. 2000). In the spring and summer, bowhead whales reside in continental-slope waters and favour inner-shelf waters during the fall (Moore et al. 2000). Quantification of $\delta^{34}S$ in the bowhead whale may provide additional insight into the feeding ecology of this species. While no study to date has investigated the application of $\delta^{34}S$ to describe the feeding ecology of any cetacean, stable sulfur isotope analysis was performed to investigate the hypothesis that energy intake by bowhead whales may be influenced by feeding in nearshore areas and reflected by seasonal changes in $\delta^{34}S$ signatures.

Previous studies have characterized the heterogeneity of stable carbon isotopes in herbivorous and carnivorous zooplankton from the Bering, Chukchi, and Beaufort seas (Saupe et al. 1989; Schell et al. 1998). An oscillation in seasonal $\delta^{13}C$ signatures has been characterized in baleen plates from bowhead whales migrating between the Beaufort and Bering seas (Schell et al. 1989; Hobson and Schell 1998). As well, Schell et al. (1989) showed that the change in $\delta^{13}C$ signatures between fall and spring migrations diminished with increasing baleen length. The results of these studies suggest that as bowheads increase in age (inferred from increased body length), most of the annual energy intake occurs in the winter range (i.e., the Bering Sea) and that the Beaufort Sea may not be an important feeding ground for mature bowhead whales (Schell et al. 1989).

The objective of this study was to determine if isotopic trends described in previous studies are similar to values in more metabolically active tissue such as muscle. We also investigated seasonal changes in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ with migra-tion and variability of isotopes within the Bering–Chukchi–Beaufort Sea stock, based on harvest season and whale length (i.e., age). Trophic positioning was studied relative to that of other marine species from the study area to provide an ecological context for our findings.

Methods

Sampling

Lumbar-muscle samples from bowhead whales were provided by Native Alaskan (Inuit) subsistence hunters at Barrow, Alaska (71°17′N, 156°45′W), and Kaktovik, Alaska (70°10′N, 143°50′W) (Fig. 1) through the North Slope Borough Department of Wildlife Management (DWM) and Alaska Department of Fish and Game (ADFG). Samples were collected in 1997–2000 during spring and fall subsistence harvests with approval of the Alaskan Eskimo Whaling Commission (Barrow). Personnel from DWM and ADFG recorded specimen data (body length, baleen length, sex, etc.) from each whale sampled. Whale were classified into three cohorts based on body length: juveniles 6–8.9 m; subadults 9–12.9 m; and adults >13 m (George et al. 1999). Muscle from other marine mammals and fish was sampled for an interspecies comparison of trophic positions. Invertebrate samples were collected using a 100 µm mesh plankton tow in Holman, N.W.T. (70°43′N, 117°43′W), and Barrow. Additional copepod samples were collected from the eastern Beaufort Sea (near Kaktovik) by LGL Limited, Sidney, B.C., coincidentally with observed bowhead whale feeding.

Stable-isotope analysis

Sample preparation

Bowhead whale muscle tissues (approximately 100 g from each specimen) were collected and temporarily archived at the Arctic Research Facility in Barrow. Tissue specimens were subsampled with clean titanium-blade knives to remove excess bioorganic materials and sealed in Whirl-packs™. Samples were transported to the National Water Research Institute (Environment Canada), Burlington, Ont., and stored at –20°C. Muscle and whole tissues (zooplankton) were homogenized. Approximately 10 g of tissue from each sample was freeze-dried for 24–48 h and ground into a fine powder.

A portion of tissue was subsampled to test the effect of lipid removal on stable-isotope signatures in biota. The methodology for lipid extraction was developed and described by Pinnegar and Polunin (1999). Samples were weighed (approximately 3 g) and washed in a 10-mL solution of chloroform, methanol, and water (2:1:0.8). Samples were agitated for 30 min and then centrifuged (2000 × g for 10 min). The supernatant was discarded and the process was repeated twice (three exposures). The sample was dried at 60°C, reweighed, and reground prior to analysis. The percentage of lipids in each sample was determined gravimetrically.

Stable-isotope determination

Tissue (1.0–1.5 mg) was weighed using a microbalance (Mettler ME 30) and loaded into a 5 × 8 mm tin capsule. The capsule was subsequently folded and crushed into a cube. All samples were analyzed in triplicate for both stable carbon and nitrogen isotope ratios using a Micromass Optima

Fig. 1. Annual migration route of bowhead whales (*Balaena mysticetus*) between the wintering (W) and summering (S) grounds in the Bering Sea and Beaufort Sea, respectively. Arrows with solid and broken lines indicate spring and fall migrations, respectively. Biota-sampling location for this study are indicated (●).
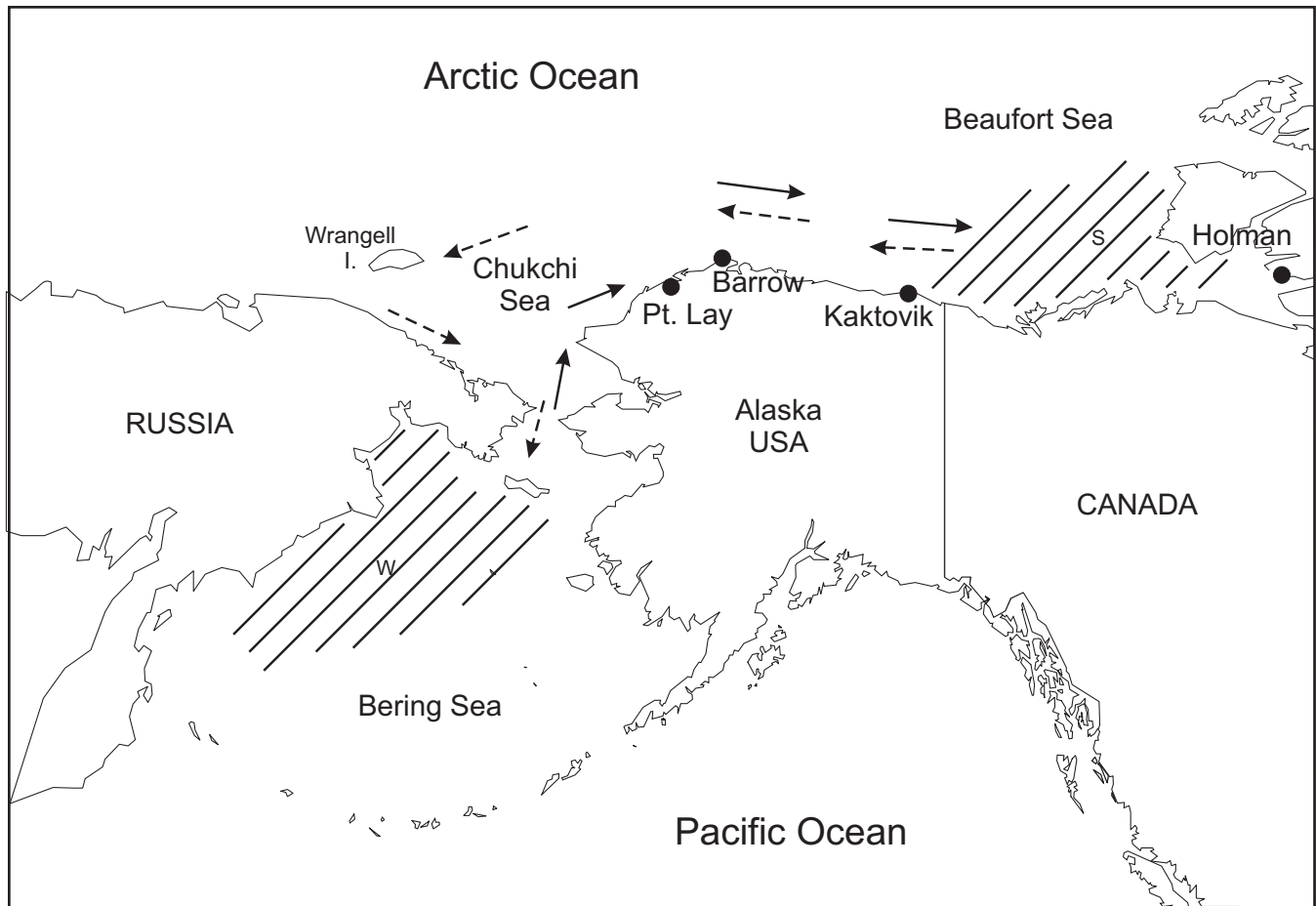
continuous-flow isotope-ratio mass spectrometer directly coupled to a Carlo Erba NA1500 elemental analyzer (Environment Canada, Saskatoon, Sask.). Samples were flash-combusted at 1030°C, followed by on-line removal of water and on-line chromatographic separation of sample N_2 and CO_2 (He carrier gas). The sulfur content of selected lipid-extracted samples (3–6 mg) was converted directly to SO_2, purified, and analyzed on a MicroMass 602D dual-collector mass spectrometer (University of Waterloo, Waterloo, Ont.). Enrichment of a particular isotope was reported using the following notation:

$$[1] \quad \delta R‰ = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where the differential notation (δR) represents the relative difference between isotope ratios of the sample and standard gases ($^{13}C/^{12}C$, $^{15}N/^{14}N$, and $^{34}S/^{32}S$). Samples analyzed for $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were standardized with a synthetic gelatine (PU-gel, Princeton University, Princeton, N.J.). The standardized isotope values for atmospheric N_2 in air and NBS-19 (National Institute of Standards and Technology (NIST), Gaithersburg, Md.) were $5.60 \pm 0.1‰$ for $\delta^{15}N$ and $-12.62 \pm 0.08‰$ for $\delta^{13}C$, respectively. Sulfur analysis was compared against sulfide and sulfate standards (NBS-123 and NBS-127) obtained from NIST. The standardized value of $\delta^{34}S$ in

NBS-123 and NBS-127 was 17.44 ± 0.31 and $20.32 \pm 0.36‰$, respectively. A laboratory working standard (albumen) was run every 10 samples during analysis. External instrument reproducibility for both $\delta^{13}C$ and $\delta^{15}N$ analysis was ± 0.2 and $\pm 0.3‰$ for $\delta^{34}S$ analysis. The standard deviation for carbon-, nitrogen-, and sulfur-isotope values in samples was $\pm 0.2‰$.

Statistical analysis

Paired *t* tests ($\alpha = 0.05$) were used to compare $\delta^{13}C$ and $\delta^{15}N$ values in lipid-extracted and non-lipid-extracted biotic samples. Stable nitrogen isotope values in bowhead whale muscle (all samples pooled) were compared with those in other biota by means of analysis of variance (ANOVA, $\alpha = 0.05$). Derivation of relative trophic levels was based on the most depleted $\delta^{15}N$ value for *Calanus* species. Calanoid copepods are generally considered to be primary herbivores and were assumed to occupy trophic level (TL) 2. Assuming constant isotopic enrichment at a rate of $+3.8‰$ per trophic level, relative trophic levels for biota were calculated (Hobson and Welch 1992):

$$[2] \quad TL = 2 + (\delta^{15}N_{consumer} - \delta^{15}N_{Calanus \ spp.})/3.8$$

Tukey's test ($\alpha = 0.05$) was used to compare stable nitrogen

Table 1. Mean stable isotope values and derived trophic positions of the bowhead whale and other biota.

	Season and year	Sampling location[a]	n	Trophic level[b]	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{34}S$ (‰)
Bowhead whale	Fall 1997	Barrow	21	2.9	13.3 (0.3)	−21.1 (0.2)	17.3 (0.2)
		Kaktovik	4	2.9	13.1 (0.2)	−21.8 (0.3)	17.6 (0.5)
	Spring 1998	Barrow	9	3.0	13.5 (0.4)	−19.8 (0.3)	17.0 (0.2)
	Fall 1998	Barrow	16	2.9	13.1 (0.2)	−21.0 (0.2)	17.1 (0.2)
		Kaktovik	3	2.8	12.8 (0.4)	−21.8 (0.2)	17.2 (0.1)
	Spring 1999	Barrow	15	2.9	13.3 (0.3)	−20.1 (0.3)	na
	Fall 1999	Barrow	5	2.8	12.5 (0.3)	−21.0 (0.1)	na
		Kaktovik	3	3.1	13.6 (0.6)	−21.2 (0.3)	na
	Spring 2000	Barrow	4	2.8	12.9 (0.6)	−19.6 (0.2)	na
	Fall 2000	Barrow	2	2.9	13.1 (0.2)	−20.9 (0.4)	na
		Kaktovik	2	3.0	13.5 (0.9)	−23.2 (0.9)	na
Beluga whale	1998–1999	Point Lay	22	3.8	16.6 (0.1)	−18.7 (0.2)	17.7 (0.2)
Ringed seal	1998–1999	Barrow	33	3.9	16.9 (0.2)	−18.7 (0.2)	na
Bearded seal	1998–1999	Barrow	6	3.9	16.8 (0.4)	−17.2 (0.2)	na
Arctic cod	1998	Barrow	20	3.1	13.7 (0.2)	−20.3 (0.2)	na
Broad whitefish	1998	Chip River	10	2.0	9.8 (0.8)	−27.1 (1.9)	6.4 (2.2)
	1998	Meade River	10	2.4	11.3 (0.7)	−24.8 (1.1)	9.9 (0.6)
Chum salmon	1998	Barrow	3	2.6	11.8 (0.2)	−20.8 (0.2)	na
Pink salmon	1998	Barrow	7	2.3	10.8 (0.6)	−20.4 (0.2)	na
Arctic flounder	1998	Barrow	3	2.8	12.6 (0.2)	−19.7 (0.5)	na
Calanoid copepod	1998	Kaktovik[c]	20	2.2	10.4 (0.5)	−22.8 (0.4)	na
(*Calanus* spp.)	1999	Holman[c]	10	2.2	10.4 (0.4)	−24.3 (0.5)	na
	2000	Barrow[c]	10	2.0	9.8 (0.2)	−20.8 (0.1)	na

Note: Values in parentheses are 95% confidence values; n is the number of samples analyzed; na, not analyzed.
[a]All locations are in Alaska, except Holman, N.W.T.
[b]Non-extracted (whole tissue).
[c]Calculated as follows: TL = 2 + ($\delta^{15}N_{consumer} - \delta^{15}N_{Calanus\ spp.}$)/3.8 (from Hobson and Welch 1992).

isotope values in the bowhead whale with those in other marine biota.

ANOVA was applied to determine the influence of sex, sampling season, and (or) length cohort on $\delta^{13}C$ signatures. Tukey's multiple-comparison test ($\alpha = 0.05$) was used to examine significant differences in stable-isotope patterns between seasonal groups and cohorts of harvested bowhead whales. The relationships among $\delta^{34}S$, $\delta^{15}N$, and $\delta^{13}C$ in muscle tissue were analyzed with linear regression. All statistical analysis was performed using SYSTAT® version 8.0 (SPSS, Chicago, Ill.).

Results

Table 1 is a summary of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values for the bowhead whale and other marine and anadromous species. The $\delta^{13}C$ and $\delta^{15}N$ values in lipid-extracted and non-lipid-extracted tissues from selected biota were not significantly different ($p > 0.05$ for all pairwise comparisons). As a result, only isotope values from non-lipid-extracted tissues were considered in the subsequent statistical analysis and interpretation.

Stable nitrogen isotope values and assigned trophic levels calculated in this study are in agreement with current knowledge on the diets of Arctic marine species (Table 1 and Fig. 2). Bowhead whales were found to have significantly different nitrogen-isotope signatures than other marine biota ($F_{[5,178]} = 362.4$, $p < 0.001$; Tukey's test, $p < 0.001$ for all

comparisons) except Arctic cod (*Boreogadus saida*) ($p > 0.05$).

The $\delta^{34}S$ values were not significantly influenced by harvest season or length cohort ($p > 0.10$ for all comparisons). Additionally, $\delta^{34}S$ values were independent of $\delta^{15}N$ ratios in the bowhead whale samples from 1997–1998 ($F_{[1,51]} = 0.10$, $p = 0.754$). However, $\delta^{34}S$ signatures in both beluga and bowhead whales were significantly different from those in the broad whitefish (*Coregonus nasus*) ($p < 0.001$). Broad whitefish from the Chip and Meade rivers had significantly different $\delta^{34}S$ signatures ($p = 0.01$).

A significant seasonal oscillation in $\delta^{13}C$ values between whales landed in the fall and spring was observed (ANOVA, $F_{[1,80]} = 89.1$, $p < 0.001$; Tukey's test, $p < 0.01$ for all comparisons; Fig. 3). The $\delta^{13}C$ values for adult and subadult whales from Barrow and Kaktovik landed during the fall harvest were significantly different (t test, $p = 0.002$; Fig. 4). Since no juvenile whales were harvested at Kaktovik during the 1997–2000 sampling period, this cohort was omitted from the above comparison.

Seasonal changes in feeding habits of the bowhead whale with increasing age (as interpreted from body length) were investigated by determining the $\delta^{13}C$ values in fall- and spring-harvested specimens. A significant interaction with season (fall versus spring migration) was found (ANOVA, $F_{[1,76]} = 90.0$, $p < 0.001$). However, neither length cohort (main effect) nor season × length (interaction effect) was significant ($p > 0.08$). The $\delta^{15}N$ and $\delta^{34}S$ signatures in bowhead whale

Fig. 2. Mean $\delta^{15}N$ values in bowhead whale muscle tissue and in other marine biota from the Beaufort and Chukchi seas. Numbers in parentheses indicate the number of specimens analyzed. Vertical lines denote +95% confidence intervals. Columns with the same letters are not statistically different ($\alpha = 0.05$).
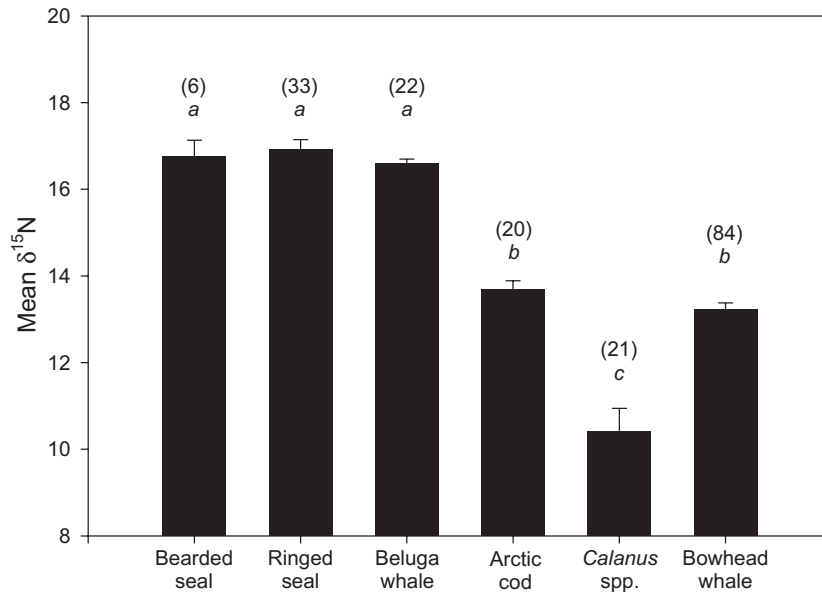
muscle tissue did not fluctuate with oscillating $\delta^{13}C$ patterns ($\delta^{15}N$: $F_{[1,80]} = 1.64$, $p = 0.20$; $\delta^{34}S$: $F_{[1,51]} = 0.08$, $p = 0.776$)

Discussion

Trophic position interpreted from $\delta^{15}N$ values

Stable nitrogen isotope ratios varied among the species analyzed and are in reasonable agreement with current knowledge concerning the diets of Arctic marine biota (Table 1). Bowhead whales were found to have significantly different $\delta^{15}N$ values than other marine biota ($p < 0.001$ for all comparisons) except Arctic cod ($p > 0.05$; Fig. 2). Mean $\delta^{15}N$ values of bowhead whales were significantly lower than those of carnivorous marine mammals (–3 to –3.5‰), demonstrating that the bowhead whale is a full trophic position lower than other marine mammals analyzed in this study.

The foods selected by the bowhead whale and other selected species explain the differences observed in $\delta^{15}N$ values. The diet of the bowhead whale consists primarily of calanoid copepods, euphausiids, and other planktonic organisms, as well as epibenthic organisms in the case of subadult whales (Hazard and Lowry 1984; Lowry 1993). The derived trophic position of the bowhead whale was less than one complete trophic level (TL = 2.8–3.0) higher than that of the calanoid copepods sampled (TL = 2.0–2.2). This is most likely due to the nonselective filter-feeding behaviour of the bowhead whale and the influence of planktonic organisms on the overall $\delta^{15}N$ signatures in the bowhead whale.

The isotope values from this study are similar to those from other reports and suggest that the diets of ringed seals (*Phoca hispida*), bearded seals (*Erignathus barbatus*), and beluga whales (*Delphinapterus leucas*) comprise a mixture of fish species, possibly including Arctic cod, as well as a variety of benthic and pelagic invertebrates (Lowry et al. 1980; Heide-Jorgensen and Teilmann 1994; Holst 2000).

Arctic cod play an important role in the trophic transfer of energy from lower trophic level taxa to marine mammals and birds (Bradstreet and Cross 1982). The $\delta^{15}N$ values in Arctic cod are consistent with the known ecology of this species, which feeds on copepods and amphipods prior to maturity (Bradstreet et al. 1986; Hobson and Welch 1992; Hobson et al. 2001). The trophic positions of the broad whitefish, chum salmon (*Oncorhynchus keta*), pink salmon (*Oncorhynchus gorbuscha*), and Arctic flounder (*Liposetta glacialis*) inferred from $\delta^{15}N$ signatures are consistent with their omnivorous and (or) detrital feeding strategies.

The $\delta^{34}S$ values in the bowhead whale and marine biota

Stable sulfur isotope analysis was performed to test the hypothesis that seasonal changes in habitat selection may influence the trophic status of the bowhead whale. The $\delta^{34}S$ signatures of both the beluga and the bowhead whale were significantly different from those of the broad whitefish ($p < 0.001$), an anadromous species in northern Alaska. Additionally, broad whitefish from the Chip and Meade rivers had significantly different $\delta^{34}S$ signatures. The high variability associated with the $\delta^{34}S$ signatures in the broad whitefish confirms previous observations that this species interacts with both freshwater and marine ecosystems (Jarvela and Thorsteinson 1999). The results support the application of $\delta^{34}S$ signatures as a potential tracer of migration as well as in differentiating fish from specific watershed habitats in northern Alaska.

This is the first study to report the stable sulfur isotope values in species within this study region. As a result, the background $\delta^{34}S$ signatures in species in the nearshore marine environment of northern Alaska have not been well characterized. The significant difference among the two cetacean species and the anadromous broad whitefish suggests that both belugas and bowhead whales derive most of their

Fig. 3. Mean stable carbon and nitrogen isotope values in bowhead whale muscle tissue according to season of harvest. Vertical lines denote +95% confidence intervals. The seasonal pattern of $\delta^{13}C$ values in bowhead whale muscle was consistent for all length cohorts ($p < 0.01$ for all multiple comparisons). No significant effect of harvest season was observed for $\delta^{15}N$ ($p > 0.05$ for all comparisons).
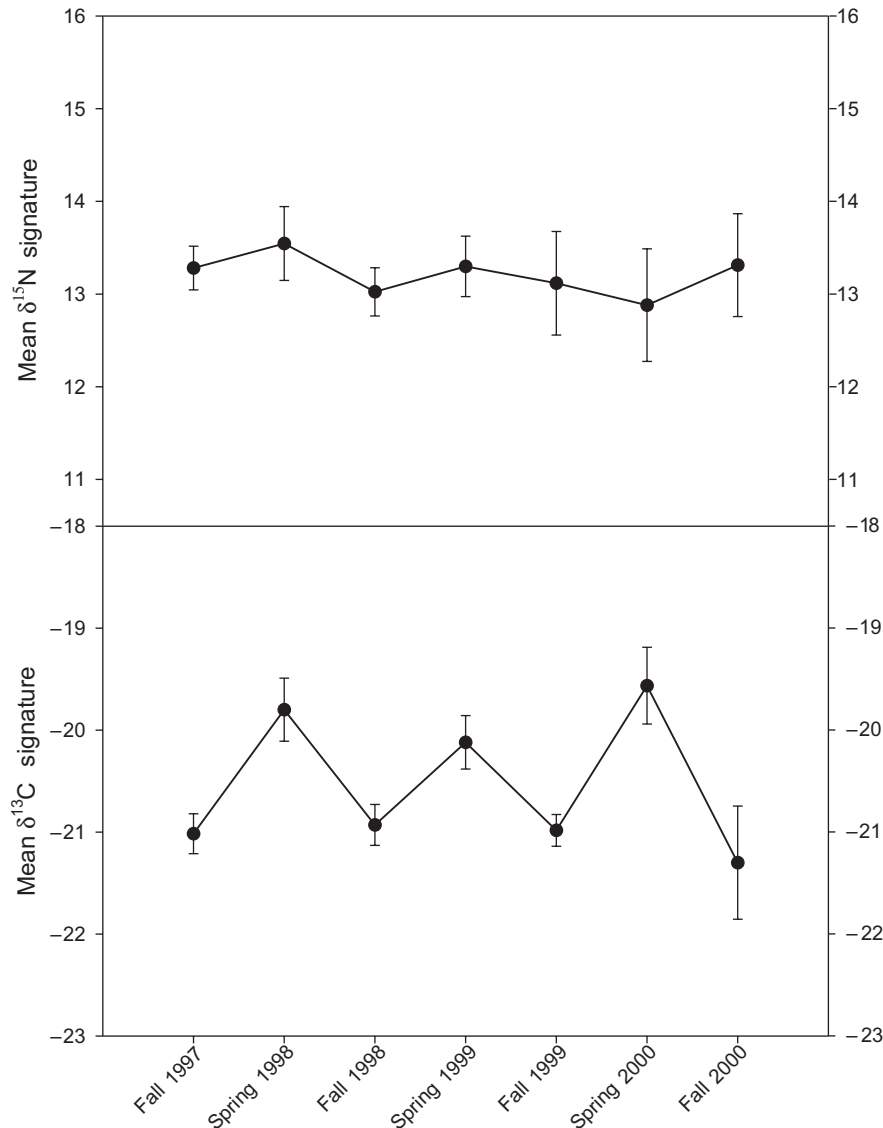
energy inputs from the marine environment. Results suggest that the nearshore relationship of the bowhead whale is constant during the spring and fall harvest seasons. However, our finding cannot be extrapolated to the long-term behaviour of the bowhead whale, as samples from only three consecutive seasons were analyzed for $\delta^{34}S$. The variability associated with these comparisons may be due to fluctuations in $\delta^{34}S$ signatures derived from various terrestrial inputs (Petersen et al. 1986; Hesslein et al. 1988, 1991). As well, the decomposition process of sulfate reduction in marine sediments may effect the distribution of stable sulfur isotopes in the aquatic environment (Jorgensen 1979).

### The $\delta^{13}C$ values in bowhead whale muscle tissue

Influence of season on $\delta^{13}C$ values

Significant seasonal changes in $\delta^{13}C$ values were observed between fall- and spring-harvested bowhead whales in Bar-

row (Fig. 3). The $\delta^{13}C$ patterns in the bowhead whale muscle analyzed in this study were consistent with previous observations of $\delta^{13}C$ patterns in baleen (Schell et al. 1989; Hobson and Schell 1998), suggesting that the bowhead whales harvested from 1997 to 2000 were feeding in both the Bering Sea and the Beaufort Sea. The seasonal changes of $\delta^{13}C$ in baleen are believed to reflect the changes in abundance of ^{13}C relative to ^{12}C in bowhead whale prey, based on geographic location and time of year (Saupe et al. 1989; Schell et at. 1998). Plankton species from the summer range of the bowhead whale in the Beaufort Sea – Amundsen Gulf are ^{13}C-depleted, owing to terrestrial inputs of carbon with low $\delta^{13}C$ values from the Mackenzie and Colville river basins. In contrast, the wintering grounds of the bowhead whale in the Bering Sea contain ^{13}C-enriched zooplankton and invertebrates (Schell et al. 1998).

Seasonal patterns of stable carbon values in bowhead whale muscle tissues analyzed in this study were observed

Fig. 4. Stable carbon isotope ratios in muscle tissue from subadult and adult bowhead whales harvested during Native subsistence hunts (fall only) at Kaktovik (○) and Barrow (●). The $\delta^{13}C$ values for adult and subadult whales harvested at these two locations were significantly different ($p < 0.05$ for both comparisons).
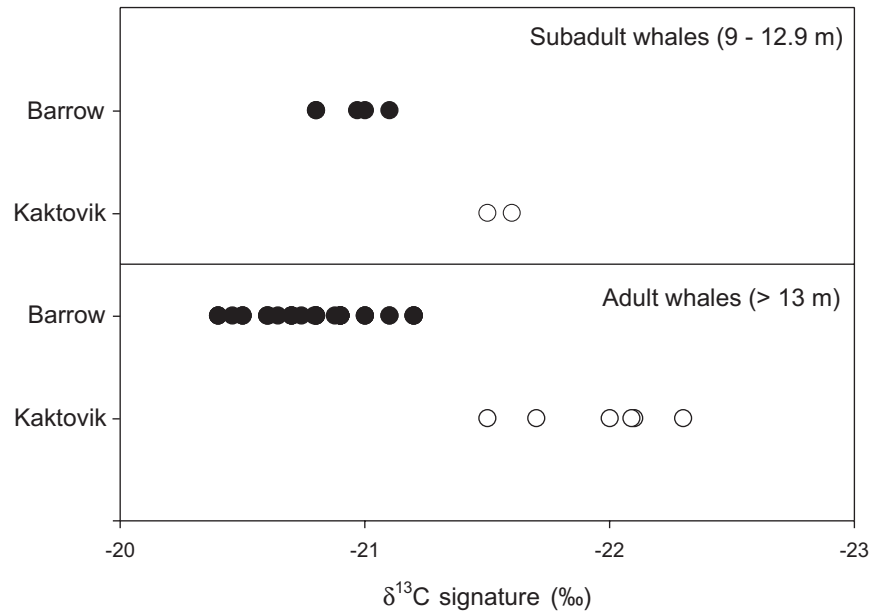
for all length cohorts ($p > 0.10$ for all comparisons). Previous reports have suggested that the Beaufort Sea may not be a significant feeding ground compared with the Bering Sea for adult bowhead whales (Schell et al. 1989; Hobson and Schell 1998). Schell et al. (1989) reported that the $\delta^{13}C$ values in subadult bowhead whales reflected the differences in $\delta^{13}C$ between the Bering and Beaufort seas, while the seasonal pattern of $\delta^{13}C$ was reduced or absent from muscle and baleen samples from adult whales (Schell et al. 1989; Hobson and Schell 1998). However, in both studies it was acknowledged that more samples would be desirable to support these observations.

In addition to $\delta^{13}C$ values in muscle, the profile of persistent organochlorine contaminants (OCs) in blubber from bowhead whales harvested from 1997 to 2000 also varied with season (Hoekstra et al. 2002). Hoekstra et al. (2002) found that contaminant profiles in bowhead whale blubber generally reflected the spatial differences in OC concentrations in surface waters in the Bering and Beaufort seas. While a direct comparison of the aforementioned investigations is difficult because of the influence of compounding variables (i.e., tissue type, sample size, and other variables that affect seasonal OC bioaccumulation), the interpretation of the stable-isotope and OC analysis provides further evidence that the bowhead whales were feeding in both the Beaufort Sea and the Bering Sea during the 1997–2000 sampling period.

Influence of tissue type on $\delta^{13}C$ values

The differences in $\delta^{13}C$ values observed in muscle samples from this study were not as pronounced as the seasonal shift in baleen as reported by Hobson and Schell (1998) and Schell et al. (1989). The potential differences in $\delta^{13}C$ fractionation between muscle and baleen may explain this discrepancy. Schell et al. (1989) reported $\delta^{13}C$ values in muscle from spring-harvested whales (–18.8 to –20.7‰) that were

similar to those found in this study (Fig. 3). Laboratory and field observations have indicated that $\delta^{13}C$ fractionation is tissue-dependent and that the relative enrichment of ^{13}C in hair and bone is greater than in other tissues, including muscle (Tieszen et al. 1983; Hobson and Clark 1992; Hobson et al. 1996).

As the isotope composition of muscle tissue is not static relative to that of baleen, feeding by the bowhead whale during migration may diminish the overall difference in $\delta^{13}C$ values obtained from muscle (Fig. 4). The $\delta^{13}C$ signatures in subadult whales from Kaktovik (eastern Beaufort Sea) during the southwest (fall) migration to the Bering Sea were significantly different from those found in subadult whales harvested from Barrow ($p = 0.002$) during the same season. The $\delta^{13}C$ values in adult whales harvested from these two sites were also significantly different ($p = 0.04$). These results suggest that feeding along the coast of Alaska may reduce the magnitude of seasonal differences in $\delta^{13}C$ values found in muscle tissue from bowhead whales harvested in Barrow.

Relationships with $\delta^{15}N$ and $\delta^{13}C$

Stable nitrogen isotope ratios in bowhead whale muscle did not differ significantly between fall- and spring-harvested whales (Fig. 3). However, a seasonal shift in $\delta^{15}N$ signatures in baleen has been previously observed (Schell et al. 1989; Hobson and Schell 1998). Hobson and Schell (1998) suggested that the seasonal differences in $\delta^{15}N$ might be caused by whales migrating between isotopically distinct $\delta^{15}N$ regions and (or) protein catabolism due to seasonal fasting. Schell et al. (1998) revealed that the $\delta^{13}C$ and $\delta^{15}N$ values and community structure of various invertebrates are heterogeneous within the Bering, Chukchi, and Beaufort seas.

The lack of seasonal differences in $\delta^{15}N$ values in the bowhead whale muscle tissue analyzed in this study suggests

that either the relative composition of $\delta^{15}N$ values in invertebrate prey of the bowhead whale fluctuates within this region or that fractionation rates of stable nitrogen isotopes in muscle and baleen are different. Tissue-specific fractionation of both stable carbon and nitrogen isotopes has been observed in other marine mammals (Hobson et al. 1996). While metabolically active tissue such as muscle may provide a short-term account of the feeding ecology of a species, periods of physical activity (or inactivity) during seasonal migration may alter $\delta^{15}N$ turnover rates in the bowhead whale. More research is required to determine the effects of physiological stress on stable-isotope fractionation in biological systems.

This investigation has provided additional understanding of the trophic ecology of the Bering–Chukchi–Beaufort Sea bowhead whale population relative to that of other marine species in the Alaskan and western Canadian Arctic marine environment. Our results demonstrate that a large sample from multiple seasons is needed to address spatial and temporal variation in trophic ecology as interpreted from stable-isotope analysis. The analysis of stable carbon and nitrogen isotopes illustrates that the bowhead whale occupies a lower trophic position than other marine mammals and suggests that the Bering and Beaufort seas are important regions for feeding by this species, regardless of age class.

Acknowledgements

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