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Marine Pollution Bulletin 52 (2006) 301–319
MARINE POLLUTION BULLETIN
www.elsevier.com/locate/marpolbul

Stable isotope and trace element status of subsistence-hunted bowhead and beluga whales in Alaska and gray whales in Chukotka

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Abstract

Tissues of bowhead, beluga, and gray whales were analyzed for Ag, Cd, Cu, Se, Zn, THg and MeHg (belugas only). $\delta^{15}N$ and $\delta^{13}C$ in muscle were used to estimate trophic position and feeding habitat, respectively. Trace element concentrations in tissues were significantly different among whale species. Hepatic Ag was higher in belugas than bowheads and gray whales. Gray whales had lower Cd concentrations in liver and kidney than bowhead and belugas and a sigmoid correlation of Cd with length was noted for all whales. Renal and hepatic Se and THg were higher in belugas than in baleen whales. The hepatic molar ratio of Se:THg exceeded 1:1 in all species and was negatively correlated to body length. Hepatic and renal Zn in subsistence-harvested gray whales was lower than concentrations for stranded whales. Se:THg molar ratios and tissue concentrations of Zn may show promise as potential indicators of immune status and animal health.

Keywords: Bowhead whale; Beluga whale; Gray whale; Trace elements; Stable isotopes; Feeding ecology; Arctic

1. Introduction

Bowhead (*Balaena mysticetus*), beluga (*Delphinapterus leucas*) and gray whales (*Eschrichtius robustus*) have been of subsistence and cultural importance to the Inuit of Alaska and other Arctic areas for centuries. Accumulation of toxic elements is of growing concern to the consumers of subsistence foods in Alaska and Russia, and the cold water of the Arctic has been proposed as a sink for many contaminants (Ponce et al., 1997; Egeland et al., 1998; Bard, 1999). Continuous bioaccumulation and biomagnification of trace elements have been repeatedly reported in marine mammal tissues (Honda et al., 1983; Hansen et al., 1990; Dietz et al., 2000; Woshner et al., 2001). In addition, the effect of longevity in cetaceans, in particular the bowhead whale (George et al., 1999), may lead to high levels of trace element accumulation.

The bowhead whale is the largest mysticete in Arctic waters. The Bering–Chukchi–Beaufort seas stock (BCBS or western Arctic stock) of bowheads migrates annually from the Bering Sea in winter to the Beaufort Sea in summer (Moore and Reeves, 1993). Commercial whalers decimated the bowhead population in the 19th century, but the BCBS stock is recovering at an estimated rate of 3.4% a year and sustains a controlled subsistence harvest (George et al., 2004). However, effects of offshore and coastal industrial development and thus health status and contaminant burden are of great importance for conservation and management of this culturally important species. Generally, trace elements in tissues of bowhead whales are low compared to other cetaceans, e.g., beluga, narwhal (*Monodon monoceros*), minke whale (*Balaenoptera acutorostrata*) and harbor porpoise (*Phocoena phocoena*) (Honda et al.,

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0025-326X/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.marpolbul.2005.09.001

1987; Hansen et al., 1990; Mackey et al., 1995; Wagemann et al., 1996; Woshner et al., 2001). Several studies have linked the lower trace element concentrations found in mysticetes to their low position in the food chain (Honda et al., 1987; Hansen et al., 1990; Bratton et al., 1997; Woshner et al., 2001). However, compared to domestic animals, cadmium (Cd) concentrations in kidneys of bowheads are at levels of concern to whale health and subsistence consumers (Puls, 1994; Bratton et al., 1997).

Gray whales are primitive mysticetes and unique in their reliance on benthic invertebrates (Rice and Wolman, 1971). Benthic gammaridean amphipods (e.g., *Ampelisca* spp.) are found most commonly in their stomachs (Rice and Wolman, 1971; Bogoslovskaya et al., 1981). In 1999 the number of gray whales involved in fatal strandings increased from an average of about 50 animals per year to 274 animals (Le Boeuf et al., 2000). Contaminants, in particular sediment-associated compounds, have been proposed as possible causes for the die-offs (Varanasi et al., 1994; Le Boeuf et al., 2000; De Luna and Rosales-Hoz, 2004). However, very little baseline information is available on trace elements in healthy gray whales, making inference on the cause of strandings difficult. Tilbury et al. (2002) have reported trace element concentrations in juvenile gray whales harvested in Russia for subsistence use. Other information on trace elements consists of data of stranded animals (mostly juveniles) of varying specimen condition (Varanasi et al., 1994; Méndez et al., 2002; Ruelas-Inzunza and Paez-Osuna, 2002; De Luna and Rosales-Hoz, 2004).

The beluga is a medium sized odontocete and is widely distributed throughout the Arctic. Five stocks of beluga whales are currently recognized in Alaskan waters, including the small isolated Cook Inlet stock (O'Corry-Crowe et al., 1997). Little information is available on beluga feeding ecology. Various species of fishes have been identified from stomach contents, and benthic and epibenthic prey (e.g., octopus, shrimp, polychaetes) seem to be of importance (Seaman et al., 1982). Some beluga stocks are declining in Alaska and Canada, and contaminants have been proposed as significant factors in this decline (Wagemann et al., 1990; Gauthier et al., 1998; Becker et al., 2000). Belugas in the isolated St. Lawrence estuary are exposed to elevated contaminants and show signs of disease (e.g., neoplasia) and immune suppression associated with contaminant burden (Gauthier et al., 1998, 2003; Martineau et al., 2003; Brousseau et al., 2003).

Bowheads, beluga, and gray whales utilize very different trophic niches in the Arctic marine food web, and a comparison between tissues of these cetaceans may help to discriminate trace element pathways. Thus, it is of importance to identify trophic level and predator–prey relationships for these species. Studies of feeding ecology that rely on fecal or stomach contents analysis are strongly biased toward prey with identifiable hard parts and often underestimate soft prey (Sheffield et al., 2001). In addition, the frequency of empty stomachs is high in marine mammals, especially during migration, and empty stomachs will not yield any prey-based information (Rice and Wolman, 1971; Oliver et al., 1983; Kasuya, 1995).

Stable isotopes have been increasingly important in feeding ecology studies. They occur naturally, and nitrogen isotope ratios of prey are reflected in tissues of the consumer with slight enrichment occurring at each trophic step (Kelly, 2000). Carbon isotope ratios are not reliable indicators of trophic position, but are powerful in distinguishing between benthic and pelagic foodwebs, inshore versus offshore environments and fresh- and saltwater habitats (Tieszen et al., 1983; France, 1995; Smith et al., 1996; Burton and Koch, 1999). Schell et al. (1998) showed distinct regional differences in carbon isotope signatures of zooplankton from the Beaufort Sea versus the Bering and Chukchi seas. These differences have also been detected in muscle and baleen of migrating bowhead whales (Schell et al., 1989; Hoekstra et al., 2002). However, little or no comparative information is available on stable carbon and nitrogen isotope ratios in tissues of bowheads, belugas, and gray whales.

The objectives of this study are to provide reference concentrations of selected trace elements and stable isotopes of apparently healthy whales taken during subsistence harvests in Alaska and Russia to evaluate the effects of age (length) and trophic level ($\delta^{15}N$) on trace element pathways and biomagnification in Arctic cetaceans. This may aid in the conservation and management of these important subsistence species.

2. Materials and methods

2.1. Sample collection

All whale samples were obtained during Native subsistence harvests. Basic morphometrics, e.g., body length, blubber thickness, and sex were recorded. Standard body length (rostrum to fluke notch) was used as a proxy for age (Sergeant and Brodie, 1969; Rice and Wolman, 1971; George et al., 1999). Most whales were grossly examined for lesions. Bowhead epidermis, lumbar muscle, kidney, and liver were predominantly collected in Barrow, Alaska during either spring or fall harvest 1998–2001 ($n = 99$). Data from bowheads harvested during 1995–1997 ($n = 21$) (Woshner et al., 2001) and harvested from 1983 to 1990 ($n = 41$) (Bratton et al., 1997) were included in the data set. Samples of belugas harvested in Point Lay and Wainwright, Alaska in 1998–1999 ($n = 24$) were combined with data obtained during 1996–1997 ($n = 24$) (Woshner et al., 2001) and 1992–1995 ($n = 19$) (Tarpley et al., 1995) that displayed the appropriate biological variables to increase sample size and statistical power. Additionally, belugas sampled during 1996 and 1997 and bowheads sampled during 1997 were analyzed for stable carbon and nitrogen isotopes as part of this study. Tissues of gray whales were collected in Lorino and Lavrentiya, Russia in 2001. Amphipods and zooplankton were obtained in the Bering Strait and near Kaktovik, Alaska, respectively.

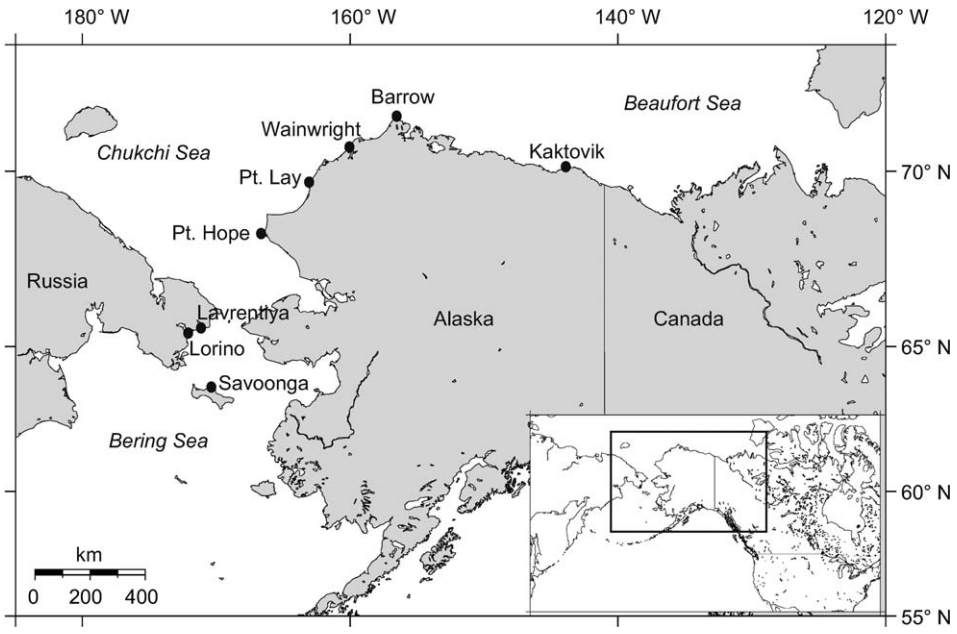

Fig. 1. Alaskan and Russian communities where samples of subsistence harvested Arctic cetaceans were collected.

Table 1
Whale samples collected in Alaskan and Russian villages

Species	Sampling location	*n*			
		Epidermis	Muscle	Kidney	Liver
Bowhead whale	Barrow	96	77	140	143
	Kaktovik	4	9	12	14
	Wainwright	–	–	4	3
	Savoonga	–	–	–	1
Beluga whale	Pt. Lay	32	31	49	51
	Wainwright	2	–	2	2
	Pt. Hope	2	9	9	9
	Barrow	4	4	3	4
	Kaktovik	1	1	1	1
Gray whale	Lorino/Lavrentiya	27	17	28	29

n: sample size.

Fig. 1 shows communities where samples were collected and Table 1 summarizes sample sizes. All tissues were subsampled 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 scintillation vials or Whirlpacks™ until analysis. Marine mammal samples were collected and analyzed under the authority of Permit No. 932-1489-03 issued to Dr. T. Rowles of the Marine Mammal Health and Stranding Response Program.

2.2. Stable isotope analyses

Muscle of bowhead, beluga, and gray whales and total body homogenates of prey (unsorted zooplankton and amphipods) were freeze-dried and ground into a fine powder with mortar and pestle. For each sample, 0.2–0.4 mg of tissue was weighed into a 4.75×4 mm tin capsule, which were folded into a cube. Samples were analyzed for both stable isotope ratios of carbon and nitrogen at the University of Alaska Fairbanks (UAF) using a Finnigan MAT Delta^{Plus}XL Isotope Ratio Mass Spectrometer (IRMS) directly coupled to a Costech Elemental Analyzer (ESC 4010). Samples were flash-combusted at 1020 °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:

$$\delta R‰ = \left((R_{\text{sample}}/R_{\text{standard}}) - 1\right) \times 1000,$$

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‰.

2.3. Trace element analyses

Silver (Ag), cadmium (Cd), copper (Cu), selenium (Se), and zinc (Zn) were analyzed at Texas A&M University (TAMU) following US Environmental Protection Agency (EPA) procedures (200.3, 200.7, 200.8 and 200.9) with slight modifications (EPA, 1992). Briefly, sub-sampled tissues were homogenized, and approximately 0.8–1.0 g of sample was digested in a microwave wet ash procedure using HNO_3, H_2O_2 and HCl. A second preparation followed for determination of Se in tissues using excess HCl to completely reduce Se(VI) to Se(IV) in a CPI ModBlock digester. For bowhead and beluga whales, Cd and Ag were analyzed using Graphite Furnace Atomic Absorption Spectrometry (Perkin-Elmer Model SIMAA 6000 equipped with an AS-72 autosampler and Zeeman background correction). Cu and Zn were determined by Flame Atomic Absorption Spectrometry (Perkin-Elmer Aanalyst 100). Se in all whale tissues was analyzed using Atomic Fluorescence Spectrometry (PSA Millennium Excalibur with CETAC autosampler) and metals (Ag, Cd, Cu and Zn) in gray whales were analyzed by ICP-MS (Perkin-Elmer Elan Model 6100 DRC-II). The detection limit was 0.01 μg/g for elements analyzed with Graphite Furnace AAS, Flame AAS and Atomic Fluorescence Spectrometry. The detection limits were 0.01 μg/g for Cd, 0.05 μg/g for Zn and Cu and 0.005 μg/g for Ag using ICP-MS. All element concentrations are expressed as μg/g wet weight (ww) unless otherwise noted.

2.4. Total mercury

Total mercury (THg) was analyzed at UAF following the procedure established by Bloom and Crecelius (1983). Briefly, sub-sampled tissues were homogenized, and approximately 1 g of tissue was digested in 7:3 HNO_3/H_2SO_4 and oxidized with 10% BrCl in 12 N HCL. The sample was reduced to Hg^0 with $SnCl_2$ and purged with N_2 onto gold-coated quartz sand traps followed by dual thermal desorption to a Cold Vapor Atomic Fluorescence Spectrometer (Tekran Model-2500 CVAFS Mercury Detector) with argon as carrier gas. The detection limit was 0.001 μg/g. Concentrations are expressed as μg/g wet weight (ww) unless otherwise noted.

2.5. Methyl mercury

Methyl mercury (MeHg) was analyzed in beluga tissues at UAF following the procedure established by Bloom (1989). About 1 g of tissue was homogenized and digested in 20% KOH in methanol. Aqueous phase ethylation was initiated with $NaB(C_2H_5)_4$ resulting in volatile methylethylmercury which was purged with N_2 from solution onto a carbotrap™. MeHg was thermally desorbed from the trap and volatile ethyl-analogs were separated by isothermal (100 °C) gas chromatography followed by CVAFS (Tekran Model-2500) with argon as carrier gas. The detection limit was 0.001 μg/g. Concentrations are expressed as μg/g wet weight (ww) unless otherwise noted.

2.6. Quality control

All trace element analyses were performed under a thorough quality control program (Table 2). Reference materials (DOLT-2, DOLT-3 and DORM-2) were obtained from the National Research Council, Canada and BLS 1577b from NIST. Marine mammal reference material (liver of pilot and beluga whale) was provided by NIST as part of annual interlaboratory comparison exercises for the determination of trace elements in marine mammals (Wise et al., 1993; Christopher, 2002, 2004). Spikes and duplicate samples as well as method and instrument blanks were run routinely (with each group of 20 samples) during analysis.

2.7. Trace element ratios

The ratio or relative occurrence of organic Hg (MeHg) to total Hg (THg) is referred to as %MeHg in the text and was calculated (for belugas only) as

$$\%\mathrm{MeHg} = (\mathrm{MeHg}\ \mu g/g\ \mathrm{ww}/\mathrm{THg}\ \mu g/g\ \mathrm{ww}) \times 100.$$

The molar ratio of Se to THg was calculated for all three species as

$$\mathrm{Se:THg\ molar\ ratio} = (\mathrm{Se}\ \mu g/g\ \mathrm{ww}/\mathrm{THg}\ \mu g/g\ \mathrm{ww}) \times (200.59\ g/\mathrm{mole}/78.96\ g/\mathrm{mole}),$$

where 200.59 g/mole and 78.96 g/mole are the atomic weights of Hg and Se, respectively.

2.8. Statistical analysis

The variables in the data set (body length, $\delta^{15}N$, $\delta^{13}C$, Ag, Cd, Cu, Se, Zn, THg, MeHg, %MeHg, and Se:THg molar ratio) were ranked prior to analysis to reduce the risk of violations of normality and homogeneity of variance assumptions. Two-way ANOVA (with interaction term − species × sex) followed by Tukey's multiple comparison test was applied to compare variable means between cetacean species and sex. Sample sizes did not allow for a comparison between localities or analysis of temporal variation. A residual analysis was implemented to determine possible violations of assumptions. Spearman rank correlation was calculated within a species to determine correlations between the variables. LOESS smoothing followed by nonlinear regression analysis was utilized on non-ranked raw data to estimate suitable functions between two variables and compare regression surfaces between whale species. Graphing and nonlinear regression analyses were conducted using Sigma-Plot (Version 7.0). All other

Table 2
Results for trace element analysis of reference materials for quality assurance/quality control

		Ag	Cd	Cu	Se	Zn	THg	MeHg
Dogfish muscle	Dorm-2							
	Certified value	0.041 ± 0.09	0.043 ± 0.008	2.34 ± 0.16	1.4 ± 0.09	25.6 ± 2.3	4.64 ± 0.26	4.47 ± 0.32
	Measured mean	–	–	–	1.3	–	4.55	3.88
	Standard deviation	–	–	–	0.08	–	0.25	0.11
	% Recovery	–	–	–	96.4	–	98.0	86.8
	n	–	–	–	25	–	17	5
Dogfish liver	Dolt-2							
	Certified value	0.608 ± 0.032	20.8 ± 0.5	25.8 ± 1.1	6.06 ± 0.49	85.8 ± 2.5	2.14	0.693 ± 0.06
	Measured mean	0.606	21.6	25.7	5.53	92.7	2.05	–
	Standard deviation	0.068	1.1	1.6	0.31	10.3	0.09	–
	% Recovery	99.7	103.7	99.5	91.2	108.0	95.9	–
	n	23	15	25	30	25	8	–
Dogfish liver	Dolt-3							
	Certified value	1.20 ± 0.07	19.4 ± 0.6	31.2 ± 1.0	7.06 ± 0.48	86.6 ± 2.4	3.37 ± 0.14	n.e.
	Measured mean	1.04	18.1	31.4	6.54	83.3	3.39	–
	Standard deviation	0.19	1.3	0.9	0.55	1.8	0.35	–
	% Recovery	87.0	93.2	100.7	92.6	96.2	100.6	–
	n	12	12	10	10	10	10	–
Bovine liver	SRM1577b							
	Certified value	0.039 ± 0.007	0.50 ± 0.03	160 ± 8.0	0.73 ± 0.06	127 ± 16.0	n.e.	n.e.
	Measured mean	0.042	0.52	168	0.71	135	–	–
	Standard deviation	0.001	0.05	2.1	0.05	8.4	–	–
	% Recovery	108.2	103.1	105.0	96.9	106.2	–	–
	n	6	18	11	6	18	–	–
Pilot whale liver	QC91LH1							
	Certified value	0.181 ± 0.005	8.51 ± 0.22	2.96 ± 0.20	11.0 ± 0.3	32.2 ± 0.7	28.2 ± 1.1	1.36
	Measured mean	0.194	8.90	3.21	11.0	32.3	27.5	1.38
	Standard deviation	0.002	0.08	0.01	0.2	0.0	2.4	0.06
	% Recovery	107.0	104.6	108.4	100.4	100.5	97.4	101.3
	n	3	3	3	3	3	17	10
Beluga whale liver	QC97LH2							
	Consensus mean[a]	13.24 ± 2.41	2.433 ± 0.040	13.10 ± 0.188	24.35 ± 0.484	26.92 ± 0.359	40.31 ± 1.28	n.e.
	Analyzed mean	23.48	2.497	12.91	23.93	26.63	39.98	1.47
	Standard deviation	0.43	0.016	0.039	0.344	0.081	2.82	0.09
	% Recovery	177.3	102.6	98.5	98.3	98.9	99.2	–
	n	5	5	5	5	5	7	10

Concentrations are given in μg/g ww. n.e. = not established.
[a] Established by 19 laboratories Christopher (2002, 2004).

statistical analyses were performed using SAS (Version 8) with $\alpha = 0.05$. In order to include element concentrations below the minimum detection limit (MDL) in summary statistics and statistical tests, they were expressed as one-half the MDL (Gilbert, 1987). If more than 50% of samples had element concentrations below the MDL they were highlighted in summary statistics and excluded from further statistical tests. Results are reported as mean ± standard deviation (SD) unless otherwise noted. In addition, the sample median is reported as it is robust to outliers and is appropriate for censored data sets.

3. Results

3.1. Stable isotopes

Stable carbon and nitrogen isotope ratios were significantly different for the three cetacean species analyzed ($p = < 0.0001$ for both $\delta^{13}C$ and $\delta^{15}N$). $\delta^{15}N$ was highest in belugas (16.8 ± 0.6‰), followed by bowheads (13.3 ± 0.6‰) then gray whales (12.0 ± 0.9‰). Carbon isotope values were more enriched in gray whales (−17.3 ± 1.0‰) than in bowheads (−20.7 ± 0.8‰) and belugas were intermediate (−18.4 ± 0.6‰). Averages, standard deviations, medians and ranges of stable carbon and nitrogen isotope ratios in whales are given in Table 3. No sex difference and no significant interaction term (species × sex) were noted for $\delta^{13}C$ and $\delta^{15}N$ in the three whale species.

Nitrogen and carbon isotope ratios in the mysticete prey examined were significantly different ($p = < 0.0001$ for both $\delta^{13}C$ and $\delta^{15}N$). Total body homogenates of unsorted zooplankton (including copepods and euphausids) had higher $\delta^{15}N$ than homogenates of benthic gammaridean amphipods (10.4 ± 1.2‰ and 7.9 ± 0.8‰ for zooplankton and amphipods, respectively). In contrast, amphipods showed more enriched ^{13}C values than zooplankton

Table 3
Mean trace element concentration ± standard deviation (SD) in μg/g ww, concentration range, median and sample size (*n*) in tissues of bowhead, beluga and gray whales harvested in Alaska and Russia

	$\delta^{15}N$	$\delta^{13}C$	Zn	Cu	Cd	Se	Ag	THg	Se:THg molar ratio
Bowhead whale									
Liver									
Median	–	–	31.60	4.89	3.93	1.06	0.04	0.04	74.41
Mean ± SD	–	–	35.99 ± 17.08	9.13 ± 21.67	7.27 ± 8.97	1.23 ± 0.69	0.13 ± 0.28	0.05 ± 0.07	121.62 ± 136.20
Range	–	–	6.99–135.11	1.09–203.81	0.03–50.91	0.06–4.19	0.002–2.37	0.001–0.59	3.88–971.83
n	–	–	161	161	161	161	127	154	151
Kidney									
Median	–	–	24.80	1.85	12.66	1.45	0.01[a]	0.03	156.68
Mean ± SD	–	–	25.90 ± 9.20	2.27 ± 1.17	15.08 ± 14.94	1.45 ± 0.43	0.01 ± 0.01[a]	0.03 ± 0.03	252.96 ± 251.18
Range	–	–	9.07–56.31	0.76–7.94	0.01–64.00	023–3.21	0.002–0.06	0.001–0.18	20.25–1386.00
n	–	–	156	156	156	157	128	145	144
Muscle									
Median	13.16	−20.62	33.85	0.65	0.04	0.20	0.002[a]	0.02	31.52
Mean ± SD	13.28 ± 0.62	−20.65 ± 0.82	35.38 ± 9.64	0.65 ± 0.10	0.07 ± 0.10	0.21 ± 0.07	0.003 ± 0.001[a]	0.02 ± 0.01	134.22 ± 596.58
Range	11.81–14.74	−25.06 to −19.20	9.47–74.10	0.47–1.07	0.01–0.61	0.08–0.77	0.001–0.01	0.00–0.05	11.06–5255.00
n	110	110	86	86	86	86	84	123	79
Epidermis									
Median	–	–	13.82	0.37	0.01[a]	0.71	0.002[a]	0.01	198.97
Mean ± SD	–	–	14.20 ± 2.63	0.38 ± 0.07	0.01 ± 0.01[a]	0.70 ± 0.23	0.003 ± 0.003[a]	0.01 ± 0.01	480.87 ± 897.66
Range	–	–	10.50–28.80	0.25–0.70	0.01–0.07	0.24–1.42	0.002–0.03	0.00–0.04	44.72–5855.00
n	–	–	100	100	100	100	100	98	98
	$\delta^{15}N$	$\delta^{13}C$	Zn	Cu	Cd	Se	Ag	THg	Se:THg molar ratio
Gray whale									
Liver									
Median	–	–	29.70	9.66	0.24	0.83	0.06	0.02	99.58
Mean ± SD	–	–	41.07 ± 51.78	18.90 ± 34.67	0.47 ± 0.63	0.83 ± 0.26	0.11 ± 0.14	0.02 ± 0.01	127.81 ± 101.98
Range	–	–	9.57–300.48	0.24–154.45	0.01–2.20	0.34–1.32	0.004–0.67	0.004–0.07	23.80–515.81
n	–	–	29	29	29	29	29	28	28
Kidney									
Median	–	–	19.27	2.55	0.71	1.56	0.004[a]	0.02	293.67
Mean ± SD	–	–	20.09 ± 5.12	2.51 ± 0.71	1.19 ± 1.50	1.50 ± 0.40	0.01 ± 0.001[a]	0.01 ± 0.01	401.50 ± 345.38
Range	–	–	14.30–33.30	1.34–4.64	0.01–5.11	0.50–2.24	0.003–0.01	0.001–0.03	128.02–1805.00
n	–	–	28	28	28	28	28	28	28
Muscle									
Median	11.87	−17.05	33.50	2.80	0.01	0.19	0.004[a]	0.02	28.65
Mean ± SD	12.04 ± 0.86	−17.32 ± 1.03	39.47 ± 18.68	3.17 ± 2.54	0.02 ± 0.01	0.19 ± 0.04	0.004 ± 0.0004[a]	0.02 ± 0.01	27.09 ± 9.05
Range	11.12–14.62	−20.00 to −15.96	19.10–74.80	0.46–8.01	0.01–0.05	0.13–0.29	0.003–0.004	0.01–0.04	9.93–45.71
n	17	17	17	17	17	17	17	17	17
Epidermis									
Median	–	–	18.10	1.00	0.01[a]	3.36	0.003[a]	0.01	1251.47
Mean ± SD	–	–	16.71 ± 6.77	1.58 ± 2.17	0.01 ± 0.001[a]	3.75 ± 2.08	0.01 ± 0.003[a]	0.01 ± 0.01	1717.00 ± 1560.00
Range	–	–	0.03–26.04	0.01–8.29	0.01–0.01	0.85–10.60	0.003–0.01	0.001–0.03	180.04–7582.00
n	–	–	27	27	27	27	27	24	24

	δ^{15}N	δ^{13}C	Zn	Cu	Cd	Se	Ag	THg	MeHg	%MeHg	Se:THg molar ratio
Beluga whale											
Liver											
Median	–	–	36.80	17.00	2.84	25.70	11.33	11.99	1.41	13.20	4.46
Mean ± SD	–	–	36.21 ± 8.29	24.98 ± 27.23	3.05 ± 1.52	31.39 ± 25.95	12.84 ± 9.09	15.95 ± 15.17	1.43 ± 0.78	17.60 ± 14.57	6.91 ± 6.37
Range	–	–	18.50–53.20	4.90–156.84	0.05–7.05	0.93–113.20	1.77–51.70	0.28–72.48	0.19–3.89	2.51–63.10	1.05–31.73
n	–	–	67	67	67	67	48	48	46	46	48
Kidney											
Median	–	–	33.89	1.99	10.20	4.86	0.05	3.53	0.48	11.50	2.86
Mean ± SD	–	–	34.49 ± 5.71	1.98 ± 0.29	10.16 ± 4.25	5.04 ± 1.96	0.05 ± 0.03	4.41 ± 3.00	0.50 ± 0.32	12.80 ± 5.13	4.99 ± 6.69
Range	–	–	24.04–49.30	1.29–2.92	0.46–20.40	1.65–10.82	0.01–0.15	0.10–12.26	0.07–1.67	4.98–28.98	1.31–42.14
n	–	–	64	64	64	64	32	46	44	44	46
Muscle											
Median	16.72	−18.32	28.40	1.01	0.03	0.32	0.01[a]	1.10	1.05	96.05	0.84
Mean ± SD	16.74 ± 0.56	−18.41 ± 0.62	31.72 ± 12.16	0.96 ± 0.33	0.06 ± 0.06	0.38 ± 0.19	0.01 ± 0.00[a]	1.13 ± 0.63	1.04 ± 0.52	94.63 ± 10.90	1.26 ± 1.05
Range	15.48–18.34	−20.75 to −17.21	16.30–66.66	0.41–1.51	0.01–0.21	0.20–1.26	0.01–0.01	0.13–3.27	0.13–2.40	56.83–138.20	0.30–4.62
n	49	49	45	45	32	45	47	46	46	46	45
Epidermis											
Median	–	–	86.84	0.55	0.01[a]	7.05	0.01[a]	0.51	0.54	97.14	35.12
Mean ± SD	–	–	82.52 ± 36.00	0.53 ± 0.13	0.01 ± 0.003[a]	7.96 ± 5.06	0.01 ± 0.002[a]	0.63 ± 0.39	0.63 ± 0.39	95.99 ± 6.83	60.08 ± 81.30
Range	–	–	12.50–160.12	0.23–0.83	0.01–0.02	2.66–32.91	0.01–0.01	0.03–1.52	0.06–1.48	75.38–111.15	5.56–447.15
n	–	–	41	41	35	41	41	39	37	37	39

[a] More than 50% of samples below MDL.

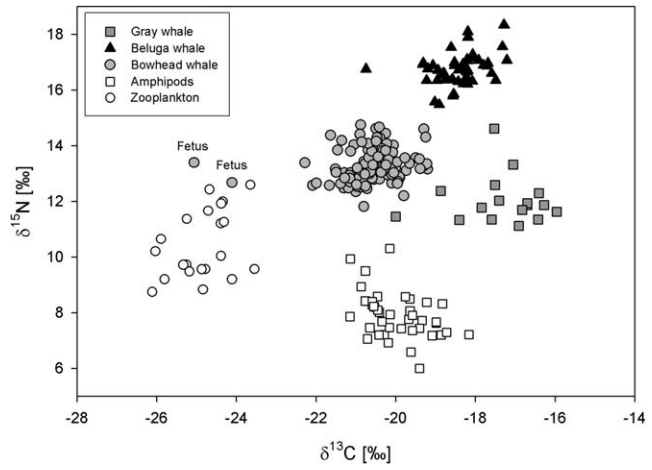

Fig. 2. δ^{15}N versus δ^{13}C in bowhead, beluga and gray whales harvested in Alaska and Chukotka. Zooplankton and amphipods were collected in Kaktovik and the Bering Strait, respectively.

(-24.9 ± 0.7‰ and -19.9 ± 0.7‰ for zooplankton and amphipods, respectively). Fig. 2 illustrates δ^{13}C versus δ^{15}N in all cetacean groups analyzed and in bowhead and gray whale prey (pelagic zooplankton and benthic amphipods, respectively).

3.2. Trace element concentrations and tissue distribution

Table 3 summarizes mean, standard deviation, median, and concentration range of trace elements (Cu, Zn, Cd, Ag, Se, THg and MeHg) and element ratios (%MeHg and Se:THg molar ratio) in epidermis, muscle, liver and kidney of bowheads, belugas and gray whales. For Ag in epidermis and muscle and Cd in epidermis, more than 50% of the samples were below the MDL in the three whale species analyzed. Ag in kidney was below MDL in more than 50% of bowheads and gray whales only.

Generally, concentrations of trace elements were highest in liver, followed by kidney and lowest in muscle and epidermis. However, renal concentrations of Cd exceeded levels in liver in all three species. Epidermal Se was higher in gray whales and belugas than concentrations in muscle and kidney, while Se in bowhead kidney showed the highest concentrations and muscle the lowest. The Se:THg molar ratio was highest in epidermis for all species analyzed. Zn was higher in bowhead muscle than in any other tissue, while belugas had the highest Zn concentration in the epidermis. MeHg was only analyzed in beluga tissues and accounted for approximately 100% of the THg measured in muscle and epidermis, while kidney and liver had less than 15% MeHg.

3.3. Species comparison

All variables in all tissues differed significantly among species analyzed, except for Zn in liver (Table 4). Zn in

Table 4
Tukey grouping and *p*-values of variables in tissues of bowhead (BM), beluga (DL) and gray whales (ER) from Alaska and Russia

Variable	Tissue	Tukey grouping	*p*-Value
$\delta^{15}N$	Muscle	DL > BM > ER[a]	<0.0001
$\delta^{13}C$	Muscle	ER > DL > BM	<0.0001
Zn	Kidney	DL > BM > ER	<0.0001
	Liver	DL = BM = ER	0.07
	Muscle	BM = ER, BM > DL, ER = DL	0.005
	Epidermis	DL > ER > BM	<0.0001
Cu	Kidney	ER = DL, ER > BM, DL = BM	0.01
	Liver	DL > ER > BM	<0.0001
	Muscle	ER = DL > BM	<0.0001
	Epidermis	DL = ER > BM	<0.0001
Cd	Kidney	BM = DL > ER	<0.0001
	Liver	BM = DL > ER	<0.0001
	Muscle	BM = DL > ER	0.04
	Epidermis[b]	–	–
Ag	Kidney[b]	–	–
	Liver	DL > ER = BM	<0.0001
	Muscle[b]	–	–
	Epidermis[b]	–	–
Se	Kidney	DL > ER = BM	<0.0001
	Liver	DL > BM > ER	<0.0001
	Muscle	DL > BM > ER	<0.0001
	Epidermis	DL > ER > BM	<0.0001
THg	Kidney	DL > BM > ER	<0.0001
	Liver	DL > BM > ER	<0.0001
	Muscle	DL > ER = BM	<0.0001
	Epidermis	DL > ER = BM	<0.0001
Se:THg molar ratio	Kidney	ER > BM > DL	<0.0001
	Liver	ER = BM > DL	<0.0001
	Muscle	ER = BM > DL	<0.0001
	Epidermis	ER > BM > DL	<0.0001

[a] DL—beluga whale, BM—bowhead whale, ER—gray whale.
[b] More than 50% of samples below MDL.

kidney and epidermis and hepatic Ag were higher in belugas than in bowheads and gray whales. Se and THg were also highest in beluga tissues compared to bowhead and gray whale tissues, while the Se:THg ratio was lowest in belugas. Cd concentrations were higher in bowheads and belugas than in gray whales, and Cu was highest in gray whale and beluga tissues and was lowest in bowheads. Results of the ANOVA and Tukey's multiple comparison tests for all variables and tissues are compiled in Table 4. No sex differences were detected for variables analyzed in this study, and no significant interaction between whale species and sex was noted.

3.4. Correlation between variables

Significant Spearman rank correlations were found between many variables within and among tissues (Table 5) for all whale species. Positive correlations of renal and hepatic Cd with length, hepatic THg with length, and Se and THg in kidney were noted in all species. Hepatic Cd was positively correlated to Se and THg in liver in bowheads, belugas, and gray whales. Trophic level as determined by $\delta^{15}N$ was not consistently correlated to trace elements among species. THg in liver and renal Se were negatively correlated with trophic level (based on $\delta^{15}N$) in mysticetes only, while these variables were positively correlated in belugas. Similarily, renal Cd was positively correlated with $\delta^{15}N$ in belugas, negatively correlated in bowheads and no correlation was established in gray whales. Other significant correlations consistent for bowheads and gray whales included Cu with Ag in liver and hepatic Ag with THg. Hepatic Se was correlated to hepatic THg in belugas and bowheads, but not in gray whales. Similarly, Cu in liver was negatively correlated with length in bowheads and belugas, but was not correlated in gray whales. Hepatic %MeHg was negatively correlated to length in belugas, while THg and MeHg were positively correlated to length in all beluga tissues. Significant correlations that were noted in all species are underlined in Table 5, and correlations consistent among mysticetes were highlighted in bold script.

Table 5
Correlation matrix of all variables in tissues of bowhead, beluga and gray whales

		Liver	Kidney	Muscle	Epidermis
Bowhead whale					
	Length	−Cu, +Cd, −Ag, +Se, +THg	+Zn, +Cd, +Se, +THg	$-\delta^{15}$N, +Cd, +Se, +THg	+Zn, +Se, +THg
	δ^{13}C	+Zn, +Cu, +Se	−Cu	$+\delta^{15}$N	–
	δ^{15}N	+Cu, −Cd, +Ag, −Se, **−THg**	−Zn, −Cd, **−Se**, −THg	+Cu, −Cd, −Se, −THg	−Se, −THg
Liver	Zn	+Cu, +Cd, +Ag, +Se, +THg	+Zn, +Cd, +THg	–	–
	Cu	**+Ag**	+Cu, −Cd, +Ag	−THg	−Se, −THg
	Cd	−Ag, +Se, +THg	+Zn, +Cd, +Se, +THg	+Cd, +Se, +THg	+Zn, +Se, −THg
	Ag	**−THg**	−Cd, −Se, −THg	−THg	−Zn, −THg
	Se	+THg	+Zn, +Cu, +Cd, +Se, +THg	+Cd, +Se, +THg	+Zn, +Cu, **+Se**, +THg
	THg	–	+Zn, +Cd, +Se, +THg	+Cd, +Se, +THg	+Se, +THg
Kidney	Zn	–	+Cd, +Se, +THg	+Cd, +Se, +THg	**+Zn**, +Se, +THg
	Cu	–	+Se	–	–
	Cd	–	+Se, +THg	+Cd, +Se, +THg	+Zn, +Se, +THg
	Ag[a]	–	–	–	–
	Se	–	+THg	+Cd, +Se, +THg	**+Se**, +THg
	THg	–	–	+Cd, +Se, +THg	+Zn, **+Se**, +THg
Muscle	Zn	–	–	+Se	–
	Cu	–	–	–	−Se
	Cd	–	–	+THg	+THg
	Ag[a]	–	–	–	–
	Se	–	–	+THg	−Se, +THg
	THg	–	–	–	+Se, +THg
Epidermis	Zn	–	–	–	+Cu, +Se
	Cu	–	–	–	+Se
	Cd[a]	–	–	–	–
	Ag[a]	–	–	–	–
	Se	–	–	–	**+THg**
Gray whale					
	Length	+Cd, +THg	+Cu, +Cd	–	−Zn
	δ^{13}C	–	–	–	–
	δ^{15}N	**−THg**	**−Se**	–	–
Liver	Zn	–	+Zn	–	+Zn
	Cu	**+Ag**	–	–	+Zn
	Cd	+Se, +THg	+Cd, −Zn	–	+Cu, −Zn
	Ag	**−THg**	–	−Se	+THg
	Se	–	+Cd, +THg	−Cu	**+Se**, +THg
	THg	–	–	−Zn	+THg
Kidney	Zn	−Cd	–	–	+Cu, +Zn
	Cu	–	−Se, −THg	–	−Se
	Cd	–	+Se	–	−Zn
	Ag[a]	–	–	–	–
	Se	–	+THg	–	**+Se**
	THg	–	–	–	**+Se**, +THg
Muscle	Zn	–	–	–	−Zn
	Cu	–	–	–	–
	Cd	–	–	–	–

(*continued on next page*)

Table 5 (*continued*)

		Liver	Kidney	Muscle	Epidermis
Ag[a]	–	–	–	–	
Se	–	–	–	–	
THg	–	–	–	–	
Epidermis	Zn	–	–	–	–
	Cu	–	–	–	–
	Cd[a]	–	–	–	–
	Ag[a]	–	–	–	–
	Se	–	–	–	**+THg**
Beluga whale					
	Length	−Cu, +Cd, +Se, +THg, +MeHg, −%MeHg	+Cd, +Se, +THg, +MeHg	−Cu, +THg, +MeHg	+THg, +MeHg
	$\delta^{13}C$	−Cu, +Cd, +Se, +MeHg	−Cu, +Cd, +MeHg	$+\delta^{15}N$, −Cu, −Se, +THg, +MeHg	−Zn, −Cu, +THg
	$\delta^{15}N$	−Cu, +Se, +MeHg	−Cu, +Cd, +Se, +THg, +MeHg	+THg, +MeHg	−Zn, −Cu
Liver	Zn	+Cd	+Zn, +Cd, +Se	−Cu	+Se
	Cu	−THg, −MeHg	+Cu, −Cd, −MeHg	−THg, −MeHg	+Zn, +Cu
	Cd	+Ag, +Se, +THg, +MeHg	+Zn, −Cu, +Cd, +Ag, +Se, +THg, +MeHg	−Cu, +THg, +MeHg	−Cu, +THg, +MeHg
	Ag	+Se	+Zn, +Ag, +Se	+%MeHg	+Se
	Se	+THg, +MeHg, −%MeHg	+Zn, +Cd, +Ag, +Se, +THg, +MeHg, −%MeHg	−Cu, +THg, +MeHg	−Cu, +THg, +MeHg, +%MeHg
	THg	+MeHg, −%MeHg	+Zn, +Cd, +Ag, +Se, +THg, +MeHg, −%MeHg	+Se, +THg, +MeHg	+THg, +MeHg
	MeHg	–	−Cu, +Cd, +Ag, +Se, +THg, +MeHg	−Cu, +THg, +MeHg	−Cu, +THg, +MeHg
	%MeHg	–	−Zn, −Cd, −Ag, −THg, +%MeHg	−Cd, −Se, −THg, −MeHg, +%MeHg	−Zn, −THg, −MeHg
Kidney	Zn	–	+Cd, +Ag, +Se, +THg, +MeHg, −%MeHg	–	+THg, +MeHg
	Cu	–	−%MeHg	+Cd, +Se	+Zn
	Cd	–	+Ag, +Se, +THg, +MeHg	−Cu, +THg, +MeHg	−Cu, +THg, +MeHg
	Ag	–	+Se, +THg, +MeHg	+THg	+THg
	Se	–	+THg, +MeHg, −%MeHg	−Cu, +THg, +MeHg	−Cu, +THg, +MeHg
	THg	–	+MeHg, −%MeHg	+THg, +MeHg	+THg, +MeHg
	MeHg	–	–	−Cu, +THg, +MeHg	−Cu, +THg, +MeHg, +%MeHg
	%MeHg	–	–	−Se	−Zn
Muscle	Zn	–	–	–	−%MeHg
	Cu	–	–	−THg, −MeHg	−Cu, −THg, −MeHg
	Cd	–	–	–	+Zn
	Ag[a]	–	–	–	–
	Se	–	–	–	+Zn
	THg	–	–	+MeHg	−Cu, +THg, +MeHg
	MeHg	–	–	–	−Cu, +THg, +MeHg
	%MeHg	–	–	–	–
Epidermis	Zn	–	–	–	–
	Cu	–	–	–	−THg, −%MeHg
	Cd[a]	–	–	–	–
	Ag[a]	–	–	–	–
	Se	–	–	–	–
	THg	–	–	–	+MeHg
	MeHg	–	–	–	+%MeHg

Only significant relationships were noted and slope of correlated variables is indicated by either + (positive) or−(negative). Correlated variables that are underlined are consistent for all whale species. Correlations consistent between mysticetes are highlighted in bold script.

[a] More than 50% of samples below MDL.

4. Discussion

4.1. Stable isotopes

Beluga whales occupy a higher trophic level (based on $\delta^{15}N$) than both mysticete species analyzed. Seaman et al. (1982) suggested competition for prey between belugas and piscivorous spotted seals (*Phoca largha*). However, nitrogen isotope ratios were lower in belugas than reported for spotted seals, indicating that this odontocete does not eat fish exclusively (Dehn, 2005). Though a variety of fish species are clearly important to the beluga diet, cephalopods and shrimp are commonly eaten and 90–100% of stomachs analyzed by Seaman et al. (1982) contained invertebrates. $\delta^{15}N$ in beluga muscle analyzed in this study was similar to values reported for belugas from the St. Lawrence estuary (15.1–16.3‰ range) and the closely related narwhal analyzed from Greenland waters (16.3 ± 1.0‰), suggesting similar prey utilization by these whales (Lesage et al., 2001; Dietz et al., 2004). Narwhals rely on deep benthic prey, with squid, octopus, and fish making up the majority of the diet, while crustaceans were present in about 60% of stomachs (Finley and Gibb, 1982). Stable nitrogen isotope ratios in assumed prey of beluga whales range from 13.6 ± 1.2‰ in cephalopods to 15.5 ± 1.0‰ in Arctic cod (*Boreogadus saida*) (Hobson and Welch, 1992; Hobson et al., 1997; Dehn, 2005).

Stable nitrogen isotope ratios suggest that bowheads are foraging on a higher trophic level than gray whales, thus pointing to differences in prey consumed. Typical bowhead prey (e.g., euphausids and copepods) had higher $\delta^{15}N$ than benthic gammaridean amphipods that make up the majority of the gray whale diet (Fig. 2). This indicates a stepwise trophic enrichment of 3.0‰ for $\delta^{15}N$ in whale muscle, corresponding to enrichment factors reported by Hobson et al. (1996). Stable nitrogen isotope ratios of unsorted amphipods and zooplankton in this study are in agreement with values reported for gray whale prey (7.0 ± 0.4‰ and 8.3 ± 0.3‰ for *Ampelisca eschrichti* and *Ampelisca macrocephala*, respectively) and bowhead dietary items (9.6 ± 1.6‰ and 10.1 ± 0.7‰ for euphausids and copepods, respectively) (Highsmith and Coyle, 1991). Minke whale nitrogen isotope ratios in baleen are generally similar to those found in bowhead muscle (12–14‰ and 12–15‰ for minke and bowhead whales, respectively) with baleen and muscle tissue showing comparable isotope ratios (Hobson and Schell, 1998; Born et al., 2003; Hobson et al., 2004). However, in contrast to bowheads, minke whales are known to consume capelin (*Mallotus villosus*) and herring (*Clupea harengus*) and may switch to krill only if fish is not available (Sigurjónsson et al., 2000; Haug et al., 2002).

Carbon-13 is significantly enriched in gray whales as compared to bowhead and beluga whales (Fig. 2). Stagnant boundary layers and low turbulence, as found in benthic ecosystems, will lead to enrichment of ^{13}C (Fry and Sherr, 1984; France, 1995; Hemminga and Mateo, 1996; Burns et al., 1998), thus explaining the enriched carbon isotope values in benthic-feeding gray whales. In contrast, bowheads feed mostly in the water column on euphausids and copepods (Lowry, 1993; Lowry and Sheffield, 2002), displaying the more depleted carbon isotope signatures of the pelagic foodweb. However, carbon isotope signatures are significantly different between Arctic regions, and bowhead whales migrating from the Beaufort Sea in fall are more depleted in ^{13}C than whales migrating from the Bering Sea in spring (Schell et al., 1989; Hoekstra et al., 2002). Bowheads analyzed in this study were taken during both spring and fall harvests; therefore, the sample includes animals with both carbon signatures. Two bowhead whale fetuses exhibited highly depleted carbon isotope signatures (highlighted in Fig. 2). Selective fractionation of carbon isotopes leads to depleted ^{13}C in body fat compared to other tissues (DeNiro and Epstein, 1977), and the low ratios in fetuses suggest mobilization and transfer of maternal carbon to fetal development.

Belugas have intermediate $\delta^{13}C$ values between bowhead and gray whales, suggesting that both pelagic and benthic foods are important components of their diet. As discussed, narwhals rely heavily on epibenthic prey, but Arctic cod is also of importance (Finley and Gibb, 1982). Similarly, saffron cod (*Eleginus gracilis*), shrimp, and octopus dominate the beluga diet (Seaman et al., 1982). The majority of beluga stomachs analyzed by Seaman et al. (1982) contained sediment and pebbles, and about 27% of narwhal stomachs contained sand (Finley and Gibb, 1982). Carbon isotope signatures of belugas in this study and narwhal (Dietz et al., 2004) were almost indistinguishable (-18.5 ± 0.4‰ and -18.4 ± 0.6‰ for narwhal and beluga, respectively), further supporting similar prey utilization by these two odontocetes.

4.2. Trace elements

4.2.1. Mercury and selenium

The beluga occupies a higher trophic level compared to the mysticetes analyzed in this study, and, as expected, concentrations of Hg in all beluga tissues are up to two orders of magnitude higher. Both MeHg and THg are positively correlated to trophic level (based on $\delta^{15}N$) in belugas only. Hepatic Hg in this work falls within the range reported for Alaska belugas by Becker et al. (1995) and Woshner et al. (2001), but is higher than for belugas analyzed from the Cook Inlet stock (Becker et al., 2000). Hepatic Hg concentrations of belugas harvested in Alaska are intermediate to values reported by Wagemann et al. (1996) for whales from Western and Eastern Canada (11.3 ± 7.1 and 19.2 ± 32.7 μg/g ww, respectively, in liver), while belugas from the St. Lawrence estuary were an order of magnitude higher (Wagemann et al., 1990). Thus, concentrations of Hg in tissues ranges widely in these whales and may be interpreted as differences in feeding habits and feeding grounds due to geographically separate stocks or populations (Becker et al., 1995; Kunito et al., 2002; Born et al.,

2003). THg and MeHg in this study were positively correlated to length (as a proxy for age), and heterogeneity in age structure of the sampled beluga stocks may also explain the large variations in Hg concentrations reported for this species. However, concentrations of THg in belugas in this study are low compared to other odontocetes, e.g., rough-toothed dolphins (*Steno bredanensis*), pilot whales (*Globicephala melas*), and striped dolphins (*Stenella coeruleoalba*) (Honda et al., 1983; Becker et al., 1995; Caurant et al., 1996; Mackey et al., 2003).

THg in tissues of bowhead and gray whales is very low in comparison to other mysticetes, e.g., minke whales (Hansen et al., 1990; Born et al., 2003) and hepatic THg is negatively correlated to $\delta^{15}N$, in contrast to belugas. The overall higher concentrations of Hg in minke whale tissues in contrast to bowhead and gray whales are likely due to the higher prevalence of fish in the minke whale diet (Haug et al., 2002). Fish consumption has been correlated to elevated Hg levels in a variety of studies (Dietz et al., 1996; Wagemann et al., 1997; Egeland et al., 1998), and the low concentrations of THg in bowhead and gray whales are in agreement with the invertebrate-dominated diet of these mysticetes. THg in tissues of bowheads is comparable to levels reported by Bratton et al. (1997) and Woshner et al. (2001). Hg concentrations in gray whales analyzed in this study are among the lowest reported for marine mammals and MeHg analyzed in four stranded gray whales accounted for 22%, 18% and 75% of the THg burden in liver, kidney and muscle, respectively (Ruelas-Inzunza et al., 2003). Tissue levels of THg in whales stranded along the Pacific West coast of North America were lower (0.06 ± 0.01 μg/g ww for gray whale liver) (Varanasi et al., 1994) than for juvenile gray whales sampled during subsistence harvests in Russia (0.16 ± 0.06 μg/g ww for liver) (Tilbury et al., 2002) and whales examined in this study.

THg is positively correlated to length (as a proxy for age) in liver of all three species analyzed in this study ($r = 0.43$, 0.57 and 0.55 for bowhead, beluga and gray whale, respectively). In addition, MeHg was positively correlated to length in all beluga tissues ($r = 0.45$, 0.38, 0.60 and 0.53 for liver, kidney, muscle and epidermis, respectively). This likely results from the continuous uptake of Hg/MeHg via diet, slow elimination, or storage (e.g., tiemannite), and thus a relatively long half-life of THg of about 10 years as discussed by Wagemann et al. (2000). However, studies on captive bottlenose dolphins (*Tursiops truncatus*) inferred that only about 50% of ingested Hg (administered as dietary fish) is retained and the remainder is eliminated via bilary excretion in the feces, while pulmonary elimination is negligible (Nigro et al., 2002). A half-life of less than 1000 days for Hg in whale tissues was postulated (Nigro et al., 2002). Wagemann et al. (1996) suggested that the epidermis of cetaceans might be a significant route of elimination of Hg compounds. For belugas in this study, about 100% of THg in epidermis was present as organic Hg. The highest Hg concentration is found in the outer epidermal layer, and during skin molt approximately 14% of epidermal MeHg can be eliminated (Wagemann et al., 1996). The fraction of MeHg (%MeHg) in beluga liver was inversely correlated to length ($r = -0.46$). A similar decay function of hepatic %MeHg with age was also described for other marine mammals (Becker et al., 1995, 2000; Dehn et al., 2005).

Storage of Hg as biologically inert tiemannite (Hg–Se granules) requires Se and thus leads to the often discussed protective effect of Se on Hg toxicosis. This is supported by a strong correlation between THg and Se in liver of beluga and bowhead whales ($r = 0.72$ and 0.58 for beluga and bowhead, respectively). This relationship is commonly observed in marine mammal tissues (Koeman et al., 1973; Mackey et al., 1996, 2003; Das et al., 2004a), although it was not noted for gray whales in this study ($r = 0.31$, $p = 0.11$). Several authors report that both elements occur in a 1:1 ratio when expressed as molar concentrations (Koeman et al., 1973; Caurant et al., 1994; Becker et al., 1995; Dietz et al., 2000; Endo et al., 2002). Unity between Se and Hg on a molar basis was only observed in one adult beluga whale, and other cetaceans in this study had ratios in liver of approximately 10:1 in belugas or 100:1 (Se:THg) for mysticetes (Fig. 3). Se is an essential element and is incorporated into selenoproteins involved in hormone homeostasis, reproduction, and anti-oxidant enzyme systems, e.g., glutathione peroxidase (Bedwal and Bahuguna, 1994; Bates et al., 2000; Whanger, 2001). A molar ratio of 1:1 would indicate that all available Se is bound to Hg, leaving animals, in particular diving marine mammals, vulnerable to oxidative stress. Becker et al. (1995) and Ikemoto et al. (2004) argued that not only Hg binds Se, but also Ag may compete for binding sites on Se in belugas and other marine mammals, thus making the assumed unity of Hg:Se even more improbable. In addition, the Se:THg molar ratio is negatively correlated to body length in all three species, and a similar decay function of Se:THg

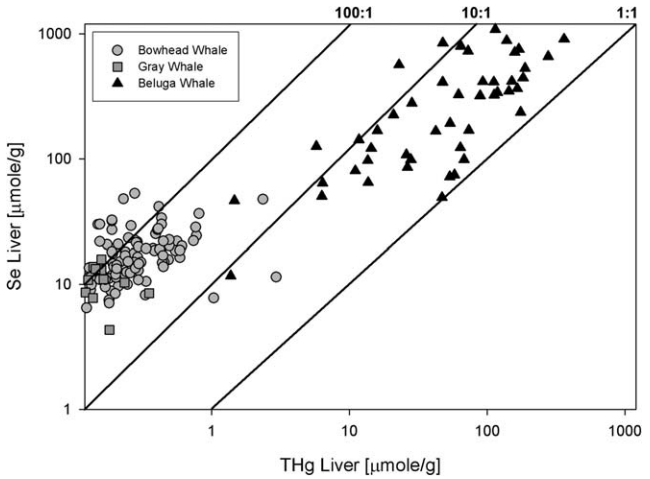

Fig. 3. Hepatic THg [μmole/g] versus hepatic Se [μmole/g] of bowhead, beluga and gray whales. The lines indicate the 1:1, 10:1 and 100:1 molar ratio of Se:THg.

with age was also noted for ice seals (Dehn et al., 2005). This illustrates the importance of Se for maturation of the antioxidant system and endocrine, reproductive, and neuronal development (Bedwal and Bahuguna, 1994; Hagmar et al., 1998; Whanger, 2001). Thus, tissue ratios of Se:THg close to 1:1 could suggest compromised health of the animals (Dietz et al., 2000; Dehn et al., 2005). Wagemann et al. (2000) postulated that only marine mammals with exceedingly high concentrations of Hg show a Se:THg ratio approaching unity. Se in liver of stranded gray whales was higher than for subsistence-harvested gray whales examined here (Varanasi et al., 1994). Hepatic Se concentrations have been reported to be elevated in stranded and emaciated animals (Bennet et al., 2001; Das et al., 2004a). Ketone body metabolism requires Se, and it is possible that during starvation Se is elevated to increase turnover of lipids and ketone bodies (Olsson, 1985).

Epidermal Se in this study was highest in belugas and lowest in bowhead whales. Elevated concentrations of Se were also reported in epidermis of harbor porpoise from Greenland and belugas and narwhals from the Canadian Arctic (Dietz et al., 1990; Paludan-Müller et al., 1993; Wagemann et al., 1996). Se in epidermis does not seem to be associated with Hg as tiemannite, as most of the Hg in epidermis is present in the organic form. Paludan-Müller et al. (1993) considered a possible storage mechanism or excretion of Se via skin molt as described for Hg. Leccia et al. (1993) and Burke et al. (2003) suggested that Se in the form of glutathione peroxidase protects against ultraviolet (UV) induced skin damage and carcinogenesis caused by generation of reactive oxygen species. As belugas lose their skin pigmentation with adulthood at approximately 6 years of age (Sergeant, 1973), it is feasible that this species will need more UV protection than the dark pigmented bowhead whale. Se in epidermis of belugas analyzed in this study was higher than reported by Wagemann et al. (1996) for belugas and narwhals from the Canadian Arctic. However, epidermal Se concentrations in harbor porpoise exceeded levels established for belugas by an order of magnitude (Dietz et al., 1990; Paludan-Müller et al., 1993).

4.2.2. Cadmium

Although bowheads feed low in the food chain, renal and hepatic Cd concentrations of bowheads were similar to or even higher than those of belugas that occupy a higher trophic level. Renal and hepatic Cd in gray whales was considerably lower than in both bowheads and belugas. Most invertebrates have higher Cd levels than fish (Bohn and McElroy, 1976; Bustamante et al., 2003), and cephalopods, in particular, display elevated Cd concentrations (Martin and Flegal, 1975; Bustamante et al., 1998a,b). High variability in Cd levels has been described for different species of crustaceans that make up typical mysticete prey. Elevated levels of Cd were reported for pelagic amphipods (*Parathemisto libellula*) and copepods, ranging from 3 μg/g dry weight (dw) in copepods to 11 μg/g dw in amphipods (Bohn and McElroy, 1976; Hamanaka and Ogi, 1984; Macdonald and Sprague, 1988). However, benthic amphipods have very low concentrations ranging from 0.2 to 1.3 μg/g ww in the Alaskan Beaufort Sea (Presley, 1997). Similarly, concentrations of Cd in mysids and euphausids are up to an order of magnitude lower than in *Parathemisto* and copepods (Hamanaka and Ogi, 1984; Macdonald and Sprague, 1988), and Cd concentrations in euphausids from Greenland are below the limit of detection (Dietz et al., 1996). However, the overall lower concentrations of Cd in gray whale prey would not account for the 1–2 orders of magnitude difference in renal Cd levels of the two mysticetes. According to daily consumption estimates based on body mass and metabolic rate, adult bowheads consume between 1083 and 1453 kg of prey, while adult gray whales take in approximately 268–538 kg of amphipods (Tamura and Ohsumi, 2000; Thompson, 2002). In addition, gray whales feed mainly for about five months in their summering grounds, while there is still disagreement about seasonality of bowhead feeding (Rice and Wolman, 1971; Schell et al., 1989; Lowry, 1993; Hoekstra et al., 2002). Thus, differences in prey Cd concentrations and daily and seasonal intake of prey may account for the overall higher exposure to Cd in bowhead whales compared to gray whales. Renal Cd concentration in minke whales is intermediate to bowheads and gray whales, and the seasonal importance of fish to this species may explain much of this difference (Hansen et al., 1990; Haug et al., 2002).

The relatively high concentrations of Cd in kidneys of belugas indicate the importance of invertebrates and/or cephalopods to this species. Bustamante et al. (1998a) suggested that cephalopods, in particular benthic rather than neritic species, are a main vector for Cd in the food chain. Cd levels in narwhal tissues are higher than established for belugas in this study, ranging from 0.76 to 168 μg/g ww (Wagemann et al., 1996). This may indicate higher prevalence of invertebrates and cephalopods in narwhals or regional differences in Cd concentrations as described by Wagemann et al. (1996). Belugas from the St. Lawrence estuary are considered highly polluted, though Cd levels in these whales are among the lowest compared to belugas from other Arctic regions (Wagemann et al., 1990). Similarly, renal Cd of the declining Cook Inlet beluga stock is markedly lower than for other Alaska belugas (Becker et al., 2000). Feeding habits of Cook Inlet belugas are strongly correlated with salmon runs and other seasonally abundant fish, while invertebrates seem uncommon in their diet (Huntington, 2000). Thus, limited abundance of invertebrate prey or dietary preference for fish may explain the low Cd concentrations in these isolated beluga stocks.

Renal Cd was positively correlated to length in all three species ($r = 0.83$, 0.40 and 0.84 for bowhead, beluga and gray whale, respectively). The correlation is sigmoid rather than linear, showing plateaus of Cd levels during the fetal and neonate stage and later in adult life (Fig. 4). Cd concentrations are below detection limit in three bowhead fetuses (Fig. 4), suggesting that Cd is not transferred from

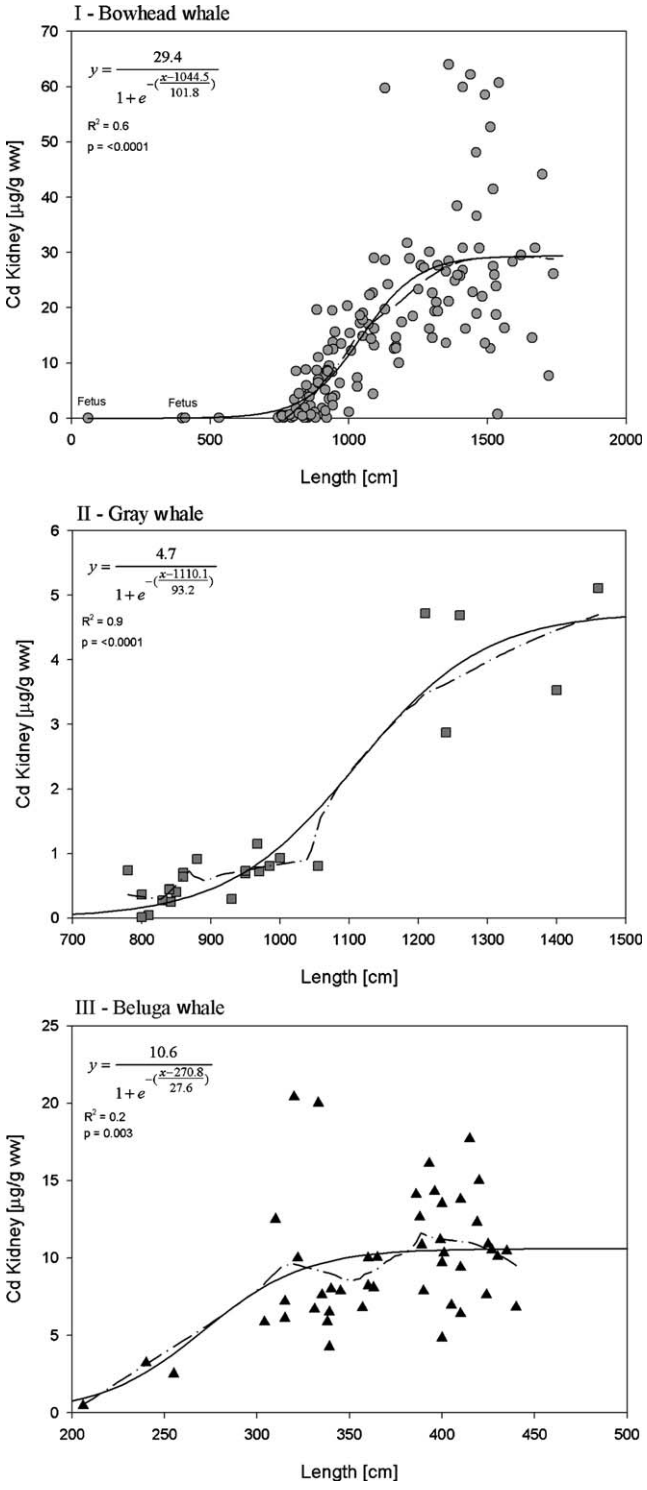

Fig. 4. Renal Cd [µg/g ww] versus length [cm] in bowhead (I), beluga (III) and gray whales (II). A sigmoid function was fitted to the data sets and LOESS nonparametric smoothing (dashed lines) was employed to estimate and compare the regression surface.

mother to fetus in this species. Some studies report that the placenta may serve as a selective Cd filter (Itoh et al., 1996; Enomoto and Hirunuma, 2001). Almost linear accumulation of Cd begins at birth via oral exposure (e.g., milk, prey). With increasing length (as a proxy for age) Cd increases to a maximum in midlife and plateaus such that Cd intake and excretion are balanced. Renal Cd concentrations at the point of curve saturation are 29.4, 10.6 and 4.7 µg/g ww in bowhead, beluga and gray whales, respectively (Fig. 4).

Metallothionein is involved in intracellular binding of divalent elements (e.g., Cd, Cu, Zn) at the renal glomerulus, though Cd is reabsorbed at the proximal tubules along with the biologically similar essential elements. The biological half-life for Cd in humans is estimated at 20–40 years as Cd is continuously accumulated until tubule cells and associated Cd are shed in the urine (Gerhardsson and Skerfving, 1996). Changes in renal physiology associated with the aging process (e.g., apoptosis, glomerulosclerosis) may lead to an increased excretion of Cd with shed cells or decreased absorption efficiency due to impaired peritubular blood flow after a critical age (Khan et al., 1999; Cardani and Zavanella, 2000). Thus, increase of Cd levels to a maximum or even decreases in renal Cd concentrations after a critical age are plausible and have been described for other marine mammals (Dietz et al., 1998; Watanabe et al., 2002; Dehn et al., 2005).

4.2.3. Silver

The high concentrations of Ag in beluga liver have long been a mystery and several authors have discussed possible causes for Ag accumulation (Becker et al., 1995, 2000; Woshner et al., 2001). Cephalopods have been associated with elevated concentrations of Ag (Martin and Flegal, 1975). Benthic snow crabs (*Chionoecetes opilio*) retained 90% of an administered Ag dose and the biological half-life was above 1000 days, while flatfish retained only 16% and rate of Ag elimination was 10–100 times faster (Rouleau et al., 2000). Thus, much higher concentrations of Ag can be reached in benthic invertebrates. As discussed above, belugas rely heavily on cephalopods; however, hepatic Ag concentrations were an order of magnitude higher in belugas than in some pinnipeds (e.g., northern fur seal (*Callorhinus ursinus*), bearded seal (*Erignathus barbatus*)) and cetaceans (e.g., pilot whale) that also rely heavily on octopus and squid (Mackey et al., 1996; Becker et al., 2000; Saeki et al., 2001; Dehn et al., 2005). Thus, the concentrations of Ag found in belugas could reflect a unique dietary source, as has been suggested by Becker et al. (1995), or feeding location, e.g., vicinity to volcanic or hydrothermal activity (Hein et al., 1999). It is also conceivable that belugas have a predilection for Ag accumulation or this trace metal serves an unknown nutritional need. Currently, there is no data available on Ag concentrations in tissues of narwhals to determine if Ag accumulation is a peculiarity in the Family Monodontidae.

Hepatic Ag concentrations of pelagic bowheads and benthic-feeding gray whales were 2–3 orders of magnitude lower than in beluga whales, suggesting that mysticete prey, e.g., zooplankton and benthic amphipods, are not retaining Ag to the extent that large crustaceans and cephalopods do. Copepods have low accumulation potential

(~17% of Ag is retained), and zooplankton molt their chitinous carapace so that Ag adsorbed to the exoskeleton is shed, hence not bioaccumulated (Ratte, 1999).

Ag in liver was not correlated to body length in gray whales or belugas ($r = -0.08$ and -0.29 for gray whales and beluga, respectively), but was negatively correlated in bowheads ($r = -0.37$). Juvenile and subadult bowhead whales have higher hepatic Ag levels than adults. Hazard and Lowry (1984) reported benthic prey in a juvenile bowhead and considered that the baleen plates of young bowhead whales are not long enough to filter plankton efficiently from the water column. Hence, differences in feeding ecology could explain higher concentrations of hepatic Ag in juvenile bowheads. However, Ag is also elevated in juvenile gray whales and belugas (data not shown). Ag and Cu are commonly intercorrelated, and Saeki et al. (2001) indicated that Ag interferes with Cu metabolism and transport. Bremner and Beattie (1990) postulated that Cu accumulates in fetal tissues due to limited efficiency of bilary excretion mechanisms. Thus, co-accumulation of Cu and Ag in liver of juvenile whales or limited bilary excretion may account for elevated concentrations of Ag.

4.2.4. Copper and zinc

Homeostasis of the essential trace metals Cu and Zn is tightly regulated. Both metals are excreted from the liver with bile or pancreatic secretions. Excretion via kidneys is limited, though Zn may be removed in urine following muscle catabolism mediated by interleukin-1 (Cousins, 1985). Cu and Zn are required for bone formation and are part of the antioxidant enzyme system superoxide dismutase. In addition, Zn contributes to tissue growth, wound-healing, and immune function and protects against UV-radiation in the epidermis (Rostan et al., 2002). Thus, Zn is found in its highest concentration in the epidermis of beluga whales, and is lower in bowhead and gray whales.

Concentrations of renal and hepatic Zn of stranded gray whales (Varanasi et al., 1994) were higher than levels of subsistence-harvested animals analyzed in this study. Zn is an inhibitor of gluconeogenesis, its absorption increases during malnutrition, and it competes with Cu for receptor binding sites (Cousins, 1985; Das et al., 2004b). In addition, high dietary Zn decreases Cu absorption (Cousins, 1985). Cu secretion from the liver is increased and its absorption is negatively influenced by stress (e. g., glucocorticoids), while elevated Zn concentrations and altered Zn kinetics are a response to stressors, poor body condition, and infection (Cousins, 1985, 1986; Frank et al., 1992; Bennet et al., 2001; Das et al., 2004b; Ilbäck et al., 2004). Thus, tissue concentrations of Zn could provide a possible indication of immune status and health in cetaceans.

Cu in liver is inversely correlated to length in bowheads and beluga, but not gray whales, such that fetal and juvenile tissues have the highest hepatic concentrations. The negative correlation of Cu with age has been noticed by a variety of studies (Honda et al., 1983; Wagemann et al., 1988, 1990; Caurant et al., 1994; Woshner et al., 2001). Liver metallothionein is increased during fetal growth, and concentrations of Cu in a Dall's porpoise (*Phocoenoides dalli*) fetus exceeded levels found in maternal tissues by 6 times (Yang et al., 2004). Thus, tissue growth, development, and DNA synthesis may require increased concentrations of Cu and Zn. However, limited efficiency of bilary excretion mechanisms in fetus and subadult animals, as discussed above, may lead to accumulation of Cu in juveniles (Bremner and Beattie, 1990).

5. Summary and conclusion

Stable nitrogen isotope ratios indicate that belugas occupied the highest trophic level. $\delta^{15}N$ values also established that bowheads forage on a higher trophic level than gray whales, thus pointing to differences in prey species consumed. Cd concentrations in whale tissues seem to be associated with invertebrate prey. The relationship between Cd and length was sigmoid in all three species. The molar ratio of Se to THg was inversely correlated to length. The observed ratios exceeded the classic 1:1 ratio by one or two orders of magnitude, and Se:THg ratios close to unity may indicate compromised health. High concentrations of Ag in liver of belugas were noticed in this study; mysticetes had much lower Ag concentrations. Se and Zn occurred in high concentrations in cetacean epidermis. Both elements are likely involved in protection against reactive oxygen species and UV radiation. Subsistence-harvested gray whales had strikingly lower concentrations of Zn in liver and kidney than stranded gray whales. Thus, Zn status may be useful in the evaluation of body condition, immune status, and animal health.

Acknowledgement

This study would not have been possible without the samples provided by Alaskan and Russian subsistence hunters and whaling captains in the communities of Barrow, Kaktovik, Wainwright, Point Lay, Point Hope, Savoonga, Lorino and Lavrentiya, and we thank them all for their support. We greatly appreciate the assistance of H. Brower, Jr., C. D. N. Brower, B. Akootchook, T. Hepa, C. George, R. Suydam, G. Zelensky, G. Sheffield, V. Woshner, G. York and many others in the field and N. Haubenstock, T. Howe, T. Bentzen and P. Hoekstra for support with analysis. We also thank P. Krahn and G. Ylitalo for making additional gray whale samples available and R. Highsmith and B. Bluhm for collection of amphipod samples from the Bering Strait. P. Becker and S. Christopher provided marine mammal reference material and coordinated interlaboratory comparison exercises for the determination of trace elements in marine mammals. The comments of two anonymous reviewers improved the manuscript. This study was primarily funded by the Cooperative Institute for Arctic Research. Additional support was provided by the Experimental Program for Stimulation

of Competitive Research; the Biomedical Research Infrastructure Network; the North Slope Borough Department of Wildlife Management; the Institute of Arctic Biology and the Department of Biology and Wildlife, UAF.

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