

# Inter-annual variation in environmental factors affect the prey and body condition of beluga whales in the eastern Beaufort Sea

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**ABSTRACT:** Declines in individual growth rates in eastern Beaufort Sea (EBS) beluga whales *Delphinapterus leucas* over the past 20 yr are hypothesized to be the result of changing environmental conditions. To better understand short-term variation in diet, we examined inter-annual variation in body condition indices, fatty acid composition, and stable isotope ratios in EBS beluga whales in relation to environmental conditions. We also examined if differences in dietary tracers in beluga whales reflect sex- and size-based habitat selection. During a warm year anomaly (2012), belugas demonstrated greater overlap in dietary tracers among sex and size classes, whereas greater differences occurred during years with greater sea ice extent over the Mackenzie Shelf (2013 and 2014). Body condition indices (maximum girth and blubber thickness) were highest in belugas in 2011 and 2012 and lowest in 2014. Total *Calanus* markers 20:1n-9 and 22:1n-11 contributed the most to annual variability and had the lowest proportions in females and small males in 2014, a year that coincided with low Arctic cod *Boreogadus saida* biomass. Age and year were the strongest predictors of fatty acid composition and  $\delta^{13}\text{C}$  values in beluga whales, whereas length influenced  $\delta^{15}\text{N}$  values, possibly a reflection of larger whales diving to greater depths to feed on Arctic cod. Annual variability in sea ice conditions and prey availability may be associated with inter-annual variation in dietary tracers and condition in beluga whales. As Arctic marine ecosystems are currently undergoing rapid change, understanding the factors causing inter-annual variation in diet should be a conservation priority for this beluga whale population.

**KEY WORDS:** Fatty acid signatures · *Delphinapterus leucas* · Beaufort Sea · Arctic · Stable isotope ratios · Climate change · Dietary tracers · Body condition

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## INTRODUCTION

As the most abundant Arctic odontocetes with a circumpolar distribution, beluga whales *Delphinapterus leucas* are a potential indicator species for Arctic climate change (Tynan & DeMaster 1997, Laidre 2008, Moore & Huntington 2008, Laidre et al. 2015). The eastern Beaufort Sea (EBS) beluga whale population is one of Canada's largest, with an estimated population of 40 000 individuals (Allen & Angliss 2015). Departing from Alaska in April, the EBS beluga stock arrives in the Canadian Beaufort Sea in

May to late June, where parturition, nursing, and possibly moulting take place near the waters of the Mackenzie River estuary. By September, whales return to their wintering grounds in the Bering Sea (Richard et al. 2001, Harwood & Smith 2002). Habitat selection of the EBS beluga population is affected by sex, size, and reproductive status during the open-water season (Richard et al. 2001, Loseto et al. 2006). Large males select offshore pack ice habitat and have a larger summer range than females, whereas smaller males and females with young calves select coastal habitat (Loseto et al. 2006). Tagging data re-

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vealed that in July, males travelled to offshore habitats of the Canadian Beaufort Sea, Arctic Ocean, and Viscount Melville Sound, whereas females travelled between Amundsen Gulf and the Mackenzie River estuary or the continental shelf (Richard et al. 2001).

Recently, there has been concern over the decline in body condition in marine mammals, seabirds, and forage fish species in the Beaufort Sea (Harwood et al. 2012, 2014, 2015, Divoky et al. 2015). EBS beluga whales harvested by Inuvialuit subsistence hunters significantly declined in body size-at-age from 1989 to 2008 (Harwood et al. 2014). Male belugas also experienced a decline in blubber thickness from 2000 to 2007, with the thinnest blubber in 2005, a year that coincided with poor body condition in ringed seals *Pusa hispida* and polar bears *Ursus maritimus* (Harwood et al. 2014). Declines in body condition are believed to be caused by climate-induced ecosystem shifts that may have resulted in reduced availability of prey (Harwood et al. 2014). Fatty acid signatures in blubber from whales sampled in 2004 and 2005 revealed their diet to be primarily Arctic cod *Boreogadus saida* (Loseto et al. 2009), the most abundant fish in the Canadian Beaufort Sea (Benoit et al. 2008). However, growth and physical condition of Arctic cod is compromised by increasing temperature, making cod vulnerable to climate change (Laurel et al. 2016). In addition, the loss of sea ice has led to the northward range expansion of temperate and subarctic species, such as Pacific sand lance *Ammodytes hexapterus* that have been recently detected in the Beaufort Sea and are predicted to displace Arctic cod (Falardeau et al. 2014).

In response to the observed decline in body condition, monitoring of beluga diet has increased to determine the vulnerability of the population to future environmental change. Whales harvested by Inuvialuit subsistence hunters typically have empty stomachs (Harwood & Smith 2002), and observations of feeding behaviours are difficult to obtain; therefore, ecological tracers that are transferred from prey to predator, such as fatty acids and carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios, can provide useful information on the diets of marine mammals (Falk-Petersen et al. 2004, Iverson et al. 2004, Budge et al. 2006, Newsome et al. 2010). Most essential fatty acids (FAs) such as long-chained monounsaturated FAs (MUFAs) and polyunsaturated FAs (PUFAs) are obtained from an organism's diet, with the exception of a few long-chained MUFAs and PUFAs (e.g. 22:5n-3, 18:1n-11) that can be biosynthesized due to metabolism of other FAs (Iverson et al. 2004). Short-chained FAs (<14 carbons) in blubber are produced

by de novo synthesis and are not incorporated from prey, as they are immediately oxidized in the liver (Budge et al. 2006). Likewise, stable isotope ratios of predators reflect the stable isotope ratios of their prey (Hobson et al. 1996, Parnell et al. 2013, Phillips et al. 2014).  $\delta^{15}\text{N}$  values typically increase 3 to 5‰ with every trophic transfer, whereas  $\delta^{13}\text{C}$  varies with differences in baseline primary producers, increasing approximately 0 to 1‰ per trophic transfer (Peterson & Fry 1987). The combination of FA signatures and stable isotope ratios is a powerful technique for the interpretation of trophic linkages in aquatic ecosystems (El-Sabaawi et al. 2009).

To investigate if shifts in diet and body condition are linked to changing environmental conditions, we examined inter-annual variation in FA signatures and stable isotope ratios of Beaufort Sea beluga whales from 2011 to 2014. As sea ice conditions influence the habitat and range of beluga whales (Heide-Jørgensen et al. 2010, Hornby et al. 2016), we first examined whether variability in diet in beluga whales was influenced by habitat selection. Using sex- and size-based habitat groups defined by Loseto et al. (2006, 2008a), we predicted that dietary tracers found in large males would differ from those in females and small males due to differences in habitat use. We also predicted that annual differences in habitat selection due to changing environmental conditions would be reflected in dietary tracers. Our next objective was to assess body condition indices in beluga whales using morphometrics from harvested whales, to examine if higher body condition in whales corresponds with favourable environmental conditions. Finally, we investigated biological factors influencing FA composition and stable isotope ratios in beluga whales. As Arctic marine ecosystems are undergoing rapid change, our goal was to increase our understanding of inter-annual variations in beluga diet in response to environmental conditions, as well as to establish a baseline for monitoring the response of belugas to environmental changes.

## MATERIALS AND METHODS

### Sample collection

Blubber and liver samples were collected from 26 female and 151 male adult beluga whales harvested at Inuvialuit hunting camps in July to early August 2011 to 2014 at Hendrickson Island, Brown's Harbour, Kendall Island, and East Whitefish in the Inuvialuit Settlement Region, Northwest Territories,

Canada (Fig. 1). Sex, body length, maximum half girth (indicated by the dorsal ridge), and axillary blubber thickness were recorded for each specimen. Age was estimated by counting growth layer groups, in which 1 growth layer group (comprised of a dark and light layer) equals 1 yr, from teeth collected from lower jaws (Stewart et al. 2006). Blubber samples (approximately 10 cm by 10 cm, throughout the entire blubber depth) were removed from the mid thoracic region near the front flipper. All individuals had empty stomachs. Samples were frozen at  $-20^{\circ}\text{C}$  in portable freezers and shipped to Fisheries and Oceans Canada in Winnipeg, Manitoba, for laboratory analysis.

### FA extraction

Blubber was divided into 3 equal layers: inner, middle, and outer. Total lipid content was extracted from 0.5 g of blubber using chloroform:methanol containing 0.01% butylated hydroxytoluene (2:1 v/v/w) and 0.7% NaCl, for a final proportion of chloroform/methanol/water of 8:4:3 following a method modified

from Folch et al. (1957) as described by Budge et al. (2006). FA methyl esters (FAMES) were prepared using the lipid extract through transesterification using 1.5 ml of dichloromethane and Hilditch reagent (0.5 N  $\text{H}_2\text{SO}_4$  in dry methanol) and incubated for 1 h at  $100^{\circ}\text{C}$ . The purified FAMES were dissolved in hexane.

Gas chromatography was performed using an Agilent Technologies 7890N coupled to a flame ionization detector. Run procedures are described in detail by Giraldo et al. (2016). Briefly, FAME samples were analysed using gas chromatography (Hewlett-Packard HP series 6890) with a mass spectrometer detector (Hewlett-Packard 5973). FA standards were obtained from Supelco (37 component FAME mix; Sigma-Aldrich Canada) and Nu-Chek (54 component mix GLC-463; Nu-Chek Prep). FAs that were not present in the Supelco standard were quantified using response factors for FAs of similar chain length and retention time. In total, 72 FAs were identified by retention time based on Supelco and Nu-Chek standards and reported as the percentage of the total FAs. Dietary FAs identified by Iverson et al. (2004) are best represented in the inner blubber layer (Koopman et al. 2002) and were used for analysis.

Thirty FAs identified by Iverson et al. (2004) as having dietary origins and mean proportions greater than 0.1% were kept for analyses.

### Stable isotope analysis

Liver samples for 2011–2013 were freeze-dried for at least 48 h and analysed for C and N stable isotope ratios at the University of Waterloo Environmental Isotopes Laboratory as described by Choy et al. (2016). Samples for 2014 were analysed at the Freshwater Institute biotracers lab as described by Rosenberg et al. (2015). To ensure data were comparable, 10 liver samples were compared for inter-laboratory variability and reported to have a mean difference of  $0.07\text{‰}$  for  $\delta^{13}\text{C}$  and  $0.30\text{‰}$  for  $\delta^{15}\text{N}$ ; the standard deviations between laboratories were  $0.05\text{‰}$  for  $\delta^{13}\text{C}$  and  $0.22\text{‰}$  for  $\delta^{15}\text{N}$  (Rosenberg et al. 2015).

As lipids significantly affect  $\delta^{13}\text{C}$  values in beluga tissues, a lipid correction model ( $\delta^{13}\text{C}_{\text{extracted}} = -1.868 + 0.839 \times \delta^{13}\text{C}_{\text{bulk}}$  for liver) was used on bulk  $\delta^{13}\text{C}$  values (Choy et al. 2016).

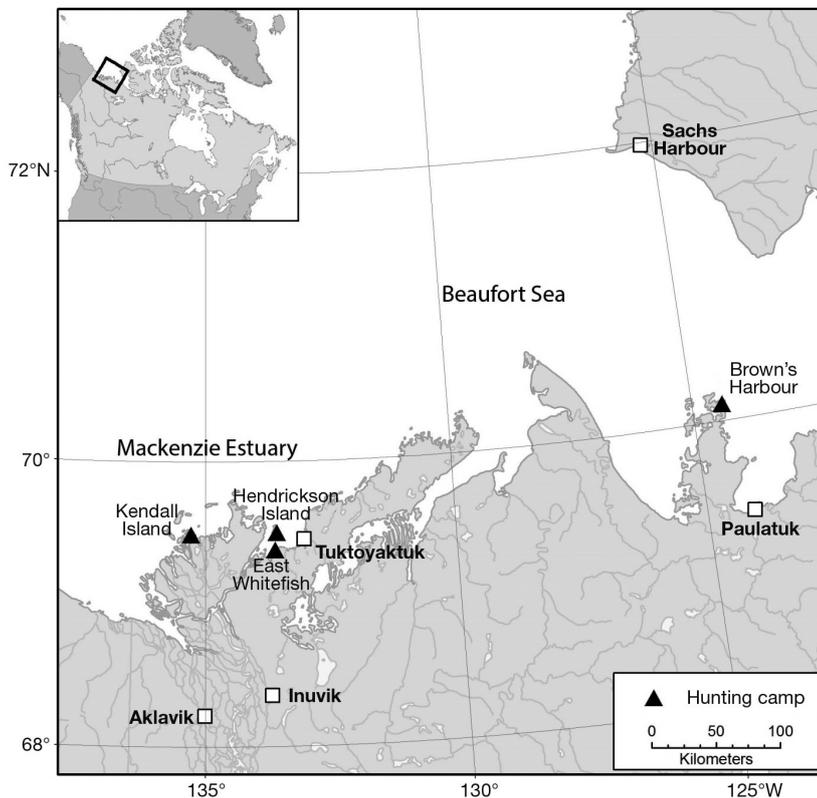


Fig. 1. Sample collection sites for beluga whale *Delphinapterus leucas* tissues at traditional Inuvialuit hunting camps (▲) located in the Inuvialuit Settlement Region, Northwest Territories, Canada

## Statistical analyses

### Body condition

Using an approach similar to that of George et al. (2015) for bowhead whales *Balaena mysticetus*, we developed 2 body condition indices based on maximum girth and blubber thickness. Each body condition index was computed from the residuals of the most parsimonious model based on Akaike's information criterion corrected for small sample sizes (AICc) with length, age, and sex as factors using the package nlme for linear models (Pinheiro et al. 2015) in R 3.2.5 (R Core Team 2016). Models were assessed for multicollinearity using a variance inflation factor (<2.5) for each predictor, and for normality of residuals using a Shapiro-Wilk test. Variables were log-transformed when appropriate to meet assumptions of normality. Differences in body condition indices among years were tested using 1-way analysis of variance (ANOVA) followed by a post hoc Tukey HSD test.

### Dietary tracers

Although dietary tracers can provide insights into the diets of free-ranging cetaceans, the relative turnover rates of FAs in blubber and stable isotope ratios have not been quantified in belugas or other cetaceans (Newsome et al. 2010). Turnover of FAs in blubber are approximately 1.5 to 3 mo in newly weaned harbour seals *Phoca vitulina* (Nordstrom et al. 2008); however, significant changes in FAs during prey-switching experiments have been detected after 14 d in harp seals *P. groenlandica* (Kirsch et al. 2000). Stable isotope ratios in liver typically have the fastest turnover rate relative to other tissues in mammals, ranging from a few days in small rodents to 37.3 d in alpacas *Lama pacos* (Tieszen et al. 1983, Arneson et al. 2006, Sponheimer et al. 2006, Miller et al. 2008, DeMots et al. 2010). Therefore, we assumed the relative turnover rate of FAs in the inner blubber and stable isotope ratios in the liver to be approximately 2 to 5 wk and indicative of the spring-summer diet of Beaufort Sea belugas.

### FA signatures

To determine if different FA signatures reflected differences in habitat use, we divided males into 3 size classes defined by Loseto et al. (2008a): small

males (<3.8 m total body length) that use coastal habitat, medium-sized males (3.8–4.2 m) that use mixed sea ice, and large males (>4.2 m) that select pack ice. We kept females as 1 class due to small sample size ( $n = 26$ ). Non-parametric multivariate analyses were performed using Plymouth routines in multivariate ecological research (PRIMER) v.7.0 (Clarke & Gorley 2015) and PERMANOVA + (Anderson et al. 2008). We ran a 2-factor permutational multivariate ANOVA (PERMANOVA) to investigate the variation in FA composition by year and sex and size class, followed by post hoc pairwise tests. PERMANOVA partitions variation of multivariate data in an ANOVA design using permutational methods (Anderson et al. 2008). PERMANOVA is not affected by violations of the assumption of normality, but is sensitive to dispersion of multivariate data. We did not include the single female sampled in 2011 since there is no dispersion for a group with a sample size of 1 (Anderson et al. 2008). FAs among beluga whales ( $n = 175$ ) were homogeneously dispersed by year (PERMDISP,  $F_{3,171} = 0.79$ ,  $p = 0.60$ ) and sex and size class ( $F_{3,171} = 1.28$ ,  $p = 0.37$ ). PERMANOVA tests used fixed factors, and Type III sums of squares, and significance was determined using 9999 unrestricted permutations of the raw data and Monte Carlo generated p-values when the number of unique permutations was <100. To identify the influential FAs contributing to dissimilarities between sex and size classes and year, we performed a 2-way similarity percentage routine (SIMPER) analysis. SIMPER first tabulates FA contributions to the average similarity of individuals within each group followed by the average dissimilarity (Clarke et al. 2014, Clarke & Gorley 2015). We designated a cut-off from the dominant FAs that characterized up to 80% of dissimilarities.

We used distance-based linear models (DISTLM) to examine the variation of FA signatures explained by biological factors and year. DISTLM partitions variation of a multivariate dataset according to a multiple regression model. Unlike PERMANOVA, DISTLM allows predictor variables to fit individually or together and allows for the testing of significance of continuous predictor variables. Parsimonious models can be built using model selection criteria (Anderson et al. 2008). FAs were  $\log(x + 1)$ -transformed to increase the weighting of FAs found in lower proportions. Predictor variables included continuous (age, length, girth, blubber thickness) and categorical variables (sex and year) coded as binary variables. Missing values were inputted into the worksheet of the predictor variables using an expectation maximum likelihood algorithm

(Clarke & Gorley 2015). To control for scaling and sexual dimorphism, predictor variables were normalized within each sex by subtracting the value of each variable by their mean and dividing by their standard deviation. A draftsman plot was used to check assumptions of multicollinearity between predictor variables, revealing an  $r < 0.65$  for every pairwise comparison. We used a stepwise selection procedure with 9999 permutations and using adjusted  $r^2$  as the selection criterion. The full model was visualized using distance-based redundancy analysis (dbRDA) ordination, which shows the percentage of fitted variation of the model explained by the first 2 axes and the remaining unexplained variation. Vector overlays displayed the multiple partial correlations of significant predictor variables with the dbRDA axes.

#### Stable isotope ratios

A 2-factor PERMANOVA was also run on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values to investigate the effect of year and sex and size class, followed by post hoc pairwise tests. Due to violation of homogeneity of dispersion,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were log-transformed (using  $x + 40$  for  $\delta^{13}\text{C}$  and  $x + 1$  for  $\delta^{15}\text{N}$  to make all values non-negative). Based on the significant predictor variables of the PERMANOVA, we examined the influence of sex and size class and year on isotopic niche breadth using Stable Isotope Bayesian Ellipses in R (SIBER) tools (Jackson et al. 2011) in the package Stable Isotope Analysis in R (SIAR 4.2.2; Parnell & Jackson 2013). Stable isotope data were visualized using the standard ellipse areas ( $\%2$ ) corrected for small sample size, which characterized spatial variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in 2-dimensional space and encompassed approximately 40% of the data (Jackson et al. 2011). Using pairwise comparisons between year and sex and size class, we calculated the overlap area between ellipses followed by the percentage of overlap for each standard ellipse area. We also compared standard ellipse areas by calculating the probability that the posterior distribution of one ellipse was smaller than another, using Bayesian inference based on Markov chain Monte Carlo simulations using  $10^4$  posterior draws (Layman et al. 2007, Jackson et al. 2011) using the script provided by Parnell & Jackson (2013).

We assessed the influence of biological variables and year on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values using the package nlme for linear models (Pinheiro et al. 2015) following the same approach we used for body condition indices. A Kruskal-Wallis rank sum test was selected as a non-parametric comparison followed by Dunn's test for post hoc multiple comparisons tests. Significance was judged at  $\alpha = 0.05$  for all statistical procedures. All univariate analyses were conducted using R 3.2.5 (R Core Team 2016).

## RESULTS

### Annual differences in body condition indices

The most parsimonious models included log(length) + sex  $\times$  age as predictors for log(maximum girth) ( $F_{4,154} = 48.77$ ,  $r_{\text{adj}}^2 = 0.55$ ,  $p < 0.01$ ) and length + age for blubber thickness ( $F_{2,156} = 13.01$ ,  $r_{\text{adj}}^2 = 0.13$ ,  $p < 0.01$ ; see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m579p213\\_supp.pdf](http://www.int-res.com/articles/suppl/m579p213_supp.pdf)). In our models for body condition, maximum girth was significantly influenced by length and the interaction sex  $\times$  age, whereas only length was a significant factor for blubber thickness (Table 1). The body condition index for maximum girth differed among years (ANOVA,  $F_{3,155} = 6.64$ ,  $p < 0.01$ ). Residual maximum girth was higher in 2012 than in 2011 (Tukey HSD test,  $t = 2.80$ ,  $p = 0.03$ ), 2013 ( $t = -3.53$ ,  $p < 0.01$ ), and 2014 ( $t = -3.96$ ,  $p < 0.01$ ; Fig. 2a). The body condition index for blubber thickness also differed among years ( $F_{3,155} = 4.97$ ,  $p < 0.01$ ) and was lowest in 2014 compared to 2011 ( $t = -3.46$ ,  $p < 0.01$ ) and 2012 ( $t = -2.90$ ,  $p = 0.02$ ) (Fig. 2b).

Table 1. Multiple linear regression models for body condition indices based on maximum girth ( $n = 159$ ) and blubber thickness ( $n = 158$ ) for eastern Beaufort Sea beluga whales *Delphinapterus leucas*. Results are presented for the most parsimonious model based on Akaike's information criterion adjusted for small sample sizes ( $\text{AIC}_c$ )

Dependent	Predictor	Value	$t$	$p$
Log(maximum girth) (cm)	Intercept	0.36	0.50	0.62
	Sex	-0.11	-1.31	0.19
	Age	$4.9 \times 10^{-4}$	0.28	0.78
	Log(Length)	0.72	5.97	<0.01
	Sex $\times$ Age	$6.00 \times 10^{-3}$	2.80	0.01
Blubber thickness (cm)	Intercept	-3.37	-1.35	0.18
	Age	-0.04	-1.92	0.06
	Length	0.03	4.99	<0.01

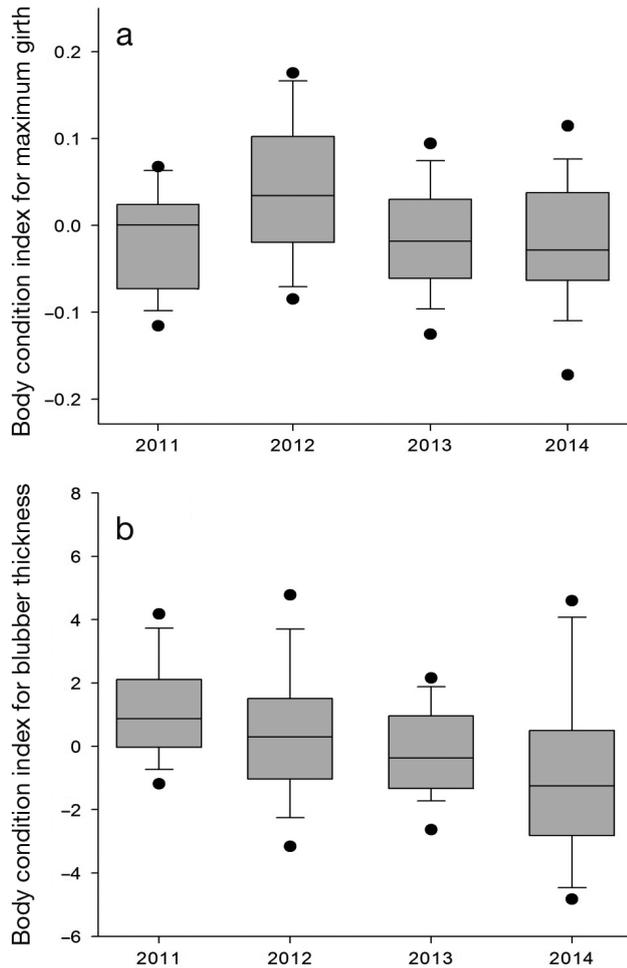


Fig. 2. Medians and quartiles of the body condition index based on (a) maximum girth and (b) blubber thickness for eastern Beaufort Sea beluga whales *Delphinapterus leucas* ( $n = 159$ ). Whiskers: 10th and 90th percentiles; black dots: 5th and 95th percentiles

### Inter-annual variation and biological factors affecting FA signatures

FA signatures of EBS beluga whales ( $n = 175$ ) varied by year (2-way PERMANOVA, pseudo- $F_{3,160} = 6.07$ ,  $p < 0.01$ ) and sex and size class (pseudo- $F_{3,160} = 7.87$ ,  $p < 0.01$ ), with a significant year  $\times$  sex and size class interaction (pseudo- $F_{8,160} = 2.00$ ,  $p = 0.01$ ). Pairwise comparisons of this interaction (Table S2 in the Supplement) demonstrated that there was a significant difference in FAs between large and small males in 2011, 2013, and 2014, but not in 2012. There was also a significant difference between large males and females in 2013 and 2014, but not 2012. Medium-sized males were also different from small males in 2013 and 2014, but not in 2012 and 2011. There was also a significant difference between large and medium-

sized males and small males and females in 2013, and between medium-sized males and females in 2014. In 2012, FA compositions did not differ among sex and size classes, with the exception of females and medium-sized males. For comparisons of FA signatures between years (Table S2), there was a significant difference between 2012 and 2013 for large and medium-sized males. FA signatures were different between 2012 and 2014 for small males and females. FAs of females were different between 2013 and 2014, and for small males between 2011 and 2014.

Across all years and sex and size classes, 14 FAs comprised between 83.2 and 90.5% of the total FAs (Fig. 3). 16:1n-7 was the predominant FA in small males in 2013 (19.7%) and 2014 (18.1%) and was lowest in medium-sized males in 2012 (10.6%). 20:1n-9 and 22:1n-11 were predominant in large males in 2013 (13.8 and 13.5%, respectively) and 2011 (12.9 and 13.1%) and were lowest in females (8.5 and 6.9%) and small males (9.6 and 6.9%) in 2014. 16:1n-7, 20:1n-9, and 22:1n-11 contributed the most to dissimilarities among sex and size classes, accounting for 61.1 to 76.4% (2-way SIMPER; Table S3 in the Supplement). 16:1n-7 accounted for the most differences among all size classes except large males and females, for which 22:1n-11 contributed to most of the differences (25.1%). 16:1n-7 and 22:1n-11 accounted for the most inter-annual variation (36.6 to 54.5%), with 20:1n-9, 18:1n-9, 20:1n-11, 22:6n-3, and 16:0 also contributing to differences between years.

Among environmental variables, the DISTLM analysis revealed that age (9.4%) explained most of the total variation. Year (7.9%), girth (7.7%), length (5.7%), and sex (4.6%) followed as the next most important variables (Table S4 in the Supplement). Blubber thickness was the only variable tested that was not significant ( $p = 0.62$ ). The first 2 dbRDA axes accounted for 82.5% of the variability of the fitted model and 19.8% of the variation of the entire FA dataset (Fig. 4). The first axis explained 67.9% of the variability of the fitted model and 16.3% of the total variation in FAs. Age ( $r = -0.56$ ), maximum girth ( $r = -0.44$ ), length ( $r = -0.36$ ), and males ( $r = -0.30$ ) were negatively correlated to the first axis whereas year 2014 ( $r = 0.36$ ) and females ( $r = 0.30$ ) were positively correlated. On the second axis, years 2012 ( $r = -0.59$ ) and 2011 ( $r = -0.24$ ) had the strongest negative correlations, whereas 2014 ( $r = 0.50$ ), age ( $r = 0.44$ ), and 2013 ( $r = 0.34$ ) had the strongest positive correlations. Along the first axis, there was a sex and size class gradient, with large males located at one extreme and small males and females at the opposite.

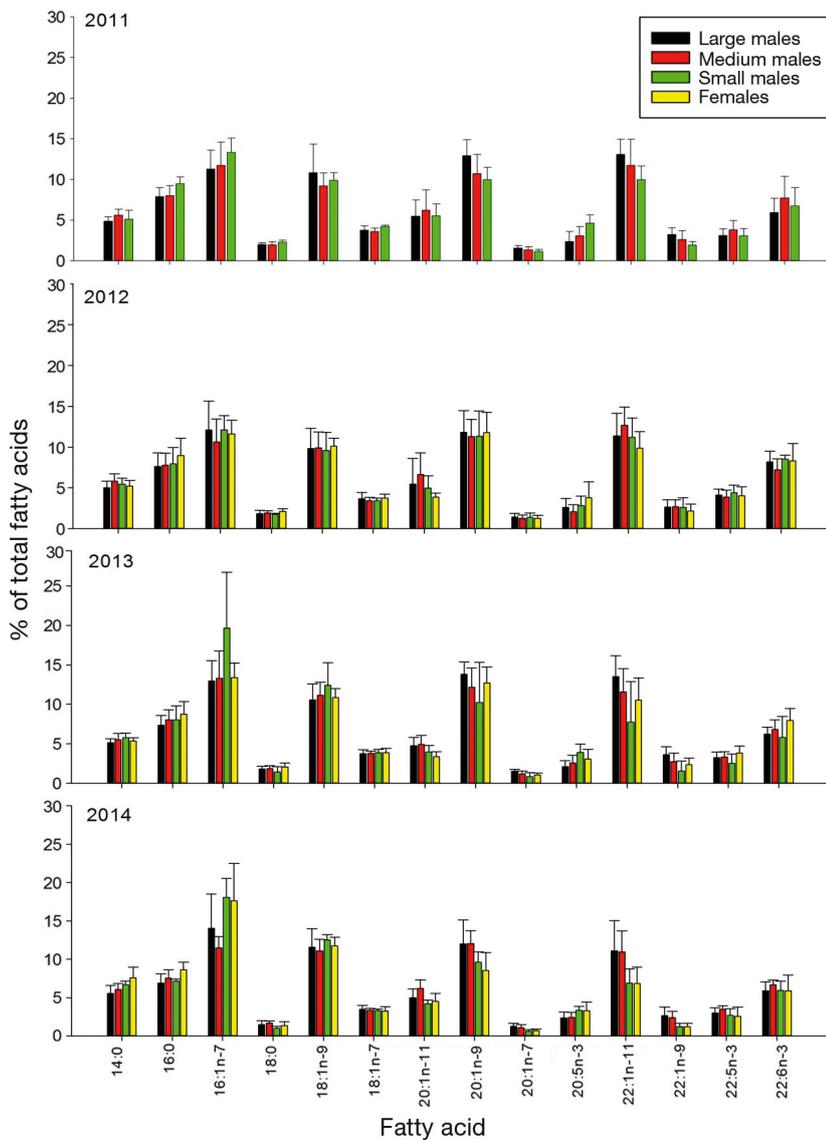


Fig. 3. Annual mean  $\pm$  SD percentages (%) of fatty acids in eastern Beaufort Sea beluga whales *Delphinapterus leucas* ( $n = 175$ ) according to sex and size class. Only fatty acids transferred through diet that contribute to more than 1% of the total percent fatty acids are shown

The results of the sequential stepwise test using adjusted  $r^2$  as a selection criterion procedure for each data set are shown in Table 2. The cumulative variation explained by the full model was 23.9% with an adjusted  $r^2$  of 0.21.

#### Inter-annual variation and biological factors affecting stable isotope ratios

Stable isotope ratios among beluga whales ( $n = 169$ ) differed by year (pseudo- $F_{3,154} = 3.30$ ,  $p < 0.01$ ) and sex and size class (pseudo- $F_{3,154} = 4.11$ ,  $p < 0.01$ ).

Unlike FAs, there was no significant interaction (pseudo- $F_{8,154} = 1.45$ ,  $p = 0.13$ ). Post hoc pairwise tests revealed that stable isotope ratios between large and small males, and between medium and small males were significantly different, as well as for large males and females, and medium-sized males and females, but not small males and females or medium and large males (Table S5 in the Supplement). Between years, pairwise tests showed that 2011 and 2013, 2012 and 2013, and 2013 and 2014 had significantly different stable isotope ratios, but not 2011 and 2012, 2011 and 2014, and 2012 and 2014 (Table S5).

Isotopic niche breadth estimates for the beluga population by year were 2011 =  $0.54\text{‰}^2$ , 2012 =  $0.81\text{‰}^2$ , 2013 =  $0.60\text{‰}^2$ , and 2014 =  $1.01\text{‰}^2$  (Fig. 5). The standard ellipse area was largest in 2014, displaying the most overlap with 2011 (84.7%), 2012 (64.0%), and 2013 (86.4%). 2012 had the second largest standard ellipse area and overlapped with 2011 (51.9%), 2013 (67.4%), and 2014 (51.5%). There was no overlap between ellipses for 2011 and 2013. The standard ellipse area was smaller for 2011 (Bayesian  $p = 0.90$ ), 2012, ( $p = 0.87$ ), and 2013 ( $p = 0.99$ ) than 2014. The standard ellipse area was also smaller for 2013 than 2012 ( $p = 0.91$ ). Isotopic niche breadth estimates by sex and size class were: small males =  $0.52\text{‰}^2$ , medium males =  $0.75\text{‰}^2$ , large males =  $1.25\text{‰}^2$ , and females =  $0.75\text{‰}^2$ . The standard ellipse area of large males displayed the greatest overlap with medium-sized males (94.5%; Fig. 5). The ellipse of small males overlapped least with large males (25.2%), and the ellipse of females also demonstrated the lowest overlap with large males (33.8%). The standard ellipse area was smaller in small males ( $p = 0.92$ ), medium-sized males ( $p = 1.00$ ), and females ( $p = 0.88$ ) than in large males.

The most parsimonious model included age + year ( $F_{4,154} = 9.99$ ,  $r_{\text{adj}}^2 = 0.19$ ,  $p < 0.01$ ) as predictors for  $\log(\delta^{13}\text{C} + 40)$  and length + age ( $F_{2,156} = 13.34$ ,  $r_{\text{adj}}^2 = 0.14$ ,  $p < 0.01$ ) for  $\delta^{15}\text{N}$  in liver (Table S1).  $\delta^{15}\text{N}$  values increased with length but had no relationship with age (Table 3).  $\delta^{13}\text{C}$  values decreased with age ( $r_{\text{adj}}^2 =$

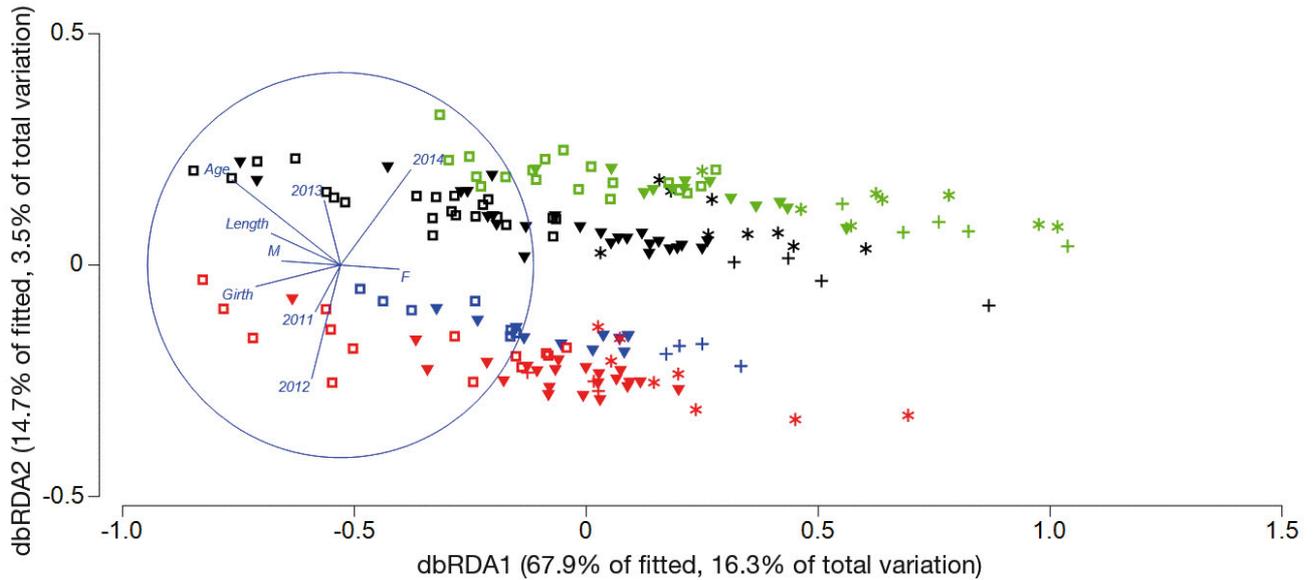


Fig. 4. Biplot of distance-based redundancy analysis (dbRDA) relating the variation of fatty acid signatures in eastern Beaufort Sea beluga whales *Delphinapterus leucas* explained by predictor variables based on the full distance-based linear model. Vector overlays demonstrate the strength of the relationship of significant predictor variables (multiple partial correlations  $r > 0.2$ ) with the dbRDA axes. Large males (M) are represented by open squares, medium males by closed triangles, small males by crosses, and females (F) by asterisks. The year 2011 is indicated by blue, 2012 by red, 2013 by black, and 2014 by green

Table 2. Percentage of variation and cumulative variation of fatty acid signatures attributed to explanatory variables in a distance-based linear model with sequential stepwise tests using the adjusted  $r^2$  selection criterion for fatty acids in eastern Beaufort Sea beluga whales *Delphinapterus leucas*.  $SS_{\text{trace}}$  is the portion of the sum of squares that is related to the predictor variable

Variable	$r^2_{\text{adj}}$	$SS_{\text{trace}}$	Pseudo- $F$	p	Variation (%)	Total variation (%)	df
Age	0.09	13.43	17.88	<0.01	9.37	9.37	2,173
Year	0.16	11.71	5.61	<0.01	8.17	17.54	5,170
Sex	0.20	6.11	9.22	<0.01	4.26	21.80	6,169
Girth	0.21	2.19	3.35	0.02	1.53	23.33	7,168
Length	0.21	0.88	1.35	0.23	0.62	23.95	8,167

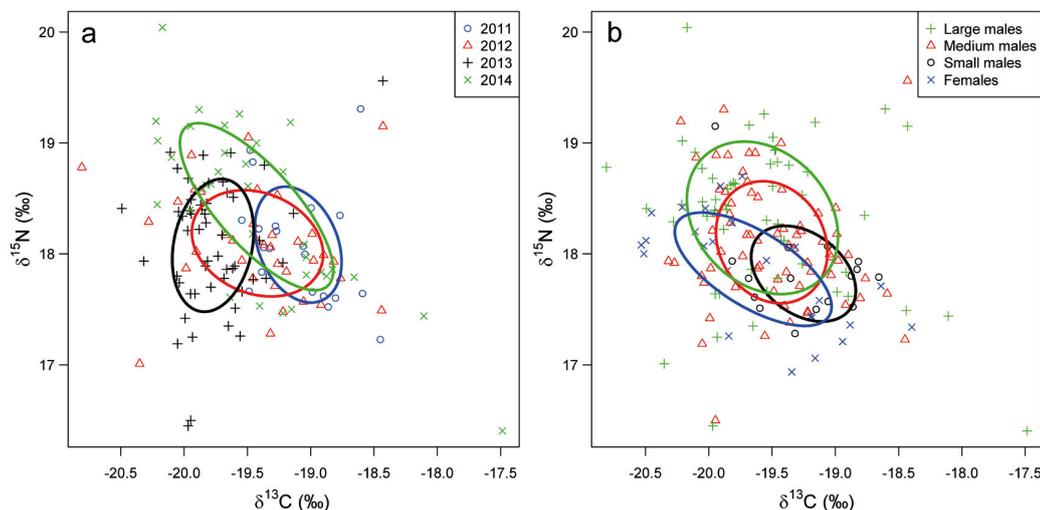


Fig. 5. Isotopic niche breadth based on the standard ellipse area for liver samples from eastern Beaufort Sea beluga whales *Delphinapterus leucas* across different (a) years (males only) and (b) sex and size classes

Table 3. Multiple linear regression models for factors influencing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in liver tissues of eastern Beaufort Sea beluga whales *Delphinapterus leucas* ( $n = 169$ ). Results are presented for the most parsimonious model based on Akaike's information criterion adjusted for small sample sizes ( $\text{AIC}_c$ )

Dependent variable	Predictor	Value	$t$	$p$
$\text{Log}(\delta^{13}\text{C} + 40)$	Intercept	3.05	422.79	<0.001
	Age	$-6.00 \times 10^{-4}$	-2.93	<0.01
	Year2012	$-1.30 \times 10^{-2}$	-1.94	0.05
	Year2013	$-2.70 \times 10^{-2}$	-4.15	<0.001
	Year2014	$-7.0 \times 10^{-3}$	-1.08	0.28
$\delta^{15}\text{N}$	Intercept	15.04	24.9	<0.01
	Length	$7.60 \times 10^{-3}$	5.13	<0.01
	Age	$5.25 \times 10^{-4}$	0.11	0.91

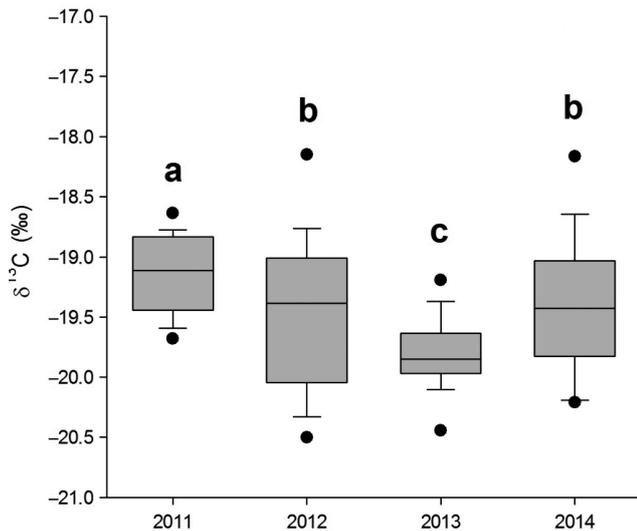


Fig. 6.  $\delta^{13}\text{C}$  ratios of beluga whale *Delphinapterus leucas* liver tissue by year ( $n = 169$ ). Boxes with the same letters are not statistically different ( $\alpha = 0.05$ ) according to a Dunn's test. Whiskers: 10th and 90th percentiles; black dots: 5th and 95th percentiles

0.08,  $p < 0.01$ ) and differed by year (Kruskal-Wallis test,  $\chi^2 = 33.83$ ,  $\text{df} = 3$ ,  $p < 0.01$ ), with values highest in 2011 and lowest in 2013 among all years; there was no difference between 2012 and 2014 (Dunn's test; Fig. 6).

## DISCUSSION

Body condition indices based on blubber thickness and maximum girth varied annually and appeared to be highest during years with greater open-water conditions and lower sea ice extent (Perovich et al. 2011, 2012, 2013, 2014, Hornby et al. 2014). The body

condition index for girth was highest in 2012 relative to all years, whereas the index for blubber was highest in 2011 and 2012. During the study period, the largest loss of sea ice in the Western Arctic occurred in 2012, with record lows occurring in June and September (Perovich et al. 2012). Sea ice extent rebounded in 2013 although it was lower in 2014 than 2013, but still higher than in 2012 and 2011 (Perovich et al. 2011, 2013, 2014). Open-water conditions may be favourable to beluga whales, similar to bowhead whales in the Beaufort Sea (George et al. 2015). Long-term

temporal trends showed an increase in fall body condition in bowhead whales with the reduction of sea ice in the Beaufort Sea, along with a significant correlation between summer open-water conditions and body condition (George et al. 2015). Although both condition indices followed similar trends in belugas, maximum girth may be better suited as a condition index because it was a significant predictor of FA signatures in the present study. Girth also incorporates changes in thickness in the hypothalamic layer, muscle mass, and visceral fat (George et al. 2015). Similarly, maximum girth was recommended as a body condition index for belugas longer than 290 cm from the St. Lawrence River, since it was positively correlated with the scaled mass index, whereas blubber thickness was not (Larrat 2014). Because blubber has an important function in thermoregulation (Worthy & Edwards 1990, Dunkin et al. 2005), belugas and other Arctic cetaceans may avoid using energy reserves from blubber, instead utilizing energy reserves in muscle and other tissues (Koopman 2001, Koopman et al. 2002, Irvine et al. 2017).

FA signatures varied according to year, age, and sex and size class. Beluga whales demonstrated the greatest overlap in diet among sex and size classes in 2012. In all years except 2012, small males and females differed in their FAs from large males. Females and small males did not differ in their FA signatures, nor did medium-sized males and large males (with the exception of 2013), supporting the observation that they share similar habitats (Loseto et al. 2006). Overall, there were greater differences in FA signatures among sex and size classes in 2013 and 2014 than in 2011 and 2012. Our findings of dietary overlap among sex and size classes in 2012 support the findings by Hornby et al. (2016), in which decreased sea ice extent in June 2012 allowed EBS

belugas access to a wider range of habitats over the continental shelf, whereas beluga habitat use was restricted in 2013 due to heavier ice conditions (Hornby et al. 2016). Aerial surveys conducted in June 2012 and 2013 found EBS beluga whales to be most often associated with light ice conditions, but contrasting spring conditions resulted in the selection of different classes of habitat variables between years (Hornby et al. 2016). Open-water conditions and low sea ice extent have resulted in the range expansion of other beluga populations, such as belugas from West Greenland (Heide-Jørgensen et al. 2010).

Although 16:1n-7 was the predominant FA accounting for differences among years and individual belugas, 20:1n-9 and 22:1n-11 combined contributed to the greatest dissimilarities among years and sex and size classes. The FAs 20:1n-9 and 22:1n-11 are synthesized de novo by *Calanus* copepods, which are consumed by Arctic cod (Falk-Petersen et al. 2009b), the main species of prey fish of EBS beluga whales (Loseto et al. 2009, Quakenbush et al. 2015). Therefore, dissimilarities in 20:1n-9 and 22:1n-11 may be related to differences in Arctic cod consumption among whales or *Calanus* consumption by cod. Acoustic surveys conducted in the Canadian Beaufort Sea and on the Mackenzie Shelf from 2010 to 2014 revealed that the integrated biomass and abundance of Arctic cod decreased with delays in ice break-up dates and decreases in spring–summer sea surface temperature (Geoffroy 2016). Mean standard length of Arctic cod as well as the proportions of age-2 cod in the mesopelagic layer (100 to 500 m) were significantly lower in 2014 than in 2013 and 2012 (Geoffroy 2016). Although the highest biomass of Arctic cod in the mesopelagic layer was measured in 2012 (Geoffroy 2016), the highest relative abundance of Arctic cod was observed in 2013 across all stations and depths (Majewski et al. 2016). Additionally, Geoffroy (2016) reported the biomass of Arctic cod in 2014 to be unable to sustain the energetic requirements of ringed seals *Pusa hispida* and beluga whales, a year that coincides with our findings of low body condition. The proportions of 20:1n-9 and 22:1n-11 were lowest in small males and females in 2014, which may be related to lower consumption of Arctic cod. Large males had the highest proportions of 22:1n-11 and 20:1n-9 and likely had greater access to Arctic cod at greater depths (Richard et al. 2001). Although a diatom marker (Dalsgaard et al. 2003), 16:1n-7 can be synthesized in marine mammals as a result of  $\Delta 9$  desaturase enzyme activity (Iverson 2009); however, without access to the FA signatures of prey, we can only speculate on the meaning of 16:1n-7 in beluga whales.

Stable isotope ratios supported FA signatures, reflecting differences in habitat selection among certain sex and size classes. Age and year most influenced  $\delta^{13}\text{C}$  values, whereas  $\delta^{15}\text{N}$  was most influenced by length, similar to previous findings by Loseto et al. (2008a). Stable isotope ratios of beluga whales may be influenced by the variation in the values of their main prey, Arctic cod. Arctic cod in the Canadian Beaufort Sea demonstrate a  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  gradient with depth (Stasko et al. 2016). Cod collected from the lower shelf (750–1000 m, mean  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ : 14.57,  $-23.41\text{‰}$ ) and upper slope (350–500 m, 14.07,  $-23.59\text{‰}$ ) have higher  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values and are larger in body size than those from the nearshore shelf (18–50 m; 12.57,  $-24.04\text{‰}$ ; Stasko et al. 2016). Therefore, larger beluga whales may dive to greater depths than smaller whales to feed on larger Arctic cod from the lower shelf, resulting in higher  $\delta^{15}\text{N}$  values.  $\delta^{13}\text{C}$  values were higher in adult versus subadult bowhead whales, and were hypothesized to be the result of older whales feeding on  $^{13}\text{C}$ -enriched prey from the Bering-Chukchi Sea and younger whales feeding on  $^{13}\text{C}$ -depleted prey from the western Beaufort (Schell et al. 1989). Arctic cod from the Canadian Beaufort Sea have lower  $\delta^{13}\text{C}$  values than those from the Bering-Chukchi Sea ( $-20.3\text{‰}$ ; Hoekstra et al. 2002). As our whales have recently migrated from the Bering-Chukchi Sea, perhaps the  $\delta^{13}\text{C}$ –age relationship is indicative of older whales arriving earlier to the Canadian Beaufort Sea relative to younger whales, or differential feeding areas. Comparisons of isotopic niche breadth also supported differences in habitat use, with large males having the widest isotopic niche breadth, likely due to their larger summer habitat range and ability to exploit a higher diversity in habitats (Richard et al. 2001). Likewise, lack of an isotopic niche overlap between 2011 and 2013 suggests that belugas were feeding from different areas.  $\delta^{13}\text{C}$  values decreased with year from 2011 until 2013, but were not different between the years 2012 and 2014. Belugas had greater access to multiple habitats in 2012, which may be reflected by the wider range in  $\delta^{13}\text{C}$  values from their prey. As belugas from 2012 and 2014 had the greatest contrast in FA signatures, the wider range in  $\delta^{13}\text{C}$  values for those years may reflect different influences. Since Arctic cod were at their lowest abundance in 2014, belugas may have been more opportunistic in their prey choice, resulting in a greater range in stable isotope ratios and niche breadth.

Recent declines in individual growth rates of EBS beluga whales have been identified over a 20 yr time-scale and are hypothesized to be due to changes in the prey base (Harwood et al. 2014). Our results show

high inter-annual variability in diet and body condition over short time periods. To understand whether declines in growth rates are ongoing and reflect an ecosystem change, we must first understand the factors that affect short-term variability. Annual variation in sea ice extent and biomass fluctuations of Arctic cod may be linked to inter-annual changes in diet and body condition of beluga whales. The year 2012 experienced the largest loss of Arctic sea ice, resulting in beluga whales having greater access to a wider range of habitats and displaying greater overlap in diet among sex and size classes than in other years. Differences in proportions of *Calanus* markers 20:1n-9 and 22:1n-11 contributed the most to variability in FA signatures within the EBS beluga population. High levels of *Calanus* 20 and 22 MUFA levels have been linked to improved body condition in pinipeds (Kirsch et al. 2000, Falk-Petersen et al. 2004, 2009a). Therefore, 20:1n-9 and 22:1n-11 may be effective indicators for prey abundance, body condition, and overall ecosystem changes. Lower proportions of *Calanus* markers in small males and females in 2014 suggest less consumption of Arctic cod, and therefore, small or young males and females may be most sensitive to environmental changes as documented in other species such as polar bears *Ursus maritimus* (Molnár et al. 2010, Rode et al. 2010, Stirling & Derocher 2012). Our results support the conclusions of Laidre et al. (2008), who identified beluga whales as moderately sensitive marine mammals with high flexibility to changes in sea ice and diet. However, as a long-lived species with a low reproductive rate, climate-induced effects on beluga fitness may take a long period of time to become detectable within the population (Gilg et al. 2012).

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