Variability in polar bear *Ursus maritimus* stable isotopes in relation to environmental change in the Canadian Beaufort Sea

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ABSTRACT: Diets of apex predators can be used to understand the effects of environmental changes within an ecosystem and to monitor shifts in community dynamics. Using stable isotopes of nitrogen and carbon ($\delta^{15}N$ and $\delta^{13}C$) in polar bear *Ursus maritimus* guard hairs, we examined their diet in the Canadian Beaufort Sea from 2003 to 2011. We investigated how $\delta^{15}N$ and $\delta^{13}C$ were related to population demographics, sea ice dynamics, climate indices, air temperatures, and ringed seal *Pusa hispida* ovulation rates. Bayesian stable isotope models were used to determine annual variation in prey contributions and niche widths. Diet contributions from ringed seal, bowhead whale *Balaena mysticetus*, beluga *Delphinapterus leucas*, and bearded seal *Erignathus barbatus* varied by sex, reproductive status, and year. Polar bear ringed seal consumption was lowest and niche widths were highest in 2004 following ringed seal reproductive failure in the early 2000s, and polar bear $\delta^{15}N$ decreased when ringed seal ovulation rate was high. Polar bear $\delta^{15}N$ and $\delta^{13}C$ were linked to capture locations, which may reflect geographic gradients in stable isotopes within the Beaufort Sea. Climate indices were not related to polar bear $\delta^{15}N$ and $\delta^{13}C$. Sea ice dynamics were related to polar bear $\delta^{13}C$, suggesting that the bears' diets shift in response to environmental change. Overall, these results highlight the biological link between polar bears and ringed seals, as well as sea ice dynamics, and the importance of considering geographic location in stable isotope studies.

KEY WORDS: *Ursus maritimus* · Polar bear · Beaufort Sea · Sea ice dynamics · Environmental change · Stable isotopes · Diet · Niche width

1. INTRODUCTION

Fluctuations in the environment can cause shifts in ecosystem structure and function, resulting in species altering their foraging behaviors and habitat use in response to variation in resources (Post et al. 2009). Such alteration or plasticity in diet is driven by optimal foraging, in which resource selection by an individual is directed by attempts to maximize energy gain at a reduced search and handling cost (MacArthur & Pianka 1966, Pyke et al. 1977). Food sources with low availability may be rare to encounter, resulting in animals switching to resources that are more abundant and accessible (Pyke et al. 1977). Therefore, shifts in diet may indicate changes in the availability and distribution of resources within the ecosystem (Montevecchi & Myers 1996). Dietary shifts in high trophic level species may have pronounced ecosystem effects (Ripple & Beschta 2004). As such, monitoring the diets of apex predators can be used both to indicate changes within the community and to understand the effects of environmental fluctuations on the ecosystem. Studies on predator diets have documented alterations to community

composition and prey population density, and have been supported by research on shifts in population dynamics and distributions of prey (Montevecchi & Myers 1996).

Sea ice loss due to climate change is modifying the structure and dynamics of Arctic marine ecosystems (Post et al. 2009). Temperatures within the Arctic are increasing faster than other areas, resulting in rapid and accelerating reductions in sea ice extent and thickness (Stroeve et al. 2007, Galley et al. 2016, Stern & Laidre 2016). For several organisms within this ecosystem, including polar bears *Ursus maritimus* and ringed seals *Pusa hispida*, sea ice is critical to various aspects of their life history (Smith 1980, Reeves 1998).

Polar bears are apex predators dependent on sea ice to catch ringed seals and bearded seals *Erignathus barbatus* (Stirling & Archibald 1977, Smith 1980). The bears accumulate most of their energy from adult seals and newborn pups during a hyperphagic spring period and, following ice break-up, undergo a fasting period in late summer/fall (Lunn & Stirling 1985, Amstrup 2003). Loss of sea ice reduces the temporal availability of seals for polar bears (Stirling et al. 1999, Cherry et al. 2013) and decreases in sea ice are associated with lower seal productivity (Harwood et al. 2012), potentially affecting predator–prey dynamics.

Reduced available sea ice limits opportunities for polar bears to hunt seals, and as a result they may exploit alternative food sources, such as seabird eggs (Dey et al. 2017). However, terrestrial food sources may not provide adequate nutrition compared to lipid-rich marine mammal prey (Rode et al. 2015). While an unreliable food source, whales may supplement polar bear diets, as they are a large source of protein and fats that may sustain many individuals and offset nutritional stress (McKinney et al. 2017, Laidre et al. 2018, Whiteman et al. 2018). Polar bears may scavenge or hunt belugas *Delphinapterus leucas* from openings in the sea ice (Thiemann et al. 2008). In the Beaufort Sea, scavenging of bowhead whale *Balaena mysticetus* carcasses left after subsistence hunts has increased as the open water period becomes longer (Bentzen et al. 2007, Rogers et al. 2015, Whiteman et al. 2018). Within the Beaufort Sea, climate variation is linked to changes in diet, with more bowhead whales consumed in years with longer open water periods (McKinney et al. 2017).

Shifts in diet can be documented by changes in an individual's stable isotopes over time (Hobson et al. 1996). In the Beaufort Sea, $\delta^{15}N$ and $\delta^{13}C$ have been used to examine seasonal and annual diet variation in polar bears (Bentzen et al. 2007, Rogers et al. 2015, Whiteman et al. 2018). However, these studies only examined short time periods (2 to 3 yr) or subsets of the population, which may not capture diet variation.

This study examined $\delta^{15}N$ and $\delta^{13}C$ in guard hairs of Canadian Beaufort Sea polar bears from 2003 to 2011. The objectives of this study were to (1) quantify diet of Canadian Beaufort Sea polar bears using stable isotope ratios, (2) assess variation in stable isotope ratios in relation to age, sex, reproductive status, spatial distribution, sea ice dynamics, air temperature, climate indices, and ringed seal ovulation rate, and (3) assess variation in niche widths.

2. MATERIALS AND METHODS

2.1. Study area

The study area included the region of the Beaufort Sea north of the Yukon and Northwest Territories, Canada, as well as in the Amundsen Gulf (Fig. 1). Within the Beaufort Sea, sea ice begins to break up in May in the Cape Bathurst polynya, an area of open water off Cape Bathurst at the mouth of the Amundsen Gulf (Galley et al. 2016). In September, the Beaufort Sea's open water season typically ends, and freeze-up begins (Galley et al. 2016). Sea ice is circulated through the Beaufort Sea by the Beaufort gyre (McLaren et al. 1987).

Two polar bear subpopulations occur in the Canadian Beaufort Sea. While the subpopulations can intermix, the northern Beaufort Sea bears primarily use the northeastern Beaufort Sea, and the southern Beaufort Sea bears use the southwest side eastward to Utqiagvik (Barrow), Alaska. When the sea breaks up, the bears either migrate north following the sea ice retreat (Amstrup et al. 2000), or move to land (Pongracz & Derocher 2017).

2.2. Sampling

Samples were collected in early April to late May from 2004 to 2012. Polar bears were live-captured using a helicopter, within 150 km of the coast, following standard immobilization techniques. Using a scalpel, guard hairs were shaved from the skin on the rump adjacent to the side of the tail, and all underfur was removed from the sample. Bears were aged using a vestigial premolar, and grouped as subadults (3 to 4 yr) or adults (≥5 yr) (Calvert & Ramsay 1998). Cubs were aged by tooth eruption. Straight-line
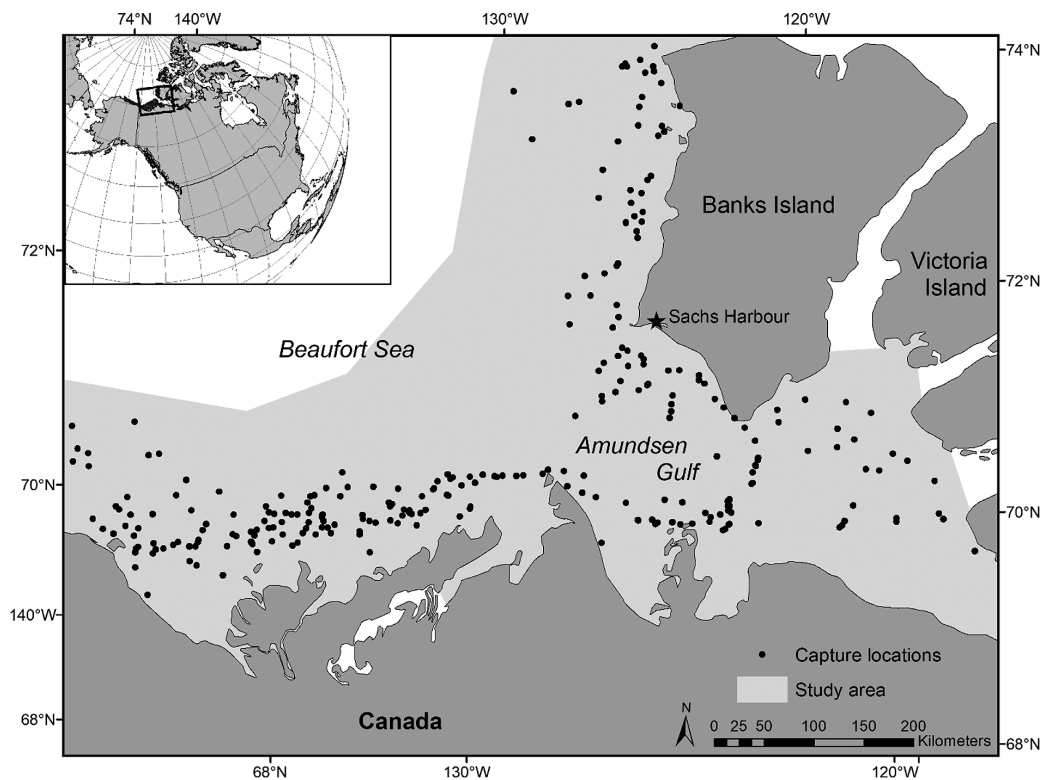
Fig. 1. Beaufort Sea study area with sampling locations (n = 315) of polar bears *Ursus maritimus* from the Canadian Beaufort Sea, sampled between 2004 and 2012. Shaded region: area where sea ice metrics were calculated; star: Environment and Climate Change Canada climate station at Sachs Harbour

body length (SLEN; tip of nose to the last tail vertebra) and axillary girth (AXG; body circumference behind forelimbs) were measured to the nearest cm. Body mass (*M*; in kg) was estimated following Thiemann et al. (2011), using SLEN and AXG measurements:

$$M = 0.00006039 \times AXG^{1.762} \times SLEN^{1.249} \qquad (1)$$

A 2:1 chloroform:methanol solution was used to wash the hair samples, followed by rinsing with deionized water. Samples were air-dried, homogenized, and packed into tin capsules before $\delta^{13}C$ and $\delta^{15}N$ analysis. Stable isotope analysis was completed using a Thermo Delta V Advantage isotope ratio mass spectrometer (IRMS) attached to a Costech 4010 elemental analyzer and a ConFlo IV gas interface, at the Great Lakes Institute for Environmental Research laboratory at the University of Windsor. Stable isotope ratios were expressed using the delta (δ) notation (standards: $\delta^{15}N$: atmospheric nitrogen; $\delta^{13}C$: Pee Dee Belemnite), measured in parts per thousand (‰). Analytical error was ±0.1‰ for $\delta^{15}N$ and $\delta^{13}C$, based on standard deviations of within-run sample replicates (n = 20) and standard deviations for internal laboratory standards (NIST 1577c, Tilapia,

USGS 40, Urea IVA 33802174) run for every 12 samples (n = 28). We did not correct consumer or prey $\delta^{13}C$ for the Ocean Suess effect, as this correction would be negligible over our study duration (Keeling 1979).

2.3. Data analysis

Polar bear hair growth occurs between approximately May to October–November (Amstrup 2003). Our sampling was completed before the moult and likely represents diet from the previous year (Rogers et al. 2015), so all environmental variables were examined for the year of hair growth, rather than the sampling year.

Bears were grouped by age (subadults and adults), and by class, which we defined as a combination of sex and reproductive status (males, females, females with cubs up to 2 yr old). As cub presence for females without cubs at the time of capture was unknown during hair growth, the female category could include solitary adult females, females that weaned 2 yr old cubs and did not breed, and females that may have lost offspring.

We used sea ice concentrations from Special Sensor Microwave Imager (SSM/I) daily satellite images, at a resolution of 25 km, obtained from National Snow and Ice Data Center (Boulder, Colorado). Sea ice concentration percentage was determined by averaging the sea ice concentration value for all pixels within the study area, which included the extent of helicopter flight paths (Fig. 1). We derived the following sea ice metrics within the study area: break-up date, freeze-up date, and open water duration (Table S1 in the Supplement at www.int-res.com/articles/suppl/m630p215_supp.pdf). Break-up date was defined as the first day in which sea ice concentration dropped below 50%, and freeze-up date was the first day in which sea ice concentration remained above 50%. We chose 50% as it is a common metric for spring ice conditions for polar bears (Stirling et al. 1999, Stern & Laidre 2016), and below 50% sea ice concentration, polar bears will typically abandon the sea ice and retreat to land (Stirling et al. 1999, Durner et al. 2006, Cherry et al. 2013). Open water duration was the number of days between break-up and freeze-up.

Mean values for 3 climate indices were included in the models: the Arctic Oscillation (AO), the Pacific Decadal Oscillation (PDO), and the Arctic Ocean Oscillation (AOO). The AO index is a pattern of sea level pressure anomalies in high latitudes (Rigor et al. 2002). The PDO is a pattern characterized by sea surface temperature anomalies, and fluctuates between warm and cool phases (Mantua & Hare 2002). Both the AO and the PDO affect the strength of the Beaufort Sea gyre, as well as sea ice thickness, retention, and transport within the Beaufort Sea (Rigor et al. 2002, Stroeve et al. 2011). The AOO focuses on wind-driven sea surface height circulation regimes in the Arctic, and measures both the direction (cyclonic and anticyclonic) and strength of the circulation (Proshutinsky & Johnson 1997, Proshutinsky et al. 2015). The AOO affects the amount of freshwater in the Beaufort Sea, as well as sea ice drift (Proshutinsky et al. 2015). Mean climate index values were used in the models for the time of hair growth (May–November), except for AOO, which was only available as an annual value. These climate indices are expected to affect prey availability and accessibility, due to their impact on sea ice dynamics.

We obtained mean air temperatures during the period of hair growth (May–November) from the Environment and Climate Change Canada weather station at Sachs Harbour in the Northwest Territories, Canada (Fig. 1). Air temperature is correlated with sea surface temperatures, which influence sea ice and water conditions in the Beaufort Sea (Stroeve et al. 2007), and may influence food webs.

Lastly, we included ringed seal ovulation rates (%) determined by Harwood et al. (2012) for the eastern Amundsen Gulf, which describes ringed seal productivity in the Canadian Beaufort Sea. Ovulation rates were matched to the year of polar bear hair growth. Ovulation rate has been correlated with seal body condition and recruitment (Harwood et al. 2012).

All analyses were conducted in R v.3.4.3. (www.r-project.org). Before modeling, we compared factors using Pearson's correlation coefficients and did not use factors with coefficients of >0.7 within the same model. Linear models were used to relate age (subadult, adult), class (females, females with cubs, males), mass (kg), geographic location (latitude and longitude coordinates of capture location), climate indices (AO, AOO, PDO), sea ice metrics (break-up date, freeze-up date, open water duration), and air temperature to either $\delta^{13}C$ or $\delta^{15}N$. Following model fit, we assessed variance inflation factors (VIF) to further assess multicollinearity, with values >5 indicating multicollinearity. Residual plots were used to determine whether the models met assumptions. Levene's test for homogeneity of variance was used to determine whether the models met the assumption of homoskedasticity. Stepwise model selection was used to determine the top models. Model fit was assessed using Akaike's information criterion for small sample sizes (AIC_c), and the most parsimonious model was selected in cases with multiple models of $\Delta AIC_c < 2.00$, where $\Delta AICc$ is the difference between the AICc of the model of interest and that of the model with the lowest score. Effect size was assessed using Cohen's f^2, where small, medium, and large effect sizes are represented by $f^2 \geq 0.02$, $f^2 \geq 0.15$, and $f^2 \geq 0.35$, respectively. The significance level was $\alpha \leq 0.05$.

2.4. Bayesian mixing models

Bayesian mixing models, with uninformative priors, were implemented using MixSIAR v.3.1 (Stock & Semmens 2016) to determine the contribution of prey species to the diet of Canadian Beaufort Sea polar bears. We chose to use uninformative priors (corresponding to generalist diet, i.e. consumption of prey species in equal proportions) because it allows for equal probability of obtaining each combination of dietary proportions. We obtained ringed seal ($\delta^{15}N = 18.3 \pm 1.3‰$, $\delta^{13}C = -20.6 \pm 0.7‰$, n = 45), bearded seal ($\delta^{15}N = 16.8 \pm 1.0‰$, $\delta^{13}C = -17.8 \pm 1.3‰$, n = 10), bow-

head whale (δ^{15}N = 14.3 ± 1.0‰, δ^{13}C = −19.2 ± 0.4‰, n = 3), and beluga (δ^{15}N = 17.7 ± 0.6‰, δ^{13}C = −18.1 ± 0.4‰, n = 11) muscle δ^{15}N and δ^{13}C from Cherry et al. (2011), sampled between 2003 and 2007 in the Canadian Beaufort Sea. Prey muscle δ^{15}N and δ^{13}C has been used in mixing models to examine polar bear diet (Rogers et al. 2015, Whiteman et al. 2018). We did not use prey isotope data from adipose tissue because lipids are nitrogen-deficient (Bearhop et al. 2002), and therefore would only allow for use of a single isotope (δ^{13}C) model. Only the main prey of polar bears were included in the model, as other food sources likely do not significantly contribute to their stable isotope ratios (Bentzen et al. 2007). We aggregated medium-sized prey (bearded seal and beluga) *a priori* following Stock et al. (2018), as both species have similar isotopic values, and benthic prey are important within both species' diets (Dehn et al. 2006, 2007).

Diet estimates produced by Bayesian mixing models are sensitive to choice of discrimination factor (Bond & Diamond 2011), and therefore we evaluated mixing model assumptions *a priori* for polar bear diet-hair discrimination factors from L'Hérault et al. (2018) (Δ^{15}N = 2.41 ± 0.20‰, Δ^{13}C = 2.59 ± 0.42‰, n = 3) and Rode et al. (2016) (Δ^{15}N = 2.5 ± 0.2‰, Δ^{13}C = 2.0 ± 0.6‰, n = 4). We used methods from Smith et al. (2013) to test the point-in-polygon assumption (consumer isotopic values are bounded by the mixing polygon of prey isotopic values) for each discrimination factor; this assumption is violated when samples fall outside of the 95% mixing region. We selected the discrimination factor that best (i.e. fewest samples outside of the 95% mixing region) satisfied the assumption and excluded samples that fell outside the 95% mixing region from the mixing model.

We ran Bayesian mixing models with either class (female, female with cubs, male) or year (2003 to 2011) as a factor. Each model was run with 1 000 000 iterations (burning = 500 000, thinning = 500). We checked for model convergence using Gelman-Rubin and Geweke diagnostics, and visual analysis of diagnostic plots. Diet comparisons were made using Bayesian inference.

2.5. Niche comparisons

Niche comparisons were completed using Stable Isotope Bayesian Ellipses in R (SIBER) v.2.1.3, which uses standard ellipses area as a Bayesian estimate (SEA$_b$) to estimate niche width of groups (Jackson et al. 2011). We compared polar bear niche widths in each sampling year using Bayesian inference. Groups with a sample size < 5 were not included due to statistical constraints. The model was run with 2×10^6 iterations.

3. RESULTS

3.1. δ^{15}N and δ^{13}C models

Polar bear samples (n = 315) included individuals from both the northern (n = 119) and southern (n = 196) Beaufort Sea subpopulations. For all bears within the study (Table 1), the mean (±SE) for δ^{13}C values was −17.1 ± 0.44‰ (range: −18.14 to −15.39‰), while δ^{15}N was 20.8 ± 0.66‰ (range: 18.55 to 22.92‰). The mass of bears ranged from 123 to 647 kg.

AIC$_c$ supported 2 top δ^{13}C models (Table S2). Both models had VIFs < 2.60. The most parsimonious model included class, mass, latitude, longitude, and freeze-up (Table 2). δ^{13}C decreased with decreasing body mass (f^2 = 0.20), eastward longitudes (f^2 = 0.47), southern latitudes (f^2 = 0.13), and later freeze-up dates (f^2 = 0.28). Females with cubs had lower δ^{13}C than solitary females or males (f^2 = 0.40).

Two top δ^{15}N models were supported by AIC$_c$ (Table S2). Models had VIFs < 1.11. The most parsimonious model included latitude, class, and ringed seal ovulation rate (Table 2). δ^{15}N declined with southern latitudes (f^2 = 0.42) and increasing ringed seal ovulation rate (f^2 = 0.30). Solitary female polar bears had higher δ^{15}N than females with cubs or males (f^2 = 0.18).

3.2. Diet estimation

The discrimination factor from L'Hérault et al. (2018) best satisfied the point-in-polygon mixing model assumption, with 18 samples outside of the

Table 1. Sample size (n), and mean (±SD) mass and guard hair δ^{13}C and δ^{15}N for adult female with cubs, adult female, adult male, subadult female, and subadult male polar bears *Ursus maritimus* in the Canadian Beaufort Sea, captured from 2004 to 2012

Group	n	Mass (kg)	δ^{13}C (‰)	δ^{15}N (‰)
Adult female with cubs	35	197 ± 21	−17.39 ± 0.41	20.50 ± 0.70
Adult female	117	198 ± 31	−17.20 ± 0.41	20.91 ± 0.65
Adult male	97	370 ± 81	−16.92 ± 0.44	20.73 ± 0.66
Subadult female	40	166 ± 25	−17.27 ± 0.39	20.74 ± 0.64
Subadult male	26	246 ± 58	−17.14 ± 0.40	20.62 ± 0.63
All	315	251 ± 97	−17.13 ± 0.44	20.76 ± 0.66

Table 2. Estimate, standard error, *t*-value, and p-value for coefficients included in the top models for $\delta^{13}C$ and $\delta^{15}N$ guard hair stable isotopes of Canadian Beaufort Sea polar bears *Ursus maritimus*, 2003 to 2011

Model	Variables	Estimate	SE	*t*	p
$\delta^{13}C$	Intercept	−22.906	2.014	−11.373	<0.001
	Class (female with cubs)	−0.153	0.069	−2.227	0.027
	Class (male)	0.039	0.068	0.571	0.568
	Freeze-up	−0.017	0.004	−4.575	<0.001
	Latitude	0.092	0.018	4.996	<0.001
	Longitude	−0.031	0.004	−7.874	<0.001
	Mass	0.001	0.0003	3.588	<0.001
$\delta^{15}N$	Intercept	10.761	1.956	5.503	<0.001
	Latitude	0.150	0.027	5.527	<0.001
	Ringed seal ovulation rate	−0.785	0.150	−5.222	<0.001
	Class (female with cubs)	−0.276	0.110	−2.502	0.013
	Class (male)	−0.172	0.071	2.439	0.015

95% mixing polygon (Fig. S1). The discrimination factor from Rode et al. (2016) violated the point-in-polygon assumption, with 30 samples outside of the 95% mixing polygon. Therefore, we selected the discrimination factor from L'Hérault et al. (2018) for presentation and interpretation of results (see Figs. S2 & S3 for diet estimates using the discrimination factor from Rode et al. 2016). We excluded samples that violated the point-in-polygon assumption from the mixing models (see Figs. S4 & S5 for diet estimates without consumer exclusion). All mixing models converged and produced unimodal

posterior distributions for each prey contribution.

Ringed seal and medium-sized prey contributed the most to Beaufort Sea polar bear (n = 297) diet estimates for all classes and years (Figs. 2 & 3). The probability that ringed seal contributed more to the diet of females with cubs than solitary females and males was 0.68 and 0.94, respectively. Males had a high probability of having a greater diet contribution of medium-sized prey than females (0.91) and females with cubs (0.94). Polar bears of all classes had higher diet contributions of ringed seal and medium-sized prey than bowhead whale.

Prey contributions varied between years (Fig. 3). Ringed seal had a high probability (0.78 to 0.96) of contributing the least to the diet in 2004 out of all other years within the study. In 2003 and 2005, ringed seal had a high probability (0.76 to 0.91 and 0.68 to 0.88, respectively) of contributing the least when compared to later years (2006 to 2011) but had a low probability (0.22 and 0.16, respectively) when compared to 2004. Medium-sized prey had high probability of higher contributions to polar bear diet during 2004 (0.78 to 0.96) compared to other years within the study.
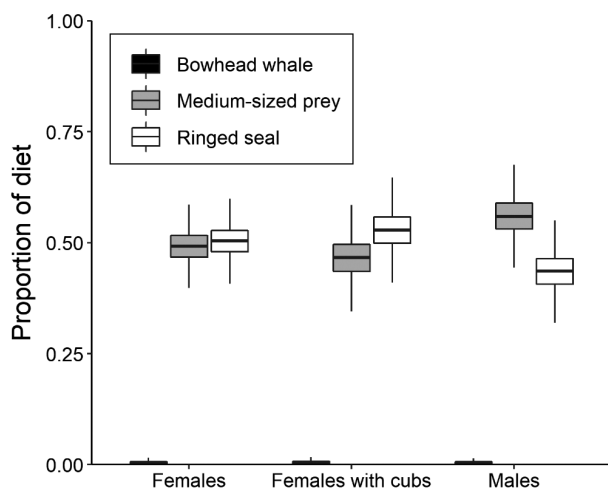

Fig. 2. Prey contributions to diets of polar bear females (n = 146), females with cubs (n = 34), and males (n = 117) in the Canadian Beaufort Sea, 2003 to 2011. Prey contributions and 95% credible intervals were generated from MixSIAR, using the discrimination factor from L'Hérault et al. (2018) for polar bears. Bearded seal *Erignathus barbatus* and beluga *Delphinapterus leucas* were aggregated as medium-sized prey, *a priori*
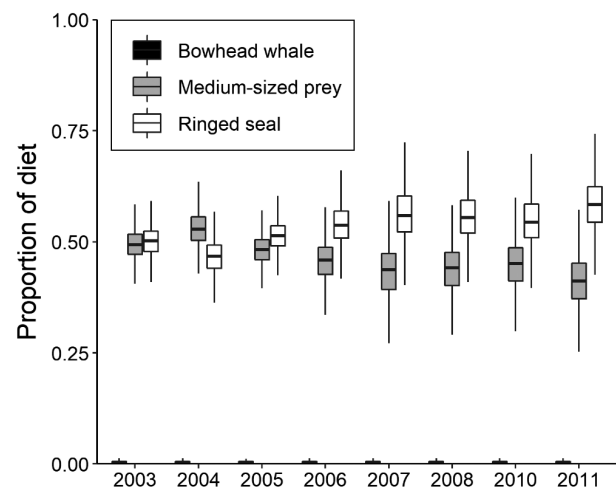

Fig. 3. Temporal change in prey contributions, with 95% credible interval bands generated by MixSIAR, for polar bears *Ursus maritimus* (n = 297) from the Canadian Beaufort Sea, 2003 to 2011. Prey contributions and 95% credible intervals were generated from MixSIAR, using the discrimination factor from L'Hérault et al. (2018) for polar bears. Bearded seal *Erignathus barbatus* and beluga *Delphinapterus leucas* were aggregated as medium-sized prey, *a priori*
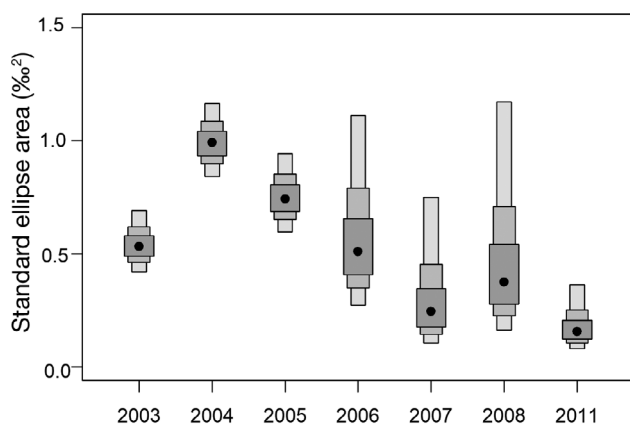
Fig. 4. Density plot generated from guard hair $\delta^{13}C$ and $\delta^{15}N$ from Canadian Beaufort Sea polar bears *Ursus maritimus* showing the standard ellipse area of the Bayesian estimate for each sampling year (2003: n = 63; 2004: n = 147; 2005: n = 75; 2006: n = 9; 2007: n = 5; 2008: n = 5; and 2011: n = 8). Black circles: mode; shaded boxes: 50, 75, and 95% credible intervals

3.3. Niche comparison

Polar bear (n = 312) niche width, as represented by SEA_b (‰^{2}), varied between years in the Canadian Beaufort Sea (Fig. 4). We excluded 2010 due to low sample size (n = 3). Niche width had a probability of 0.92 to 1.00 of being larger in 2004 compared to all other years within the study, followed by 2005 with a probability of 0.75 to 1.0. The probability of 2011 having a lower niche width than earlier years (2003 to 2008) was high (0.82 to 1.0). Credible intervals were large in 2006 to 2008 due to small sample size.

4. DISCUSSION

For Canadian Beaufort Sea polar bears, variation in $\delta^{15}N$ and $\delta^{13}C$ was linked to both intrinsic and extrinsic factors, including demographics, geographic location, sea ice dynamics, and prey availability. Polar bear diet differed between sex, reproductive status, and years. Variation in stable isotope ratios, diets, and niche widths suggest that polar bears forage adaptively in response to resource availability, accessibility, and distribution.

4.1. Diet estimates and demographic comparison

For Canadian Beaufort Sea polar bears, $\delta^{15}N$ and $\delta^{13}C$ was not related to age, but differed between classes. Subadults may have comparable hunting

ability to adults (Stirling & Latour 1978), and therefore these age categories may have similar diets. Between classes, variation in stable isotopes and diet estimates was within a narrow isotopic range. Analytical error was low; however, it is possible that this variability was an artefact of the IRMS analysis or for diet estimates, the MixSIAR analysis (e.g. selection of inputs, sample size). Therefore, only conservative conclusions can be made regarding the comparison of stable isotopes and diet estimates of females, females with cubs, and males.

The pattern of prey contributions to the diet estimate of each class was similar, with ringed seal and medium-sized prey consumed more than bowhead whale. Consistent with research from the Beaufort Sea (Bentzen et al. 2007, Thiemann et al. 2008), ringed seals contributed a large proportion to the polar bear diet. Males had the lowest diet contribution of ringed seals and a higher contribution of medium-sized prey than the other classes. Male polar bears are typically larger than females, and their size allows them to prey upon larger species (Thiemann et al. 2008, Cherry et al. 2011). Mass was positively correlated with $\delta^{13}C$, and larger-bodied species (e.g. beluga) have higher $\delta^{13}C$ than ringed seals (Cherry et al. 2011). Diet contributions of bowhead whale were lower than other studies in the Beaufort Sea (Bentzen et al. 2007, Cherry et al. 2011, Rogers et al. 2015). Canadian Beaufort Sea polar bears may have reduced access to bowhead whale carcasses compared to Alaskan southern Beaufort Sea polar bears, as bowhead whale hunting is limited in Canada (Moshenko et al. 2003). Carcasses from whales that perish naturally or are struck and lost may be available to Canadian Beaufort Sea polar bears, although these carcasses are uncommon (DFO 2014).

Some sources of uncertainty exist within our mixing models which may have influenced our diet estimates. For both discrimination factors, a subset of consumers lay outside of the mixing polygons due to high $\delta^{15}N$ and were deemed outliers within this study. However, it is possible that a dietary source was missing within the model (Smith et al. 2013), that nutritional stress resulted in bears with higher $\delta^{15}N$ (Hobson et al. 1993), or that bears with elevated $\delta^{15}N$ were feeding further north. It is unlikely that a missing source resulted in the high $\delta^{15}N$, as alternative food sources are limited in availability within the Beaufort Sea, uncommon within the diet (e.g. cannibalism of cubs) (Amstrup et al. 2006, Bentzen et al. 2007), or have low $\delta^{15}N$ (e.g. walrus $\delta^{15}N$ = 13.5 ± 1.0‰; Dehn et al. 2007). It is possible that bears may have been fasting during hair growth, which would

have resulted in enriched ^{15}N (Hobson et al. 1993, Polischuk et al. 2001) and may have inflated our estimate of medium-sized prey and ringed seals. In addition, our study examined the protein-metabolic pathway, and as a result, may have overestimated ringed seals within the polar bear diet compared to the lipid-metabolic pathway (Cherry et al. 2011). As well, the discrimination factor we chose may have influenced diet estimates, as mixing models are sensitive to choice of discrimination factor (Bond & Diamond 2011). However, both the L'Hérault et al. (2018) and Rode et al. (2016) discrimination factors produced similar diet estimates. Lastly, it is possible that stable isotopes reflect spatial distribution in polar bear foraging. Polar bears foraging further north may have consumed foods with less terrestrially derived nitrogen, which is depleted in ^{15}N (Dunton et al. 2012), thereby increasing their $\delta^{15}N$. While we found that polar bear stable isotope ratios were related to capture location, we do not have GPS tracking data to confirm polar bear space use throughout the region. However, we hypothesize that the outliers within the mixing model are due to the underlying isotopic gradient within the region.

4.2. Geographic location

We found that $\delta^{15}N$ and $\delta^{13}C$ of polar bears was related to capture location, reflecting spatial variation in stable isotopes at the base of the food chain. $\delta^{13}C$ decreased eastward and southward, which is consistent with the $\delta^{13}C$ gradient in sediments (Dunton et al. 2012) in the Beaufort Sea. This gradient in $\delta^{13}C$ has been found in ringed seals (Dehn et al. 2007), and bowhead whales (Schell et al. 1989). As well, low $\delta^{13}C$ may indicate increased foraging within a pelagic food web for polar bears in the southeastern region of the Canadian Beaufort Sea (St. Louis et al. 2011). As a result of this isotopic gradient, ringed seal may have been overestimated within the diet estimates of polar bears foraging in southern or eastern areas.

Lower $\delta^{15}N$ in polar bears with southern capture locations may be due to increased terrestrially derived $\delta^{15}N$ and availability of bowhead whale carcasses along the coast. Terrestrially derived $\delta^{15}N$ is depleted in ^{15}N, and therefore $\delta^{15}N$ will increase further from shore (Dunton et al. 2012). Consumption of bowhead whale carcasses leftover from subsistence hunts along the coast may have also decreased $\delta^{15}N$, as bowhead whales are depleted in ^{15}N due to feeding on invertebrates (Lowry et al. 2005, Cherry et al. 2011). However, bowhead whale contribution was

low within our diet estimates, suggesting that terrestrially derived $\delta^{15}N$ may affect the spatial pattern in polar bear $\delta^{15}N$.

4.3. Environmental change

Ringed seal ovulation rate was negatively correlated with polar bear $\delta^{15}N$, suggesting that increased productivity of ringed seals may affect nutritional stress or protein consumption in polar bears. Severe fasting events may elevate $\delta^{15}N$ due to protein catabolism (Hobson et al. 1993). In addition, increased protein consumption relative to lipids can elevate $\delta^{15}N$ (Rode et al. 2016). Polar bears prefer fat as it is high in calories, but will eat protein when food availability is low (Best 1985). Therefore, in years when ringed seal productivity is high, polar bears may be less nutritionally stressed and consume less protein compared to fats.

During 2000 to 2005, ringed seal body condition and productivity declined within the Canadian Beaufort Sea (Harwood et al. 2012, Nguyen et al. 2017). Polar bear diets reflected this decline, with 2003 to 2005 having lower diet contributions of ringed seal relative to later years. In years of ringed seal reproductive failure, polar bears had larger niche widths, with a peak of niche width size in 2004 followed by 2005. Polar bears are opportunistic foragers and utilize different prey sources in years of reduced ringed seal availability (Lunn & Stirling 1985, McKinney et al. 2017). In years of ringed seal reproductive failure, polar bears may scavenge more, forage for a broader diversity of prey, or hunt more challenging prey (e.g. beluga), which will increase their isotopic niche width. After 2005, ringed seal ovulation rates and the number of seal pups in the subsistence harvest increased (Harwood et al. 2012). Polar bear niche width was lower following 2005 suggesting a lower diversity of foods within the polar bear diet, which was reflected by our diet estimate. Our results suggest that polar bear niche widths and diet estimates may be used as an index of ringed seal population dynamics. However, current population estimates and trends for seals in the Beaufort Sea are unknown, and therefore we could not verify the use of polar bear diet metrics as an index of seal population dynamics.

The ability of polar bears to access and hunt seals is dependent upon the presence of sea ice (Stirling & Archibald 1977, Smith 1980, Thiemann et al. 2008); however, the only sea ice metric significantly related to polar bear stable isotopes was freeze-up date. We found that $\delta^{13}C$ decreased with later freeze-up dates,

which may be due to freeze-up influencing polar bear distribution and prey availability. Polar bears in the Beaufort Sea move either towards land or northward to multiyear ice for the open water season (Amstrup et al. 2000, Pongracz & Derocher 2017). Later sea ice freeze-ups may result in bears remaining longer in the south over the continental shelf where ringed seal density is higher (Stirling et al. 1977, Frost et al. 2004). Ringed seals have low $\delta^{13}C$ compared to other prey species (Cherry et al. 2011), and coastal areas are depleted in ^{13}C (Dunton et al. 2012). While offshore regions are ^{13}C-enriched, it is likely that polar bears that move to multiyear sea ice are not feeding, as ringed seals have dispersed to open water (Reeves 1998) and other prey species (e.g. bearded seals) are less abundant (Stirling et al. 1977).

Sea ice dynamics within the Beaufort Sea are linked to air temperature and climate indices (Rigor et al. 2002, Stroeve et al. 2011, Proshutinsky et al. 2015, Galley et al. 2016), and sea ice availability is important for polar bear foraging. However, climate indices, other sea ice metrics (break-up date, open water duration), and air temperature were not included within the top $\delta^{15}N$ and $\delta^{13}C$ models. Climate indices may be too broad-scale to detect variation in stable isotopes, compared to finer-scaled measures such as freeze-up date. To detect patterns in $\delta^{15}N$ and $\delta^{13}C$ relative to these environmental variables, a longer study duration is likely necessary. For example, during the years of our study, AOO remained within an anticyclonic circulation regime, allowing only comparisons of circulation regime strength.

5. CONCLUSIONS

We demonstrated that polar bear stable isotopes are linked to capture location, sea ice dynamics, prey availability, and intrinsic factors. This complexity should be considered when interpreting polar bear diet from stable isotopes within a changing ecosystem. Monitoring the impacts of climate change on Arctic marine ecosystems represents a significant challenge in light of forecasted declines in sea ice (Stroeve et al. 2007), and documenting trends in diets of high trophic level species will likely be an important tool to investigate changes in ecosystem structure and function.

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