Feeding habits of Baffin Bay polar bears *Ursus maritimus*: insight from stable isotopes and total mercury in hair

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ABSTRACT: Loss of sea ice brought on by climate change affects polar bear *Ursus maritimus* access to prey. Here we investigated variation in feeding habits of the Baffin Bay (BB) polar bear subpopulation in relation to sea ice, habitat use, season, and demography using hair carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) stable isotope values and total mercury (THg) concentrations as ecological tracers. We analyzed hair samples from BB polar bears (n = 131) of all age and sex classes live-captured in West Greenland during the spring in 2009–2013. BB polar bears occupied a narrow isotopic space, suggesting limited variation in carbon sources and trophic position within the subpopulation. THg concentrations (median ± SE: 5.1 ± 0.2, range: 0.3–12.5 µg g^{-1} dry weight, DW) were related to age class, and nearly half exceeded the suggested threshold for neurological effects in polar bears at 5.4 µg g^{-1} DW. Although distinct coastal and offshore space-use strategies have been reported for BB polar bears, our results suggest that both strategies lead to similar carbon sources and trophic positions. We found seasonal variation in $\delta^{13}C$ and $\delta^{34}S$ across both space-use strategies, with $\delta^{34}S$ suggesting that all BB polar bears may prey on a higher proportion of benthic-feeding bearded seals *Erignathus barbatus* in late summer relative to spring. Despite wide fluctuations in inter-annual sea ice conditions and differences in space-use strategies among individuals, stable isotope values and THg concentrations suggested limited variation in feeding habits among BB polar bears. The variation of habitat tracers ($\delta^{13}C$ and $\delta^{34}S$) was related to season, whereas trophic tracer ($\delta^{15}N$ and THg) variation was driven by demographic group. The specialized BB polar bear diet suggests limited feeding plasticity under continued climate warming.

KEY WORDS: Arctic · Polar bear · *Ursus maritimus* · Feeding ecology · Dietary tracers · Greenland · Mercury

1. INTRODUCTION

Arctic food webs are less stable and resilient to climate change compared to those at lower latitudes (McCann et al. 2005, McMeans et al. 2015). In these food webs, apex predators are important for top-down ecosystem regulation of prey density (Horswill et al. 2016, Florko et al. 2020). Polar bears *Ursus maritimus* are specialized top predators that rely on a lipid-rich diet to sustain high energy intake obtained

from ringed seals *Pusa hispida* and bearded seals *Erignathus barbatus* in particular (Stirling & Archibald 1977, Galicia et al. 2015). The rapid decrease of Arctic sea ice has resulted in longer open-water seasons, with earlier onset of break-up and later dates of freeze-up (Overland & Wang 2013, Stern & Laidre 2016). Decreased sea ice reduces access to ice-associated marine mammal prey (Moore & Huntington 2008). As a result, polar bears experience longer fasting periods which lead to increased energetic stress and reduced body weight and reproductive success, with lower juvenile survival rates (Rode et al. 2014, Laidre et al. 2020a). The response of a polar bear subpopulation to climate change varies with local sea ice regimes, status of regional prey populations, and ecosystem productivity (Regehr et al. 2010, Rode et al. 2014, 2018, Whiteman et al. 2015, Laidre et al. 2020b). Polar bears in different subpopulations, and even in different habitats within a subpopulation, may show sea ice-associated dietary shifts (McKinney et al. 2013). Studies of polar bear foraging are therefore necessary for understanding how diets may change with loss of sea-ice habitat and increased use of coastal habitats.

Stable isotopes integrate and record dietary patterns over a timescale proportional to tissue growth rate (Bowen & Iverson 2013). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes have been used to show individual variation in polar bear diet and trophic level related to age and contaminant load (Polischuk et al. 2001, Horton et al. 2009). Values of $\delta^{15}N$ are primarily tracers of trophic position, and $\delta^{13}C$ is used to trace carbon sources from pelagic and sympagic primary producers that eventually reach top predators (Hobson et al. 2002, Horton et al. 2009). Sulfur isotopes ($\delta^{34}S$) are especially effective at distinguishing between terrestrial and open-ocean feeding (Barros et al. 2010, Matthews & Ferguson 2015, Szpak & Buckley 2020). Combining $\delta^{13}C$ and $\delta^{34}S$ signals is the most effective for distinguishing between primary producers (Connolly et al. 2004). Total mercury (THg) concentrations are informative for monitoring health in relation to biological effects thresholds and can also provide an additional metric to quantify polar bear foraging ecology (Dietz et al. 2011, 2013, McKinney et al. 2017, Yurkowski et al. 2020). Together, the use of a combination of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ (CNS) stable isotopes and THg facilitates insight into polar bear subpopulation feeding habits, trophic position, and potential health threats.

Baffin Bay (BB) is one of 5 polar bear subpopulations within the seasonal sea-ice ecoregion, which is characterized by having an ice-covered winter and an al-most ice-free summer (Amstrup et al. 2008, Laidre et al. 2013, 2018a,b). Polar bears in BB use large proportions of accessible habitat while moving across the pack ice, and the dates of arrival to and departure from Baffin Island are closely correlated with sea ice retreat and advance (Laidre et al. 2013, 2020a, SWG 2016). BB bears that make long-distance movements across the pack ice ('offshore bears') spend their summer on land (Baffin Island) without access to marine prey resources and are likely to fast for 3 mo or more (Laidre et al. 2020a). Another subset of BB bears has been observed with satellite telemetry in recent years and documented using traditional ecological knowledge to be resident at glacier fronts ('coastal bears') in Northwest Greenland year-round (Born et al. 2011, SWG 2016, Laidre et al. 2020a). The use of glacier fronts by some BB polar bears during the open-water season may become more common due to the abundance of ringed seals in Melville Bay (e.g. Born et al. 1999, Laidre et al. 2020a) and the need for year-round access to a hunting platform as loss of sea ice continues (Ferguson et al. 2001, Laidre et al. 2020a). Previous studies have investigated polar bear dietary and contaminant patterns related to distinct coastal and offshore movement patterns (Rogers et al. 2015, Boucher et al. 2019a, Blévin et al. 2020), but none to date has focused on an ecoregion of seasonal sea ice or the BB subpopulation in particular. Understanding the intersection of sea ice dynamics, movement patterns, and resource use for subpopulations experiencing a completely ice-free season is increasingly important as sea ice continues to decline throughout the Arctic.

In this study, we assessed the feeding habits of BB polar bears from 2009 to 2013 using hair CNS stable isotope values and THg concentrations as ecological tracers. First, we evaluated whether intra-population variation in stable isotope values and THg concentrations are associated with population demographics and sea ice metrics. Second, using tracer measurements in segmented guard hair of a subset of adult females, we compared how these tracers vary with seasons and coastal or offshore space-use strategies. Finally, we examined stable isotope values and THg concentrations across the 5 yr study period and through comparison of values from recaptured bears.

2. MATERIALS AND METHODS

2.1. Study site and sampling

The BB polar bear subpopulation occupies an area of close to 1 million km² bounded by Green-

land to the east and Baffin Island, Canada, to the west (Taylor et al. 2005). Polar bears were captured in the fast and pack ice of West Greenland in March and April of 2009–2013. Briefly, helicopter searches occurred ~150 km from the coast and bears were temporarily sedated for sample collection (see Laidre et al. 2020a for capture methods). A premolar tooth was collected from each bear, excluding cubs-of-the-year, to estimate age from the tooth cementum layers (e.g. Hensel & Sorensen 1980). Captured individuals (n = 131; Table 1, Fig. 1) were grouped into 5 age classes: cub-of-the-year (COY), yearling (YRL), 2 yr old (2YR), subadult (ages 3–4), and adult (ages 5+). Hair samples were trimmed from the coat about 2–5 mm from the skin on the rump using scissors and frozen in a plastic bag. Total body mass (TBM) was estimated using axillary girth and body length (Derocher & Wiig 2002; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m677p233_supp.pdf). A body condition index (BCI) was calculated for each bear using the TBM in kg and straight-line body length in cm in the equation specific to polar bears (Table S1; Cattet et al. 2002). BCIs were not calculated for 6 bears (1 adult male, 1 2YR, and 4 COYs) due to missing TBM estimates. All female bears (n = 42) were fitted with a Telonics TAW-4610H satellite radio collar to collect movement data (Laidre et al. 2018a,b, 2020a). These movement data were used to differentiate between 'coastal bears' (n = 6) that remained resident on the fast ice in Melville Bay near glacier fronts and 'offshore bears' (n = 36) that used larger areas across the pack ice of BB, between West Greenland and Baffin Island (Fig. S1; see Laidre et al. 2018a, 2020a).

2.2. Stable isotope and THg analysis

For each captured bear, multiple guard hairs were pooled to meet the required minimum sample weight (450 µg) for chemical analysis. Field-collected hair samples consisted of both underfur and guard hair; prior to analysis, we separated and excluded underfur from analysis. Additional guard hair samples from a subset of adult females (n = 27) were measured and cut into 2 cm long segments. Two segments, the first nearest to the root (referred to hereafter as the 'base') and the second nearest to the tip of the hair were analyzed separately to evaluate isotope variation between the spring and summer seasons. We assumed that the collected guard hair was grown determinately during the gradual molting period, presumed to be between April and August (Kolenosky 1987, Born et al. 1991, St. Louis et al. 2011, K. L. Laidre pers. obs.), though the exact timing of polar bear hair growth is unknown and has never been quantified. For segmented guard hairs, the tip of the hair was assumed to roughly represent growth in spring (April–May), whereas the hair near the root represented growth in the summer (July–August), in the year prior to sampling (Born et al. 1991, Rogers et al. 2015). The subset of samples included all available coastal bears (n = 6) and a subset of offshore bears (n = 21) across the study period. We assumed that the hair growth period does not overlap with the fasting period, as adult female bears arrive on Baffin Island (and thus, enter their fasting period) in early August (SWG 2016).

Hair samples processed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were first cleaned via immersion in 2:1 chloroform: methanol for 24 h at 30°C, then rinsed with a second

Table 1. Mean guard hair $\delta^{13}C$ and $\delta^{15}N$ (‰) and median guard hair concentrations (µg g^{-1} dry weight, DW) of total mercury (THg) with standard errors (SE), and THg concentration ranges (min.–max., µg g^{-1} DW) for each class and sample size (n [with THg n in parentheses, if different]) in the Baffin Bay polar bear *Ursus maritimus* subpopulation. COY: cub-of-the-year; YRL: yearling cub; 2YR: 2 yr old cub

| Class	n	$\delta^{13}C$	$\delta^{15}N$	THg	THg range
Adult females (solitary)	12	−16.2 ± 0.1	18.9 ± 0.1	6.0 ± 0.7	3.2–11.4
Adult female with COY	7	−16.0 ± 0.2	19.4 ± 0.1	5.1 ± 0.9	3.6–10.2
Adult female with YRL	14	−16.4 ± 0.1	18.6 ± 0.1	6.8 ± 0.5	4.8–12.2
Adult female with 2YR	9	−16.2 ± 0.1	18.6 ± 0.2	6.3 ± 0.9	4.5–12.3
Adult male	28 (27)	−16.1 ± 0.1	19.4 ± 0.1	5.8 ± 0.3	3.8–12.5
Subadult female	6	−16.5 ± 0.2	18.8 ± 0.2	5.0 ± 0.4	3.7–6.2
Subadult male	6	−16.5 ± 0.1	18.8 ± 0.2	4.1 ± 0.2	4.0–5.3
COY	13 (8)	−16.6 ± 0.1	21.0 ± 0.1	0.4 ± 0.1	0.3–1.0
YRL	21	−16.5 ± 0.1	19.3 ± 0.1	2.5 ± 0.2	1.6–4.4
2YR	15 (14)	−16.3 ± 0.1	19.1 ± 0.1	4.8 ± 0.4	2.0–7.5
All	131 (124)	−16.3 ± 0.03	19.3 ± 0.07	5.1 ± 0.2	0.3–12.5
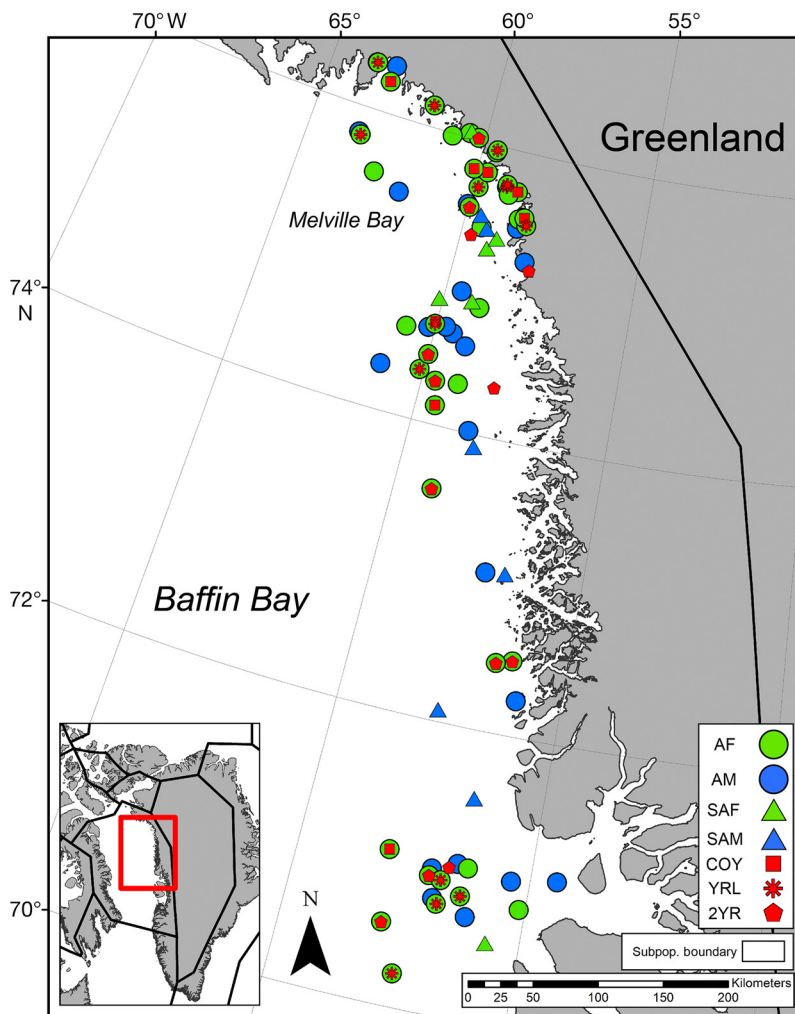
Fig. 1. Capture and sampling locations (n = 131) of polar bears *Ursus maritimus* in Baffin Bay between 2009 and 2013 according to age and sex class. Demographic groups are defined as follows: adult female (AF), adult male (AM), subadult female (SAF), subadult male (SAM), cub-of-the-year (COY), yearling (YRL), and 2 yr old (2YR). The PBSG (2018) subpopulation boundaries are shown on the inset map with black lines

aliquot of 2:1 chloroform:methanol, followed by 3 rinses with deionized water. After drying for 24 h at 50°C, hairs were cut into small pieces using surgical scissors. Approximately 450–600 µg of the hair was weighed and packed for analysis via a Costech 4010 elemental analyzer and a Thermo Delta V Advantage ($\delta^{13}C$, $\delta^{15}N$) / Delta V Plus ($\delta^{34}S$) isotope ratio mass spectrometer in the Fisk lab at the University of Windsor (Canada) using the method of McKinney et al. (2012) for stable isotope analyses. Precision was assessed by the standard deviation of replicate analyses of multiple standards for each element: NIST 1577c ($\delta^{13}C$, $\delta^{15}N$: n = 16; $\delta^{34}S$: n = 4), internal lab standard – tilapia muscle ($\delta^{13}C$, $\delta^{15}N$: n = 16; $\delta^{34}S$: n = 4), USGS 40 ($\delta^{13}C$, $\delta^{15}N$: n = 16), urea ($\delta^{13}C$, $\delta^{15}N$: n = 16), USGS 42

($\delta^{34}S$: n = 4), and NIST 8529 ($\delta^{34}S$: n = 4). For all standards, precision values averaged 0.21‰ for $\delta^{15}N$ and 0.11‰ for $\delta^{13}C$. Accuracy, based on the certified values of USGS 40 ($\delta^{13}C$, $\delta^{15}N$: n = 16) and USGS 42 ($\delta^{34}S$: n = 4), showed a mean absolute difference from the certified value of 0.09‰ for $\delta^{13}C$, 0.06‰ for $\delta^{15}N$, and 0.01‰ for $\delta^{34}S$.

For THg analysis, the cleaned hairs were acid-digested in plastic centrifuge tubes and then analyzed using a Perkin Elmer FIMS Cold-Vapor Atomic Absorption Spectrometer by the Metals Division at the University of Connecticut Center for Environmental Science and Engineering (McKinney et al. 2017). All concentrations of THg are reported as µg g^{-1} dry weight (DW). Based on an average sample size of ~0.001 g, the detection limit was determined to be 0.2 µg g^{-1}. Only 2 samples were under the limit of detection and thus excluded from analysis. All blanks were below the detection limit. Precision was indicated by relative percent difference of duplicate samples and was between 4.4 and 11.2%. Recoveries of matrix spikes ranged from 85.1 to 88.3%, and recoveries of laboratory control samples ranged from 95.4 to 105.2%. Accuracy was indicated by the percent THg measured relative to that of the certified standard values from the National Research Council of Canada and was 95.0 ± 12.6% for DOLT-4 (n = 5) and 88.4% for DORM-3 (n = 1).

2.3. Sea-ice metrics

We calculated the March sea-ice extent and area within the BB subpopulation boundary using daily data from the National Snow and Ice Data Center (Cavalieri et al. 1996, Stern & Laidre 2016). We used the initiation dates of spring sea-ice retreat and fall sea-ice advance, as well as the duration of the open-water period as calculated by Stern & Laidre (2016). We defined spring retreat and fall advance dates as the dates on which the sea-ice concentration reached below/above 311×10^3 km^2, a threshold halfway between the historical (1979–2014) mean September

and mean March sea-ice areas in BB (Stern & Laidre 2016). The open-water period was defined as the number of days between the spring sea-ice retreat and fall sea-ice advance dates. Sea-ice metrics fluctuated throughout the 5 yr study period with a full month (31.4 d) between the minimum and maximum open-water periods. The March sea-ice extent is not weighted by the sea-ice concentration and ranged from 628 347.3 to 656 356.7 km^2. The March sea-ice area is weighted by sea-ice concentration and ranged from 574 470.5 to 632 446.5 km^2.

2.4. Statistical analysis

Subadult and adult bears were separated by age and sex, whereas dependent bears were grouped for analysis by age class only (COY, YRL, 2YR). Adult females were further divided into the following reproductive categories: solitary, with COYs, with YRLs, and with 2YRs (Table 1). Summary statistics for all stable isotopes are reported as arithmetic means and standard errors of the mean. Normality and homogeneity of variances of CNS stable isotopes and THg were assessed using Shapiro–Wilk and Levene's tests, respectively. Concentrations of THg were log transformed to meet normality prior to any statistical analysis. A Pearson's product-moment correlation was run between THg and both stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) for all adult age classes. Outliers were determined by identifying values that exceeded 3 times the interquartile range. All statistical tests were run using R v.4.0.3 (R Core Team 2017).

We used the isotopic niche width to examine variation in dietary breadth for each demographic class. Niche width, represented by the mode Bayesian estimate of the standard ellipse area (SEA_B), was calculated using Stable Isotope Bayesian Ellipses in R (SIBER) version 2.1.3 (Jackson et al. 2011). To calculate SEA_B and the 95% credible interval for each demographic class, 2 chains were used in the Markov Chain Monte Carlo process with a burn-in of 1000 iterations, a thinning rate of 10, and 20 000 iterations for each posterior distribution. Space-use strategies (coastal vs. offshore) were pooled among adult female reproductive statuses for this niche analysis.

We fit either a generalized linear model (GLM) or generalized linear mixed model (GLMM) to separately examine variation in $\delta^{13}C$, $\delta^{15}N$, and log-transformed THg concentrations. Explanatory variables included demographic group/reproductive status of the bears referred to as Class (i.e. solitary adult fe-

male, female with COY, female with YRL, female with 2YR, adult male, subadult female, subadult male) and sea-ice metrics important to polar bears (Stern & Laidre 2016) and specific to BB, either fall sea-ice advance date of the previous year (FreezeUp. lag), spring sea-ice retreat of the previous year (BreakUp.lag), open-water period duration of the previous year (OpenWater.lag), March sea-ice extent of the previous year (IceExtent.lag), or March sea-ice area of the previous year (IceArea.lag). Models only included one sea-ice variable to avoid autocorrelation, and model selection was conducted using the function 'dredge' in the 'MuMIn' package (Bartoń 2020). Space-use strategies were pooled among adult female reproductive statuses for this analysis. The BCI was also included in THg models to account for variation related to body condition. Because $\delta^{34}S$ was only examined in base and tip hair segments in a subset of adult females, no whole-hair models were feasible to include in this study.

We conducted a likelihood ratio test with a parametric bootstrap approach (n = 1000) to construct the distribution of the likelihood ratio statistic (McLachlan 1987, Tekle et al. 2016) to determine whether a model was improved with 'Capture Year' included as a random effect and if a GLMM should be used. If a model required a random effect, we used the 'lme4' package to fit a GLMM (Bates et al. 2015). If not, we used the 'stats' package to fit a GLM (R Core Team 2017).

Akaike's information criterion (Akaike 1974), corrected for small sample size (AIC_c), was used to determine the models of best fit with penalties for overfitting (defined as $\Delta AIC_c = 0$). The estimate and 95% confidence interval are reported for each predictor in the models of best fit (Table S2). The residuals of every top model were checked for normality by examining the residual plots and using the Shapiro-Wilk normality test in the 'stats' package (R Core Team 2017). Models with a ΔAIC_c of <2 were considered competing models (Table 2), and all models with ΔAIC_c <4 are reported (Table S3). We calculated the deviance explained (R^2) for the GLMs using the 'rsq' package (Zhang 2021) and the marginal and conditional R^2 values for GLMMs using the 'MuMIn' package (Bartoń 2020). We used a Type II analysis (Yates's method of fitting constants) to calculate the relative amount of variance explained by each predictor (partial R^2) via the 'car' package (Langsrud 2003, Fox & Weisberg 2011).

The CNS stable isotopes and THg values of 6 coastal adult females were compared to values of 36 offshore females using Welch's 2-sample t-tests (Table S4). Niche width (SEA_B) and the 95% credible

Table 2. Model selection to assess demographic and environmental variables affecting δ^{13}C, δ^{15}N, and total mercury (THg) values of Baffin Bay polar bears *Ursus maritimus*. Models with a change in Akaike's information criterion corrected for small sample size $\Delta AIC_c \leq 2$ are included and are considered to be competing. All models with $\Delta AIC_c < 4$ are shown in Table S2

Response	Rank	Model	df	Deviance explained (R^2)	AIC_c	ΔAIC_c
δ^{13}C	1	Class + OpenWater.lag + (1 | Capture Year)	10	0.408	54.8	0
	2	Class + (1 | Capture Year)	9	0.396	54.9	0.08
	3	Class + BreakUp.lag + (1 | Capture Year)	10	0.423	55.5	0.64
δ^{15}N	1	Class	8	0.348	131.4	0
	2	Class + IceArea.lag	9	0.366	131.6	0.26
	3	Class + BreakUp.lag	9	0.349	131.8	0.43
	4	Class + IceExtent.lag	9	0.338	131.9	0.50
log(THg)	1	Class	8	0.198	35.4	0
	2	Class + OpenWater.lag	9	0.202	37.4	2.01
	3	Class + FreezeUp.lag	9	0.202	37.4	2.03

interval were calculated for coastal and offshore female polar bears (Jackson et al. 2011). Additional separate GLMs were fit for only adult females in order to include an additional covariate (Habitat) derived from the satellite collar data (i.e. coastal or offshore movement patterns), and the top 5 models are reported (Table S6). For these analyses, we did not distinguish between reproductive statuses within space-use strategy groups.

The CNS stable isotopes and THg values in the base and tip segments of hair were compared among individual adult females using paired *t*-tests (Table S5). Welch's 2-sample *t*-tests were used to compare between coastal and offshore base sections and between coastal and offshore tip segments (Table S5). We ran a Pearson's product-moment correlation for δ^{13}C, δ^{15}N, and THg for solitary adult females (as a representative group) across the 5 yr study period. We also examined inter-annual differences in δ^{13}C, δ^{15}N, and THg for 7 bears (including 1 'coastal bear') that were recaptured during the 5 yr study period. The GLMs and GLMMs included data from only the first capture if a bear was captured more than once to avoid pseudo-replication.

3. RESULTS

3.1. Demographic variation

Polar bears in BB occupied a narrow range of carbon sources (2.1‰) and the 95% credible intervals of the niche width for all sex/age classes fully overlapped (Fig. S2). Despite this, demographic group was important in all competing δ^{13}C, δ^{15}N, and THg models. There was variation in δ^{13}C ($F_{9,118} = 5.17$, p < 0.0001) and δ^{15}N ($F_{9,120} = 23.15$, p < 0.0001) among

multiple age and sex classes (Table 1, Fig. 2). Similar to δ^{13}C and δ^{15}N (CN) isotopes, THg concentrations varied between age and sex classes ($F_{9,114} = 69.94$, p < 0.0001). The Pearson's product-moment correlation showed few significant linkages between THg and CN isotopes among demographic groups (Table S7).

The THg concentrations varied for all bears between 0.3 and 12.5 µg g^{-1} DW, with a median THg concentration of 5.1 ± 0.2 µg g^{-1} DW (Table 1). Only the median THg concentration of solitary adult females exceeded 5.4 µg g^{-1}, a concentration at which negative correlations with N-methyl-D-aspartate activity have been reported for East Greenland polar bears (Basu et al. 2009, Dietz et al. 2013). When examined individually, nearly half of the BB bears exceeded this threshold. Two-thirds (66.7%) of both solitary adult females and adult males exceeded the threshold. The lowest percentage of adult females exceeding the neurological effects level threshold was found for females with COYs (28.6%), as compared to percentages of females with YRLs (85.7%) and with 2YRs (88.9%). Of all cub age classes, only 2YRs (21.4%) exceeded the neurological effects level threshold.

3.2. Overall model results

There were 3 competing models for δ^{13}C, which included Class, ice variables (either OpenWater.lag or BreakUp.lag), and Capture Year (Table 2). A GLMM was used in δ^{13}C model selection as δ^{13}C data supported the inclusion of capture year (p < 0.001) as a random effect. The variance of the random effect (Capture Year) was smaller than the residual variation of the GLMM ($s^2_{\text{Capture Year}} = 0.02$; $s^2_{\text{residual}} = 0.08$). The overall deviance explained (R^2) for the com-
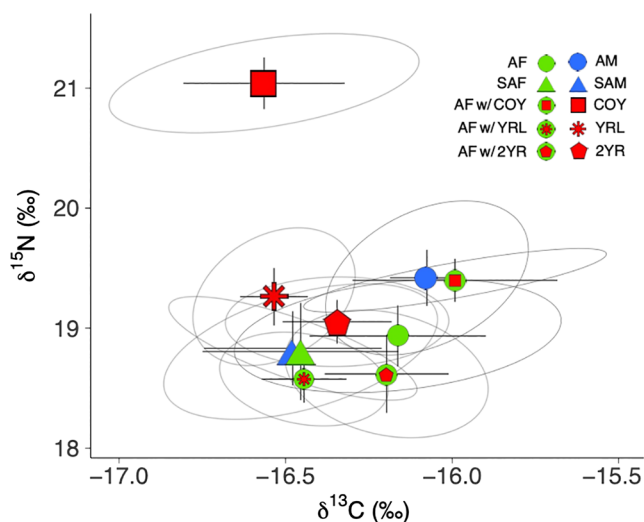
Fig. 2. Mean guard hair $\delta^{13}C$ and $\delta^{15}N$ with standard error (SE) bars separated by age class, sex, and reproductive status in the Baffin Bay polar bear *Ursus maritimus* subpopulation. Demographic groups are defined as in Fig. 1. Adult females with dependent cubs are denoted as AF w/ COY, YRL or 2YR. Standard ellipses are shown for each demographic class in gray. Ellipses were calculated using SIBER version 2.1.3 (Jackson et al. 2011) and contain approximately 95% of the data

peting models ranged between 0.396 and 0.423 (Table 2). Limited variance was explained by Class in the top models for $\delta^{13}C$ (partial R^2 = 0.161). Two of the 3 competing models for $\delta^{13}C$ included ice metrics, OpenWater.lag or BreakUp.lag, for $\delta^{13}C$. However, the confidence intervals for both OpenWater.lag and BreakUp.lag overlapped zero and therefore they were not considered significant variables in their respective models.

There were 4 competing models for $\delta^{15}N$, which included Class and either IceArea.lag, BreakUp.lag, or IceExtent.lag as an ice variable (Table 2). A GLM was used in $\delta^{15}N$ model selection because the inclusion of capture year as a random effect was not supported (p = 0.515). The overall deviance explained (R^2) for the competing models ranged between 0.348 and 0.366 (Table 2). Most of the variance was explained by Class in the top models for $\delta^{15}N$ (partial R^2 = 0.318–0.349). The confidence intervals for adult males did not overlap zero in any $\delta^{15}N$ models, and thus this age class was considered important in explaining $\delta^{15}N$ variation. The confidence intervals for IceArea.lag, BreakUp.lag, and IceExtent.lag overlapped zero and they were therefore not considered significant variables in their respective models.

There were 3 competing models for THg, which included Class and either FreezeUp.lag or Open Water.lag as an ice variable (Table 2). A GLM was

used in THg model selection because the inclusion of capture year as a random effect was not supported (p = 0.926). The overall deviance explained (R^2) for the competing models ranged between 0.198 and 0.202 (Table 2). Most of the variance was explained by Class in the models for THg (partial R^2 = 0.194–0.198). The confidence intervals for subadult males did not overlap zero in any THg models, and thus this age class was considered important in explaining THg variation. Two of the 3 top models for THg included ice metrics (Table 2), FreezeUp.lag or OpenWater.lag, for THg. However, the confidence intervals for both FreezeUp.lag and OpenWater.lag overlapped zero and therefore they were not considered significant variables in their respective models. The covariate BCI was not selected in the 3 competing THg models, and thus was not considered significant in describing THg variation (Table 2).

3.3. Offshore versus coastal habitat use

Coastal and offshore polar bears were similar in $\delta^{13}C$, $\delta^{15}N$, and THg. Whole-hair means for $\delta^{13}C$, $\delta^{15}N$, and THg did not significantly differ between coastal ($\delta^{13}C$ = −16.3 ± 0.2‰, $\delta^{15}N$ = 19.1 ± 0.2‰, THg = 6.6 ± 0.8 µg g^{-1} DW; Table S4) and offshore adult female bears ($\delta^{13}C$ = −16.2 ± 0.1‰, $\delta^{15}N$ = 18.8 ± 0.1‰, THg = 6.7 ± 0.4 µg g^{-1} DW; Table S4). The 95% credible intervals of the niche widths for coastal polar bears (SEA$_B$ = 0.8 ‰^{2} [0.3, 1.9]) and offshore polar bears (SEA$_B$ = 0.5 ‰^{2} [0.4, 0.7]) fully overlapped (Fig. S2). Of all the separate models for adult females to determine the influence of 'coastal' or 'offshore' space-use strategies, the Habitat covariate (partial R^2 value = 0.031) was retained in a single $\delta^{15}N$ model with an R^2 of 0.103 (ΔAIC$_c$ = 1.02, Table S6). The inclusion of capture year was not supported by likelihood ratio tests (all p > 0.4) so all adult females were modeled using GLMs.

3.4. Intra- and interannual variation

For base and tip hair comparisons, outliers were detected for $\delta^{13}C$ and $\delta^{15}N$ for 1 individual, and these values were excluded from the paired analysis. The $\delta^{34}S$ and THg values from this individual were retained, as the analyses were separate and independent. The ^{13}C and ^{34}S in the base segments were significantly depleted compared to the tip segments for both coastal and offshore bears, while $\delta^{15}N$ and THg did not significantly differ (Fig. 3, Table S5). There
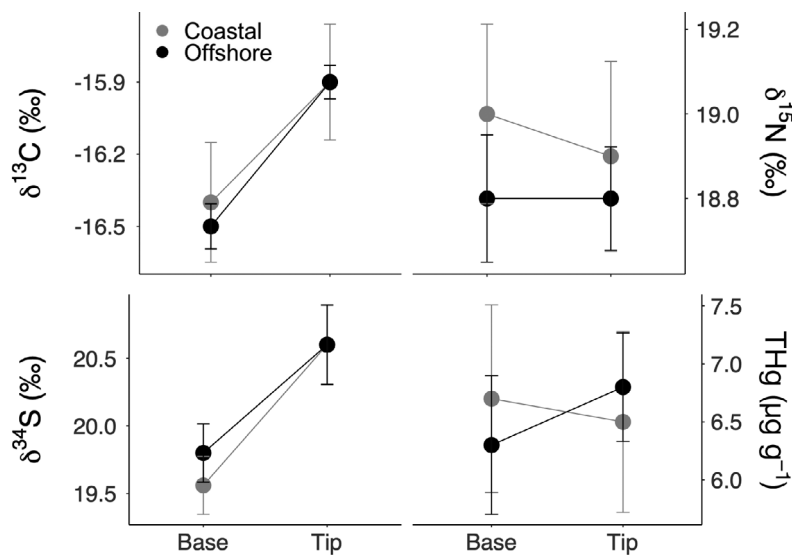
Fig. 3. Mean (±SE) guard hair $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ and total mercury (THg) concentrations (μg g^{-1} dry weight) for both base and tip guard hair segments of adult female Baffin Bay polar bears *Ursus maritimus*. Values can also be found in Table S5. Colors (gray, black) denote the space-use strategy (i.e. coastal or offshore)

were no significant differences between coastal and offshore base segments or between coastal and offshore tip segments (Table S5).

We found interannual variation between $\delta^{13}C$, $\delta^{15}N$, and THg values for recaptured bears and no significant correlation between year and tracer values for solitary adult females over the 5 yr study period. Recaptured bears (n = 7) showed interannual variation as they transitioned between age classes and/or reproductive status (Fig. S3). The recaptured bear that demonstrated the largest difference in $\delta^{13}C$ was a 'coastal' adult female bear that was without cubs in both capture years. This adult female increased in $\delta^{13}C$ by 0.3‰ and decreased in THg by 0.4 μg g^{-1} DW between 2011 and 2012.

4. DISCUSSION

We examined feeding habits of BB polar bears using $\delta^{13}C$, $\delta^{15}N$, and THg values from hair in relation to demographic class, sea ice, space-use strategy, season, and year. Our results suggest that the explanatory power of sea-ice dynamics on BB polar bear feeding habits was limited relative to demographic group and unknown drivers of variation. Of the variance explained by the model, most (at least 87%) was explained by demographic group for $\delta^{15}N$ and THg models. However, the overall deviance explained by the top model was relatively low for

$\delta^{15}N$ ($R^2 = 0.348$) and THg ($R^2 = 0.197$). Only 40% of the variance in the $\delta^{13}C$ model (partial $R^2 = 0.161$; $R^2 = 0.408$) was explained by demographic group. Geographic location, ice thickness, and sympagic versus pelagic food sources for prey can affect $\delta^{13}C$ (Hobson et al. 2002, Tremblay et al. 2006, Horton et al. 2009, Boucher et al. 2019a,b), and therefore could be considered in future models. The unclear link between sea-ice dynamics and dietary tracers may be due to the low variability within isotopic tracers for the subpopulation or a potential phenological mismatch between the effect period of selected ice metrics and when hair grows. Base hair segments were significantly depleted in ^{13}C and ^{34}S compared to the tip segments for both coastal and offshore female bears, suggesting that season explains more variation in hair stable isotope values than space-use strategy. Habitat tracers ($\delta^{13}C$ and $\delta^{34}S$) were driven by season, whereas trophic tracers ($\delta^{15}N$ and THg) were driven by demographic group.

For $\delta^{15}N$, most of the differences between sex and age classes were small (<1‰), suggesting limited variation in trophic position within the BB subpopulation. The exception was that COY $\delta^{15}N$ was higher than all other age groups; however, nutrient transfer from ^{15}N-enriched milk from the mother is the primary contributor to ^{15}N-enriched values of COY hair (Polischuk et al. 2001). Yearlings were more ^{15}N-enriched than adult females with YRLs and females with 2YRs, likely because their hair was grown at a time when the YRLs were still nursing and therefore were feeding at a trophic level higher than their mother (Polischuk et al. 2001).

Similar to other polar bear subpopulations, variation in BB polar bear THg concentrations was related to sex, age class, and reproductive status (St. Louis et al. 2011, Bechshoft et al. 2016, McKinney et al. 2017). Hair THg concentrations increased with age for BB polar bears, following well with demographic variation reported in the western Hudson Bay and Southern Beaufort Sea subpopulations (Bechshoft et al. 2016, McKinney et al. 2017). In addition to age class, reproductive status played a role in determining THg concentrations, as the highest THg means were found in BB adult females with YRLs and 2YRs. This may indicate that adult female bears with cubs need to ingest more food than solitary females to feed their cubs.

In addition to use of THg as a tracer, polar bear hair THg concentrations can be interpreted in relation to effect thresholds (Dietz et al. 2011, 2013). Percentages of individuals exceeding the neurological effects threshold have previously been calculated for multiple subpopulations, including BB (Dietz et al. 2013), but not for distinct age and reproductive statuses. For THg accumulation, we report exceedance of the neurological effects threshold for all but 2 demographic groups, ranging from 21.4% of 2YR cubs up to 88.9% of females with 2YR cubs. The median THg concentrations for subadult and adult BB polar bears in 2009–2013 was lower than previously reported, ranging from 4.1 to 6.0 µg g^{-1} DW (Table 1) versus 7.6 µg g^{-1} DW in 1985–1994 (Dietz et al. 2006) and 9.4 µg g^{-1} DW in 2000–2008 (Dietz et al. 2011). However, the bears sampled by Dietz et al. (2006, 2011) were harvested in the Qaanaaq region, an area further north than capture locations in this study and were potentially more representative of bears in the Kane Basin subpopulation. The somewhat lower subadult and adult THg medians in recent years could be related to this difference in geography, changes in Hg transport, deposition, or biogeochemical cycling in the Arctic (Wang et al. 2019), and/or related to the long-term changes in the food web or BB polar bear diets, as documented in other subpopulations (e.g. East Greenland; McKinney et al. 2013).

Despite telemetry-based evidence of contrasting space-use strategies (Laidre et al. 2018a, 2020a), we did not detect any differences in δ^{13}C, δ^{15}N, and THg in hair between coastal and offshore polar bears, although we are cautious to reach a firm conclusion due to low coastal sample size (n = 6). A lack of differences in δ^{13}C and δ^{15}N between space-use strategies was recently also found for Barents Sea and Southern Beaufort Sea polar bears (Boucher et al. 2019a, Blévin et al. 2020). Only 1 BB adult female δ^{15}N model retained Habitat as a covariate, and even then, space-use strategy explained little of the variation (partial R^2 = 0.031; R^2 = 0.103). However, we assume that movement strategies of the captured bears is consistent over 2 years (i.e. coastal bears stay coastal bears) for the current year of satellite tracking and the lagged data of diet and ice metrics. Also, the foraging period reflected in the guard hair isotopic values of coastal and offshore BB bears may at least partially occur when the bears overlap in habitat use (i.e. out on the ice in the spring and summer), although the exact timing of hair growth is not well understood in polar bears. We therefore suggest further investigation of hair

growth rates in captive and wild polar bears, especially during the spring and summer seasons. An improved understanding of the tissue growth timeline, a larger sample size of coastal polar bears, and/or the use of a higher-resolution tracer (i.e. fatty acids, compound-specific stable isotopes, persistent organic pollutants) should be employed to detect differential patterns in feeding habits related to space-use strategies (Bowen & Iverson 2013).

Seasonal variation in dietary patterns was examined through comparisons of base and tip hair segments. For both coastal and offshore BB bears, the base end (grown in summer) was depleted in ^{34}S and ^{13}C when compared to the tip end (grown in spring). A nearshore–offshore/benthic–pelagic gradient of ^{13}C exists in the BB food web, with depleted ^{13}C signifying an increased reliance on offshore/pelagic prey (Hobson et al. 2002, Yurkowski et al. 2020). There is also a well-established benthic–pelagic gradient in ^{34}S in the opposite direction of ^{13}C, with depleted ^{34}S signifying an increased reliance on coastal/benthic-feeding prey (Matthews & Ferguson 2015). We thus expected offshore BB bears would have depleted ^{13}C and enriched ^{34}S in both base and tip segments of the hair relative to coastal bears. We expected the offshore δ^{34}S value would be around 21‰, the value found in the well-mixed pool of sulfate in the open ocean (Böttcher et al. 2007, Barros et al. 2010). Conversely, we expected that coastal BB bears would exhibit a benthic isotopic signal via enriched ^{13}C and depleted ^{34}S in both base and tip segments of the hair.

Both offshore and coastal polar bears had a δ^{34}S tip value of 20.6‰, and values were more depleted in the base segment. This suggests that both coastal and offshore bears may feed on a higher proportion of nearshore/benthic-feeding bearded seals later in the summer when remnant sea ice facilitates access to shallow, coastal areas. If interpreted using only the nearshore–offshore/benthic–pelagic gradient of ^{13}C, our results would imply that the depleted base end signifies an increased reliance on offshore/pelagic prey later in their primary feeding season, a finding contrary to both our expectations and the δ^{34}S results. Szpak & Buckley (2020) also found δ^{13}C opposing δ^{34}S patterns and expectations for walrus *Odobenus rosmarus* and ringed seals across multiple regions. Our results support the fact that δ^{34}S may be a more appropriate indicator of the contribution of benthic-feeding versus pelagic-feeding prey than δ^{13}C in Arctic consumers (Szpak & Buckley 2020).

The δ^{13}C, δ^{15}N, and THg concentrations were examined in 7 bears recaptured after periods of 1–3 yr to assess how values changed for bears transitioning

between age classes and/or reproductive status. A solitary 'coastal' adult female had the highest increase in $\delta^{13}C$, which may indicate that this individual foraged over a larger area than the other recaptured bears. Both females captured with cubs were somewhat depleted in ^{15}N compared to when recaptured as solitary adults, although the magnitude of difference was small. We highlight the degree of interannual variation that can occur within an individual bear and the importance of including reproductive status and age class information in diet studies.

5. CONCLUSIONS

We examined feeding habits of BB polar bears using $\delta^{13}C$, $\delta^{15}N$, and THg values from hair in relation to demographic class, sea ice, space-use strategy, season, and year. Overall, there was little variation in feeding habits of BB polar bears across demographic groups, multiple years of sampling, and variable sea-ice conditions. Demographic group was the most important predictor of the limited differences in $\delta^{15}N$ and THg concentrations. We found that a high percentage of adult bears exceeded the neurological effects threshold, which confirms that BB polar bears will face multiple stressors in a rapidly warming Arctic. For adult females, seasonal variation of $\delta^{34}S$ between hair segments suggests that bearded seals may be increasingly important prey in the late summer, which may have implications for phenological changes caused by climate change. We detected no differences in CNS stable isotopes and THg concentrations between adult female space-use strategies, suggesting that these tracers may not have sufficient resolution to distinguish more fine-scale variation in foraging patterns. Further investigation between coastal and offshore space-use strategies in BB polar bears will be important for understanding how differences in space use under climate change translate to diet and pollution levels. Continued monitoring of polar bear diet is necessary to understand the resilience of an apex predator across the changing Arctic ecosystem.

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