



Are tissue samples obtained via remote biopsy useful for fatty acid-based diet analyses in a free-ranging carnivore?

MELISSA P. GALICIA,^{*,} GREGORY W. THIEMANN,[°] MARKUS G. DYCK, AND STEVEN H. FERGUSON

Department of Biology, York University, Toronto, Ontario, Canada (MPG)

Faculty of Environmental and Urban Change, York University, Toronto, Ontario, Canada (GWT)

Wildlife Research Section, Department of Environment, Government of Nunavut, Igloolik, Nunavut, Canada (MGD)

Fisheries and Oceans Canada, Central and Arctic Region, Winnipeg, Manitoba, Canada (SHF)

* Correspondent: mgalicia@yorku.ca

Fundamental knowledge on free-ranging animals has been obtained through capture-based studies; however, these may be logistically intensive, financially expensive, and potentially inconsistent with local cultural values. Genetic mark–recapture using remote tissue sampling has emerged as a less invasive alternative to capture-based population surveys but provides fewer opportunities to collect samples and measurements for broader ecological studies. We compared lipid content, fatty acid (FA) composition, and diet estimates from adipose tissue of polar bears (*Ursus maritimus*) obtained from two collection methods: remote biopsies ($n = 138$) sampled from helicopters and hunter-collected tissue ($n = 499$) from bears harvested in Davis Strait and Gulf of Boothia, Nunavut, 2010 – 2018. Lipid content of adipose tissue was lower in remote biopsies than harvest samples likely because remote biopsies removed only the outermost layer of subcutaneous tissue, rather than the more metabolically dynamic innermost tissue obtained from harvest samples. In contrast, FA composition was similar between the two collection methods with relatively small proportional differences in individual FAs. For diet estimates in Davis Strait, collection method was not a predictor of prey contribution to diet. In Gulf of Boothia, collection method was a predictor for some prey types, but the differences were relatively minor; the rank order of prey types was similar (e.g., ringed seal; *Pusa hispida* was consistently the primary prey in diets) and prey proportions differed by $< 6\%$ between the collection methods. Results from both methods showed that diets varied by geographic area, season, year, age class, and sex. Our study demonstrates that adipose tissue from remote biopsy provides reliable estimates of polar bear diet based on FA analysis and can be used to monitor underlying ecological changes in Arctic marine food webs.

Key words: adipose lipid content, Arctic, diet, fatty acids, harvest samples, polar bears, quantitative fatty acid signature analysis (QFASA), remote biopsy, *Ursus maritimus*

The Arctic has experienced profound climate change and rapid sea ice loss, leading to ecosystem-wide impacts (Walsh 2008; Post et al. 2013). Monitoring wildlife populations in association with environmental conditions is essential to understanding how individuals, and in turn populations, will respond to continued environmental change. However, untangling the mechanistic relationships between Arctic wildlife and their habitat at times requires the capture and handling of free-ranging animals. Live capture of large mammals is logistically complex, invasive, expensive and does not always coincide with research priorities of northern Indigenous people (Henri et al. 2010; Wong et al. 2017).

Capture of free-ranging polar bears (*Ursus maritimus*) involves chemical immobilization via remote injection, typically a dart fired from a helicopter (Stirling et al. 1989). Capture-based studies have been essential in addressing important questions about polar bear ecology, including: population size (Regehr et al. 2007; Lunn et al. 2016); vital rates (Regehr et al. 2010); movement and habitat use (Durner et al. 2009; Laidre et al. 2018); body condition (Rode et al. 2012; Sciullo et al. 2016); energetic demand (Durner et al. 2017; Pagano et al. 2018); diet (Thiemann et al. 2008a; Sciullo et al. 2017); and genetic structure (Paetkau et al. 1999; Viengkone et al. 2016). However, live-capture population surveys are expensive and complex, and may not be feasible on the spatial and

temporal scales necessary to detect rapid demographic change in polar bears (Vongraven et al. 2012). Although studies have found no evidence of long-term negative effects from chemical immobilization and handling (Thiemann et al. 2013; Rode et al. 2014), Inuit have nonetheless expressed concerns about live-capture studies (Henri et al. 2010; Peacock et al. 2011; Wong et al. 2017).

Polar bear research has increasingly emphasized less invasive methods, including aerial surveys (Stapleton et al. 2016; Obbard et al. 2018), scat collection (Gormezano and Rockwell 2013; Iversen et al. 2013), and genetic mark–recapture, either through passive hair snags (Lillie et al. 2019) or remote biopsy darting (Pagano et al. 2014; Aars et al. 2017). Tissue samples from harvested polar bears have provided important ecological insights (e.g., Galicia et al. 2020) without additional capture or handling, but harvest may be subject to seasonal or demographic restrictions. For instance, polar bear family groups legally cannot be hunted, and females with dependent cubs thus are excluded from harvest samples. Harvest-based sampling also may be biased toward bears that are closer to human settlements. Although remote biopsies are primarily intended to collect skin for DNA extraction, samples often include a small amount of subcutaneous adipose tissue (McKinney et al. 2014; Pagano et al. 2014). Analysis of adipose tissue of polar bears has provided data on diet composition (Thiemann et al. 2008a; Galicia et al. 2015) and body condition (Thiemann et al. 2006; Sciullo et al. 2016; Galicia et al. 2020). Thus, tissue samples obtained from remote biopsies may provide important information on foraging ecology of polar bears, without seasonal or demographic constraints, if the composition of this tissue: 1) can be accurately determined; and 2) is representative of overall subcutaneous fat stores.

The fatty acid (FA) composition of adipose tissue can be used to infer the feeding patterns of free-ranging animals based on the knowledge that ingested FAs are predictably incorporated into the fat stores of a consumer and reflect integrated diet composition over the preceding weeks to months (Iverson et al. 1997, 2004; Budge et al. 2008). The relative lipid content of adipose tissue can provide insight into overall fatness because adipocytes (fat cells) shrink and swell as lipid is mobilized and deposited, respectively (Schemmel 1976; Pond et al. 1992). In polar bears, FAs were uniformly distributed across the depth of subcutaneous adipose tissue, whereas relative lipid increased with distance from the skin (Thiemann et al. 2006). The uniform distribution of FA in adipose tissue of polar bears contrasts with pinnipeds and cetaceans, which show vertical stratification in their FA across blubber depth (e.g., Koopman et al. 1996; Strandberg et al. 2008; Waugh et al. 2014). Pagano et al. (2014) found that FAs could be identified in most remote biopsy samples from polar bears but did not compare the results to bears sampled contemporaneously via other methods. There have been no attempts to date to quantitatively estimate diet composition via FA analysis of a free-ranging carnivore from remote biopsy samples.

The objective of our study was to evaluate the utility of adipose tissue obtained from remote biopsies used in genetic mark–recapture studies of polar bears. We hypothesized that

lipid content in adipose tissue would be low in remote biopsies compared with harvest samples, and thus be unreliable in measuring body condition (see Thiemann et al. 2006; McKinney et al. 2014; Pagano et al. 2014). However, given evidence that FAs remain uniform across the depth of adipose tissue, we hypothesized that remote biopsy samples would accurately reflect total FA composition and thus diet estimates of biopsied bears, and would be comparable to those from bears harvested contemporaneously in the same subpopulation. Remote biopsy darting has become increasingly common in population surveys of polar bears (SWG 2016; Aars et al. 2017) and other species (e.g., Beausoleil et al. 2016; Frasier et al. 2020). If remote sampling can generate accurate estimates of diet, then genetic mark–recapture surveys could yield additional ecological data, and reveal relationships between wildlife and their habitat in a manner that is cost-effective, minimally invasive, and more compatible with Inuit perspectives.

MATERIALS AND METHODS

Sample collection.—We compared adipose tissue samples collected from remote biopsy darts and harvest samples (Fig. 1). We collected remote biopsies during the fall (late August – September) of 2017 in Davis Strait ($n = 64$) and the spring (April–May) of 2015 – 2016 in Gulf of Boothia ($n = 74$) as part of a genetic mark–recapture population survey. Once a bear was located, a small sample of tissue (< 5 mm diameter), mostly skin with some attached adipose tissue (Pagano et al. 2014), was taken using a biopsy dart (SCC Polar Bear Biopsy DNA Dart, Pneu-Dart Inc., Williamsport, Pennsylvania). All sampled bears were darted in the rump area from inside a helicopter at an approximate distance (or altitude) of 3–7 m. The biopsy darts are designed to fall to the ground after impact and are retrieved without physically handling a bear. The effectiveness of these darts for sampling polar bears has been previously demonstrated in Pagano et al. (2014) and SWG (2016). On average, it takes < 4 min from when a bear is initially spotted to the time when the dart is retrieved. The design and relatively low velocity of the dart means that risk of injury to an individual is minimal. Typically, bears show no or very little response to the impact of the dart and are left with no visible marks. To facilitate dart recovery, we tied a 10 – 15 cm long and ~ 2 cm wide strip of brightly colored flagging tape (C.H. Hanson, Naperville, Illinois; or Johnson, Montreal, Quebec, Canada) around the distal end of the dart. We stored collected skin and adipose tissue (ca. 1 cm in length) in 2-ml cryovials kept frozen at -20°C until analysis.

Harvest samples were collected by Inuit hunters from 2010 to 2018 in Davis Strait ($n = 221$) and in Gulf of Boothia ($n = 278$). Samples were collected year-round from adult (5+ years old) and subadult (3 – 4 years old) polar bears of both sexes. Subcutaneous adipose tissue samples (ca. 6 cm \times 6 cm) were taken from the rump of each bear, wrapped in aluminum foil, sealed in a labeled Whirl-Pak, and stored at -20°C until analysis.

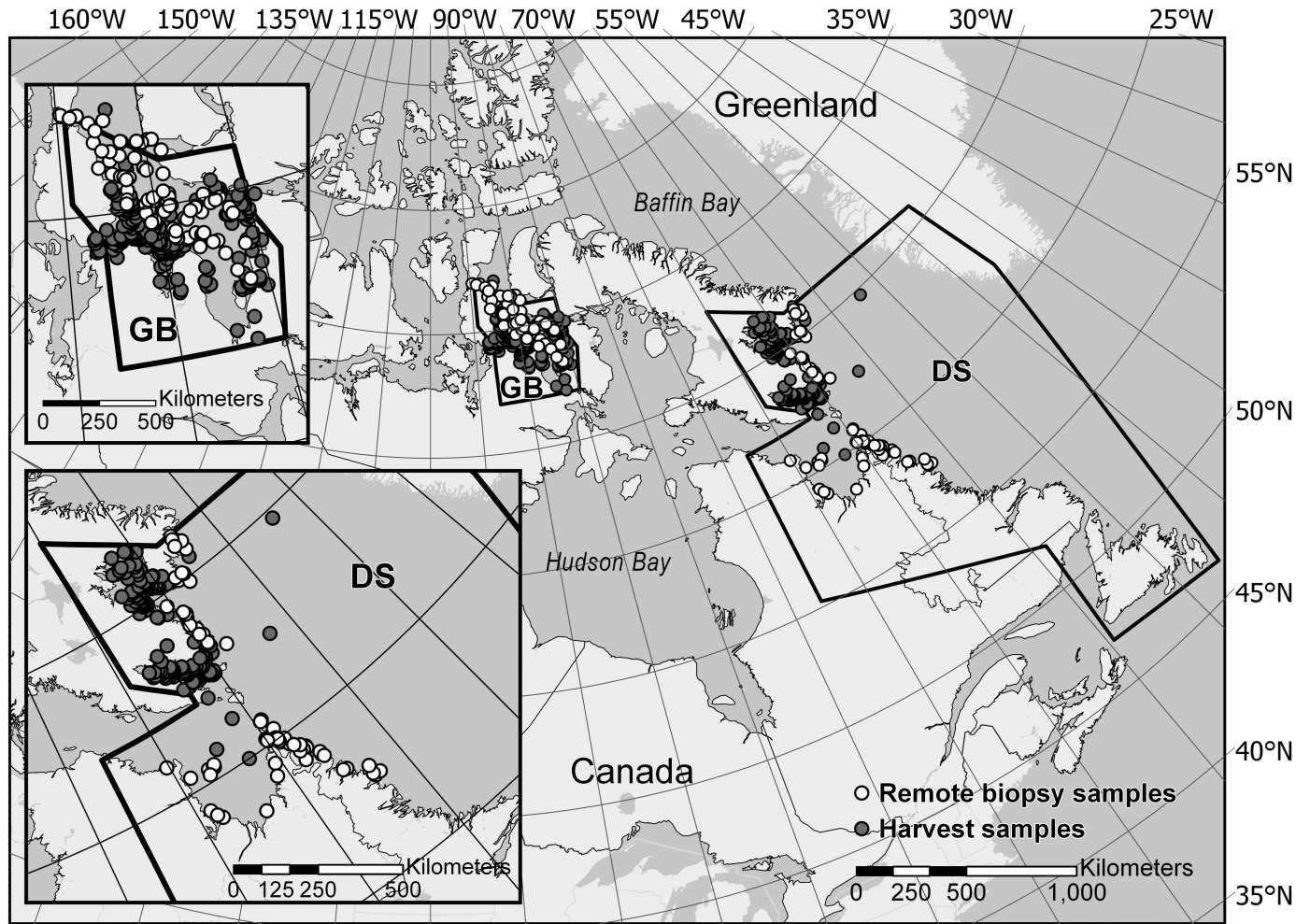


Fig. 1.—Location of polar bear adipose tissue samples collected from remote biopsy darts ($n = 138$) and harvest samples ($n = 499$) in Davis Strait (DS) and Gulf of Boothia (GB). The black outline represents the subpopulation boundaries.

Laboratory analysis.—We weighed remote adipose tissue biopsies after removing the epidermis. For harvest samples, we took a subsample of approximately 0.5 g from the interior of each sample to avoid any desiccated or oxidized surfaces. Lipid was quantitatively extracted following Iverson et al. (2001) and lipid content expressed as percent total wet weight. We used sulfuric acid as a catalyst to derive FA methyl esters (FAMES) from the extracted lipid (Budge et al. 2006). FAME samples were analyzed using gas-liquid chromatography and flame-ionization detection at the Canadian Institute for Fisheries Technology at Dalhousie University, Halifax. Typically, over 70 FAs are identified in each adipose tissue sample and expressed as the mass percentage of the total FA \pm SEM. FAs are identified using the nomenclature A:Bn-X, where A is the carbon chain length, B is the number of double bonds, and X is the position of the first double bond in relation to the terminal methyl group.

Diet estimation.—We used quantitative FA signature analysis (QFASA) to estimate diet composition of polar bears both for remote biopsies and harvest samples (Iverson et al. 2004). Briefly, QFASA models a predator FA profile (or “signature”) as a linear combination of average prey signatures and estimates diet as the proportional combination of prey that minimizes the distance

between the observed and modeled predator (Bromaghin et al. 2015). For Davis Strait diet estimates, we used existing FA data from 144 marine mammals including bearded seals (*Erignathus barbatus*), harbor seals (*Phoca vitulina*), harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), ringed seals (*Pusa hispida*), and Atlantic walrus (*Odobenus rosmarus rosmarus*), sampled across Nunavut from 1994 to 2015 (Thiemann et al. 2008b; Galicia et al. 2016). For Gulf of Boothia diet estimates, we used existing FA data from 243 marine mammals including bearded seals, beluga whales (*Delphinapterus leucas*), harp seals, narwhal (*Monodon monoceros*), ringed seals, and Atlantic walrus sampled from 2005 to 2016 across Nunavut (Galicia et al. 2015).

A combination of prey species that are most ecologically relevant to each subpopulation (i.e., prey library) is important to accurately quantify predator diet (Iverson et al. 2004). Thus, the analysis of prey library performance is a necessary step for reliable diet estimation. For instance, the more distinct prey species’ signatures are from each other, the better the model should perform. The performance of the prey library was analyzed using two diagnostic functions in the qfasar package (version 1.2.0—Bromaghin 2017) in R (version 3.5.1—R

Development Core Team 2018): “leave-one-prey-out” analyses, and divisive magnetic clustering (DIMAC). The “leave-one-prey-out” function temporarily removes a single prey FA signature from the prey library, then computes the mixture of the remaining prey FA signatures that best represents the signature of the removed prey, and subsequently repeats this for each prey sample. The output reflects the proportion of samples attributed to the correct species (distinctiveness within library), and the proportion that was misidentified (confounding within library—Bromaghin et al. 2017a). DIMAC is a clustering technique that identifies substructure across FA signatures within a prey type. It partitions the prey library into clusters that are more similar than the original prey groups (i.e., species) with the goal of minimizing confounding and maximizing distinctiveness within the library (Bromaghin et al. 2017a).

Calibration coefficients derived from a captive carnivore with a controlled marine-based diet (mink, *Neovison vison*) were used to account for FA metabolism in the predator (Iverson et al. 2004; Thiemann 2006; Thiemann et al. 2008a; Bromaghin et al. 2017b). We used the Aitchison distance to compare modeled and observed predator signatures (Bromaghin et al. 2015, 2016) and a set of 30 dietary FAs (Galicia et al. 2015). All diet estimates were produced using the qfisar package (version 1.2.0—Bromaghin 2017) in R (version 3.5.1—R Development Core Team 2018).

Statistical analysis.—We compared adipose lipid content from remote-biopsied and harvested polar bears using Mann–Whitney *U*-tests. Because polar bears undergo known seasonal changes in food intake and body condition (Galicia et al. 2020), adipose lipid content of harvest and biopsy samples were limited to the same sampling season. This would result in a more seasonally relevant comparison between collection methods. Thus, we limited Davis Strait harvest samples to August and September ($n = 21$) and Gulf of Boothia harvest samples to April and May ($n = 108$) for adipose tissue lipid analysis. We included season as a predictor variable in the model to test collection method, intraspecific (sex and age class), and spatiotemporal effects on FA composition and diet estimates (see below).

We used principal component analysis (PCA) and Akaike’s information criterion for small sample size (AIC_c) to test whether there was a difference in FA composition between collection method (i.e., remote biopsy and harvest samples) while controlling for other covariates. We used a set of 18 of the most abundant FAs transformed by calculating the log of the ratio of each FA to 18:0 to improve normality (Budge et al. 2002, 2006). Broken stick models revealed PC1 and PC2 were significant axes in both subpopulations, PC1 accounted for 55% and 47% and PC2 accounted for 47% and 36% of the variation in FA signatures in Davis Strait and Gulf of Boothia, respectively. We used linear models with PC1 and PC2 scores to encompass variation of all 18 FAs into two parameters. Separate models were used for each PC axis and subpopulation. We included collection method (remote biopsy or harvest), year, sex, age class (adult or subadult), and season (defined as per Sahanatien et al. 2015), as possible predictors in models. In Davis Strait, seasons were defined as ice-free (August – November), freeze-up (December – January), winter (February – March),

spring (April – May), and break-up (June – July). In Gulf of Boothia, seasons were defined as ice-free (September), freeze-up (October – November), winter (December – March), spring (April – May), and break-up (June – August). In Davis Strait, remote biopsy and harvest samples were not evenly distributed across the subpopulation, with more remote biopsies collected in the southern portion and more harvest samples in the northern portion. The two collection methods were more evenly distributed in Gulf of Boothia (Fig. 1). Moreover, FA composition and diet estimates have been found to vary spatially within Davis Strait (Iverson et al. 2006). We separated the subpopulation by latitude into northern (above 61°N) and southern (below 61°N) areas and included geographic area as a predictor in the Davis Strait models. We used AIC_c to select from a set of ecologically relevant candidate models defined a priori (Burnham and Anderson 2002). Log-likelihood (LL), AIC_c values, ΔAIC_c , and AIC_c weights (w_i —relative likelihood of the model) were calculated using MuMIn package in R (version 1.43.17—Bartón 2018). To evaluate the relative importance (i.e., strength of evidence) of individual model parameters, we computed cumulative AIC_c weights by calculating the sum of Akaike model weights across all models that included the variable (Arnold 2010).

We used AIC_c to analyze variation associated with collection method in estimates of polar bear diet while controlling for other covariates (Burnham and Anderson 2002). Separate models were used for each prey type within Davis Strait and Gulf of Boothia. We used prey contribution to diet as the response variable for each generalized additive model with a zero-inflated beta distribution (Douma and Weedon 2019) and used the same possible explanatory predictors as in the FA signature models. Again, LL, AIC_c values, ΔAIC_c , and AIC_c weights (w_i —relative likelihood of the model) were calculated using MuMIn package in R (version 1.43.17—Bartón 2018). We also computed the cumulative AIC_c weight of each parameter to evaluate its relative importance within the model set (Arnold 2010).

RESULTS

Adipose lipid content.—Remote biopsies of adipose tissue weighed 0.015 ± 0.002 g (mean \pm SEM) and 0.013 ± 0.001 g for Davis Strait and Gulf of Boothia, respectively. Harvest subsamples weighed 0.423 ± 0.007 g and 0.439 ± 0.006 g for Davis Strait and Gulf of Boothia, respectively. Adipose lipid content was significantly higher (Mann–Whitney *U*, $P < 0.001$) in harvest samples in both Davis Strait ($83.7 \pm 1.0\%$) and Gulf of Boothia ($68.6 \pm 4.0\%$) than in biopsies from either region ($51.6 \pm 2.6\%$ and $54.9 \pm 2.6\%$, respectively; Fig. 2). There was a seasonal/regional difference within harvest samples; Davis Strait (August – September) had a higher adipose lipid content than Gulf of Boothia (April – May); however, this trend was not observed in remote biopsy samples.

FA composition.—In Davis Strait and Gulf of Boothia, the top-ranked models explaining variation in FA composition included a combination of predictor variables. In Davis Strait, none of the top models included collection method. The

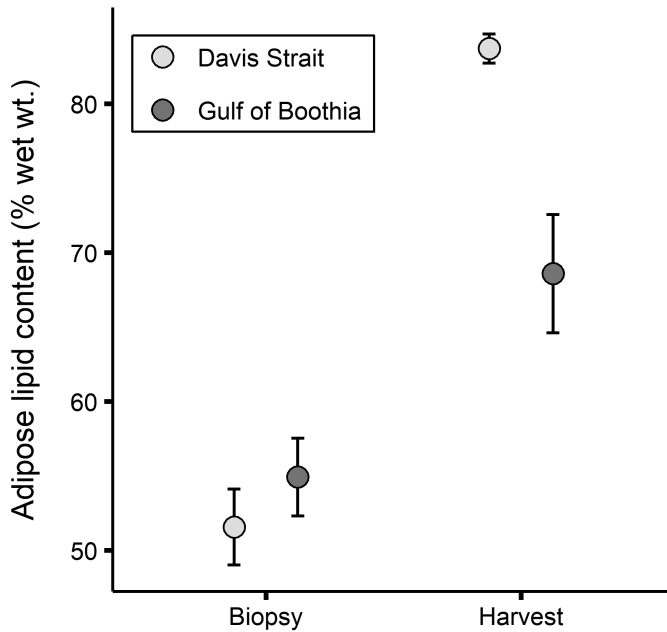


Fig. 2.—Body condition (expressed as lipid content of adipose tissue; mean \pm SEM) for polar bears sampled in Davis Strait and Gulf of Boothia. Davis Strait polar bears sampled (harvest 2010–2017, $n = 21$ and remote biopsy 2017, $n = 64$) in August and September. Gulf of Boothia polar bears sampled (harvest 2011–2018, $n = 108$, remote biopsy 2015–2016, $n = 74$) in April and May.

top-ranked model for FA composition included geographic area and season for PC1, and sex and season for PC2 (Supplementary Data SD1). In addition, collection method had a relatively low cumulative AIC_c weight compared with geographic area (PC1), season (PC1 and PC2), and sex (PC2; Table 1). In Gulf of Boothia, the top-ranked model for variation in FA composition included sample collection method, sex, and season for PC1, and collection method, sex, and year for PC2 (Supplementary Data SD1). Both collection method and sex had high cumulative AIC_c weights for both PC1 and PC2 (Table 1).

Remote biopsies contained the same number of FAs (> 70) in adipose tissue as harvest samples, although there was variability between collection method in the proportion of specific FAs. In Davis Strait and Gulf of Boothia bears, the largest differences between collection method occurred in 16:0 and 16:1n-7, which were consistently higher in biopsies (by 2.8% and 4.2%, respectively, in Davis Strait; 1.0% and 1.5%, respectively, in Gulf of Boothia), and 20:1n-9 which was consistently higher in harvest samples (by 5.3% in Davis Strait and 1.4% in Gulf of Boothia; Fig. 3; Supplementary Data SD2).

Diet composition.—The leave-one-prey-out function indicated that prey types were distinguishable within prey libraries used for diet estimates (see Supplementary Data SD3) and DIMAC indicated no significant substructure within prey types. In both Davis Strait and Gulf of Boothia, the variables that explained the contribution of a given prey to polar bear diet varied across prey types.

In Davis Strait, both collection methods identified harp seal as the primary prey of polar bears (biopsy: $25 \pm 2.78\%$ and

Table 1.—Cumulative Akaike's information criterion for small sample size (AIC_c) weights of fatty acid composition (PC1 and PC2) model parameters for polar bears harvested and remote-biopsied in Davis Strait and Gulf of Boothia, 2010–2018. PC = principal component.

Model parameter	Davis Strait		Gulf of Boothia	
	PC1	PC2	PC1	PC2
Collection method	< 0.01	0.08	0.98	1.00
Geographic area	1.00	0.15		
Sex	0.04	0.47	0.97	0.99
Age class	0.23	0.21	< 0.01	< 0.01
Year	0.35	0.13	0.08	0.46
Season	0.77	1.00	0.75	0.01

harvest: $37 \pm 1.42\%$; Fig. 4A). Bearded seal, hooded seal, and ringed seal had the next largest contributions to diet; however, the order of contribution varied between collection methods. Bearded seal contributed the second most to diet in biopsies but was fourth in harvest samples, whereas ringed seal contributed the second most to diet in harvest samples. The second largest difference in contribution between biopsy and harvest samples after harp seal occurred in bearded seal, which differed by 11% (biopsy: $23 \pm 2.39\%$ and harvest $12 \pm 2.39\%$), whereas hooded seal differed by 2%, and ringed seal by 4% between the two collection methods (Fig. 4A). Harbor seal and walrus consumption was lowest in both biopsy and harvest samples with a difference of 4% and 3% between collection methods, respectively (Fig. 4A).

Collection method was not included in any top-ranked models for bearded seal, harbor seal, harp seal, or hooded seal (Supplementary Data SD4) with a low cumulative AIC_c weight across all prey types in Davis Strait (Table 2). Although collection method was included in the fifth-ranked model ($\Delta AIC_c < 2.00$) for ringed seal, it also included year and sex (Supplementary Data SD4). The beta coefficient suggested no relationship between ringed seal dietary levels and collection method with a confidence interval that overlapped zero ($\beta = 0.15$, 95% CI = -0.17 to 0.48 from fifth-ranked model), regardless of year and sex. The cumulative weight of collection method was also relatively low compared with sex, geographic area, age class, and year (Table 2) and thus collection method likely was an uninformative parameter in the model. The top-ranked model for walrus included only season with a low overall model weight of 0.11 and nine models for walrus had a $\Delta AIC_c < 2.00$ with four of those models containing collection method as a predictor variable (Supplementary Data SD4). Model uncertainty was apparent in the relatively low cumulative weights of all model parameters (Table 2) and proportional differences in walrus contribution remained low (by 3%). Season and sex were the most important explanatory variables in harp seal contribution to diet (Table 2) and by limiting the comparison to the ice-free season (July – November) and by sex, the difference between remote biopsy and harvest samples was reduced to 1% in females (biopsy: $24 \pm 3.77\%$ and harvest: $25 \pm 11\%$) and 4% in males (biopsy: $26 \pm 4.17\%$ and harvest: $30 \pm 4.42\%$).

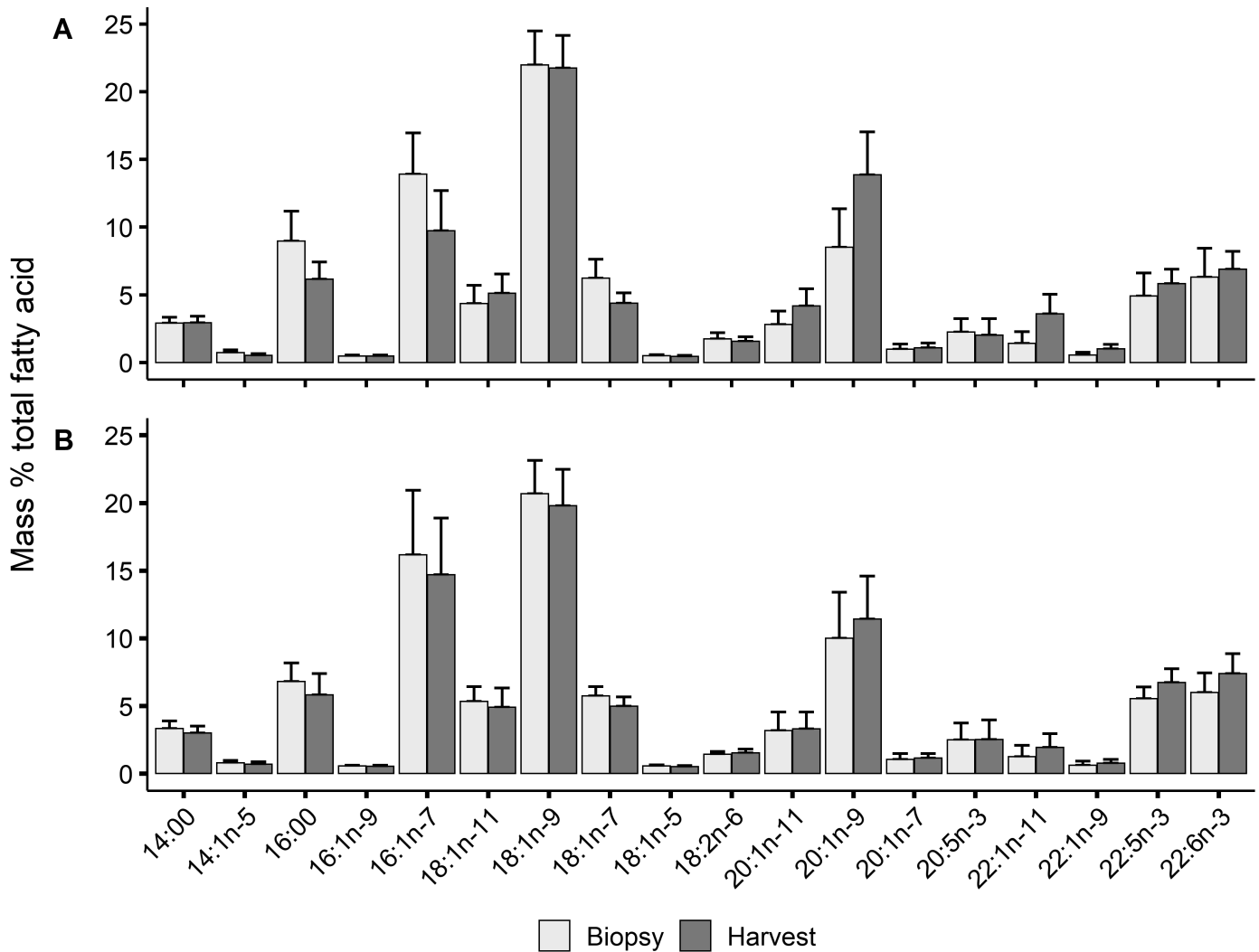


Fig. 3.—The 18 most abundant fatty acids (mass % of total \pm SEM) of (A) Davis Strait polar bears from remote biopsy (2017, $n = 64$) and harvest (2010–2018, $n = 221$) samples. (B) Gulf of Boothia polar bears from remote biopsy (2015–2016, $n = 74$) and harvest (2010–2018, $n = 278$) samples.

Variation in contribution of bearded seal, harbor seal, and hooded seal, to diet between the two collection methods can be attributed to spatial variation in sampling within the Davis Strait subpopulation because geographic area was common in all top-ranked models with a high cumulative AIC_c weight > 0.76 (Supplementary Data SD4; Table 2). While geographic area was included in the top-ranked model for ringed seal, the variation in contribution was driven by sex, because geographic area had a relatively lower cumulative AIC_c weight compared with sex (Table 2). Geographic area, year, and sex were important explanatory variables for bearded seal contribution to diet (Table 2). By limiting the comparison to the northern portion within 2017 and sex, the difference between collection methods was reduced from 11% to 1% in females (biopsy: $5 \pm 1.61\%$ and harvest: $6 \pm 1.52\%$) and 2% in males (biopsy: $11 \pm 3.70\%$ and harvest: $9 \pm 1.79\%$). Sample size of harvested bears in the southern portion of Davis Strait was too low for further comparison. While controlling for variables with high cumulative AIC_c weights for harbor seal (geographic area) and

hooded seal (geographic area and year; Table 2), proportional differences between sample types remained low, differing by 2% (biopsy: $5 \pm 1.61\%$ and harvest: $4 \pm 0.37\%$) and by 3% (biopsy: $22 \pm 2.38\%$ and harvest: $19 \pm 1.92\%$), respectively.

In Gulf of Boothia, ringed seal made the highest contribution to polar bear diets in biopsy ($52 \pm 1.93\%$) and harvest samples ($54 \pm 1.21\%$). Bearded seal consistently had the second-highest biomass and varied by 4% between collection methods (biopsy: $19 \pm 1.35\%$ and harvest: $15 \pm 0.74\%$; Fig. 4B). Cumulative AIC_c weights indicated that collection method had little or no influence on bearded seal or ringed seal contribution to diets (Table 2). The top-ranked model for bearded seal included only age class, and ringed seal included sex, age class, and season (Supplementary Data SD5). Walrus had the lowest contribution to diets with no difference between collection methods. The largest difference in contribution to diets occurred in harp seals by 6% between biopsy ($5 \pm 1.06\%$) and harvest ($11 \pm 0.58\%$) samples, whereas beluga whale differed by 3% and narwhal by 2% between the two collection

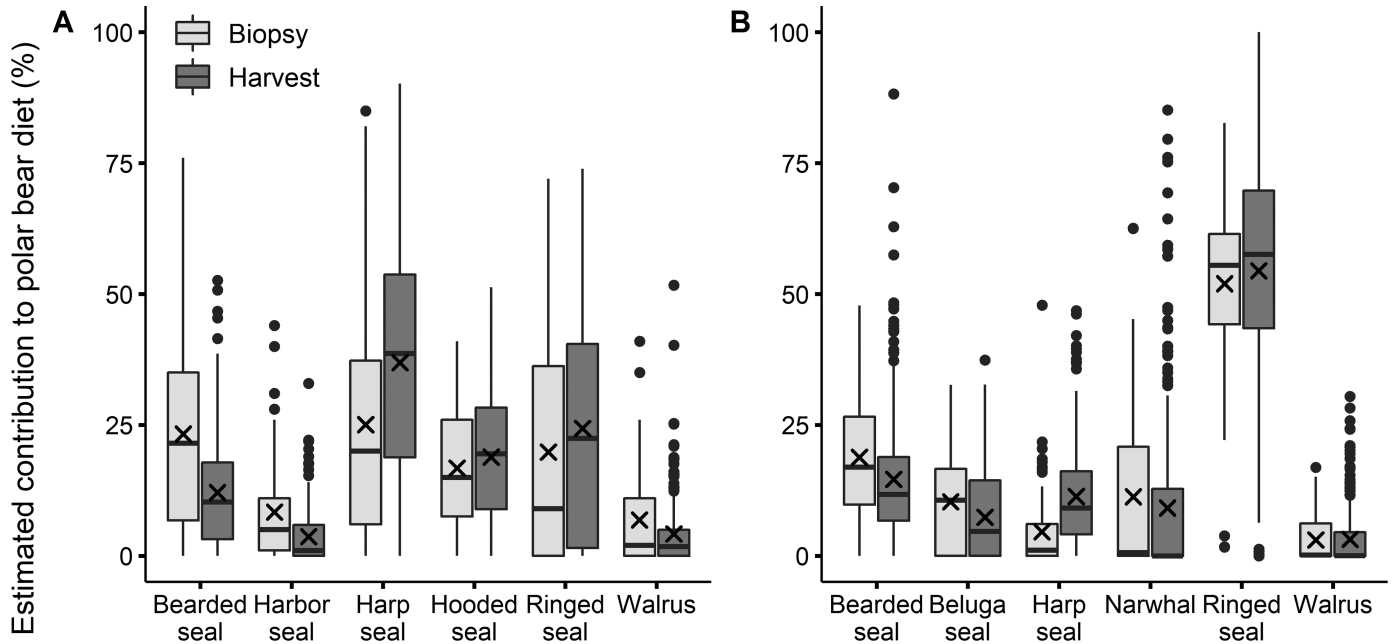


Fig. 4.—Diet composition of polar bears from (A) Davis Strait subpopulation (remote biopsy, $n = 64$ and harvest, $n = 221$) and (B) Gulf of Boothia subpopulation (remote biopsy, $n = 74$ and harvest, $n = 278$). Data represent each prey species' biomass contribution to diet estimates shown as boxplots showing the 25th quartile, median, 75th quartile, and outliers shown as solid circles. Mean proportion for each prey is represented by "x."

Table 2.—Cumulative Akaike's information criterion for small sample size (AIC_c) weights of diet composition model parameters for polar bears harvested and remote-biopsied in Davis Strait and Gulf of Boothia, 2010–2018.

Model parameter	Prey						
	Bearded seal	Harbor seal	Harp seal	Hooded seal	Ringed seal	Walrus	
Davis Strait							
Collection method	0.17	0.24	0.10	0.20	0.24	0.44	
Geographic area	0.83	0.76	0.07	0.80	0.53	0.28	
Sex	0.81	0.32	0.78	0.19	1.00	0.29	
Age class	0.01	0.47	0.32	0.21	0.40	0.22	
Year	1.00	0.24	0.11	1.00	0.35	0.22	
Season	0.17	0.04	0.92	0.06	0.03	0.48	
Gulf of Boothia							
	Bearded seal	Beluga whale	Harp seal	Narwhal	Ringed seal	Walrus	
Collection method	0.12	1.00	1.00	1.00	< 0.01	1.00	
Sex	0.32	0.83	1.00	0.49	0.96	0.78	
Age class	0.75	< 0.01	< 0.01	< 0.01	0.96	0.17	
Year	0.20	0.23	0.97	0.45	0.02	0.15	
Season	0.14	< 0.01	< 0.01	0.17	1.00	< 0.01	

methods (Fig. 4B). Collection method was common in all top-ranked models for beluga whale, harp seal, narwhal, and walrus with high cumulative AIC_c weights (Table 2). However, sex also was included in top-ranked models for beluga whale, narwhal, and walrus (Supplementary Data SD5), with high cumulative AIC_c weights (> 0.78) for beluga whale and walrus (Table 2). Sex and age class had similar importance values for narwhal contribution but were lower than collection method (Table 2). The variation in collection method for beluga was attributed to the difference (5%) within females, whereas contribution in males remained consistent between biopsy and harvest samples (Table 3). Conversely, male bears had the largest difference in contribution of narwhal (7% between collection methods compared to females with a difference of 1%; Table 3). Males consistently had higher levels of walrus in diets than

females, although within both sexes, the contribution only varied by 1% between collection methods (Table 3). The top-ranked model for harp seal included collection method, year, and sex (Supplementary Data SD5), and all three parameters had high cumulative weights in models (Table 2). Harp seal consistently varied by 4–5% in contribution to diets within year and sex across the two collection methods (Table 3).

DISCUSSION

Remote biopsy darting is increasingly common in wildlife research, typically in the context of genetic mark–recapture surveys (e.g., Mijeje et al. 2016; Aars et al. 2017; Frasier et al. 2020). Our study assessed the feasibility of using remote biopsy samples from genetic mark–recapture studies to generate

Table 3.—Mean (\pm SEM) contribution of beluga whale, harp seal, narwhal, and walrus to diets of polar bears sampled in Gulf of Boothia. Estimated contribution (%) are separated by top-ranked model variables for each prey type.

Prey		Collection method	Estimated contribution (%)
Beluga whale	female	biopsy	13 \pm 1.38
		harvest	8 \pm 0.83
Model: collection method + sex	male	biopsy	7 \pm 1.53
		harvest	7 \pm 0.59
Harp seal	2015, female	biopsy	1 \pm 0.37
		harvest	5 \pm 1.46
Model: collection method + year + sex	2016, female	biopsy	1 \pm 0.82
		harvest	6 \pm 3.33
	2015, male	biopsy	5 \pm 1.18
		harvest	10 \pm 1.17
	2015, male	biopsy	13 \pm 3.03
		harvest	9 \pm 2.39
Narwhal	female	biopsy	7 \pm 2.29
		harvest	8 \pm 1.71
Model: collection method + sex	male	biopsy	16 \pm 2.76
		harvest	9 \pm 1.16
Walrus	female	biopsy	1 \pm 0.47
		harvest	2 \pm 0.51
Model: collection method + sex	male	biopsy	5 \pm 0.91
		harvest	6 \pm 0.42

reliable estimates of adipose lipid content, FA data, and diet composition, in free-ranging polar bears. Remote biopsies did not provide comparable estimates of lipid content in adipose tissue to harvest samples and therefore currently are not useful for estimating body condition of polar bears. Collection method had no effect or a minor effect on FA composition. In Davis Strait, collection method was not an informative predictor of diet estimates. Although collection method was a significant predictor of diet estimates in Gulf of Boothia, the proportional differences were low across prey types (< 6%). Overall, variation in FA composition and diet estimation was primarily attributable to a combination of intraspecific (e.g., sex) and spatiotemporal factors, rather than sampling technique per se.

Adipose lipid content.—Adipose tissue lipid was lower in remote biopsies relative to harvest samples both in Davis Strait and Gulf of Boothia even though comparison was restricted to the same sampling season. Live-capture biopsies of adipose tissue (Thiemann et al. 2006) and harvest samples (Galicia et al. 2020) are taken through the entire depth of the subcutaneous fat layer, whereas remote biopsies are collected superficially, close to the skin (McKinney et al. 2014; Pagano et al. 2014). For example, the average weight of a full-layer adipose tissue biopsy from a captured bear was 20 \times greater (0.270 ± 0.010 g; Thiemann 2006) than the average weight from a remote biopsy (0.014 ± 0.001 g) in our study. Thiemann et al. (2006) also found that lipid content of subcutaneous adipose tissue was strongly related to tissue depth, with the outermost tissue having the lowest lipid content. Moreover, remote biopsies may have contained some nonadipose tissue (e.g., epidermis and connective tissue) generating negative bias in lipid content (Ylitalo et al. 2001; Thiemann et al. 2006). Finally, although the strong seasonal variation in polar bear body condition (Galicia

et al. 2020) was evident within our harvest samples, remote biopsy samples showed consistent lipid values between April/May and August/September. Our results therefore indicate that remote biopsies are not a reliable technique to measure body condition, a finding consistent with other studies (McKinney et al. 2014; Pagano et al. 2014).

FA composition.—The overall distribution of individual FAs between remote biopsy and harvest samples was similar, such that composition was dominated by monounsaturated and polyunsaturated FAs. Pagano et al. (2014) also found that remote biopsies provided similar proportions of routinely identified FAs in polar bears, although they did not undertake statistical comparisons. Although vertical stratification of blubber FA has been identified in pinnipeds (Strandberg et al. 2008; Guerrero et al. 2016; Tverin et al. 2019) and cetaceans (e.g., Krahn et al. 2004; Waugh et al. 2014), the composition of subcutaneous adipose tissue in polar bears is considered uniform through its depth (Thiemann et al. 2006). Thus, the FA differences we detected between remote biopsy (adipose tissue close to the skin) and harvest samples (full depth of adipose layer) likely reflect regional, intraspecific, and temporal, differences as opposed to vertical stratification (i.e., collection method difference per se).

Fatty acid composition has been found to vary geographically within our study area, particularly between southern Davis Strait (south of 61°N—Northern Labrador) and northern Davis Strait (Frobisher Bay—63°N, and Cumberland Sound—65°N—Iverson et al. 2006). The majority (69%) of remotely darted bears were sampled in the southern portion of the subpopulation with the remaining samples taken in the northern region (see Fig. 1). This spatial bias in sampling likely contributed to some of the collection method effect (biopsy versus harvest) we found in individual FA proportions. For example, of the three most abundant FAs, 16:0 and 16:1n-7 were found in higher and 20:1n-9 in lower proportions in southern areas relative to northern areas of Davis Strait, consistent with a trend found by Iverson et al. (2006). FA composition in Gulf of Boothia was influenced by collection method and sex; however, the overall magnitude of differences across individual FAs was small (less than 2%; see Supplementary Data SD2) between remote biopsy and harvest samples. The high surface-area-to-volume ratio of remote biopsy samples could promote surface oxidation (Budge et al. 2006), but the similarity of FA composition across collection methods suggests oxidation was not a significant factor in our study. Our results suggest that remote biopsy samples provide reliable information on overall FA stores in polar bears, and thus could be used to infer general dietary differences between groups of bears (e.g., Tartu et al. 2016, 2017) or potentially be used in quantitative estimates of diet composition (see below).

Diet composition.—Overall diet composition of bears both in Davis Strait and Gulf of Boothia was similar between remote biopsy and harvest samples. Although collection method was a significant predictor primarily in Gulf of Boothia, variability in diet composition was influenced by geographic area (in Davis Strait), sex, age class, and annual and seasonal variability. Sex and age class differences in polar bear diet composition are

well-documented and may be due to larger more experienced adult male bears having more success catching larger-bodied prey (Thiemann et al. 2008a; Galicia et al. 2015, 2016). Interannual variability in polar bear diet composition previously has been attributed to interannual shifts in environmental conditions and local prey availability (Thiemann et al. 2008a; Sciullo et al. 2017).

Despite potential spatial and seasonal effects, Davis Strait diet estimates were broadly similar in both collection methods: harp seal contribution was highest in bear diets, followed by lower proportions of bearded, hooded, and ringed seal, a pattern consistent with Iverson et al. (2006). In Davis Strait, bearded, hooded, and ringed seal dietary contribution varied by intraspecific factors and interannually. However, dietary contributions of these three prey species also varied spatially, which is consistent with Iverson et al. (2006), who found that ringed and hooded seal consumption was higher in northern Davis Strait, whereas bearded seal consumption was higher in southern Davis Strait. In addition, when we controlled specific model parameters with high AIC_c cumulative weights, differences between collection methods were reduced. For example, the proportional differences between collections methods were low for harp seal (< 4%) while controlling for season and sex, and low for bearded seal (< 2%) while controlling geographic area, year, and sex. The proportional differences to diets between collection method were < 4% in other prey. Our results suggest that differences in prey contribution were a function of geographic area where the bear was sampled, or variability between sexes, year, or season as opposed to collection method.

In Gulf of Boothia, both collection methods identified ringed seal as the dominant prey followed by bearded seal, with similarly lower proportions of beluga whale, harp seal, narwhal, and walrus. These results also are consistent with previous studies (Galicia et al. 2015). Differences in ringed seal and bearded seal were attributable to intraspecific (sex and age class) and seasonal effects, with relatively low (< 4%) proportional differences between remote biopsy and harvest samples. The proportional differences between collection methods were similarly low for harp seal, beluga whale, narwhal, and walrus, ranging from 1% to 7% after controlling for variables with high cumulative AIC_c weights (sex and year). The remaining variation between collection methods may be explained by spatial differences (e.g., harvested bears closer to shore) or other ecological factors. For example, females with dependent offspring were included in biopsy samples but not subject to harvest (hunting of family groups is prohibited). Mothers with cubs are known to have different habitat preferences and target different prey than solitary females (Stirling et al. 1993; Sciullo et al. 2017; Johnson and Derocher 2020). Overall, the relatively low proportional differences in prey contribution between collection methods both in Davis Strait and Gulf of Boothia suggest remote biopsies accurately reflected the FA stores of polar bears and thus, can be used to estimate diet.

Capture-based studies have provided a wide breadth of knowledge on polar bear population dynamics and life history. However, less invasive methods of sample collection are becoming increasingly important in wildlife research (e.g., Miller et al. 2005; Stansbury et al. 2014; Sittenthaler et al. 2020).

Genetic mark–recapture has emerged as a key method of estimating polar bear abundance (SWG 2016; Aars et al. 2017), at least partly because it is more compatible with Inuit research perspectives and acceptance of research techniques (Henri et al. 2010; Wong et al. 2017). Our study validates the utility of remote biopsies to investigate the feeding patterns of polar bears but does not support the use of remote biopsies for quantifying body condition. Moreover, the diets of bears not typically subject to harvest (e.g., females with dependent offspring) can be estimated with remote biopsies. Declines in sea ice habitat are having complex effects on Arctic ecosystems (Leu et al. 2011; Stirling and Derocher 2012; Post et al. 2013; Ramírez et al. 2017). Ongoing remote biopsy darting could provide important insights into how food webs are responding to environmental change, in a manner that requires no additional sampling effort and is congruent with emerging Inuit contributions to northern research methodologies and priorities.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Model selection for the variation in fatty acid composition of polar bears harvested and remote-biopsied in Davis Strait and Gulf of Boothia, 2010–2018. The two subpopulations and principal component (PC) axes were modeled separately, and the top four ranked models are shown with the top-ranked model in bold. Included in the table are number of estimated parameters (K), log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c) values, ΔAIC_c , and AIC_c weights (w_i), and are shown for each model. Geographic area (i.e., north and south Davis Strait) is represented by lat in model.

Supplementary Data SD2.—The 18 most abundant fatty acids in polar bear adipose tissue (by major lipid class; % mass of total fatty acid [FA] \pm SEM).

Supplementary Data SD3.—Proportion of leave-one-prey-out estimates attributed to the correct prey type within the prey library in Davis Strait and Gulf of Boothia.

Supplementary Data SD4.—Model selection for the variation in contribution of prey to polar bear diet in Davis Strait. Contribution of each prey species was modeled separately, and the top five ranked models are shown with the top-ranked model in bold. Included in the table are number of estimated parameters (K), log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c) values, ΔAIC_c , and AIC_c weights (w_i), and are shown for each model. Geographic area (i.e. north and south Davis Strait) is represented by lat in model.

Supplementary Data SD5.—Model selection for the variation in contribution of prey to polar bear diet in Gulf of Boothia. Contribution of each prey species was modeled separately, and the top five ranked models are shown with the top-ranked model in bold. Included in the table are number of estimated parameters (K), log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c) values, ΔAIC_c , and AIC_c weights (w_i), and are shown for each model.

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