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Diet energy density estimated from isotopes in predator hair associated with survival, habitat, and population dynamics

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Abstract

Sea ice loss is fundamentally altering the Arctic marine environment. Yet there is a paucity of data on the adaptability of food webs to ecosystem change, including predator–prey interactions. Polar bears (*Ursus maritimus*) are an important subsistence resource for Indigenous people and an apex predator that relies entirely on the under-ice food web to meet its energy needs. In this study, we assessed whether polar bears maintained dietary energy density by prey switching in response to spatiotemporal variation in prey availability. We compared the macronutrient composition of diets inferred from stable carbon and nitrogen isotopes in polar bear guard hair (primarily representing summer/fall diet) during periods when bears had low and high survival (2004–2016), between bears that summered on land versus pack ice, and between bears occupying different regions of the Alaskan and Canadian Beaufort Sea. Polar bears consumed diets with lower energy density during periods of low survival, suggesting that concurrent increased dietary proportions of beluga whales (*Delphinapterus leucas*) did not offset reduced proportions of ringed seals (*Pusa hispida*). Diets with the lowest energy density and proportions from ringed seal blubber were consumed by bears in the western Beaufort Sea (Alaska) during a period when polar bear abundance declined. Intake required to meet energy requirements of an average free-ranging adult female polar bear was 2.1 kg/day on diets consumed during years with high survival but rose to 3.0 kg/day when survival was low. Although bears that summered onshore in the Alaskan Beaufort Sea had higher-fat diets than bears that summered on the pack ice, access to the remains of subsistence-harvested bowhead whales (*Balaena mysticetus*) contributed little to improving diet energy density. Because most bears in this region remain with the sea ice year

round, prey switching and consumption of whale carcasses onshore appear insufficient to augment diets when availability of their primary prey, ringed seals, is reduced. Our results show that a strong predator–prey relationship between polar bears and ringed seals continues in the Beaufort Sea. The method of estimating dietary blubber using predator hair, demonstrated here, provides a new metric to monitor predator–prey relationships that affect individual health and population demographics.

KEYWORDS

Beaufort Sea, bowhead whale, energetics, land use, polar bear, ringed seal, sea ice, stable isotopes, *Ursus maritimus*

INTRODUCTION

Changes in the seasonal availability of Arctic sea ice are altering species distributions and trophic relationships, including how predator–prey systems are coupled (Gilg et al., 2009; Hamilton et al., 2017; Higdon et al., 2011; Yurkowski et al., 2020). Ringed seals (*Pusa hispida*) are the most abundant ice-associated seal species throughout the Arctic and are the primary prey species for polar bears (*Ursus maritimus*), composing up to 75%–80% of the bears' diet (Boucher et al., 2019a; Rode, Regehr, et al. 2021; Sciullo et al., 2017; Thiemann et al., 2008). In some areas, polar bear predation results in the loss of 29% of annual ringed seal pup production (Hammill & Smith, 1991). Although the role of polar bears as a predator of ringed seals is well documented (Reimer, Brown, et al., 2019; Stirling, 1995, 2002), the strength of this predator–prey relationship and its flexibility in response to a rapid changing Arctic are poorly understood. Further, measuring predation rates and estimating abundance and demographics of these wide-ranging species in remote habitats is challenging. Understandably, there has been a focus on the direct effects of sea ice loss as a hunting platform due to its importance for the long-term demographics of polar bear populations as sea ice loss continues (Atwood, Marcot, et al., 2016; Durner et al., 2017; Molnár et al., 2020). In the near term, however, management of Arctic marine mammals, which includes modeling to predict abundance and the effects of harvest (e.g., Regehr et al., 2017), requires a better understanding of the ecological factors that affect demography.

In regions where a substantial decline in sea ice habitat has occurred, the strength of the predator–prey relationship between polar bears and ringed seals appears to be weakening, which may signal this change as a generalized response of polar bears to sea ice loss (Hamilton et al., 2017; Yurkowski et al., 2020). Increased summer land use by polar bears in many parts of their range has the potential to further affect this predator–prey relationship as bears use alternative food resources to replace lost hunting opportunities on the sea ice (Hamilton et al., 2017; Jagielski et al., 2021). Because polar bears are a specialist predator with low dietary diversity, they are particularly sensitive to declines in the availability and condition of their primary prey (Rode, Regehr, et al., 2021; Stirling, 1995). The necessary data to track the status of prey populations, however, are lacking in most parts of polar bear range, and a major gap in our understanding of Arctic ecosystems is the interrelationship in the demographics of top predators and their marine mammal prey. It has become increasingly important, considering declines in Arctic sea ice, to develop consumer dietary inference that moves beyond the estimation of prey composition and toward the fitness-related effects of dietary change.

A number of studies have estimated polar bear diets using molecular tracing techniques, such as quantitative fatty acid analysis (QFASA; e.g., Florko et al., 2020; Thiemann et al., 2008) and stable isotopes (e.g., Boucher et al., 2019a, 2019b; Rogers et al., 2015). To date, applications of these techniques provide estimates of prey composition but cannot estimate total energy and nutrient intake. As a result, they are limited in differentiating dietary change that may be adaptive (i.e., prey switching or diet supplementation that results in similar energy intake) from those associated with reduced consumer energy intake. This limitation makes it difficult to interpret whether dietary change may be a factor affecting polar bear body condition and vital rates.

A new stable isotope–based diet modeling approach that exploits the typically large difference in $\delta^{13}C$ between prey blubber and muscle to expand prey resources in isotopic space, making them easier to differentiate, facilitates estimation of diet macronutrient

(i.e., lipid/protein) proportions in predator diets (Rode, Robbins, et al., 2021; Stricker et al., 2022) that may serve as a fitness-related proxy. For example, measures of dietary blubber assimilation by polar bears may reflect prey availability because they leave behind substantial portions of seal meat and preferentially consume blubber when prey are abundant (Stirling, 2002; Stirling & McEwan, 1975). Because polar bears have low protein requirements, energy intake can be maximized by consuming large dietary proportions of lipid-rich blubber ($\geq$70%; Rode, Robbins, et al., 2021; Stricker et al., 2022), which contains twice the energy per gram as proteinaceous muscle. Thus, the ratio of blubber to protein in polar bear diets affects dietary energy density (i.e., energy per gram of intake), which may be an important mechanism by which variation in diet composition, prey availability, and prey condition affects polar bear body condition and survival rates.

The southern Beaufort Sea (SB) and northern Beaufort Sea (NB) polar bear populations are among the best studied in the world. These populations occupy a region with spatial differences in prey species availability and polar bear population dynamics, providing an opportunity to better understand how predator–prey dynamics affect demography. Beaufort Sea habitats are diverse due to varying ocean depths, polynyas, and an anticyclonic circulation pattern, which affect the spatial distribution of seals (Stirling, 2002) and prey species diversity (Yurkowski et al., 2019). The bearded seal (*Erignathus barbatus*), another important prey species, is a benthic-focused predator that most commonly occurs over shallow shelf water. As a result, bearded seal density is likely higher over continental shelves compared to deeper basin regions of the Beaufort Sea. Remains of subsistence-harvested bowhead whales (*Balaena mysticetus*) are available to polar bears that summer on land in the Alaskan Beaufort Sea. These carcasses provide a predictable food resource not available in the Canadian Beaufort Sea (Schliebe et al., 2008; Wilson et al., 2017; Figure 1). In addition to differences in prey availability, the two populations have followed different trends in abundance. The NB population was stable during 1971–2006 despite sea ice loss (Stirling et al., 2011), whereas the SB population had low survival during 2003–2006, resulting in a 25%–50% decline in abundance (Bromaghin et al., 2015, 2021). Ringed seals are the primary prey of polar bears in the Beaufort Sea (Boucher et al., 2019b; Bourque et al., 2020; McKinney et al., 2017) and had periods of low productivity, as evidenced by low ovulation rates and a low proportion of pups in the 2003–2005 harvest (Harwood et al., 2012; Nguyen et al., 2017). Thus, patterns in prey species occurrence and prey condition and productivity may be affecting regional polar bear population dynamics (Rode, Regehr, et al., 2021).

Diets have been estimated for Beaufort Sea polar bears but only for portions of the region (i.e., the Alaskan or Canadian portion of the SB only or the Canadian Beaufort with or without the NB; e.g., Boucher et al., 2019b; Florko et al., 2020; McKinney et al., 2017). Various tissues have been used for dietary inference that correspond to different seasonal dietary windows (e.g., hair, fat, and blood). In addition, estimation of diet contributions has largely focused on tracking either dietary protein (i.e., stable isotopes) or lipid sources (i.e., fatty acids). Estimating diets by tracing specific macronutrients can bias estimates of prey species contributions due to variations in prey body size and associated differences in ratios of consumed protein to lipid (i.e., bears consuming more blubber from larger bodied species; Cherry et al., 2011). Thus, it is difficult to compare diet estimates across studies or in relation to other aspects of population demographics. Additionally, polar bears in the SB exhibit a dichotomy of summer behavior and habitat use that may affect diet and individual survival (Boucher et al., 2019b; Rogers et al., 2015; Ware et al., 2017; Whiteman et al., 2018). Between 2004 and 2014, 20% of SB polar bears spent an average of 60 days onshore during the summer when the continental shelf became ice-free (Atwood, Peacock, et al., 2016; Pongracz & Derocher, 2017). Bears of all sex and age classes summer onshore and feed on bowhead whale remains left by subsistence hunters in three communities on the Alaskan Beaufort Sea coast (Figure 1; Miller et al., 2015; Schliebe et al., 2008; Wilson et al., 2017). Alternatively, bears that remain with the pack ice continue to consume primarily ringed seals. However, telemetry data show that very few ringed seals follow the pack ice beyond the shelf break (Von Duyke et al., 2020) such that access to seals is likely reduced as ice retreats farther north into deeper, offshore waters well beyond the continental shelf (Von Duyke et al., 2020; Ware et al., 2017; Whiteman et al., 2018).

The goals of this study were to determine whether the percentage of blubber in the diet (as an indicator of diet energy density and prey availability) was stable with changes in prey species composition (i.e., does adaptive prey switching occur) and associated with differences in polar bear survival and summer habitat use (i.e., habitat used during the September sea ice minimum). We used carbon and nitrogen stable isotopes in polar bear guard hair collected from the two Beaufort Sea populations over 13 years. We also used prey muscle and blubber samples from the same region and period to generate quantitative diet estimates of prey species composition and dietary blubber proportions (Rode, Robbins, et al., 2021; Stricker et al., 2022). We used hair because it represents a large seasonal dietary window (primarily spring to fall; see additional details in the *Methods* section about
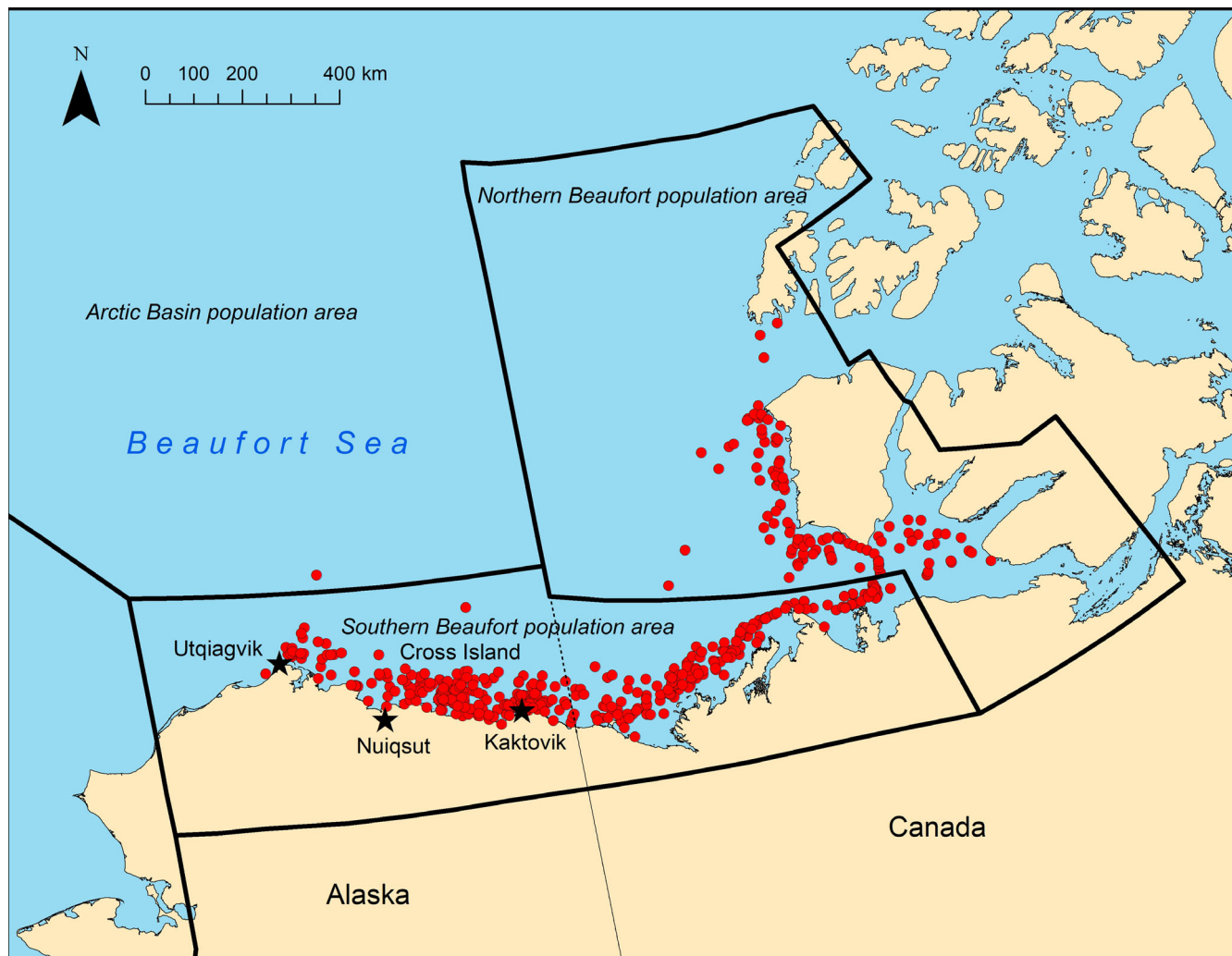
FIGURE 1 Locations of polar bears captured and sampled in the Beaufort Sea. Polar bear locations are shown as red circles. The southern and northern Beaufort Sea and Arctic Basin population boundaries (black lines) are shown as they were defined by the International Union for the Conservation of Nature's Polar Bear Specialist Group during the period of data collection (≤2016). The three study areas included the Alaskan portion of the southern Beaufort Sea population, the Canadian portion of the southern Beaufort Sea population, and the northern Beaufort population. The dashed line shows the international boundary that defined the Alaskan and Canadian southern Beaufort study areas. Polar bears have access to the remains of bowhead whales left by subsistence hunters in Utqiaġvik and Kaktovik and on Cross Island by hunters from Nuiqsut (starred locations). Samples were collected in the Canadian Beaufort Sea, primarily during 2004–2006, whereas samples were collected in the Alaskan Beaufort Sea during 2004–2016.

represented timeframes), and the necessary data on isotopic discrimination were available to support diet modeling (e.g., Rode et al., 2016; as opposed to bone collagen, which would potentially represent lifetime diet, but in that case sufficient data on isotope discrimination in bears are lacking). Specifically, our objectives were to compare diet estimates (as described in detail in Table 1) between (1) polar bears sampled in the Alaskan portion of the southern Beaufort Sea population (Alaskan SB; Figure 1) during years of low and high survival based on Bromaghin et al. (2015, 2021), (2) adult female polar bears in the Alaskan SB fit with satellite-linked radio collars that summered on land and those that summered on pack ice, and (3) polar bears sampled in three regions in

the Beaufort Sea—the Alaskan SB, the Canadian portion of the southern Beaufort Sea population (Canadian SB), and the northern Beaufort Sea (NB) population—which correspond to common separations used in analyzing the demography, behavior, and ecology of bears in this region (Figure 1).

METHODS

Polar bear hair sampling

Guard hair was collected from polar bears encountered throughout the SB and NB populations (Figure 1) during

T A B L E 1 Description of data used in stable isotope mixing models to address each study objective.

Objective	Location[a]	Years	*n*	Sex/age of bears in sample[b]	Season of polar bear sampling	Factor of interest[c]	Additional covariates[d]
1: Compare diet between years with high and low survival	Alaskan southern Beaufort	2004–2016	229	Adult males and females	Spring only	*LagSurvival and Survival*	*Sex, AgeClass*
2: Compare diet between females that summered on land versus pack ice	Alaskan southern Beaufort	2004–2016	102	Adult females only	Spring, summer and fall	*Habitat*	*Season, AgeClass*
3: Compare diet across three regions in Beaufort Sea	Alaskan and Canadian northern and southern Beaufort	2004–2006	274	Adult males and females	Spring only	*Region*	*Sex, AgeClass*

Note: Prey species, tissues, and sample sizes used in diet models are provided in Appendix S4: Table S2.

[a]Location is area from which polar bears were sampled.

[b]*AgeClass* was included as a binary variable identifying younger (age = 5–10 years) and older adult (age > 10 years) bears.

[c]*Survival* and *LagSurvival* were binary variables categorizing hair samples as collected during or before a year with high or low survival rates as reported in Bromaghin et al. (2015, 2021). *Habitat* was a binary variable indicating whether a satellite-linked radio-collared female summered on land or on pack ice. *Region* was a categorical variable identifying whether a bear ranged or was sampled in the Alaskan southern Beaufort Sea, the Canadian southern Beaufort Sea, or the northern Beaufort Sea.

[d]*Season* was a categorical variable, where spring = March–May, summer = August, and fall = September–October.

capture-based sampling in the United States (Alaska) (Rode et al., 2017) and Canada (Boucher et al., 2019a). In Alaska, guard hair was plucked with the root intact from the upper forelimb, hindlegs, or rump from March to May during 2004–2016 and August–October during 2008–2010. In Canada, polar bears were sampled from March to May during 2004–2006. Although some sampling occurred after 2006, sample sizes were substantially smaller. Therefore, analyses to address Objective 3 (regional variation) used only samples collected during 2004–2006 (Table 1). In Canada, hair was collected by shaving guard hairs from the skin of the rump beside the tail using a scalpel (Boucher et al., 2019a).

Polar bear capture and handling in Alaska followed protocols approved under U.S. Fish and Wildlife Service research permit MA 690038 and the U.S. Geological Survey's Institutional Animal Care and Use Committee. In Canada, polar bear capture and handling were approved under the Environment and Climate Change Canada Western and Northern Animal Care Committee and the University of Alberta BioSciences Animal Care and Use Committee.

Polar bears molt guard hair between June and August (Derocher, 2012; Rode et al., 2016), which is consistent with observations of grizzly bears (*U. arctos*) (e.g., Derocher, 2012; Erlenbach, 2020). Hair growth occurs primarily just prior to and during the molt and reflects the current diet (Erlenbach, 2020). Thus, guard hair used in our study represent the seasonal (not annual) assimilated diets of bears primarily from June through August, when they are actively feeding and, to a lesser extent, May, September, and October, when hair growth occurs at a slower rate (Boucher et al., 2019a; Erlenbach, 2020; Rogers et al., 2015). It is unknown whether polar bear hair continues to grow during the winter, but it has been assumed that any growth outside of the primary molt is at a reduced rate such that these seasons are minimally represented in hair (e.g., Boucher et al., 2019a; Rogers et al., 2015). Denning bears (i.e., pregnant females) are unlikely to invest resource in hair growth during the winter months, when they are fasting and need resources for reproduction and survival similar to hibernating grizzly bears (Erlenbach, 2020).

We considered the potential that Beaufort Sea polar bears that remain with the pack ice during the annual sea ice minimum, which occurs in September, may be fasting because of reduced access to prey (Whiteman et al., 2018), which could increase hair $\delta^{15}N$. However, available data (Appendix S1), including hair isotope data of fasting polar bears and grizzly bears (Rode et al., 2016), suggest that if fasting affects the $\delta^{15}N$ of bears that summer on the pack ice during the latter part of the hair growth period, the potentially slight increase (0.5‰) would be diluted in our analysis using full-length hairs (three to five times longer than the 3-cm section that might increase in $\delta^{15}N$). Thus, although it is possible that fasting could elevate the $\delta^{15}N$ of bears that summered on the pack ice in our study, we assumed that those effects would be minimal in affecting our dietary estimates.

Isotope composition of polar bear and prey tissues

Our diet model required measuring $\delta^{15}N$ and $\delta^{13}C$ values in bulk (nonlipid extracted) prey blubber and muscle separately (Rode, Robbins, et al., 2021; Stricker et al., 2022), whereas typically, stable isotopes in lipid-extracted muscle are used to represent prey for diet estimation. Thus, we generated a library of isotope values for both blubber and muscle of the four primary prey species of Beaufort Sea polar bears, identified in previous diet studies: ringed seals, bearded seals, beluga whales (*Delphinapterus leucas*), and bowhead whales (Boucher et al., 2019a, 2019b; Cherry et al., 2011; Florko et al., 2020; McKinney et al., 2017; Rogers et al., 2015; Thiemann et al., 2008). Our prey isotope library spanned the spatial and temporal scale of our analyses (i.e., during 2004–2016 and across the range of both populations). We obtained $\delta^{13}C$ and $\delta^{15}N$ values for a total of 353 prey samples analyzed from previous studies (Appendix S4: Table S2; Figure 2) (Bryan, 2014; Carroll, 2012; Cherry et al., 2011; Choy, 2017; Dehn et al., 2006, 2007; Horstmann-Dehn et al., 2012; Rogers et al., 2015), and we analyzed an additional 64 samples obtained from hunters in communities along the Beaufort Sea. Further details about samples included in the prey library, their origin, and the rationale for inclusion and exclusion of prey tissues are provided in Appendix S2.

Details of the laboratory procedures used to estimate carbon and nitrogen isotope composition in polar bear hair and prey blubber and muscle samples collected in Alaska were described in Rode, Robbins, et al. (2021) and Stricker et al. (2022). Briefly, polar bear hair was cleaned in a 2:1 chloroform and methanol solution and dried overnight. Prey muscle samples were analyzed without lipid extraction after freeze-drying, whereas blubber samples were separated into lipid and nonlipid portions for isotopic analysis. Relative proportions of fat and protein in blubber and carbon and nitrogen isotopic composition and concentrations in fat and protein were used to calculate "bulk" blubber isotopic composition (Rode, Robbins, et al., 2021; Stricker et al., 2022). Bulk blubber and bulk muscle were considered as separate diet items for each species. Elemental and isotopic composition of all tissues were measured using continuous flow isotopic ratio mass spectrometry (CF-IRMS) at several laboratories, which
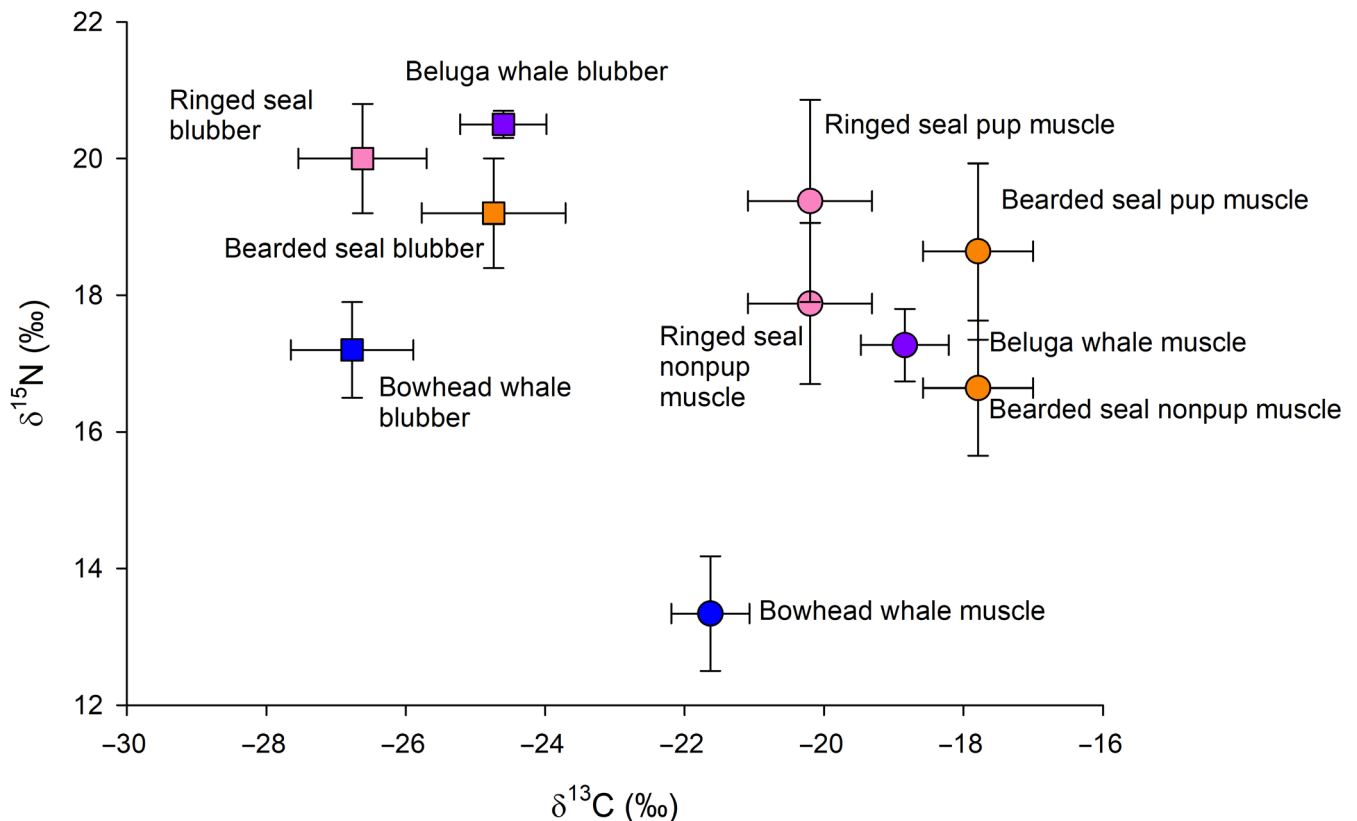
FIGURE 2 $\delta^{13}C$ and $\delta^{15}N$ values of muscle (circles) and blubber (squares) of polar bear prey sampled in Beaufort Sea. Prey tissue values are means ± 1 SD. A total of 396 samples were collected during 2004–2016 from subsistence-harvested marine mammals and polar bear kill sites. Values for each prey species are represented by a different color (ringed seal = pink, bearded seal = orange, beluga whale = purple, and bowhead whale = blue). Samples sizes for each prey tissue are provided in Appendix S4: Table S2.

followed similar normalization methods and had comparable accuracy and precision. Analyses of hair and prey samples collected in the Canadian Beaufort are described in Cherry et al. (2011) and Boucher et al. (2019a, 2019b). Additionally, estimations of $\delta^{15}N$ and $\delta^{13}C$ in the muscle of some prey included in diet models are described in Dehn et al. (2006, 2007), Horstmann-Dehn et al. (2012), and Choy (2017). For Objective 3, prey data were subsampled to match the specific timeframe of analysis as described in what follows. For all three objectives, prey muscle and blubber lipid isotope values were more readily available than blubber protein, resulting in sample size ranges of 32–100 and 9–38, respectively, across the four species (Appendix S4: Table S1). All blubber nonlipid values were obtained via species-specific sample collection and analysis resulting in sample sizes of three to six per species (Appendix S4: Table S2). Because the timeframe of our study was short (13 years) and we temporally matched prey and polar bear samples, we did not correct $\delta^{13}C$ values for changes in atmospheric CO_2 associated with increased anthropogenic fossil fuel emissions (i.e., the Suess effect; Dombrosky, 2019).

Diet modeling approach

Diets were estimated using the Bayesian stable isotope mixing model framework MixSIAR. Our three study objectives could not be addressed in a single analysis because summer habitat use was only known for a subset of adult females fitted with satellite collars (Objective 2) and sample sizes across the three regions were sufficient only for comparison during 2004–2006 (Objective 3). To address Objective 1, we needed a longer time series of diet with paired data on survival probabilities that were only available in 2004–2016 for Alaskan SB bears. The same MixSIAR model structure and trophic enrichment factors (TEFs) were used to address all three objectives as applied in Rode, Robbins, et al. (2021) and Stricker et al. (2022).

Prey values were input in diet models as means and SD for each prey species tissue (i.e., muscle or blubber) rather than the raw data because similar diet estimation with MixSIAR (Stricker et al., 2022) showed that results were the same regardless of data input method. Further, individual proportion estimates were nearly identical, with one exception—seal pup muscle, which was attributed to a spurious correlation associated with small sample size (Stricker et al., 2022). We accounted for differences in the mass fraction of C and N in prey blubber and muscle via concentration dependence in the model by inputting the carbon and nitrogen concentrations of each prey tissue (Phillips & Koch, 2002; Stock

et al., 2018). The values used to account for variable mass fractions of C and N among tissues and species were the same in all models across all objectives. To account for the net isotopic effects associated with the metabolism, routing, and integration of dietary resources into hair, we used bulk TEFs derived for guard hair from polar bears in zoos fed a diet that mimicked the high-fat, carnivorous (i.e., protein and fat only), marine diet of free-ranging polar bears (Rode et al., 2016) corrected for differential carbon concentrations in dietary fat and protein as described and applied in Rode, Robbins, et al. (2021) (corrected TEFs were $\Delta^{13}C = 7.72 \pm 0.60‰$ and $\Delta^{15}N = 1.47 \pm 1.07‰$; mean $\pm$ SD). No other studies have reported TEFs for bulk diets. However, the TEF of a lipid-extracted diet containing terrestrial meat, dry chow, and fish fed to one adult female polar bear ($\Delta^{13}C = 2.5‰$, $\Delta^{15}N = 1.6‰$; L'Herault et al., 2018) was nearly identical to lipid-extracted TEFs for the four adult polar bears fed the marine-only, high-fat diet in Rode et al. (2016; $\Delta^{13}C = 2.4 \pm 0.8‰$, $\Delta^{15}N = 1.5 \pm 1.1‰$). To run the mixing models in MixSIAR, prey data were adjusted by the TEFs. The SD of the TEF was combined with the SD of the prey data to account for the uncertainty in TEFs when estimating diet proportions using the formula

$$\sqrt{\sigma^2_{\text{prey tissue}} + \sigma^2_{\text{TEF}}}$$

where σ represents the SD. We used the noninformative priors that are defaults in MixSIAR to allow for equal prior probabilities for all prey tissues. We simulated posterior distributions using three to five Markov chains (with a range of initial values), each consisting of 100,000 to 500,000 iterations depending on model complexity (i.e., the number of factors and covariates included) and diagnostic test results. We eliminated the first 50,000 to 300,000 iterations for burn-in and then thinned by a factor of 50–500 to 1. Convergence on the stationary distribution was assessed and confirmed by examining diagnostics, including the Gelman–Rubin and Geweke statistics in the MixSIAR output as well as by visually examining the mixing of chains, autocorrelation plots, and posterior distributions. In addition, estimates of the multiplicative error terms either were <1 or, if values exceeded 1, had 95% confidence intervals that included 1, which is consistent with mixing models that conform to the underlying assumptions (Stock et al., 2018).

For each objective, we ran a set of MixSIAR models (referred to as "candidate diet models"), which were determined a priori and included models with different combinations of variables (as identified in Table 1 for

each objective) that might be important in affecting diet. Models within each set of candidate models were compared using the deviance information criterion (DIC) consistently with the application of a Bayesian model where distributions are obtained by Markov chain Monte Carlo simulation (Spiegelhalter et al., 2002). We focused our interpretations on the most supported models (i.e., models with $\Delta DIC \leq 2.0$). For the model with the lowest DIC in each model set (i.e., most-supported model), we report the diet proportion estimates and SD for individual diet components rounded to the whole number. We refer to the diets estimated from isotopic composition of polar bear hair as "assimilated diet" to acknowledge that tissue-based molecular estimates of diets reflect prey resources that are consumed, digested, and metabolized to meet energetic and nutritional needs (Pecquerie et al., 2010; Robbins et al., 2005). When percentage contributions were <2, we reported to the tenths. Because ringed seals are the primary prey of polar bears in this region, we report the percentage of ringed seals consumed as blubber as a potential indicator of ringed seal availability.

We aggregated dietary components a posteriori in two scenarios: (1) to estimate the total blubber and muscle contributions to polar bear diets from all prey species and (2) to estimate the total blubber of seal pups (nursing or recently weaned with enriched tissue isotopes from nursing) and nonpups (all nonnursing ages) for each seal species because they could not be distinguished isotopically (see details in Appendix S3; Appendix S4: Table S2). Prey tissue estimates were aggregated using the combine_sources function in MixSIAR (Stock et al., 2018). Muscle tissues of pups and nonpups were not aggregated because nursing pups had enriched $\delta^{15}N$ in muscle (Rode, Robbins, et al., 2021; Stricker et al., 2022; Young et al., 2010). None of the other prey tissues included in the model exhibited complete overlap in both $\delta^{15}N$ and $\delta^{13}C$ (Figure 2), precluding further aggregation. Aggregating typically reduces the SD associated with the proportion estimate for the combined diet components, particularly when many components are combined, as is the case for the blubber/muscle grouping (Stock et al., 2018). Whereas the SDs of blubber and muscle diet proportions were substantially reduced due to aggregating, that was less the case for aggregated estimates for each seal species. As a result, we focus our interpretations on the dietary differences in total percentage of blubber and muscle contributed from all species in the diet that had lower SDs. We cautiously interpreted estimated individual prey tissue proportions in the diet and aggregated proportions from seal species due to their relatively large SDs. However, where model results indicate that diets differed for a covariate (i.e., high vs. low survival years), we considered the potential that some of the differences in diet were biologically meaningful. We further considered where our results diverged or were consistent with previous diet estimates or expected prey species availability in interpreting our results.

Objective 1: Comparing diet between years with low and high survival rates

Diets of adult bears of both sexes ($n = 248$) sampled in spring during 2004–2016 in the Alaskan SB (Figure 1) were compared with years identified as having high or low survival rates by including a binary survival variable in candidate models (i.e., low or high survival) (Table 1). Survival rates estimated by Bromaghin et al. (2015, 2021) were used to categorize each year as either high or low survival. The years 2004 to 2008 and 2012 were defined as low survival years (and all others were high survival years) based on cub survival probabilities of <0.50, yearlings and 2-year-old survival probabilities of <0.75, and adult male and female survival probabilities of <0.90 estimated from the spring of year t to the spring of year $t + 1$ (Bromaghin et al., 2015, 2021). Reported average survival rates of these demographic groups are consistently higher than what we categorized as "low" survival years across most, if not all, polar bear populations (see table S1 in Regehr et al., 2017). Survival below these thresholds was associated with population decline in the Alaskan SB (Bromaghin et al., 2015). Only hair samples collected in spring were used for Objective 1. We assigned survival rates (i.e., low or high survival year) to hair collected in spring of year t noting that this hair grew from late spring to late fall in year $t - 1$.

We hypothesized that diets would have the greatest impact on survival of all sex and age classes the year following consumption because bears would start the year during which survival was measured with either lower or higher body condition. Female body condition affects the size of cubs produced while denning (Derocher & Stirling, 1998), which subsequently affects cub survival (Derocher & Stirling, 1996; Rode et al., 2020). Thus, adult female body condition before den entrance (year $t - 1$) could be reflected in survival probabilities of cubs during the year after diet is consumed (year t). Similarly, adult female body condition associated with the diet measured in hair grown in year t could be reflected in the survival probabilities of their yearlings, and 2-year-old cubs in the subsequent year. We therefore compared diet models that included survival, with or without a lag effect (i.e., a categorical variable of high and low survival as either *Survival* or *LagSurvival*).

We compared candidate models that estimated diets including survival as a binary variable alone or in combination with sex or age class (Table 1), as either a lagged effect (*LagSurvival*) or nonlagged effect (*Survival*) (Appendix S4: Table S3). Age class (*AgeClass*) was a binary variable identifying young adults 5–10 years old and old adults >10 years and was included separately and as an interaction with *Sex*. No subadults (bears <5 years old) were included in analyses. We compared candidate models (Appendix S4: Table S3) with all combinations of *Sex*, *AgeClass*, and either *Survival* or *LagSurvival*.

In addition to using stable isotopes to examine variation in prey and macronutrient composition of bear diets between high and low survival years, we also used an existing data set on the spring feeding behavior of bears (United States Geological Survey, 2017) sampled in the Alaskan SB during 2003–2016 to determine whether variation in predation success followed patterns observed for dietary blubber content (i.e., if periods with reduced dietary blubber proportions were concurrent with periods of less frequent predation events). In a previous study (Rode et al., 2017), serum urea and creatinine levels measured in bears sampled in the spring were used to determine the probability that a bear had not fed during the 7–10 days before sampling in mid-March to early May. Using this data set, we compared probabilities of having not recently fed (calculated as a continuous variable of fasting probability from 0 to 100) between years with low and high survival, as both a lagged and nonlagged effect (Rode et al., 2017), using a general linear model (i.e., with *Survival* or *LagSurvival* and *Sex* as factors) in IBM SPSS statistical software version 28.0.0.0. The short-term fasts represented in these data are not indicative of extended fasts that would potentially elevate hair $\delta^{15}N$ (as discussed previously).

Objective 2: Comparing diet between females that summered on land or pack ice

We compared diets between adult females fitted with satellite collars in the Alaskan SB ($n = 102$) that summered on land to those that summered on pack ice during 2004–2016 (Table 1). Females were identified as summering on land if they spent ≥21 days on land between August and October, consistent with previous categorizations of summer habitat use of polar bears in this region (Atwood, Peacock, et al., 2016; Rode et al., 2015). This designation attempted to identify bears that spent long periods of time on land in response to the retreat of pack ice away from land during the summer months. Details of summer habitat designations are further described in Appendix S2. Our sample only included adult females because adult males were not collared as their necks are larger than their heads, which reduces collar retention. We did not collar subadults because they are growing, which could result in injury as their necks become larger. Bears that summer on land have access to the remains of subsistence-harvested bowhead whales (Atwood, Peacock, et al., 2016; Pongracz & Derocher, 2017) and often range more coastally than bears that remain with the pack ice during the summer (Boucher et al., 2019b; Schliebe et al., 2008). As a result, they may have access to prey that differ from bears that remain on sea ice year round.

Summer habitat was included as a binary variable (*Habitat*) in mixing models to address Objective 2, using the same prey data described for Objective 1 (Table 1). We also included *Season* as a categorical variable in candidate models because bears in this data set were sampled in three different time periods: spring (March–May), summer (August), and fall (September/October). Spring-sampled hair ($n = 65$ with 31% summering on land) reflected diet during the previous hair growing season ($t − 1$), whereas summer and fall hair samples ($n = 37$ with 80% summering on land) represented growth that occurred during year t up to the timing of sampling. Because this analysis included only adult females, which reach maximum body size at adulthood, we did not include an *AgeClass* variable because previous analyses had suggested minimal to no dietary variation among adult females (Stricker et al., 2022). Candidate models (Appendix S4: Table S5) were compared using DIC values as described under Objective 1. Because sample sizes across the six combinations of seasons and habitat were unbalanced, we did not include a candidate model with an interaction between *Season* and *Habitat*.

Objective 3: Regional variation in diet

We investigated whether diets differed among adult male and female bears captured during the spring from (1) the Alaskan SB; (2) the Canadian SB; and (3) the NB (Figure 1; $n = 49$ Alaskan SB, $n = 139$ Canadian SB; $n = 86$ NB; Table 1). Polar bear hair samples were available in sufficient sample sizes with matching sex/age classes across all three regions during 2004–2006. Therefore, we restricted the available prey data to include only samples collected during this period ($n = 134$).

Bears were assigned to each region (categorical variable *Region*) based on either (1) the population boundary in which the majority (>50%) of available satellite-telemetry locations occurred (described in Rode et al., 2017) or (2) in the absence of satellite telemetry data,

their capture location. Some bears occupying the SB population also range north of the International Union for the Conservation of Nature's (IUCN) population boundary and into the region identified as the Arctic Basin population. These bears had all been captured within either the NB or SB population boundaries and were assigned to a region based on where the majority of their locations occurred outside of the Arctic Basin boundary (Rode et al., 2017). We used polar bear population boundaries as defined by the IUCN Species Survival Commission's Polar Bear Specialist Group during the period of data collection through 2016 (Figure 1). *Sex* was included as a binary variable in candidate models (Appendix S4: Table S6). *AgeClass* was not included because the results from Objective 1 indicated that this variable was not important in identifying dietary variation.
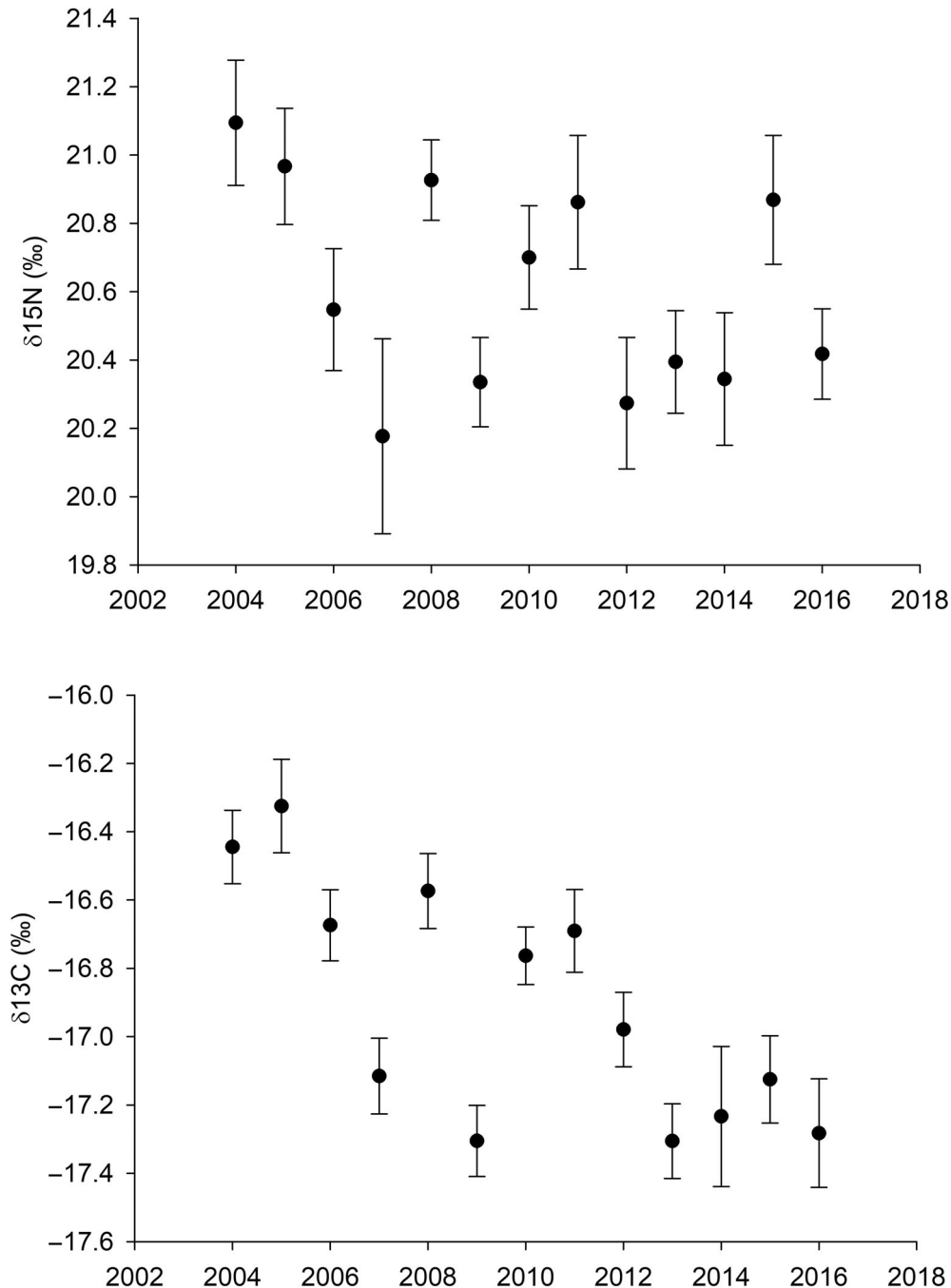
FIGURE 3 Annual variation in $\delta^{13}C$ (‰, relative to standard V-Pee Dee Belemnite) and $\delta^{15}N$ (‰, relative to air as a standard) in guard hair of male and female polar bears in Alaskan southern Beaufort Sea during 2004–2016. The years 2004–2008 and 2012 were defined as low survival years (and all others were high survival years) based on Bromaghin et al. (2015, 2021).
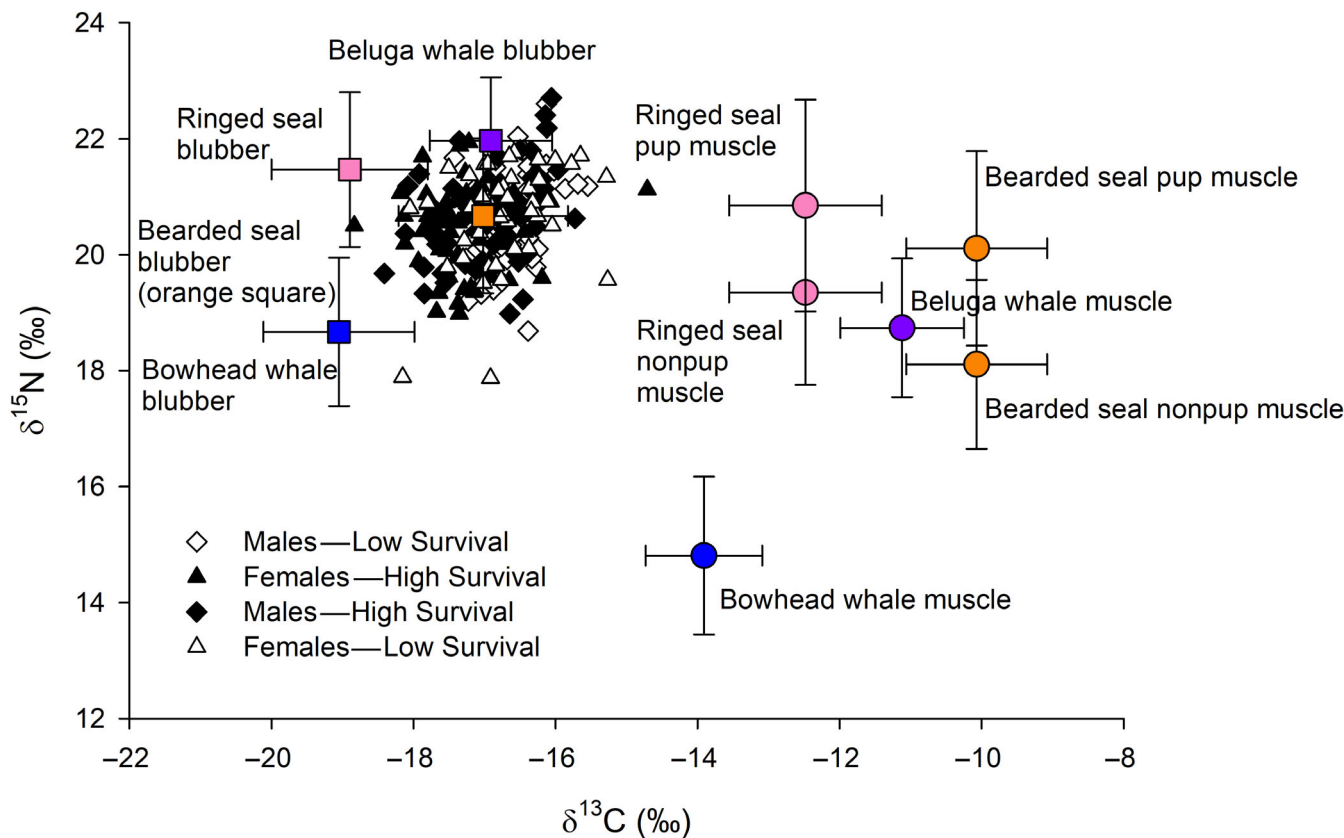
FIGURE 4 δ15N and δ13C in guard hair of adult male and female polar bears sampled in the Alaskan southern Beaufort Sea during 2004–2016 relative to isotopic values (mean and SD) of prey muscle (circles) and blubber (squares) used to address Objective 1. Prey values were corrected for trophic enrichment factors (TEFs) measured from captive feeding trials (Rode et al., 2016) and error bars represent ±1 SD associated with both TEF values and variation among individual prey samples. Hair samples were grouped to compare diets during the years before low and high survival rates based on Bromaghin et al. (2015, 2021). Values for each prey species are represented by a different color (ringed seal = pink, bearded seal = orange, beluga whale = purple, and bowhead whale = blue).

RESULTS

Objective 1: Comparing diet between years with low and high survival rates

The most supported diet model for Objective 1 included *LagSurvival* as an interactive effect with *Sex* (*LagSurvival* × *Sex*) (Appendix S4: Table S3; Figures 3 and 4). The second and third most-supported models were the additive *LagSurvival* + *Sex* model (ΔDIC = 2.3) and the univariate *LagSurvival* model (ΔDIC = 2.8). The univariate *Sex* model had little support relative to the top model (ΔDIC = 23.9) and similarly was not much of an improvement over the no-covariate model (ΔDIC = 26.6). These results indicate that the *LagSurvival* term was the most important covariate and the *Sex* effect was less important. All models with *Survival* rather than *LagSurvival* had ΔDICs >24.3.

We recognized that the dietary differences observed between years with low and high polar bear survival rates could be affected by differences in the isotopic composition of prey tissues during those periods, particularly if variability in polar bear diets reflected food web differences (i.e., prey species altering diets or consuming diets that differed isotopically). Therefore, after determining that *LagSurvival* was an important factor affecting diet, we compared the isotopic concentration of prey tissues between years with lagged low and high polar bear survival rates using ANOVAs (Figure 5). We did not use separate prey data sets to address Objective 1 initially because we wanted to ensure that we did not generate dietary differences solely by using different isotopic values for the prey. Because δ13C and δ15N did differ for some prey tissues (Figure 5), we examined models in which the prey data were specific to the high and low lagged survival years (i.e., rather than having a single prey data set for both categories of survival). We estimated diet composition for models including *LagSurvival* alone or in combination with *Sex*. It was not possible to consider a *LagSurvival* × *Sex* model in MixSIAR (which was the top model when a single prey data set was used)
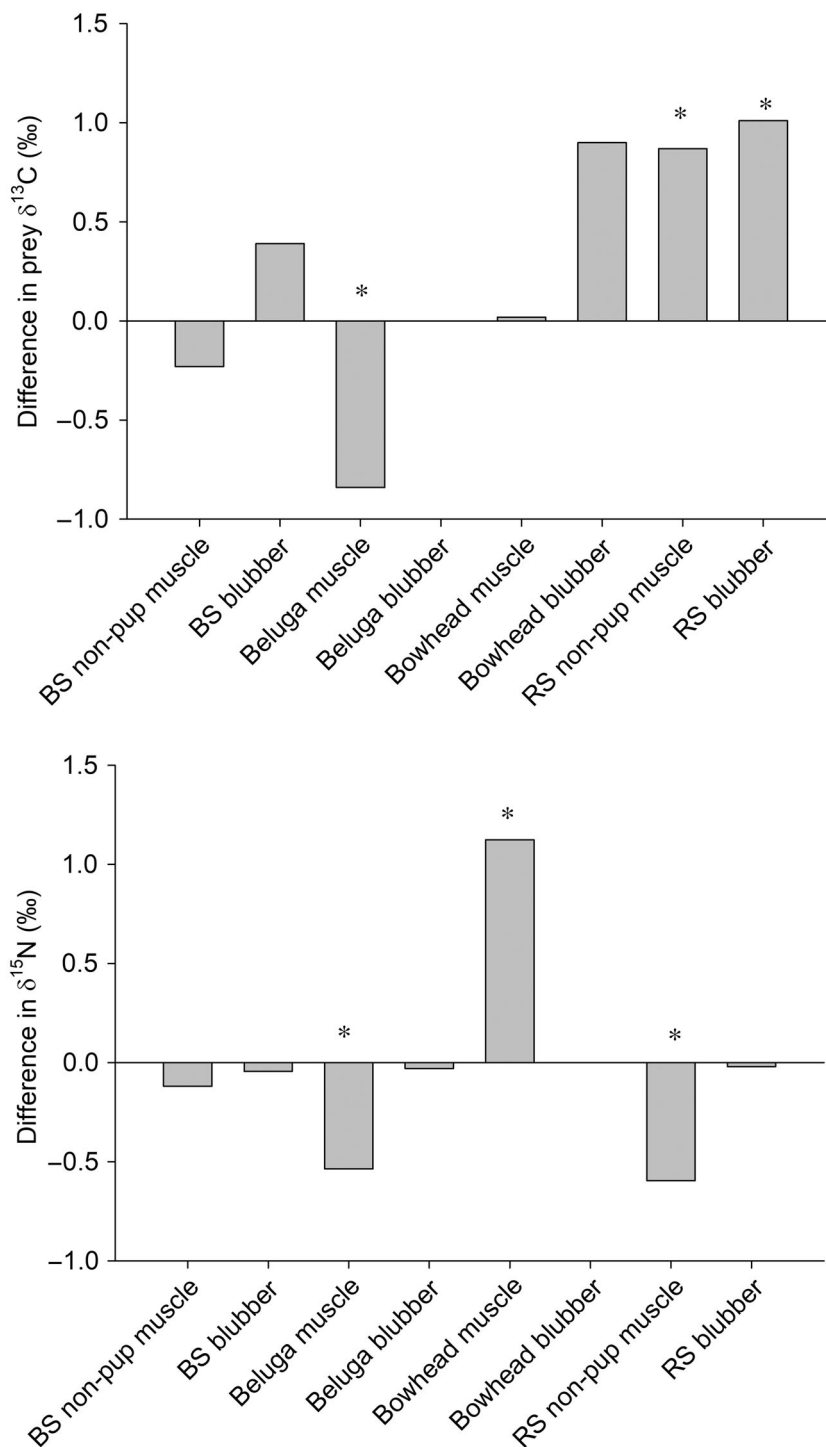
FIGURE 5 Differences in polar bear prey $\delta^{13}C$ and $\delta^{15}N$ values between years with high and low polar bear survival. Positive values indicate that the prey isotope value was higher during years when polar bears had high survival rates; negative values indicate the prey isotope value was lower when polar bears had lower survival rates. BS = bearded seal, beluga = beluga whale, bowhead = bowhead whale, and RS = ringed seal. Asterisks denote differences significant at $p < 0.05$.

when the prey data associated with the *LagSurvival* categories differed. Similar to the results for Objective 1 using a single prey data set, when using separate prey data sets for the two survival periods, the model including

LagSurvival + Sex had the lowest DIC followed by the univariate *LagSurvival* model ($\Delta DIC = 1.94$). Because dietary differences between males and females were of biological interest, we focused on the results of the model

TABLE 2 Estimated percentage contributions of prey muscle and blubber of four prey species (ringed seals, bearded seals, bowhead whale, and beluga whale) to assimilated diets of adult male and female polar bears during years before high or low survival rates were observed in Alaskan southern Beaufort Sea 2004–2016 (Objective 1).

| Tissue and species	Females[a]			Males[a]		
	High survival year ($n = 63$)	Low survival year ($n = 48$)	Difference high − low	High survival year ($n = 66$)	Low survival year ($n = 52$)	Difference high − low
Muscle						
Ringed seal pups	9 (4)	15 (10)	−6	10 (6)	16 (9)	−6
Ringed seal nonpups	1.2 (1.2)	1.4 (2.1)	−0.2	1.0 (1.3)	1.4 (2.4)	−0.4
Bearded seal pups	3 (3)	4 (6)	−1	4 (4)	5 (6)	−1
Bearded seal nonpups	0.8 (0.8)	0.7 (1.0)	0.1	0.6 (0.8)	0.7 (1.1)	−0.1
Bowhead whale	0.4 (0.4)	0.3 (0.5)	0.1	0.3 (0.4)	0.3 (0.5)	0
Beluga whale	1.0 (0.9)	1.0 (1.5)	0	0.8 (1.0)	1.0 (1.6)	−0.2
Total muscle	15 (5)	22 (11)	−7	16 (7)	24 (9)	−8
Blubber						
Ringed seal	39 (12)	24 (13)	15	36 (14)	23 (12)	13
Bearded seal	21 (12)	24 (18)	−3	19 (13)	18 (13)	1
Bowhead whale	11 (10)	7 (8)	4	9 (10)	7 (8)	2
Beluga whale	13 (10)	23 (23)	−10	19 (16)	28 (20)	−9.0
Total blubber	85 (5)	78 (11)	7	84 (7)	76 (9)	8
Total ringed seal	49 (13)	40 (19)	9	47 (16)	40 (17)	7
Percentage of ringed seal as blubber	80 (11)	61 (18)	20	76 (13)	58 (18)	19
Total bearded seal	25 (11)	29 (18)	−4	23 (13)	23 (14)	0
Percentage of bearded seal as blubber	82 (15)	83 (22)	1	77 (20)	74 (24)	4

[a]Separate prey data sets were used to match the years of data categorized as high and low survival years. Percentage contributions of prey tissues are provided with 1 SD in parentheses. Diet was estimated with stable isotope mixing models implemented in MixSIAR using stable carbon and nitrogen isotope composition in prey tissues (means and 1 SD) and polar bear hair. Results are based on diet estimated from the most-supported model (i.e., lowest deviance information criterion, Appendix S4: Table S3), which included an interaction between *LagSurvival* (survival at year $t + 1$) and *Sex*.

with the lowest DIC that included *Sex* (Table 2). In the year before years with high survival, males and females consumed more blubber (8 and 7 percentage points [pp] for males and females, respectively) than before years with low survival. This difference was primarily a result of reduced proportions of ringed seal muscle (6 pp for both males and females) and higher proportions of ringed seal blubber (13 and 15 pp for males and females, respectively) consumed before years with high survival (Table 2). Male and female polar bears consumed 76% and 79% of ringed seals as blubber, respectively, before high survival years compared to 58% and 61% before low survival years. Diet estimates using a single data set, rather than separate prey data sets, for high and low survival years also exhibited lower proportions of total dietary blubber (8 and 7 pp for males and females, respectively) before low versus high survival years (Appendix S4: Table S4).

Spring fasting probabilities differed between years with high and low survival only when survival was included as a lag effect (general linear model with sex: $F_{1,555} = 6.6$, $p = 0.01$) and not in the absence of a lagged effect with survival ($F_{1,555} = 0.79$, $p = 0.38$). Before years with high survival, the probability that a female was fasting was 10.4 ± 0.0 (SE) pp lower (34.2% probability) than before years with low survival (44.6%). Similarly, the probability of fasting in males was 5.3 ± 0.5 pp lower (63%) before years with high survival compared to lagged years with low survival (68%).

Objective 2: Comparing diet between females that summered on land or pack ice

The most supported model contained only the summer habitat variable (*Habitat*; Appendix S4: Table S5; Figure 6).
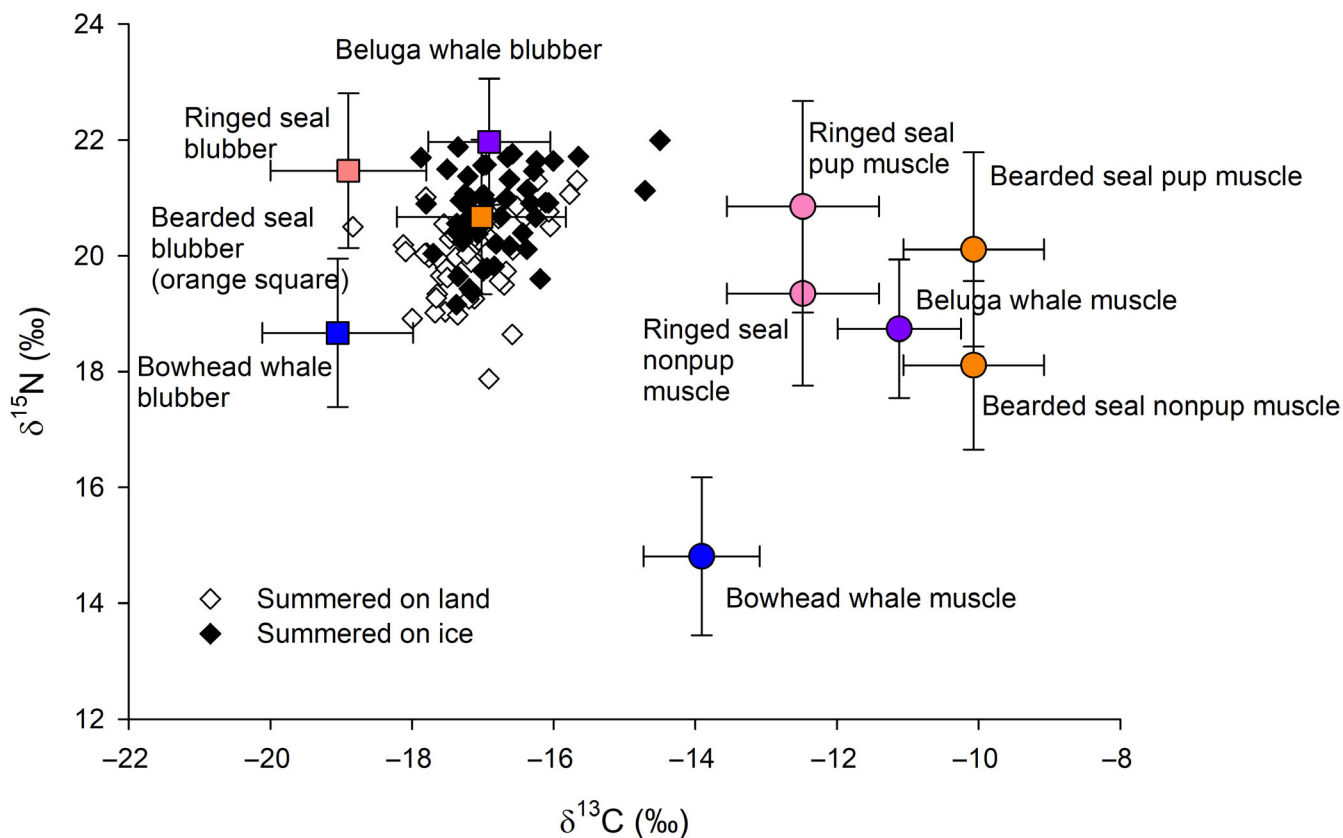
FIGURE 6 $\delta^{15}N$ and $\delta^{13}C$ in guard hair of female polar bears sampled during 2004–2016 in Alaskan southern Beaufort Sea that spent ≥ 21 days on land during summer ("summered on land") compared to those that remained with pack ice ("summered on ice") relative to mean and SD of isotopic values of prey muscle (circles) and blubber (squares) used to address Objective 2. Prey values were corrected for trophic enrichment factors (TEFs) measured from captive feeding trials (Rode et al., 2016); error bars represent ±1 SD associated with both TEF values and variation among individual prey samples. Values for each prey species are represented by a different color (ringed seal = pink, bearded seal = orange, beluga whale = purple, and bowhead whale = blue).

Bears that summered on land consumed more total blubber (7 pp), less ringed seal pup muscle (10 pp), and more blubber from each of the four prey species (Table 3). Bears that summered on the pack ice consumed 57% of ringed seals as blubber, whereas bears summering on land consumed 71% as blubber. The amount of bowhead whale blubber in the diet of bears that summered on land did not differ from that of bears that summered on pack ice (SD of dietary proportion overlapped; Table 3).

Objective 3: Regional variation in diet

The most-supported models included *Region* with *Sex* either as an additive (top model) or interactive effect (ΔDIC = 1.9) (Appendix S4: Table S6; Figure 7). We examined diets based on results from the top model (Table 4). Female bears in the Alaskan SB consumed 11 and 9 pp less blubber than females in the Canadian SB and NB populations (65% vs. 76% and 74%, respectively;

Table 4). Male bears in the Alaskan SB also consumed 7 and 3 pp less blubber than in the Canadian SB and NB, respectively (Table 4). Differences in the percentage of blubber in regional diets were largely driven by differences in the proportion of ringed seal blubber, which was 15 pp higher for females and 7 pp higher for males in the NB compared to the Alaskan SB. Bearded seal contributed 9 and 8 pp more to the diets of females and 5 and 6 pp more to the diets of males in the Alaskan and Canadian SB than in the NB, respectively (Table 4). Samples sizes of prey stable isotope data were insufficient to generate separate prey data sets to model the diets of the three regions.

DISCUSSION

Our results suggest that polar bears in the Beaufort Sea continue to maintain a strong predator–prey relationship with ringed seals, in contrast to other parts of the

TABLE 3 Estimated percentage contributions of prey muscle and blubber of four prey species (ringed seal, bearded seal, bowhead whale, and beluga whale) to assimilated diet of adult female polar bears in Alaskan southern Beaufort Sea that summered on land (≥21 days on land) versus those that summered on pack ice during 2004–2016 (Objective 2).

Tissue and species	Summer ice (n = 52)[a]	Summer land (n = 50)[a]	Difference ice − land
Muscle			
Ringed seal pups	18 (6)	8 (4)	10 (5)
Ringed seal nonpups	3 (3)	4 (4)	−1 (3)
Bearded seal pups	4 (4)	4 (4)	0 (4)
Bearded seal nonpups	1.5 (1.4)	2.0 (2.3)	−0.5 (1.8)
Bowhead whale	0.8 (0.8)	1.1 (1.3)	−0.3 (1.0)
Beluga whale	1.9 (1.6)	2.5 (2.8)	−0.6 (2.2)
Total muscle (percentage of diet)	29 (5)	21 (6)	8 (5)
Blubber			
Ringed seal	28 (11)	30 (14)	−2 (10)
Bearded seal	20 (11)	21 (13)	−1 (11)
Bowhead whale	12 (9)	14 (12)	−2 (9)
Beluga whale	12 (10)	14 (13)	−2 (10)
Total blubber (percentage of diet)	72 (5)	79 (6)	−7 (5)
Total ringed seal	49	42	7 (12)
Percentage of ringed seal as blubber	57	71	−14 (13)
Total bearded seal	25.5	27.0	−1.5 (11)
Percentage of bearded seal as blubber	78	78	0 (16)

[a]Mean diet percentages are provided with 1 SD in parentheses. Results are based on diet estimated from the most-supported model, which included only *Habitat* (Appendix S4: Table S5) using carbon and nitrogen stable isotope mixing models as implemented in MixSIAR with prey tissues (mean ± 1 SD) and polar bear hair.

Arctic, where a weakening of this relationship may have occurred (i.e., Hamilton et al., 2017; Yurkowski et al., 2020). The lowest dietary blubber proportion in any diet was that of bears in the Alaskan SB during 2004–2006 (Objective 3), when survival rates were lower than any other time during the 2001–2016 study period. This 3-year period coincided with low ringed seal productivity (Harwood et al., 2012; Nguyen et al., 2017), reduced polar bear kill rates (Pilfold et al., 2015), and reduced consumption of ringed seals (Boucher et al., 2019a). The proportion of ringed seals in the diet that was consumed as blubber (rather than muscle) by Alaskan SB polar bears declined from ~80% to 60% between years with high and low survival, respectively. In addition, the prevalence of fasting in spring (having not fed in the past 7–10 days based on serum urea and creatinine data) in the Beaufort Sea was lower during years with high survival compared to years with low survival (Rode et al., 2017). Consistency between dietary blubber proportions and patterns in short-term fasting indicate that blubber proportions in the diet were at least partially reflective of variation in prey availability (i.e., bears were feeding less frequently) and not only prey body condition. Although our data suggest that Alaskan SB polar bears may have assimilated more beluga whale in their diets during periods of low survival, it is unlikely they were able to offset the low energy density diet via increased food intake given that beluga whales are both less common and more difficult to catch due to their large size. Further, some evidence suggests that similar patterns of declining body condition of ringed seals and beluga whales in the Beaufort Sea are associated with their shared dietary preference for Arctic cod (*Boreogadus saida*) (Harwood et al., 2015). In our study, $\delta^{15}N$ was lower in beluga whales and ringed seals and higher in bowhead whales during years in which polar bears exhibited high survival (Figure 5). These patterns suggest that changes in the food web during high and low polar bear survival years affected plankton-dependent and fish-dependent food webs differently. Our results and those of others (Boucher et al., 2019a, 2019b; Florko et al., 2020; Stirling et al., 1977) indicate that Beaufort Sea polar bears both historically and presently rely heavily on ringed seals and may be limited in their ability to switch prey to offset energy intake loss during periods of low ringed seal availability.

Variation in the availability of blubber associated with prey abundance and body condition has the potential to substantially affect polar bear energy intake and expenditure. Blubber is composed of ≤10% water, is highly digestible, and provides twice the energy per gram compared to muscle, which is less digestible and contains 70% water (Best, 1985). As a result of these differences, 1 kg of ringed seal blubber contains 5.9 times the digestible energy of 1 kg of ringed seal muscle (using ringed seal water content, digestibility, and energy content from Best [1985]). Polar bears require ~20% of their energy as protein, which is the lowest protein requirement of any carnivore (Rode, Robbins, et al., 2021). Consumption of protein above these requirements increases energetic costs due to the metabolic costs of excreting excess nitrogen (Rode, Robbins, et al., 2021). Therefore, the optimal diet for polar bears maximizes energy intake by preferentially consuming high proportions of blubber, as observed in our study (up to 80% of assimilated diet) and in polar bears in the neighboring Chukchi Sea (Stricker et al., 2022). Differences in dietary blubber content, as we
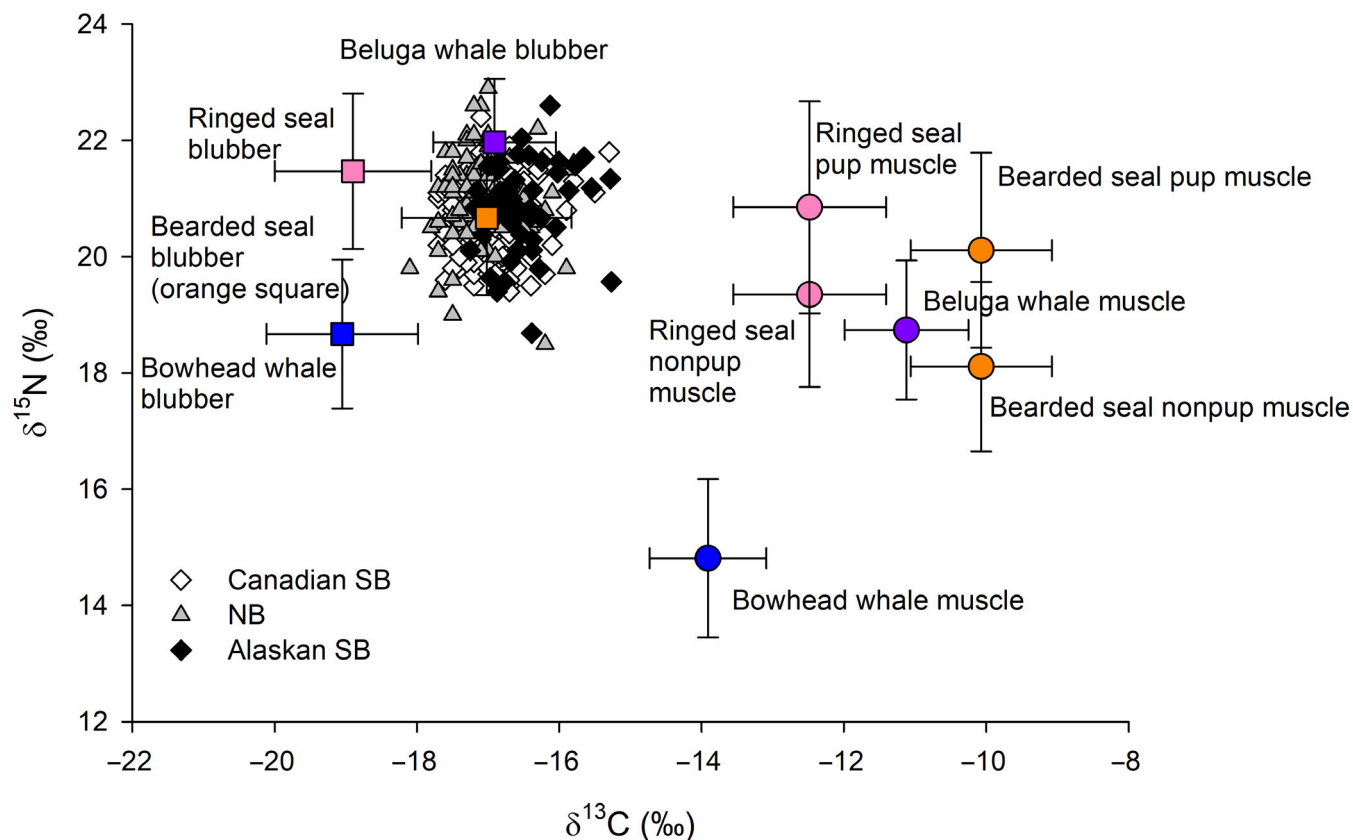
FIGURE 7 $\delta^{15}N$ and $\delta^{13}C$ in guard hair of female polar bears sampled during 2004–2006 in Alaskan southern Beaufort Sea (Alaskan SB), Canadian southern Beaufort Sea (Canadian SB), and northern Beaufort Sea (NB) relative to mean and SD of isotopic values of prey muscle (circles) and blubber (squares) used to address Objective 3. Prey values were corrected for trophic enrichment factors (TEFs) measured from captive feeding trials (Rode et al., 2016), and error bars represent ±1 SD associated with both TEF values and variation among individual prey samples. Values for each prey species are represented by a different color (ringed seal = pink, bearded seal = orange, beluga whale = purple, and bowhead whale = blue).

observed, equates to substantive changes in energy intake unless offset via increased overall food intake. For example, the daily field metabolic costs of 51.6 MJ/day of an adult female on the spring sea ice (Pagano et al., 2018) could be met with 2.1 kg of the diet (wet weight) consumed during lagged high survival years (based on the energy density of Objective 1 high survival diet) compared to 3.0 kg of the diet consumed during 2004–2006 in the Alaskan SB (the lowest energy density observed for Alaskan SB bears in Objective 3) when the population declined. If overall prey availability were lower and intake reduced simultaneously with reduced dietary energy density, the energy deficit during this period would be even greater.

Our observation that dietary differences were greatest when examining years before low or high survival (i.e., a lag effect) is suggestive that the effects of an energy deficit may be difficult to overcome in subsequent years. All but one of the low survival years in our study were consecutive, indicating that the cumulative effects of repeated years consuming a low-energy-density diet may

have played a role in survival. Further, the lowest dietary blubber proportion was observed 2004–2006 (Objective 3) during and preceding the period of low survival that continued through 2008 (Bromaghin et al., 2021). Thus, low-energy diets may precede low survival, but energy intake in subsequent years likely plays a role in determining whether bears will recover from a period of low-energy-density diets or whether energy deficits will accumulate to affect body condition and survival.

Behavioral decisions in response to sea ice loss also likely affected polar bear diets in ways that may have impacted individual health (Reimer, Mangel, et al., 2019). Bears that summered on land in the Alaskan SB had higher dietary proportions of blubber than bears that summered on the pack ice. This appeared to be a result of higher contributions from blubber versus muscle for all prey species in the diet. Bears that summer on land in the Beaufort Sea may retain greater access to productive continental shelf waters, where prey density is higher for a longer period, than bears remaining with the pack ice, which retreats far from the continental shelf (Pagano

TABLE 4 Estimated percentage contributions of prey muscle and blubber of four prey species (ringed seal, bearded seal, bowhead whale, and beluga whale) to assimilated diet of adult male and female polar bears in Alaskan southern Beaufort Sea (Alaskan SB), the Canadian southern Beaufort (Canadian SB), and the northern Beaufort (NB) during 2004–2006 (Objective 3).

Tissue and species	Female polar bears			Male polar bears		
	Alaskan SB ($n = 24$)	Canadian SB ($n = 73$)	NB ($n = 55$)	Alaskan SB ($n = 25$)	Canadian SB ($n = 66$)	NB ($n = 31$)
Muscle						
Ringed seal pups	24 (7)	14 (5)	19 (6)	21 (8)	13 (6)	20 (8)
Ringed seal nonpups	3 (3)	3 (3)	2 (2)	3 (4)	4 (4)	3 (3)
Bearded seal pups	5 (5)	4 (4)	3 (4)	4 (5)	4 (4)	4 (5)
Bearded seal nonpups	2 (2)	2 (2)	1 (1)	2 (2)	2 (2)	1.2 (1.6)
Bowhead whale	0.7 (0.7)	0.6 (0.6)	0.4 (0.5)	0.7 (0.9)	0.6 (0.6)	0.4 (0.5)
Beluga whale	2 (2)	2 (2)	1.2 (1.3)	2 (2)	2 (3)	1.4 (1.8)
Total muscle (percentage of diet)	36 (6)	25 (6)	27 (6)	32 (8)	25 (7)	30 (8)
Blubber						
Ringed seal	23 (9)	30 (11)	38 (38)	20 (12)	23 (12)	27 (12)
Bearded seal	19 (11)	19 (11)	13 (10)	20 (15)	21 (13)	16 (12)
Bowhead whale	10 (7)	12 (9)	12 (12)	10 (10)	11 (10)	10 (9)
Beluga whale	13 (10)	15 (12)	11 (11)	18 (18)	20 (16)	18 (17)
Total blubber (percentage of diet)	65 (6)	76 (6)	74 (6)	68 (8)	75 (7)	71 (8)
Total ringed seal (percentage of diet)	50 (13)	47 (15)	59 (19)	44 (20)	40 (15)	50 (16)
Percentage of ringed seal as blubber	46 (14)	64 (16)	64 (18)	45 (20)	57 (17)	54 (18)
Total bearded seal (percentage of diet)	26 (12)	25 (12)	17 (12)	26 (15)	27 (13)	21 (14)
Percentage of bearded seal as blubber	73 (19)	76 (21)	76 (22)	77 (25)	78 (21)	76 (22)

Note: Mean percentages are provided with 1 SD in parentheses. The diet was estimated from the most-supported model (i.e., lowest deviance information criterion), which included *Region* and *Sex* as additive covariates (Appendix S4: Table S6) using a stable isotope mixing model, MixSIAR, with stable carbon and nitrogen concentration in prey tissues and polar bear hair.

et al., 2020; Schliebe et al., 2008). Bears summering on the pack ice reduce feeding and activity, suggesting reduced access to prey (Ware et al., 2017; Whiteman et al., 2018). In contrast, 80% of bears observed summering on land in the Alaskan SB occurred within 15 km of a subsistence-harvested bowhead whale carcass (Schliebe et al., 2008). Similarly, 27% of bears in the Canadian Beaufort Sea visited bowhead whale carcasses in Alaska during summer (Pongracz & Derocher, 2017), and bears ranging more coastally had lower $\delta^{15}N$ in claws and hair, indicative of increased contributions from bowhead whales. We estimated that bowhead whales contributed 10%–12% of spring/summer/fall diets, a result consistent with four other studies in this region. Using isotopes in hair and lipid-extracted prey muscle, Boucher et al. (2019b) estimated that polar bear diets were composed of <10% bowhead whale, and Bentzen et al. (2007), using isotopes in red blood cells and lipid-extracted prey muscle, estimated that bowhead whale accounted for 11%–26% of the polar bear diet. Moreover, two studies estimated that bear diets consisted of 10%–20% bowhead

whale based on fatty acids for Canadian and Alaskan Beaufort Sea polar bears (winter/spring ~20% bowhead, summer/fall ~10%; see figure 1 in McKinney et al., 2017: ~10% for males and females in winter/spring and summer/fall; see figure 3 in Florko et al., 2020).

A lack of differences in bowhead whale proportions in the diets between bears that summered on shore versus on the sea ice and between the NB and SB is inconsistent with expectations based on bowhead whale availability. Our ability to detect differences may have been limited by (1) the low contribution of bowhead whale to diet over the extended seasonal timeframe represented in whole guard hairs, which resulted in potential differences being relatively small, and (2) MixSIAR's inability to accommodate different prey components by factor level (e.g., to exclude bowhead whale as a diet option for one region and not another). That said, it is also possible that polar bears have more access to bowhead whales during the period in which we measured diet (i.e., spring and summer) than previously

thought. McKinney et al. (2017) estimated bowhead whale contributions to the diet of Alaskan SB bears to be twice as high in winter–spring as in summer–fall based on fatty acids, which contrasts with the expected higher availability of bowhead whales to polar bears on land during the summer. Further, beached and floating bowhead whale carcasses have been observed in the Canadian Beaufort Sea and Amundsen Gulf (DFO, 2014), and bowhead whale carcasses also occur due to missed harvest attempts in Alaska (Suydam et al., 2019) and may be available. Thus, the similarities in bowhead whale dietary proportions regionally and relative to summer habitat use could be a limitation of the modeling, a result of diet estimates integrated over multiple seasons, or patterns of bowhead whale consumption that differ from what has been thought hitherto.

The proportion of bears summering on land has been increasing in the Alaskan SB over the past three decades in direct response to declines in summer sea ice extent (Atwood, Peacock, et al., 2016). In the Alaskan SB, females that denned on land had higher reproductive success than those that denned on the sea ice (Rode et al., 2018). Pregnant females that summer onshore may increase the energy density of their diet via consumption of bowhead whale carcasses and by maintaining longer access to areas of higher prey densities during the summer sea ice minimum compared to bears summering on sea ice far offshore. Rogers et al. (2015) modeled the diets of Alaskan SB polar bears using stable isotopes in hair sections grown while bears were on shore and prey muscle and estimated that bowhead whale contributed to ≥40% of the diet. Thus, pregnant females that summer onshore and consume higher fat diets may enter dens in better body condition than females that summer on pack ice. Because the body condition of pregnant females affects cub production and survival (Derocher & Stirling, 1996; Rode et al., 2020), females summering and denning on land may contribute more to population recruitment than those that summer on pack ice. The effects of summer land use on diet quality, however, may be unique to the SB population, where the availability of bowhead whale carcasses is a reliable and relatively high-density food resource in comparison to elsewhere in the polar bear's range (Galicia et al., 2021), including the NB. Thiemann et al. (2008) excluded bowhead whale from fatty acid models of the diets of NB polar bears based on the apparent low availability. Although bowhead whales represent a supplemental summer food resource for SB bears, this resource is currently used by only 6%–37% of the population in any given year. Although the size of bowhead whales harvested each year varies, it is a finite resource and will not equally supplement the diets of SB bears as increasing numbers summer onshore (Atwood, Peacock, et al., 2016).

Further, substantial declines in survival, and the consequent population decline, occurred in the Alaskan SB during 2004–2006 despite the availability of whale carcasses within their range.

Our diet modeling indicated a regional effect with females from the NB showing a tendency to assimilate more ringed seals and fewer bearded seals than females in the SB and males in all regions of the Beaufort Sea. These diet estimates are consistent with less shallow continental shelf habitat in the NB, which is important to benthic-feeding bearded seals (Olnes et al., 2020). Although the NB polar bear population has been stable over recent decades, it may be particularly vulnerable to changes in the local status of ringed seals due to lower species diversity and reduced access to alternative prey than the SB population (e.g., bearded seal, bowhead whale; Thiemann et al., 2008; Yurkowski et al., 2019). Diets estimated for NB polar bears included the highest proportion of ringed seals of the three regions, consistent with previous studies (Thiemann et al., 2008). The stability of the NB population may reflect more stable or abundant populations of ringed seals within their range or better ice conditions for accessing seals compared to the SB. Rode et al. (2017) found that the percentage of bears exhibiting short-term fasts was lower in the NB compared to the SB but increased between 1983–1999 and 2000–2016 in both the NB and SB.

Geographic variation in prey isotopic composition may have affected the estimated regional differences in diet we observed. Zooplankton were higher in $\delta^{13}C$ in the western Beaufort Sea compared to the eastern Beaufort Sea (Dehn et al., 2007; Schell et al., 1998). In addition, ringed seal claws exhibited higher $\delta^{13}C$ and lower $\delta^{15}N$ in the western Canadian Beaufort compared to the eastern Canadian Beaufort (Boucher et al., 2020). Diet modeling with regionally specific prey data sets would help to tease apart dietary differences within the range. However, the dietary patterns we observed are consistent with what is known about prey availability, feeding behavior, and polar bear population status. Similarly, although we recognize that our estimates of prey species tissue contributions to the diet had a high variance, we highlighted where those estimates are consistent with or divergent from other sources of information, including other diet estimates in the same regions.

Our results emphasize the need to better understand the effects of dietary change on polar bear reproduction, survival, and abundance. Even in areas with greater prey diversity, such as the Chukchi Sea, where polar bears also have access to Pacific walruses (*Odobenus rosmarus divergens*) and gray whales (*Eschrichtius robustus*), the body condition of ringed and bearded seals was the most

important factor affecting annual variation in the body condition of adult females with cubs and adult males (Rode, Regehr, et al., 2021). However, large increases in the availability of alternative prey, such as harp seals (*Pagophilus groenlandicus*) for polar bear populations in eastern Canada and Greenland, have affected population vital rates (Peacock et al., 2013) and dietary supplementation with increased availability of whale carcasses has been identified in Foxe Basin (Galicia et al., 2021). Variation in blubber contributions to diet estimated from hair isotopes is a useful indicator of the cumulative effects of variation in prey condition, abundance, or accessibility resulting from changes in sea ice and other environmental conditions. The ability to estimate blubber contributions to diet from hair, which can be collected via a variety of non-capture-based methods (e.g., hair traps), creates new opportunities for tracking diet quality and prey availability, which is vital for determining individual health, fitness, and population demographics (Rode, Robbins, et al., 2021).

CONCLUSIONS

Wildlife managers face unprecedented challenges in assessing the status of wildlife populations in areas of rapid environmental change. Identifying environmental and ecological factors that populations respond to and that can be efficiently and effectively measured will improve the available information for making management decisions. Our study demonstrated the potential for a new analytical approach using stable isotopes in hair to identify patterns of prey availability and diet energy density, in addition to the traditional application of estimating the species composition of diet, that correspond to patterns in survival and population productivity. Percentage of blubber in the diet can integrate the effects of prey fatness and abundance, as well as environmental conditions that affect predation success (i.e., sea ice extent and thickness) and energy intake. Applied to the Beaufort Sea, we found that polar bears in this region continue to be largely dependent on ringed seals and are currently limited in meeting energy needs via consumption of alternative prey when ringed seal availability is reduced. Our findings directly link diet quality to population vital rates, offer a new monitoring metric, and may help identify factors that influence overall fitness in the context of future changes in phenology and predator–prey dynamics brought about by a warming climate.

AUTHOR CONTRIBUTIONS

Karyn D. Rode, Brian D. Taras, Craig A. Stricker, Todd C. Atwood, George M. Durner, and Jeffrey F. Bromaghin designed the study. Karyn D. Rode, Todd C. Atwood, Nicole P. Boucher, George M. Durner, Andrew E. Derocher, Evan S. Richardson, Seth G. Cherry, Lori Quakenbush, and Lara Horstmann collected data. Craig A. Stricker conducted laboratory analyses. Brian D. Taras developed and ran models. Karyn D. Rode wrote the manuscript. All authors revised and contributed to the final manuscript.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Rode, 2021) are available from the U.S. Geological Survey at https://doi.org/10.5066/P9KM5FT2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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