

Temporal complexity of southern Beaufort Sea polar bear diets during a period of increasing land use

MELISSA A. MCKINNEY,^{1,†} TODD C. ATWOOD,² SARA J. IVERSON,³ AND ELIZABETH PEACOCK²

¹Department of Natural Resources and the Environment and Center for Environmental Sciences and Engineering,
University of Connecticut, Storrs, Connecticut 06269 USA

²US Geological Survey, Alaska Science Center, Anchorage, Alaska 99508 USA

³Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2 Canada

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Abstract. From 2000 to 2013, use of land as a seasonal habitat by polar bears (*Ursus maritimus*) of the southern Beaufort Sea (SB) subpopulation substantially increased. This onshore use has been linked to reduced spatial and temporal availability of sea ice, as well as to the availability of subsistence-harvested bowhead whale (*Balaena mysticetus*) bone piles. Here, we evaluated the role of climate conditions on consumption of traditional ice-associated prey relative to onshore bowhead whale bone piles. We determined seasonal and interannual trends in the diets of SB polar bears using fatty acid-based analysis during this period of increasing land use. Diet estimates of 569 SB polar bears from 2004 to 2012 showed high seasonal fluctuations in the proportions of prey consumed. Higher proportions of bowhead whale, as well as ringed seal (*Pusa hispida*) and beluga whale (*Delphinapterus leucas*), were estimated to occur in the winter–spring diet, while higher proportions of bearded seal (*Erignathus barbatus*) were estimated for summer–fall diets. Trends in the annual mean proportions of individual prey items were not found in either period, except for significant declines in the proportion of beluga in spring-sampled bears. Nonetheless, in years following a high winter Arctic oscillation index, proportions of ice-associated ringed seal were lower in the winter–spring diets of adult females and juveniles. Proportions of bowhead increased in the winter–spring diets of adult males with the number of ice-free days over the continental shelf. In one or both seasons, polar bears that were in better condition were estimated to have consumed less ringed seal and/or more bowhead whale than those in worse condition. Therefore, climate variation over this recent period appeared to influence the extent of onshore vs. on-ice food use, which in turn, appeared to be linked to fluctuating condition of SB polar bears.

Key words: Arctic oscillation; *Balaena mysticetus*; Beaufort Sea; body condition; climate change; diet; polar bear; quantitative fatty acid signature analysis; scavenging; sea ice; *Ursus maritimus*.

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† **E-mail:** melissa.mckinney@uconn.edu

INTRODUCTION

Concomitant with reduced spatial and temporal extent of their sea ice habitat, the southern Beaufort Sea (SB) polar bear subpopulation declined in size from the late 1980s to the mid-2000s (Regehr et al. 2007). Reduced body condition and vital rates in SB polar bears have also been linked to sea

ice loss over a similar time period (Regehr et al. 2010, Rode et al. 2010). Population size continued to decline from 2006 to 2009, but appeared to stabilize in 2010 despite unchanged sea ice trends (Bromaghin et al. 2015a). It was suggested that annual survival rates of SB bears may have been driven by ecological factors other than direct sea ice loss, such as reduced access to ice seals.

Polar bears in the SB have historically spent most of the year on the sea ice hunting ice-associated prey, predominantly ringed seal (*Pusa hispida*; Stirling and Archibald 1977, Thiemann et al. 2008, Cherry et al. 2013). Yet, scientific surveys and local community observations suggest a recent increase in the numbers of polar bears on the northern Alaskan coast in the fall when the sea ice retreats to its minimum annual extent (Schliebe et al. 2008). The spatial distribution of these polar bears while on shore has been linked to the geographic positions of an energy-rich, marine food subsidy, namely carcasses of subsistence-harvested bowhead whales (*Balaena mysticetus*; Herreman and Peacock 2013, Atwood et al. 2016). Often referred to as “bone piles,” this resource actually consists of trimmed blubber, meat, and bones, as well as carcasses of harvested fish, birds, and caribou (*Rangifer tarandus*) that are left behind (Herreman and Peacock 2013). The subsistence harvest previously occurred mainly on the sea ice in the spring with carcasses left to eventually descend into the water; however, changing ice conditions over the past two decades may have led to more bowhead whales being hunted, particularly in the fall, with carcasses being left onshore (Suydam and George 2012, Herreman and Peacock 2013; C. George, *personal communication*). Bone piles have been present near Barrow (until 2012), Nuiqsuit/Cross Island, and Kaktovik, with between 24 and 33 whales landed per year from 2004 to 2011, ranging in size from around 6 to nearly 20 m long (Suydam and George 2012). This resource continues to be used by polar bears throughout the year (North Slope Borough and US Geological Survey, *unpublished data*). Further, many but not all bears at the bone piles, at least anecdotally, appear to be in good or above average condition (Atwood et al. 2016).

Both stable isotope ratios and fatty acid signatures have been used to quantitatively estimate prey proportions in SB polar bear diets. Using stable isotope mixing models, Bentzen et al. (2007) estimated that the winter diets of SB polar bears comprised 11–26% bowhead whale remains in 2003 and 0–14% in 2004. Using a similar approach, Rogers et al. (2015) estimated adult female SB polar bears mainly inhabiting coastal regions in the fall actually consumed 50–70% bowhead whale remains during that period in

2008–2010. Conversely, for those adult females persisting in a pelagic foraging strategy year-round, ringed seal was consistently the predominant prey. A re-evaluation of SB polar bear diets from 2005 using stable isotopes of both protein- and lipid-rich tissues found that ringed seal was overestimated, though, and that other prey were underestimated, using traditional proteinaceous tissue-based analysis (Cherry et al. 2011). Quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004) was used to analyze SB polar bear diets in the 1980s and 1990s, or in grouped years of 1972–1991, 2000–2001, 2003, and 2004, respectively (Iverson et al. 2006, Thiemann et al. 2008). Those studies did not detect significant interannual variation in prey proportions, estimating ringed seal to be the main prey with much lower proportions of bearded seal (*Erignathus barbatus*) and/or beluga whale (*Delphinapterus leucas*). However, bowhead whale was not modeled as a potential prey in either of these temporal trends studies. More recent temporal trends of SB polar bear diets that include onshore bowhead whale bone piles as a potential food item are necessary, particularly in light of documented rapid, recent increases in land use (Atwood et al. 2016).

Here, we used the QFASA approach to evaluate seasonal and interannual trends in SB polar bear diets during the recent period of increasing land use, including all years from spring 2004–2012 and fall 2008–2012. We tested our hypothesis that climate conditions influence the consumption of traditional ice-associated prey relative to onshore bowhead whale bone piles by evaluating associations between proportions of prey species consumed and established climate indices. Given previous reports of body condition declines in SB polar bears, but possibly recent short-term stability in population size, we also examined links between body condition and consumption of onshore bowhead subsidies relative to ice-associated prey.

MATERIALS AND METHODS

Study area

The SB subpopulation of polar bears was studied along the northern Alaska coastal zone from Barrow in the west to Kaktovik in the east (157–141° W). Here, shallow productive waters over the narrow continental shelf characterize the

nearshore environment. This sea ice ecoregion is referred to as Divergent, whereby the sea ice formed tends to diverge northward from the coast in the summer (Amstrup et al. 2008). Historically, SB polar bears have remained on the retreating pack ice, making little use of onshore habitat on an annual basis (Amstrup 2003). However, recently spatially and temporally more extensive retreat of the sea ice into deeper, less productive waters of the Arctic Ocean has coincided with increased use of land by SB polar bears (Schliebe et al. 2008, Atwood et al. 2016). Compared to the years 1986–1999, during 2000–2014, radiocollared SB adult females stayed on land an average of 36 additional days, arrived on shore 15 days earlier (29 August), and departed from shore 19 days later (21 October; Atwood et al. 2016).

The communities of Barrow, Nuiqsut, and Kaktovik harvest bowhead whales in the study area in the fall when a portion of the SB subpopulation is on land. From 2004 to 2011, the three communities landed a combined average of 27.5 bowheads per year, with whales ranging in length from ~5 to 20 m (Suydam and George 2012). Although most of the harvest has been in Barrow, bone piles have not been consistently amassed there, but have been each year on Cross Island (logistical base for Nuiqsut) and Barter Island (adjacent to Kaktovik). The locations of these bone piles have been shown to influence the onshore distribution of SB polar bears (Atwood et al. 2016).

Sampling

Full details of the collection of these polar bear samples have been previously described (McKinney et al. 2014). Briefly, 569 biopsies were used from polar bears sampled from the SB subpopulation from 2004 to 2012 (Appendix S1: Table S1). We collected subcutaneous adipose tissues from the rump region of captured animals by biopsy punch and remotely from animals biopsy-darted in the spring (March to mid-May; hereafter referred to as spring-sampled) of 2004–2012 and in the late summer to early fall (August–October; hereafter referred to as fall-sampled) of 2008–2012. Biopsies were frozen at -80°C for long-term storage. First-time captured animals were aged by counting growth layer groups in the cementum of a vestigial premolar tooth. Polar bears were then grouped according to sex/age

class as cubs-of-the-year, yearlings, 2-yr-old dependent cubs, subadult (independent 2-, 3-, and 4-yr-old) females and males, and adult (5-yr-old and older) females and males. All bears were genetically identified (Pagano et al. 2014).

Fatty acid analysis

To evaluate the possible influence of potential tissue oxidation on fatty acid-based diet estimates, subjective oxidation class of the biopsies was visually assigned using a 1–5 scale: 1 = white/fresh; 2 = mainly white/slight yellow tinge; 3 = white-yellow; 4 = mainly yellow/slight white tinge; 5 = yellow/sometimes a bit dry (McKinney et al. 2013). Lipids were then extracted from the adipose samples as described in McKinney et al. (2014). Extracted fatty acids were derivatized to fatty acid methyl esters (FAMES) before gas chromatography with flame ionization detection (Budge et al. 2006, McKinney et al. 2013). Individual fatty acids were quantified as mass percentage of total FAME. The carbon chain length x , number of double bonds y , and position of the first double bond from the methyl end (n -) of the chain z are used to convey the fatty acid structure as $x:y:n-z$.

The National Institute of Standards and Technology (Charleston, South Carolina, USA) standard reference material SRM1945, pilot whale (*Globicephala melas*), was extracted with each batch of 12 samples for quality control purposes. Mass percentage values for 27 FAMES were previously reported (Kucklick et al. 2010). Our measurements were very similar to the median inter laboratory comparison values, within 17%, on average.

Quantitative fatty acid signature analysis

The QFASA approach has been used previously to estimate polar bear diets (Iverson et al. 2006, Thiemann et al. 2008, McKinney et al. 2013). Briefly, QFASA determines the proportions of individual prey species consumed by determining the weighted mixture of prey fatty acid signatures that best matches each individual polar bear signature after accounting for differences between predator and prey due to predator metabolism (Iverson et al. 2004). Specifically, the model minimizes the statistical distance over all fatty acids between the prey and predator signatures, with the constraint that the estimated diet proportions must all be non-negative and sum to 1. We used

the original Kullback-Liebler distance measure, although other distance measures have been suggested (Bromaghin et al. 2015b). We modeled SB polar bear diets using only the 31 “dietary” fatty acids and, before modeling, adjusted these fatty acid values to account for differential metabolism and deposition using simple calibration coefficients (as per Thiemann et al. 2008). We used a prey fatty acid dataset comprising 89 ringed seal, 20 bearded seal, 64 bowhead whale, and 29 beluga whale from the SB region, which was generated in previous studies (Budge et al. 2008, Thiemann et al. 2008). It should also be noted that, although we assumed bone piles were the source of bowhead whale in the SB polar bear diets, it is possible that beach-cast bowheads could also be consumed to some extent; however, no data are available on numbers or trends of beach-cast carcasses in the region. The model was run using the “QFASApack” package in R (V. 3.1.3, R Development Core Team 2014). The standard errors (SE) of the mean diet estimates were calculated from the between-bear SE, that is, from variation in diet estimates among bears (McKinney et al. 2013). Within-bear SE, that is, variation resulting from fatty acid signature variability within a particular prey species, was not used as it has been shown to be small relative to between-bear SE (Thiemann et al. 2011). Simulation studies were used to test model robustness (as fully detailed in Iverson et al. 2004). Specifically, prey-on-prey simulations showed how distinct each prey species signatures were from those of other prey species, and diet simulations indicated how well QFASA modeled diets relative to a simulated diet.

As samples were collected during two periods, it should be noted that adipose fatty acid signatures integrate marine mammal diets over weeks to months (Iverson et al. 2006). Thus, coarsely delineated, estimates from spring-sampled bears represent winter–spring diets (~November–May), while fall-sampled bears represent summer–fall diets (~May–October).

Climate and sea ice indices

Understanding climate effects on ecological processes requires knowledge of large-scale oceanographic and atmospheric parameters, as well as of local conditions (Forchhammer et al. 1998, Iverson et al. 2006, Post et al. 2013). Indeed, polar bear condition has been linked to climate and sea ice

indices at both scales (Stirling et al. 1999, Derocher 2005, Rode et al. 2010, Bechshøft et al. 2013). We therefore examined the relationship of feeding to both regional- and circumpolar-scale indices. Although a variety of climate measures can be used, we made the decision a priori to test the local measures of annual ice-free days over the continental shelf and length of the melt season in the entire SB region. These measures have been described previously and linked to variation in SB polar bear body condition (McKinney et al. 2014). For large-scale measures, we used annual minimum extent of the Arctic sea ice, as well as the winter (mean of January–March) Arctic oscillation (AO_w). Minimum extent is considered to be one of the strongest indicators of global climate change (IPCC 2013). We used annual September sea ice minimum extent data from the National Snow and Ice Data Center based on the NASA Team Algorithm (Stroeve 2003). The AO influences ice movement and distribution (Stroeve et al. 2011), variables that are not reflected in other indices such as minimum extent. The atmospheric circulation associated with a positive AO_w has been linked to thinner ice over the Arctic Ocean, earlier onset of melt, later onset of freeze-up, and increased advection of ice away from coastal areas (Rigor et al. 2002, although see Stroeve et al. 2011). AO_w was calculated based on monthly AO data from the National Oceanographic and Atmospheric Administration’s Weather Service, Climate Prediction Centre (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml).

Indices from the year before bear sampling were used. For spring-sampled bears, the minimum ice extent (September), ice-free days (July–October), and melt season length (July–October) are thus from the most recent reduced-ice season before sampling. The effects of the AO_w from the prior winter may actually represent a similar time period, that is, the most recent reduced-ice season (July–October), as “the memory” of the AO_w is known to impact ice conditions in the ensuing summer and fall (Rigor et al. 2002). Spring-sampling (March–May) thus represents a time lag of 7–10 months from the previous reduced-ice season, which may be similar to the period of feeding integrated by the fatty acid signatures, although this is not known with certainty (Budge et al. 2006). As the time lag between the reduced-ice season associated with the climate indices

and fall-sampling was longer (13–16 months), connections between the climate indices and the diets of fall-sampled bears may be weaker.

Body condition indices

Although several body condition indices have been used for polar bears, we chose subjective fatness index (FI) as it is linked to other indices and is appropriate for all demographic groups (McKinney et al. 2014). Further, FI was the only index recorded for remote-biopsied bears and, thus, was the index for which we had the most data (available for 97% of bears). The FI is determined on a 1–5 scale based on visual and/or physical examination, where 1 represents emaciated, 3 represents average, and 5 represents obese (Stirling et al. 1989).

Statistical analysis

Oxidation of fatty acids in a sample may change the fatty acid signature (reduced proportions of long-chain polyunsaturated fatty acids and higher proportions of saturated and mono-unsaturated fatty acids), which could alter fatty acid-based diet estimates for that individual. The longest, most unsaturated fatty acid in the dataset, and thus the one most subject to oxidation, would be 22:6n-3. To reduce the possible influence of sample oxidation, we thus excluded 57 samples that showed mass percentage values of 22:6n-3 below the lowest value measured for the oxidation class 1 samples (Appendix S1: Fig. S1; McKinney et al. 2013). To further test for possible confounding effects of oxidation, as well as of capture vs. remote biopsy type, we ran a permutation MANOVA on the dietary proportions for the remaining dataset including oxidation and biopsy as factors, in addition to the target variables of age/sex class, season, year, and all first-order interactions. To do so, given the compositional nature of our data, we used Bray–Curtis distance matrices and ran 10,000 permutations using the *adonis* function in the “vegan” package in R (R Development Core Team 2014).

To evaluate relationships between diet and climate indices (i.e., foraging habitat quality/quantity), we also ran permutation MANOVAs on the dietary proportions replacing year with ice-free days, melt season length, minimum ice extent, or AO_w. Univariate ANOVAs with Tukey’s honestly significant differences (HSD) for unequal *n* were

used for post hoc analysis of the influence of sex/age and season on prey proportions in the polar bear diet. Simple linear regression was used for post hoc examination of the relationship of diet to year and climate indices.

To assess associations between feeding and body condition of the polar bears, we compared prey consumption according to FI scores. Specifically, Kruskal–Wallis ANOVAs were used to examine relationships of FI to dietary proportions of traditional ice-associated ringed seal prey and onshore bowhead whale remains. This analysis was only performed for adult males and females, as juveniles did not present a sufficient range of FI scores in all seasons.

RESULTS

Model inputs and possible confounding factors

Of 69 fatty acids monitored in an initial total of 642 biopsies, 55 fatty acids were quantified in all samples including the 31 used in diet estimation (Appendix S1: Table S2; Iverson et al. 2004). We excluded 57 of these biopsy samples based on possible confounding influence of oxidation on the diet estimates (see *Statistical analysis*) and another 16 cubs-of-the-year based on unusual fatty acid patterns relative to other sex/age classes (see *Diet variation by sex/age class and season* below), leaving a final total of 569 samples for subsequent analyses (Appendix S1: Table S1). Simulation tests showed that prey species were well distinguished ($\geq 90\%$ correct identifications; Appendix S1: Fig. S2). QFASA also closely reproduced a simulated diet (Appendix S1: Fig. S3). The initial permutation MANOVA showed that neither oxidation class nor biopsy type influenced the diet estimates ($P > 0.09$). Thus, for further analysis, samples of all oxidation classes and both biopsy types were combined.

Diet variation by sex/age class and season

Overall, our estimates suggested that diets of SB polar bears from 2004 to 2012 mainly consisted of ringed seal ($43.1\% \pm 1.1\%$) and bearded seal ($37.8\% \pm 1.3\%$). Bowhead whale appeared to comprise less of the diet ($14.4\% \pm 0.8\%$), while beluga were a minor component ($4.8\% \pm 0.6\%$). These diet estimates represent the proportional biomass consumed of each prey species. It is worth noting that the proportional number of individuals of

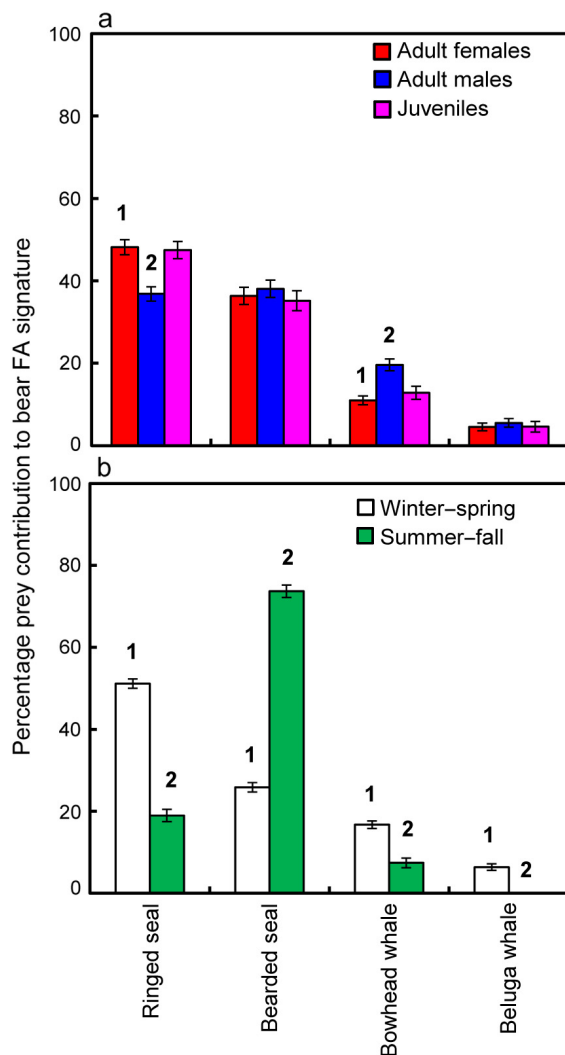


Fig. 1. Prey contribution (%) to diet estimates of 569 southern Beaufort Sea polar bears sampled over the period 2004–2012 by (a) sex/age class and (b) season. Error bars represent \pm SE of individual polar bear diet estimates. Numbers denote significant differences in diet estimates of a given prey item between sex/age classes or seasons.

each species consumed likely differs, given that the prey species vary widely in size (e.g., ringed seal are substantially smaller than bearded seal, and especially than beluga and bowhead whale). Prey proportions varied by sex/age class (permutation MANOVA; $P < 0.001$; Fig. 1a). Specifically, the proportion of ringed seal and bowhead whale differed among sex/age classes (ANOVA; $P < 0.001$).

Adult males consumed nearly twice as much bowhead whale as adult females ($19.6\% \pm 1.4\%$ vs. $11.0\% \pm 1.1\%$; post hoc Tukey's HSD; $P < 0.001$), whereas adult females consumed more ringed seal than adult males ($48.2\% \pm 1.9\%$ vs. $36.8\% \pm 1.7\%$; $P < 0.001$). Diet estimates for subadult males and females, 2-yr-old dependent cubs, and yearlings were not significantly different from each other nor from adult males or females (permutation MANOVA; $P > 0.1$), although they were more similar to adult females than adult males. Thus, these samples were subsequently considered as one group of "juveniles." Unique fatty acid patterns in cubs-of-the-year led to diet estimates ($\sim 76\%$ bearded seal, 18% ringed seal) inconsistent with those of other sex/age classes, possibly due to the influence of nursing. Thus, cubs-of-the-year were not further considered, leaving a dataset of 569 individuals for all subsequent analysis (Appendix S1: Table S1).

Prey proportions were highly variable between seasons (permutation MANOVA; $P < 0.001$; Fig. 1b). Roughly two times greater proportions of ringed seal ($51.1\% \pm 1.1\%$ vs. $18.9\% \pm 1.5\%$), bowhead whale ($16.7\% \pm 0.9\%$ vs. $7.4\% \pm 1.1\%$), and beluga whale ($6.3\% \pm 0.7\%$ vs. 0 ± 0) were estimated in the winter-spring diets compared to the summer-fall (ANOVA; $P < 0.001$). Conversely, three times the proportion of bearded seal were estimated in summer-fall than in winter-spring diets ($73.7\% \pm 1.5\%$ vs. $25.9\% \pm 1.1\%$; $P < 0.001$).

Diet variation by year and annual sea ice conditions

Overall diets of SB polar bears differed among years (permutation MANOVA; $P < 0.001$). Yet, in general, there were no increasing or decreasing linear trends in consumption of any prey species in either season (Fig. 2a, b), except for declining proportions of beluga in the winter-spring diets ($r^2 = 0.56$, $P = 0.02$). A similar lack of trends was found when adult males, adult females, and juveniles were analyzed separately, with the only significant trend being declining beluga consumption in winter-spring diets of adult males ($r^2 = 0.60$, $P = 0.01$).

We investigated whether this significant inter-annual variation in diets could be attributed to climate/ice conditions. Since melt season and minimum extent were correlated ($r^2 = 0.52$, $P = 0.03$),

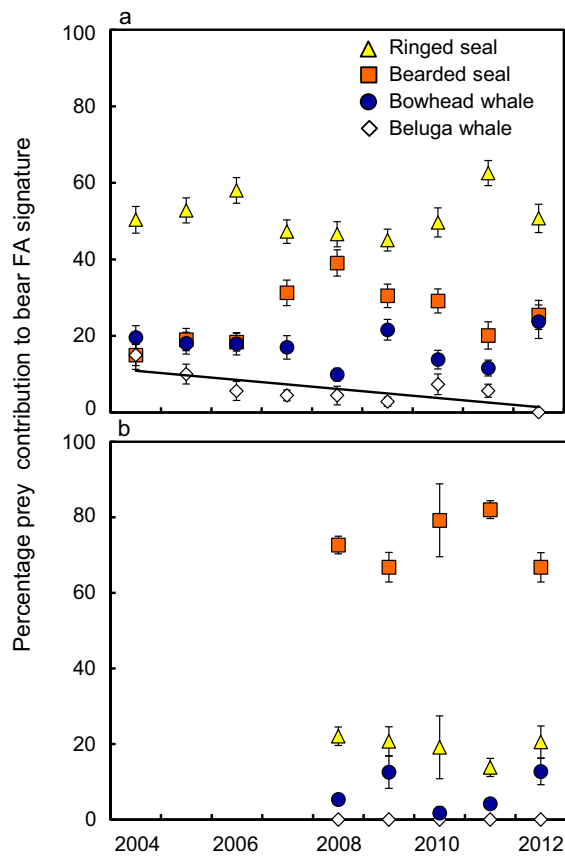


Fig. 2. Annual mean (\pm SE) prey contribution (%) to diet estimates of southern Beaufort Sea polar bears in (a) the winter-spring of 2004–2012 and (b) the summer-fall of 2008–2012. Linear regression line is provided for the statistically significant time trend only: Beluga whale proportion declines in spring-sampled bears ($r^2 = 0.56$, $P = 0.02$, $n = 9$ years). Similar patterns were also found when analyzed separately for each sex/age class (data not shown).

and melt was not correlated with annual mean proportions of any prey species ($P > 0.10$), melt was not considered further. When ice-free days, extent, and/or AO_w replaced year in the permutation MANOVA, there was a significant relationship between diet and the climate index included in the model ($P < 0.01$) and sometimes a significant interaction between climate index and season ($P < 0.002$). Further analysis showed that winter-spring diets of adult females and juveniles had lower proportions of ringed seal after higher AO_w years ($r^2 = 0.82$, $P < 0.001$ and $r^2 = 0.46$, $P = 0.04$,

respectively; Fig. 3a, b). Winter-spring diets of adult males were estimated to have lower proportions of beluga after lower minimum sea ice extent years ($r^2 = 0.67$, $P = 0.007$), but higher proportions of bowhead after years with higher numbers of ice-free days over the continental shelf ($r^2 = 0.63$, $P = 0.01$; Fig. 3c, d). However, significant relationships were not found between climate indices and prey proportions in the summer-fall ($P > 0.05$).

Relationship of diet to body condition

Fall-sampled adult females of FI 4 (higher condition) exhibited lower summer-fall ringed seal proportion estimates than those of FI 3 (normal condition; $H_{1,63} = 8.3$, $P = 0.004$; Fig. 4). A similar, but not significant, pattern was observed for adult males ($P = 0.20$). Conversely, fall-sampled adult males of FI 4 were estimated to consume proportionally more bowhead in summer-fall than those ranked FI 3 ($H_{1,25} = 5.0$, $P = 0.03$). A similar, but not significant, pattern was observed for adult females ($P = 0.19$; Fig. 4).

No differences in winter-spring bowhead consumption were observed among spring-sampled bears with different FI scores when they were captured ($P > 0.19$). Yet, spring-sampled adult males grouped by FI score showed significantly different ringed seal consumption in the winter-spring ($H_{2,181} = 5.7$, $P = 0.05$; Fig. 4); spring-sampled adult males of FI 4 were estimated to consume lower proportions of ringed seal in winter-spring than males of FI 2 ($P = 0.06$). All other diet-condition relationships were not significant.

DISCUSSION

These diet estimates suggest that ringed and bearded seals remained the predominant prey of SB polar bears in recent years, consistent with earlier studies (Iverson et al. 2006, Bentzen et al. 2007, Thiemann et al. 2008, Aars et al. 2015). We also found significant seasonal and climate-linked interannual variation in estimated diets. Our findings are consistent with the hypothesis that feeding/nutritional limitation is the mechanistic link between polar bear population health and climate/sea ice change (Rode et al. 2010). Yet, our results also reveal a complex, specific response of SB polar bears to changing climate/ice conditions, wherein an alternative human-provisioned onshore food

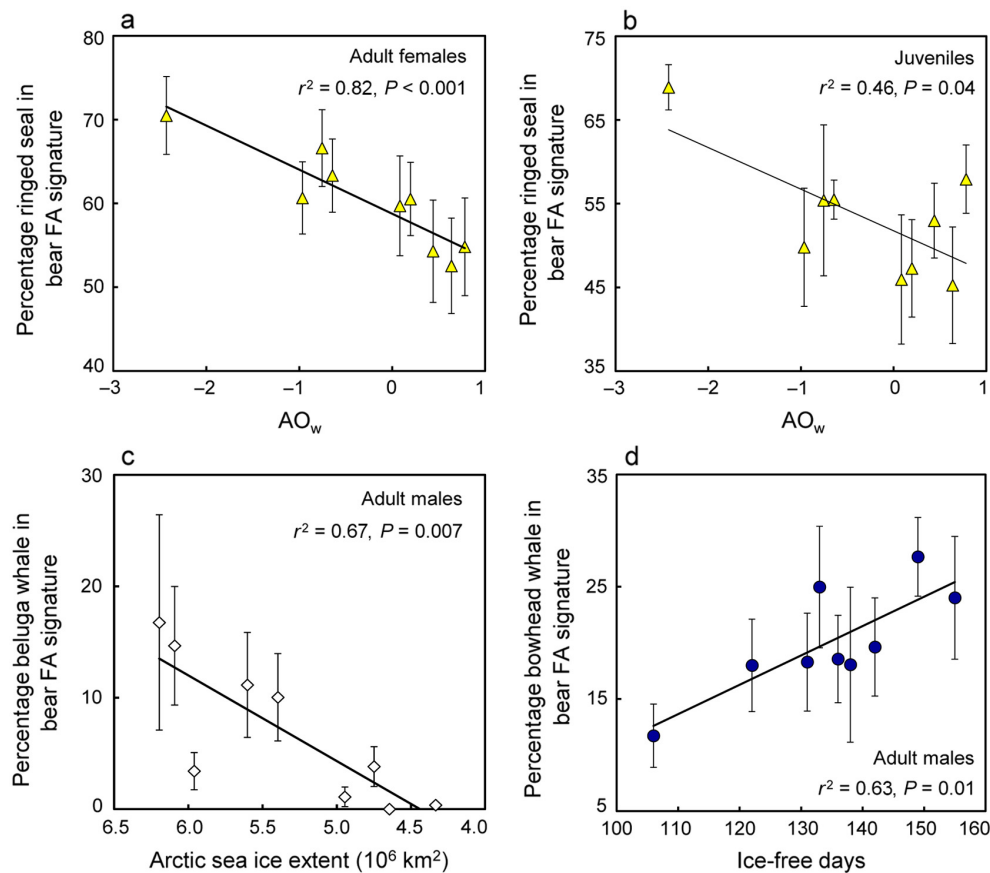


Fig. 3. Mean (\pm SE) prey contribution (%) to the winter–spring diet estimates of southern Beaufort Sea polar bears as a function of previous year climate measures. Ringed seal proportions in (a) adult female and (b) juvenile diets vs. winter Arctic oscillation (AO_w). Beluga whale proportions vs. Arctic sea ice extent (c) and bowhead whale proportions vs. ice-free days over the continental shelf (d) in adult males.

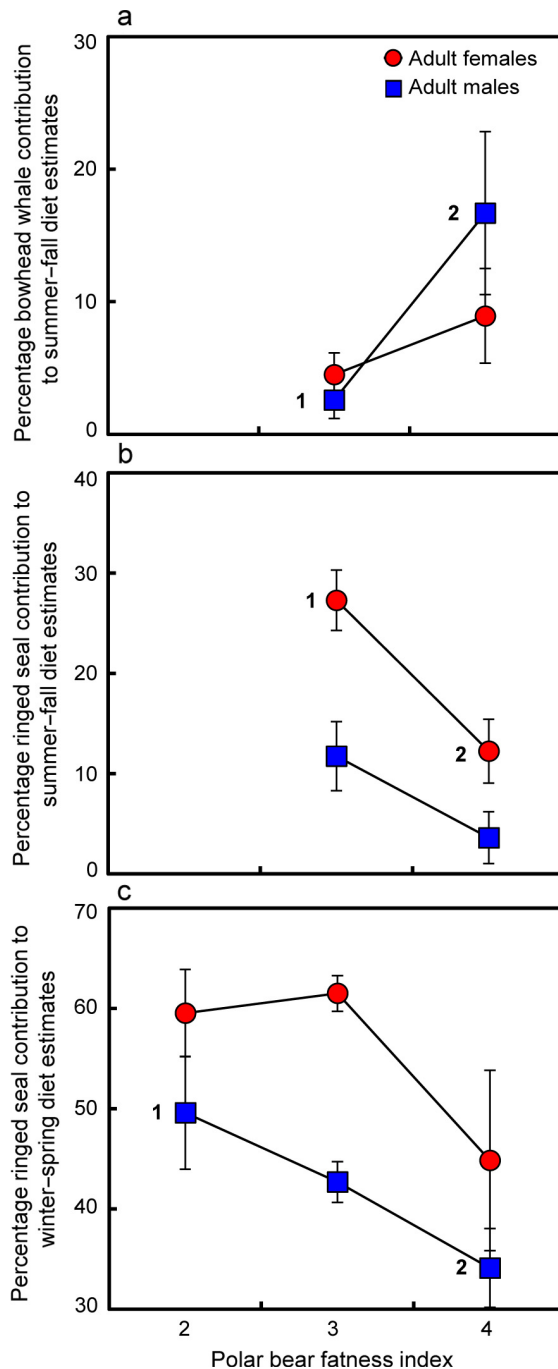
resource appears to additionally influence their foraging ecology and body condition.

Seasonal variation in diets

The predominance of bearded seal in the summer–fall diets was unexpected. Less than 20% bearded seal consumption was previously estimated in all seasons for adult SB females from 2008 to 2010 (Rogers et al. 2015). Since we did not detect differences in bearded seal consumption among sex/age classes and had similar sampling years, the difference between studies is not likely related to sample composition or collection years. It is possible that a low estimate in the earlier study is due to use of hair and blood stable isotopes (Cherry et al. 2011), which may be more biased in the case of summer–fall diet estimates.

At this time of year, polar bears are in peak condition (Stirling 2002) and may therefore be most likely to consume blubber almost exclusively, which would result in the greatest underestimate of bearded seal using proteinaceous tissue-based methods.

Thus, we tentatively suggest a previously unreported seasonal importance of bearded seal to the nutritional needs of SB polar bears of all sex/age classes. In the early days after bearded seal pupping in May, pups spend most of their time hauled out of the water (Watanabe et al. 2009), accessible to polar bears. The later pupping relative to ringed seals could, in part, explain why bearded seal consumption is better reflected in summer–fall diet estimates of SB bears. Adult bearded seals may also be more accessible in



May–June when they molt on the ice (Bengtson et al. 2005). Future modeling studies subdividing prey by age class may be informative in this regard. Regardless, given the roughly fivefold higher body mass of bearded seals vs. ringed seals (Derocher et al. 2002), even low predation rates could still achieve a high dietary biomass.

Fig. 4. Mean (\pm SE) prey contribution (%) to diet estimates of adult male and female southern Beaufort Sea polar bears by fatness index (FI). Bowhead whale (a) and ringed seal (b) proportions in summer–fall diets, and ringed seal (c) proportions in winter–spring diets. Bowhead whale proportions by FI were not significant for winter–spring diets of any bears and were therefore not shown. Numbers denote significant differences in bowhead whale or ringed seal consumption among FI groups for a given sex class.

Estimates of ringed seal, bowhead whale, and beluga whale were higher in the winter–spring than the summer–fall diets. The spring season is when ringed seal pups become available and adult ringed seals are most vulnerable to predation (Pillfold et al. 2012). Spring-sampling was likely better able to capture seasonal highs in bowhead whale bone pile resource use (i.e., the summer–fall diet). The bone piles are deposited onshore in the fall season from August to October (Suydam and George 2012). Therefore, many fall-sampled individuals were sampled before availability of the carcasses. Beluga whale consumption was only detected, and as a minor food source, in winter–spring diets. Instances of polar bear predation have been reported when belugas become entrapped in small ice openings, when moving within narrow leads, or when surfacing at small holes in the ice; these ice-linked events have been reported in the winter and during spring migration through northern Alaska (Lowry et al. 1987).

Prey consumption estimates for the winter–spring period were reasonably similar to studies from earlier time periods using fewer potential prey and either QFASA or stable isotopes approaches. Ringed seal consumption in SB polar bears using all four potential marine mammal prey was somewhat lower than reported from 1972 to 2004 (50% vs. ~60%) using the same QFASA approach (Thiemann et al. 2008), but not including bowhead whale in the prey database. We also found lower ringed seal consumption than reported for winter 2003–2005 diets (77%) estimated using blood stable isotopes, but not including beluga whale in the model (Bentzen et al. 2007). Our winter–spring bearded seal consumption estimates (~26%) were fairly comparable to those two previous SB polar bear diet studies, despite differences in prey included in the models

(Bentzen et al. 2007, Thiemann et al. 2008). Observations of April–May kills over 1985–2011 also gave reasonably similar estimates of 67% ringed seal and 33% bearded seal on a biomass basis (Pillfold et al. 2012). For beluga whale, similar proportions were reported in the diets of spring-sampled SB polar bears from 1972 to 2004 using QFASA (Thiemann et al. 2008). We found higher estimates of bowhead consumption (17%) in winter–spring than reported earlier (6%; Bentzen et al. 2007).

Some discrepancies among these studies may be due to metabolic routing; stable isotopes in proteinaceous tissues only reflect the dietary protein (Cherry et al. 2011), whereas polar bears preferentially consume blubber of kills, often leaving the meat behind, with the occasional exception of smaller prey such as ringed seal (Stirling and McEwan 1975). Since dietary proteins and lipids are metabolically routed to analogous compartments in consumer tissues, diets of polar bears are likely better estimated by methods that consider dietary lipids (Cherry et al. 2011). Thus, stable isotope approaches using blood or other proteinaceous tissues may overestimate smaller prey, such as ringed seals, and underestimate larger prey including bearded seals, beluga whales, and bowhead whales (Cherry et al. 2011). Conversely, QFASA-based diet estimates appear to be influenced by the distance measure and calibration coefficients used in the model (Bowen and Iverson 2013, Bromaghin et al. 2015b). Also, the influence of fasting on polar bear diet estimates using QFASA has not been explored, although studies on elephant and grey seals have not found overall changes in fatty acid signatures during long-term fasting (Budge et al. 2006).

Diet variation among sex/age classes

Ringed seal may have been consumed more often by adult females than males and more often in winter–spring, due to the aforementioned increased availability in March–April, when denning females emerge. Higher consumption of smaller-bodied prey (ringed seal) by adult females and higher consumption of larger prey by adult males (harp seal, hooded seal, bearded seal, and/or walrus) have also been reported elsewhere (Thiemann et al. 2008, McKinney et al. 2013). The bone piles appeared to be a more important food for adult males than females, consistent with genetic analysis of SB polar bears visiting the bone

piles (Herreman and Peacock 2013). Lack of variation in beluga whale estimates among sex/age classes suggests that predation, or at least scavenging, of beluga whales occurred to a similar extent among demographic groups.

Interannual variation in diets and relationships to climate indices

Diet estimates of SB polar bears suggested significant interannual variation over the 2004–2012 period, unlike an earlier study covering 1972–2004 (Thiemann et al. 2008). Interannual variation in estimates of winter–spring consumption of bowhead whale by adult males was largely explained by the number of ice-free days over the continental shelf. That is, in years with a longer ice-free period, adult males relied more heavily on this onshore food resource. For adult females and juveniles, who relied less on bowhead, climate-ice indices did not explain a significant amount of the interannual variation in bowhead consumption. Ice conditions may not influence bone pile use as strongly for adult females as some of them are fasting in dens in the winter–spring (Lentfer 1975), and denning draws them to shore regardless of ice conditions and bowhead availability. Thus, as a group, adult males may be better able to take advantage of this food subsidy than adult females and juveniles when ice conditions limit access to other prey. Interestingly, similar findings of consumption of bowhead by polar bears have recently been documented further east in Foxe Basin, Canada (Galicía et al. 2016). Although subsistence harvest may play a role there as well, the authors suggested that the primary mechanism may be an increased abundance of, and predation rates by, killer whales, which leave the carcasses behind.

For ringed seal, the AO_w explained much (46–82%) of the interannual variation in winter–spring consumption by adult females and juveniles, whereas simple local- (ice-free days) and large-scale (sea ice extent) ice indices did not. The leading hypothesis is that in years with less ice (e.g., reduced extent, more ice-free days), polar bear access to ringed seal as prey is reduced. However, many complex oceanographic and atmospheric parameters may influence the distribution, density, and population numbers of marine mammals and the conditions necessary for successful predation by polar bears. For instance, wind and ocean

currents can affect the size and location of flaw leads, shore leads, and polynyas, which polar bears and ringed seals frequent (Stirling 1997). Limited snow cover and high ice deformation can influence ringed seal ability to build subnivean lairs and heavy rainfall can collapse lairs, leading to greater susceptibility to predation by polar bears (Stirling and Smith 2004, Luque et al. 2014). The formation of rafted floes and pressure ridges also appears to reduce access to ringed seals for SB polar bears (Stirling et al. 2008). Multi-temporal factors influencing modeled polar bear predation on ringed seal have been reported to include ringed seal reproduction and haul-out behavior, ice concentrations, and multiple climatic indices (Pilfold et al. 2015). Thus, since the AO_w influences, and may be influenced by, climatological factors as well as sea ice movement and distribution (Stroeve et al. 2011), it may better capture environmental conditions impacting SB polar bear access to ice-associated prey than other ice indices (Stenseth et al. 2002).

Two-thirds of the interannual variation in winter–spring beluga whale consumption in adult males was explained by Arctic sea ice extent. Belugas comprised nearly 20% of the diet after a minimum extent >6 million km^2 , but $<5\%$ in recent years after ice minima were <5 million km^2 . These findings conform to our expectation that the sea ice platform is highly important for polar bear predation and scavenging on beluga whales. The lack of a similar relationship between beluga consumption and sea ice for adult females and juveniles is not readily explained. We speculate that both predation and scavenging may drive adult male consumption of beluga, while scavenging may potentially be more important for adult females and juveniles due to their smaller body size (Thiemann et al. 2008). Predation requires an ice platform, while scavenging could occur to some extent on beach-cast carcasses or those from subsistence harvest, and thus not be linked to sea ice. The contribution of onshore scavenging of beluga carcasses to SB polar bear diets is not known, however.

Bearded seal was the only prey for which interannual variation in winter–spring consumption was not linked to one of the selected climate/ice indices. Although bearded seal and ringed seal are considered to be ice-associated, they tend to prefer different ice habitats, which may

explain differences in associations with climate/ice indices relative to ringed seal. For example, bearded seal haul out on pack ice and prefer shallow nearshore environments, whereas ringed seal are more often observed on land fast ice, but also occupy near and offshore pack ice (Laidre et al. 2008). Bearded seal from neighboring areas of northern Alaska have also been reported to haul out onshore (Quakenbush et al. 2011), but the significance of potential onshore predation of bearded seal by SB polar bears is unknown.

In contrast to winter–spring variation, climate indices did not appear to influence summer–fall consumption estimates for any prey. The lack of relationship may have been due to a smaller summer–fall dataset and more limited years of data (Appendix S1: Table S1), or possibly to the longer lag time between the indices and sampling of polar bears in the fall relative to the spring.

Relationship of diet to polar bear body condition

A pattern of higher body condition was observed for those adult male and female SB polar bears that were estimated to consume higher proportions of bowhead whale. For example, in the summer–fall, bowhead whale consumption was five times higher for fat (FI 4) adult males than for those in normal condition (FI 3), whereas ringed seal consumption was two times lower for fat adult females than for those in normal condition. These results suggest that polar bears consuming greater proportions of bowhead whale remains were in better condition, possibly because the bone piles provide additional nutrition or because feeding on them requires less expenditure of effort than does predation.

CONCLUSIONS

To address the question of whether use of this onshore resource could impact vital rates at the subpopulation level, further knowledge is needed on the proportion of the population that is using the resource and the caloric value of the resources available. It has been suggested that a large portion of the subpopulation makes use of the bone piles (Herreman and Peacock 2013, Rogers et al. 2015). The proportion of radiocollared adult females that exhibited long-term land use (≥ 21 consecutive days on shore) increased over 2000–2014 to a mean of

20% of individuals (Atwood et al. 2016). In support of these data suggesting that a substantial number of SB polar bears are using the bone piles, we detected bowhead whale in the winter–spring diet estimates of 79% of the bears, nearly as high as the 88–98% detection rate of ice seals, although at a lower detection rate of 42% in the summer–fall, relative to 82–100% detections of ice seals. Nonetheless, in both seasons and in all years, the overall proportion of bowhead whale comprising the diet of SB polar bears remained low, suggesting that bowhead whale has not thus far supplanted ice seals in terms of diet importance at the population level.

The body condition of SB polar bears did not decline over the 2004–2012 period (USGS, *unpublished data*). It is unclear whether this was because the time period was too short to reflect known long-term trends or because of recent short-term changes in body condition, similar to population trends (Bromaghin et al. 2015a). Regardless, here we show that the relationship of polar bear foraging ecology and body condition to sea ice change can be complicated by other region-specific ecological factors, including human activities in the form of subsistence harvest.

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