Drivers and consequences of apex predator diet composition in the Canadian Beaufort Sea

Katie R.N. Florko, Gregory W. Thiemann, Jeffrey F. Bromaghin

K.R.N. Florko: ORCiD ID: 0000-0003-3829-7447. Department of Biology, York University, 4700 Keele Street, Toronto ON, M3J 1P3, Canada (katieflorko@gmail.com)

G.W. Thiemann: Faculty of Environmental Studies, York University, 4700 Keele Street, Toronto ON, M3J 1P3, Canada

J.F. Bromaghin: ORCiD ID: 0000-0002-7209-9500. Alaska Science Center, U.S. Geological Survey, 4210 University Drive, Anchorage AK, 99508, USA

Corresponding author: email: katieflorko@gmail.com, phone: 1-416-736-2100 x 22762[1]

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[1] Author Contributions: KRNF and GWT conceived and formulated the ideas, KRNF processed tissue samples, KRNF and JFB analysed the data, KRNF and GWT wrote the manuscript, and JFB provided editorial advice and ecological insights.

Abstract

Polar bears (*Ursus maritimus*) rely on annual sea ice as their primary habitat for hunting marine mammal prey. Given their long lifespan, wide geographic distribution, and position at the top of the Arctic marine food web, the diet composition of polar bears can provide insights into temporal and spatial ecosystem dynamics related to climate-mediated sea ice loss. Polar bears with the greatest ecological constraints on diet composition may be most vulnerable to climate-related changes in ice conditions and prey availability. We used quantitative fatty acid signature analysis (QFASA) to estimate the diets of polar bears (n = 419) in two western Canadian Arctic subpopulations (Northern Beaufort Sea and Southern Beaufort Sea) from 1999 to 2015. Polar bear diets were dominated by ringed seal (*Pusa hispida*), with interannual, seasonal, age- and sex-specific variation. Foraging area and sea ice conditions also affected polar bear diet composition. Most variation in bear diet was explained by longitude, reflecting spatial variation in prey availability. Sea ice conditions (extent, thickness, and seasonal duration) declined throughout the study period, and date of sea ice break-up in the preceding spring was positively correlated with female body condition and consumption of beluga whale (*Delphinapterus leucas*), suggesting that bears foraged on beluga whales during entrapment events. Female body condition was positively correlated with ringed seal consumption, and negatively correlated with bearded seal consumption. This study provides insights into the complex relationships between declining sea ice habitat and the diet composition and foraging success of a wide-ranging apex predator.

Key words

Foraging ecology, fatty acids, sea ice, climate change, polar bear

Introduction

Climate warming has contributed to rapid declines in sea ice extent, thickness, and seasonal duration in the Arctic (Maslanik et al. 2011, Stroeve et al. 2012, Lindsay and Schweiger 2015). Observed sea ice loss has occurred at a greater-than-forecasted rate, and declines are projected to continue and accelerate through 2100 (Stroeve and Notz 2015, Wang and Overland 2015). Although changes in sea ice conditions are well documented, the ecological consequences are more difficult to assess and likely vary by region and over time (Wassmann et al. 2011, Stern and Laidre 2016).

The response of a species to environmental change is often predicted by the relationship of the organism with its habitat (Parmesan 2006). Quantifying habitat-demographic relationships is often central to species management and conservation (e.g., Regehr et al. 2016). Apex predators are top trophic-level organisms that influence the ecology of food webs (Katona and Whitehead 1988, Horswill et al. 2016) and can serve as indicators of ecosystem change (Bowen 1997). Polar bears (*Ursus maritimus*) are apex predators with a wide geographical range, a long lifespan, and may be particularly sensitive to climate-induced ecosystem change due to their reliance on sea ice as a platform for hunting, travelling, and mating (Stirling and Derocher 1993; Durner et al. 2017, Togunov et al. 2017, Lone et al. 2018). Long-term changes in sea ice conditions have been associated with declines in polar bear body condition (Stirling et al. 1999, Rode et al. 2010, Obbard et al. 2016), reproduction (Regehr et al. 2007, Rode et al. 2010), survival (Regehr et al. 2007, Peacock et al. 2012) and abundance (Regehr et al. 2007, Bromaghin et al. 2015, Lunn et al. 2016). The effects of declining sea ice on polar bear demography are expected to be primarily mediated by changes in prey availability (i.e., spatio-temporal distribution and abundance) leading to reduced foraging opportunities.

Polar bears feed on a variety of marine mammal species throughout their range (Derocher et al. 2002, Thiemann et al. 2008a). Studies suggest polar bears feed primarily on ringed seals (*Pusa hispida*; Thiemann et al. 2008a), which have a wide distribution and high abundance throughout the Canadian Arctic (Kingsley et al. 1985). Polar bears of most age classes and both sexes are able to hunt ringed seals as they are the smallest Arctic seal (Kingsley et al. 1985). However, ringed seals are dependent on sea ice for resting, molting, and building subnivian lairs above breathing holes where they retreat to rear their pups (Smith and Stirling 1975), and are thus vulnerable to climatic change (Ferguson et al. 2005, 2017, Ferguson and Higdon 2006, Chambellant et al. 2012, Yurkowski et al. 2016, Reimer et al. 2019). During periods in the mid-1970s and 1980s when heavy ice conditions in the Beaufort Sea were not favourable for ringed seals to maintain breathing holes and birth lairs, the productivity and survival of both ringed seals and polar bears declined (Stirling 2002). Given that polar bears may feed primarily on newly weaned ringed seal pups (Stirling and Oritsland 1995), the proportion of ringed seal in polar bear diets may reflect favourable environmental conditions for both species (Pilfold et al. 2015, Hamilton et al. 2017).

Although ringed seals are the primary prey of polar bears across the circumpolar Arctic, bears also feed substantively on locally available prey, including bearded seals (*Erignathus barbatus*; Thiemann et al. 2007, 2008a), harp seals (*Pagophilus groenlandica;* Derocher et al. 2002, Galicia et al. 2015), harbour seals (*Phoca vitulina;* Thiemann et al. 2008a, Sciullo et al. 2017), walruses (*Odobenus rosmarus;* Calvert and Stirling 1989), beluga whales (*Delphinapterus leucas;* Freeman 1973), narwhals (*Monodon monoceros;* Smith and Sjare 1990), and the carcasses of bowhead whales (*Balaena mysticetus;* Bentzen et al. 2007, Schliebe et al. 2008, Herreman and Peacock 2013, Galicia et al. 2016, Lillie et al. 2019). The relative importance of alternative prey (i.e., other than ringed seal) may vary both spatially and temporally according to sea ice conditions (Hamilton et al. 2017, Boucher et al. 2019), prey life history (Young et al. 2015) and seasonal habitat use (Hornby et al. 2017). Polar bear diet may also vary within a subpopulation due to differences in body size and energetic requirements. Adult male polar bears are approximately twice the size of adult females (Derocher et al. 2005), which confers higher energetic demands but also allows them to hunt larger prey species (e.g., bearded seals; Thiemann et al. 2007, 2008a, Derocher et al. 2010).

The Southern Beaufort Sea subpopulation of polar bears has experienced recent demographic decline, with estimated abundance falling 25-50% from 2004 to 2006 followed by a period of stability through 2010 (Bromaghin et al. 2015). In contrast, the adjacent Northern Beaufort Sea subpopulation remained largely stable through the mid-2000s (Stirling et al. 2011). The ecological drivers of these divergent demographic trends are not well understood, although the decline in Southern Beaufort Sea was hypothesized to be driven by reduced sea ice in summer and increased sea ice deformation in winter, which may have negatively affected the ability of polar bears to access their prey (Bromaghin et al. 2015).

The fatty acid (FA) composition of a predator’s adipose tissue reflects its diet over the preceding weeks to months, as ingested FA are predictably incorporated into a consumer’s fat stores (Ackman and Eaton 1966, Iverson et al. 2004, Budge et al. 2006, Thiemann et al. 2008a, 2008b). Quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004) models the FA profile or “signature” of an individual predator as a linear combination of potential prey signatures. QFASA estimates diet composition by determining the relative proportion of different prey types that minimizes the distance between the observed and modeled predator signature after accounting for FA-specific patterns of metabolism (Iverson et al. 2004).

As energy is stored in adipose tissue, the proportion of lipid (relative to non-lipid components) will increase (Pond 1992). Conversely, when energy is mobilized, relative lipid content will decline. Thus, the relative lipid content of adipose tissue can serve as an indicator of body condition in polar bears (Thiemann et al. 2006, McKinney et al. 2014, Sciullo et al. 2016).

We used lipid analyses and QFASA to quantify the diet composition and body condition of polar bears harvested in the Canadian Beaufort Sea from 1999 to 2015, a period of substantial habitat and demographic change. Our objective was to examine environmental drivers of diet composition, in addition to spatial, temporal, and age- and sex-specific variation, and the implications on body condition. We hypothesized that polar bear diet composition and body condition would be affected by regional sea ice conditions, resulting in differences in diet and foraging success (i.e., body condition) over time. We further hypothesized that differences in diet and body condition across bears of different age classes and sexes would result from the ability of adult males to capture larger-bodied prey. A better understanding of the relationship between sea ice habitat and the diet composition and foraging success of top predators will allow more accurate predictions of the ecological effects of future climate warming.

Material and Methods

Sample Collection

We used adipose tissue samples collected from 419 polar bears harvested by hunters in the Inuvialuit Settlement Region of the Canadian Beaufort Sea from 1999 to 2015. Bears belonged to two recognized subpopulations: Northern Beaufort Sea and Southern Beaufort Sea, with the subpopulation boundary established by the Northwest Territories and Yukon Territory (Fig. 1). However, because the majority of samples (89%) came from the Northern Beaufort Sea and bears in the Southern Beaufort Sea were sampled close to the management unit boundary (Fig.

1), we did not use subpopulation as a factor in our models. It is illegal to harvest adult females with dependent offspring so sampled bears included males and solitary females of independent age classes (Table S1; defined as: adults = 5+ years old; subadults = 3-4 years old). Age was determined by counting growth layer groups in the cementum of an extracted vestigial premolar (Calvert and Ramsay 1998). For seasonal analyses, we defined winter/spring as January – June and summer/fall as July – December; sampling in the winter/spring was primarily from February – May, and sampling in summer/fall was primarily in November. Samples of subcutaneous adipose tissue (approx. 8 cm x 4 cm) were collected from each bear and individually wrapped in aluminum foil, sealed in a Whirl-Pak, and stored at – 20°C until analysis.

Other recent work has used QFASA to examine the diets of polar bears in the adjacent Chukchi Sea subpopulation, so to make our results comparable for future studies, we used the prey FA library from Bromaghin et al. (2017) which included ringed seals (n = 23), bearded seals (n = 83), beluga whales (n = 29), and bowhead whales (n = 64). We included additional blubber samples from 248 ringed seals harvested by Inuvialuit hunters in the eastern Amundsen Gulf for a total prey library of 447 individual animals. As with polar bear adipose tissue, marine mammal blubber was sampled from skin to muscle, wrapped in aluminum foil, sealed in a Whirl-Pak, and stored at – 20°C until analysis.

Laboratory Analyses

We subsampled the interior of polar bear adipose tissue and marine mammal blubber samples (approx. 0.3 g) to avoid any oxidized tissue (Budge et al. 2006). Tissue subsamples were weighed and lipid was quantitatively extracted using a modified Folch extraction (Folch et al. 1957, Iverson et al. 2001). Lipid content was expressed as the percent of total sample wet weight ± 1 standard error and used as an index of body condition (Thiemann et al. 2006, McKinney et al. 2014, Sciullo et al. 2016). FA methyl esters (FAME) were derived from the extracted lipid using sulfuric acid in methanol as a catalyst (Thiemann et al. 2004; Budge et al. 2006). FAME were analyzed in duplicate on a temperature-programmed gas chromatograph (GC) with a flame ionization detector fitted with a polar column (30 m x 0.25 mm inner diameter; DB-23; Agilent Technologies, Palo Alto, California, USA; Budge et al. 2006). FA were measured as mass percent of total FA ± 1 standard error, and expressed by the shorthand nomenclature of *A*:*B*n-*X*, where *A* is the length of the carbon chain, *B* is the number of double bonds, and *X* is the position of the first double bond relative to the terminal methyl group. FA identifications were based on retention times and were manually verified and corrected using CompassCDS software (Version 3.0, Bruker Daltonics Inc., Germany).

QFASA Modelling

The QFASA method developed by Iverson et al. (2004) generates estimates of predator diets by modelling the predator signature as a linear combination of available prey signatures and determining the combination of prey that minimizes the distance between the observed and modelled predator. Calibration coefficients derived from captive mink (*Neovison vison;* Thiemann et al. 2008b) were used to account for FA-specific patterns of modification and biosynthesis that occur within the predator (Iverson et al. 2004). We generated estimates of diet composition for each polar bear using the est_diet function in the R package *qfasar* (distance measure: Aitchison; estimation space: prey; Bromaghin 2017). We also used a new diagnostic function to generate a jackknifed cross-validation of the prey library: leave-one-prey-out (LOPO; function: lopo()). LOPO temporarily removes each prey sample from the prey library and models its diet estimate, as if it were a predator, before returning it to the prey library. This was done for each prey sample, and means were calculated for each type (i.e., species), which yields a measure of the prey types' distinctiveness within the library. To determine the suite of FA to use in QFASA modelling, we started with the dietary set used by Galicia et al. (2015) and removed each FA in turn, ran the LOPO analysis, and investigated the accuracy of prey classifications. LOPO outputs the mean distribution of estimates among all prey types; perfect estimation yields values of 1 for each prey type (Bromaghin 2017). If LOPO analysis showed more accurate (i.e., higher) values upon FA removal, we removed the respective FA from QFASA diet estimations. QFASA diet estimation and diagnostics were conducted using R (version 3.4.0, GUI 1.40, R Development Team 2017).

Sea Ice Data

We used sea ice data from the National Snow and Ice Data Center (NSIDC; Boulder, CO), as summarized by Stern and Laidre (2016). Although Stern and Laidre (2016) used the previous Northern-Southern Beaufort subpopulation boundary at 125°W (see Durner et al. 2018), which was slightly east of the updated boundary used in this study (133°W; Fig 1), the methods of Stern and Laidre (2016) still reflect regional sea ice conditions in the two subpopulations. Daily sea ice data were measured by satellites Nimbus-7 SSM and DMSP SSM/I-SSMIS Passive Microwave Data at a cell size of 25 x 25 km daily. Stern and Laidre (2016) derived yearly values for four sea ice metrics in Southern Beaufort Sea and Northern Beaufort Sea: date of sea ice break-up, date of sea ice freeze-up, duration of open water season, and mean summer sea ice concentration. A threshold for each year was calculated as the mid-point between the March mean sea ice concentration and the September mean sea ice concentration. Date of sea ice freeze-up and date of sea ice break-up were calculated as the day of year that sea ice concentration crossed above or below the year's threshold, respectively. Duration of the open water season was calculated as the number of days between sea ice break-up and freeze-up. Mean summer sea ice concentration was calculated for 1 June – 31 October for each year.

Statistical Analyses

We used a redundancy analysis (RDA; van den Wollenberg 1977) and a forward-selection model to examine the minimum number of variables that significantly influence polar bear diet, and ranked the models (i.e., each successive step in the forward selection model as it is building) using Akaike information criterion (AIC) to identify variables that explained the most variation in the response variables (Borcard et al. 1992). The RDA included all intraspecific (age, age class, sex), spatial (longitude, latitude), temporal (ordinal date, month, season, year), and environmental (sea ice break-up, freeze-up, duration of open-water season, mean summer sea ice concentration) predictor variables. Prior to RDA modelling we transformed the diet data (response variables) using the Hellinger transformation, which takes the square root of the sum of each proportion per prey species, reducing skewedness of more prominent response variables (i.e., ringed seal proportion in diet estimates; Legendre and Gallagher 2001).

Results from the RDA indicated which variables were driving polar bear diet; we further analyzed differences between significant binary variables (i.e., sex, season) using permutation MANOVA (for overall diet) and permutation one-way ANOVA (for individual prey types' contribution to bear diet), as diet estimates were proportional and therefore not normally distributed. We tested for age-, longitudinal-, and year-effects using Spearman rank correlations for each species' contribution to polar bear diet, when separated by sex. We also used Spearman rank correlations to examine the relationship between polar bear diet and body condition (i.e., percent lipid in the adipose tissue) independently for each prey type.

Temporal trends in sea ice metrics were tested using linear regression. The relationship between each sea ice metric and the proportion of each prey in polar bear diets was also tested in a linear regression, separated by sex; Southern Beaufort Sea bears were not included due to small sample size in some years (Table S1). Similarly, we used linear regression to investigate the relationship between sea ice and body condition of bears separated by sex. Since bears harvested in the winter/spring were mostly killed in February-March, their foraging would not be influenced by the date of sea ice break-up, freeze-up, duration of the open water season, or summer sea ice concentration of that year; thus, winter/spring bears were compared against the sea ice break-up, freeze-up, duration of open water season, and summer sea ice concentration in the year prior to sampling. All statistical analyses were conducted using R (version 3.4.0, GUI 1.40, R Development Team 2017).

Results

QFASA Modelling Diagnostics

LOPO analysis revealed the clearest separation between prey FA signatures when FA 22:1n-9 was omitted. LOPO allocation accuracy for the final set of 29 FA was 0.92 for bearded seal and beluga whale, 0.97 for bowhead whale, and 0.86 for ringed seal, thus, 22:1n-9 was excluded from QFASA diet estimations.

General Dietary Patterns

The mean (±SE) diet composition of all polar bears harvested in the Beaufort Sea was 15.1 ± 0.9% bearded seal, 17.8 ± 0.8% beluga whale, 10.0 ± 0.4% bowhead whale, and 57.1 ± 0.9% ringed seal. Polar bear diets were dominated by ringed seals irrespective of bear sex, season, or age class.

Longitude, of the single variables, was the best-fitting model of potential factors influencing polar bear diet (Table 1; $p = 0.002$). In the forward-selection, models including sex, and combining sex and age were considered the second and third best fitting models; additionally, date of sea ice freeze-up and break-up, and year were also significant covariates (Table 1).

Spatial Patterns

Longitude of sampling location, of all single variables, explained the most variation in diet composition (Table 1). For male bears, but not females, the proportional consumption of every prey type differed with longitude. Male bears' consumption of bearded seal ($\rho = -0.352$, $S = 3738400$, $p < 0.001$) and bowhead whale ($\rho = -0.150$, $S = 3177400$, $p = 0.017$) decreased, and beluga whale ($\rho = 0.349$, $S = 1800200$, $p < 0.001$) and ringed seal ($\rho = -0.137$, $S = 2384300$, $p = 0.028$) increased, as sample location moved from west (e.g., Tuktoyaktuk Peninsula, western Banks Island) to east (e.g., Amundsen Gulf; Fig. 1, S1).

Intraspecific Patterns

Polar bear diet composition differed between males and females ($p = 0.001$); males consumed proportionately more bearded seal ($p < 0.001$) and less ringed seal than females ($p < 0.001$), but there was no difference between male and female consumption of beluga or bowhead whale ($p = 0.961$, $p = 0.345$, respectively). Male polar bears also differed between age classes ($p = 0.001$) in their consumption of bearded seal ($p < 0.001$, adults highest), beluga whale ($p = 0.012$, adults highest), and ringed seal ($p < 0.001$, subadults highest), but not bowhead whale ($p = 0.216$). Specifically, the proportional consumption of bearded seal increased with the age of male bears (Fig. 2; $\rho = 0.401$, $S = 1965212$, $p < 0.001$), whereas ringed seal consumption decreased with age

($\rho = -0.387$, $S = 4550832$, $p < 0.001$). There were no significant trends between age and the consumption of any prey type for females.

Seasonal Trends

Polar bear diets differed between the summer/fall and winter/spring (Fig. 3; $p = 0.014$). In females, bearded seal consumption was higher ($p = 0.001$) and beluga whale was lower in the summer/fall ($p = 0.033$) relative to winter/spring. Bowhead whale and ringed seal consumption was not significantly different between seasons ($p = 0.298$, $p = 0.902$ respectively). Male polar bears consumed the same amount of bearded seal, bowhead whale, and ringed seal in the summer/fall and winter/spring ($p = 0.745$, $p = 0.321$, $p = 0.863$, respectively). Beluga whale contributed more to the diet of male polar bears in the winter/spring than the summer/fall ($p = 0.003$).

Body Condition and Diet

Body condition did not differ between sexes ($p = 0.263$) or age classes ($p = 0.181$). There was a positive correlation between ringed seal consumption and body condition ($\rho = 0.206$, $S = 347780$, $p = 0.016$), and a negative correlation between bearded seal consumption and body condition ($\rho = -0.169$, $S = 511840$, $p = 0.048$) in female polar bears. We found no relationship between proportional diet composition and body condition in male bears (Table S2).

Temporal Trends

Ringed seal remained the primary prey of polar bears in all years, for both males and females, with interannual variation (Fig. 4). Beluga whale consumption was higher in congruent years when ringed seal consumption was reduced. Overall, we found no directional change in the consumption of any prey type over time.

Sea Ice

Sea ice freeze-up in both the Northern Beaufort Sea and Southern Beaufort Sea subpopulation zones occurred progressively later in the year and the duration of open water increased over the course of our study (1999-2015). Moreover, sea ice break-up occurred progressively earlier and summer sea ice concentration declined over the study period in Southern Beaufort Sea but not Northern Beaufort Sea (Fig. 5).

Sea ice freeze-up and summer sea ice concentration had no significant effect on polar bear diet in Northern Beaufort Sea (Table S3). For female bears, sea ice break-up was positively related to the proportion of beluga whale (i.e., later break-up associated with higher beluga; Fig. 6; F = 7.600, R^2 = 0.398, p = 0.022), without significantly reducing the proportion of other prey in the diet. Correlations between the date of spring break-up and consumption of bowhead whale and ringed seal were non-significant but trended negative (Table S3). The diets of male bears were not related to any of the sea ice metrics (Table S3).

Sea ice dynamics were significantly related to the body condition of female polar bears in Northern Beaufort Sea, where shorter duration of the open-water season ($F_{1,11}$ = 7.219, R^2 = 0.341, p = 0.021), and later dates of sea ice break-up ($F_{1,11}$ = 11.63, R^2 = 0.470, p = 0.006), were positively related to body condition (Fig. 7). Additionally, there was a non-significant positive trend between summer ice concentration and body condition ($F_{1,11}$ = 3.769, R^2 = 0.188, p = 0.078), and no effect of the date of fall freeze-up on female body condition (Fig. 7; $F_{1,11}$ = 0.557, R^2 = -0.038, p = 0.471). Conversely, the body condition of male polar bears in Northern Beaufort Sea was not affected by the summer ice concentration ($F_{1,11}$ = 0.385, R^2 = -0.054, p = 0.547), the duration of the open-water season ($F_{1,11}$ = 0.217, R^2 = -0.070, p = 0.650), the date of fall freeze-up ($F_{1,11}$ = 0.601, R^2 = -0.034, p = 0.455), or the date of spring break-up ($F_{1,11}$ = 0.004, R^2 = -0.091, p = 0.950).

Discussion

As top predators reliant on annual sea ice habitat, polar bears and their foraging habits can provide insights into the ecological effects of climate warming. Our results reveal relationships between sea ice conditions, polar bear diet, and foraging success in a region undergoing rapid sea ice decline. Sea ice loss was associated with lower body condition among female polar bears suggesting reduced foraging success. The demonstrated differences in diet composition and response to habitat conditions among age and sex classes suggests that some bears (i.e., adult males) are better equipped to cope with changes in prey availability and habitat quality. Greater constraints on the dietary options for juvenile and female bears make them more susceptible to demographic consequences in the western Canadian Arctic.

Spatial Patterns

Of all the variables separately, the longitude of harvest location explained the most variation in polar bear diet (Table 1), specifically for male bears. Male bears consumed relatively more bearded seal and bowhead whale in the west portion of the study area, and more beluga whale and ringed seal in the east, patterns that are likely consistent with prey abundance: bearded seals primarily reside in the offshore pack-ice and may be in greater abundance in the Beaufort and Chukchi Seas than in Amundsen Gulf (Smith 1980, Quakenbush et al. 2011), and a greater abundance of ringed seal is supported in Amundsen Gulf than the Beaufort and Chukchi Seas (Harwood and Kingsley 2013, Pilfold et al. 2014, Harwood et al. 2015). Amundsen Gulf is also an important ringed seal pupping area (Harwood et al. 2000, 2012). Greater proportions of bowhead whale in the western portion of the study area is consistent with access to subsistence-harvested bowhead whale carcasses along the Alaska coast (Ashjian et al. 2010, Herreman and Peacock 2013).

Bears may have had access to beluga whales as they migrated from the Bering Sea to the Beaufort Sea in spring; whales move adjacent to the landfast ice over the Mackenzie Shelf and into Amundsen Gulf in early June (Harwood and Smith 2002), further aggregate in the Mackenzie Estuary when the landfast ice breaks up (Huntington et al. 1999, Harwood and Smith 2002, Luque and Ferguson 2009, Hornby et al. 2016) and disperse offshore across the Mackenzie Shelf in late July/August (Harwood and Kingsley 2013). Since our results suggest male polar bears consumed greater proportions of beluga whale in Amundsen Gulf than the western portion of the study area (i.e., Mackenzie Estuary), there may be more polar bear foraging opportunities on beluga whale during their Mackenzie Estuary shoulder seasons. In contrast to males, female polar bears showed no spatial structure in their diet composition, possibly as a consequence of shared feeding areas, such as around the Cape Bathurst Polynya (Thiemann et al. 2008a). Our results of female foraging on ringed seals throughout the study area are consistent with kill-sites recorded by Pilfold et al. (2014) who observed ringed seal kill-sites along the landfast ice along the Tuktoyaktuk Peninsula Region, western Banks Island, and in the Amundsen Gulf.

Intraspecific Patterns

Variability in polar bear diet between sexes and age classes may be due to differences in hunting ability, energetic requirements, and spatial segregation. Our results are consistent with previous studies (e.g., Cherry et al. 2010, McKinney et al. 2017, Thiemann et al. 2008a) that suggest female polar bears are more reliant on ringed seals than are males, which forage more on bearded seals. Females with dependent cubs may focus their hunting on ringed seals on the landfast ice, thus limiting spatial overlap with potentially infanticidal adult male bears, which may hunt in the offshore pack ice where bearded seal densities are higher (Smith 1980, Quakenbush et al. 2011). The large size of adult male bears allows them to potentially hunt large-bodied prey, like adult bearded seals, more easily (Cherry et al. 2010, Derocher et al. 2005, 2010). Solitary adult females, and subadult bears of both sexes, may have access to bearded seal pups and be able to scavenge on remains from adult bearded seal kills made by adult male polar bears.

We found males consumed proportionately more bearded seal with age (Fig. 2), likely due to increasing body mass, as male polar bears continue to grow well after sexual maturity (Derocher et al. 2010). Thiemann et al. (2007) documented a positive correlation between adult male body mass and bearded seal consumption. The clear age-driven shift away from ringed seal and towards bearded seal in male polar bears may serve to reduce intraspecific competition with adult females and juvenile bears, which are more dependent on ringed seal.

Body Condition and Diet

Body condition of female bears was positively correlated with the consumption of ringed seal and negatively correlated with bearded seal consumption (Table S2). These patterns suggest that female bears experience declining body condition when preferred ringed seal prey are less available and rely more heavily on scavenging the carcasses of large bodied prey (i.e., bearded seals). The lack of relationship between body condition and diet in male bears may be a consequence of greater dietary flexibility in male bears and their ability to exploit bearded seals as a widely available prey.

McKinney et al. (2017) examined bears in the western portion of the Southern Beaufort Sea and found a positive correlation between body condition and bowhead whale consumption, a pattern not detected in our results from the Canadian Beaufort Sea. These different spatial patterns are likely related to the distribution of bowhead carcasses, which are concentrated around the communities of Kaktovik, Nuiqsut, and Utqiagvik, AK (McKinney et al. 2017, Lillie et al. 2019). Our results suggest that Alaskan bowhead harvests have not measurably influenced the foraging ecology of polar bears in the Canadian Beaufort Sea.

Seasonal and Interannual Trends

Seasonal differences in diet composition suggest that polar bears feed on seasonally available prey, particularly increased beluga whale consumption in the winter/spring, similar to the findings of McKinney et al. (2017). Predation on beluga whale is presumably related to whale migration, which is dependent on sea ice conditions (Huntington 2002, Hornby et al. 2016). Forecasted sea ice trends may allow for the timing of beluga migration to occur progressively earlier in the winter/spring providing an important food source for polar bears in the Canadian Beaufort Sea.

Diet composition varied across years for all age classes and sexes, suggesting interannual variation in prey availability. Female bears consumed proportionately more beluga whale in years when ringed seal was reduced, and more ringed seal when beluga whale was reduced, while bowhead whale and bearded seal did not appear to be related to other prey. Our results suggest beluga whale is an important secondary prey source for both male and female polar bears in our study area. The low ringed seal consumption for all bears in 2007, and female bears in 2010 (Fig. 4), suggest a possible decrease in ringed seal availability in those years. Summer Arctic sea ice extent reached a record minimum in 2007 (Wood et al. 2013); potentially inhibiting the ability of ringed seals to produce pups and for polar bears to forage effectively. Low ringed seal consumption and low body condition of polar bears in 2007 is consistent with our hypothesis that reduced sea ice would result in a decrease of polar bear foraging on ringed seals, and increased reliance on alternative prey, such as beluga whale (Fig. 4). Recent climatic and oceanographic changes, particularly in the Beaufort Sea, such as increased upwelling of nutrients and an increase in pelagic marine productivity along the Beaufort slope (Schulze and Pickart 2012, Pickart et al. 2013), may offer favorable foraging conditions for beluga whales (Harwood and Kingsley 2013). More generally, Harwood and Kingsley (2013) report an increase in beluga whale abundance in the offshore Beaufort Sea in late August in 2007-2009 relative to the mid-1980s.

Hornby et al. (2014) conducted beluga whale aerial surveys over the Mackenzie River estuary and the Tuktoyaktuk Peninsula from 2011-2013, and found relatively low abundance of beluga in 2011 (23 whales; possibly due to logistical effects of poor weather), higher abundance in 2012 (270 beluga observed on the day of ice break up; similar to surveys done in the 1970s and 1980s), and relatively high beluga density in 2013 (305 whales observed the day after ice break-up). Our estimates of beluga whale consumption by polar bears (Fig. 4) are not consistent with these patterns of whale abundance, suggesting that years with comparatively higher numbers of beluga in the Mackenzie River estuary and near the Tuktoyaktuk Peninsula are not necessarily years polar bears are able to forage on more beluga whale. Rather, consumption of beluga appears to be more strongly affected by regional sea ice conditions (see below). Overall, our results suggest higher polar bear consumption of beluga whale than previously documented in the region (Thiemann et al. 2008a, Rode et al. 2014, McKinney et al. 2017).

Sea Ice Trends and Foraging Dynamics

Sea ice freeze-up occurred progressively later in the year, and subsequently the duration of the open water season increased over the study period (Fig. 5). However, these long-term declines in sea ice conditions were not matched by similar trends in polar bear diet composition in Northern Beaufort Sea, which showed interannual variability that was not consistently driven by sea ice conditions. However, later ice break-up (that is, “heavy” sea ice conditions) was correlated with higher beluga whale consumption. Heavy spring ice may delay beluga movements into, and out of, summer feeding areas, which may result in beluga entrapments during fall freeze-up in the Southern Beaufort Sea (Higdon and Ferguson 2012). Thus, our results suggest spring sea ice conditions are a driver of beluga whale consumption and are potentially indicative of polar bears foraging on beluga whales at entrapment events. The trend toward high beluga whale consumption at both heavy sea ice conditions may also be inversely related to ringed seal productivity, which may be reduced at heavy sea ice conditions (see below and Stirling 2002).

The positive relationship between date of spring ice break-up and body condition of female bears in Northern Beaufort Sea adds to the growing body of evidence that increased time on-ice in the spring is linked to higher foraging success and improved nutritional status (see Stirling et al. 1999, Rode et al. 2010, Obbard et al. 2016). The negative relationship between duration of open-water season and body condition also suggests on-ice foraging is essential for the nutritional health of female polar bears. In contrast to female bears, male bears showed no relationships between sea ice conditions and body condition (or diet), possibly indicative of their flexible diet and ability to exploit larger-bodied prey. Although the trend was not significant, we found evidence of reduced ringed seal consumption by Northern Beaufort Sea bears in years with delayed sea ice break-up. Heavy spring sea ice conditions have reduced the reproductive success of Beaufort Sea ringed seals in the past (Stirling 2002) and may limit the ability of polar bears to prey on newly weaned ringed seal pups (Bromaghin et al. 2015). Thus, optimal polar bear foraging will likely be realized when sea ice conditions allow for maximal ringed seal natality. That is, a stable sea ice platform that is dynamic enough to allow seals to maintain breathing holes (see Stirling 2002).

Our results suggest polar bear foraging is variable across spatiotemporal scales and intraspecific groups, possibly due to habitat-driven changes in prey availability and differences in polar bear hunting ability. These results provide novel insights into the effects of sea ice conditions (especially timing of break-up) on polar bear diet and body condition in regions undergoing rapid reductions in sea ice. Given the projected rates of sea ice decline (Stroeve and Notz 2015, Wang and Overland 2015), ongoing monitoring of the Arctic marine food web is necessary for understanding species response to climatic-driven habitat changes. A better understanding of the mechanistic relationships between habitat, foraging, and polar bear demography is essential to predicting, and potentially managing, the effects of continued climate warming on this globally vulnerable species.

Acknowledgements

We are particularly grateful to the Inuvialuit Game Council and the Inuvialuit hunters for collecting adipose tissue samples from polar bears harvested during their annual subsistence hunts. We thank Marsha Branigan and Jodie Pongracz (Government of Northwest Territories) for organizing and facilitating sample collection and providing ecological insights on the Beaufort Sea ecosystem. This work was supported by a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to GWT, the Kenneth M. Molson Foundation, Northern Scientific Training Program, and York University, Faculty of Graduate Studies. We thank S. Budge and C. Barry (Dalhousie University) for conducting gas chromatography, L. Harwood (Fisheries and Oceans Canada) and J. Alikamik for ringed seal adipose tissue samples, and H. Stern and K. Laidre for access to sea ice data. We thank K. Rode for helpful comments on an earlier draft of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not constitute endorsement by the U.S. Government. This article was

reviewed and approved under the U.S. Geological Survey, Fundamental Science Practices policy (http://www.usgs.gov/fsp).

Conflict of Interest

The authors declare that they have no conflict of interest.

Statement of Animal Rights

The polar bear subsistence hunt and sample collection were carried out under Canadian law.

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Figure Captions

Figure 1 Locations of polar bears (red circle) harvested in the Beaufort Sea from 1999 to 2015. Bears were located in the boundaries of the Southern Beaufort Sea (SB) or the Northern Beaufort Sea (NB) subpopulation.

Figure 2 Effect of age on estimated contribution (mean ± SE) of ringed seal and bearded seal in the diet of male polar bears in the Canadian Beaufort Sea (1999-2015). Results from Spearman rank correlation shown on figure with 95% confidence intervals (grey shading).

Figure 3 Seasonal diet composition (mean ± SE) of polar bears in the Beaufort Sea, 1999 to 2015, as estimated from QFASA. Winter/spring is defined as January-June and summer/fall as July-December.

Figure 4 Temporal trends in polar bear diet composition (mean ± SE) and body condition (% lipid content in adipose tissue; mean ± SE; dotted line) of polar bears in the Beaufort Sea.

Figure 5 Temporal trends in sea ice in the Northern and Southern Beaufort Sea polar bear subpopulations. Statistical results from linear regression are shown on the figure with 95% confidence intervals (grey shading). Data from Stern and Laidre 2016.

Figure 6 Effects of sea ice break-up (ordinal date; data from Stern and Laidre 2016) on proportional contribution (mean ± SE) of beluga whale to the diets of female polar bears in the Northern Beaufort Sea (2003-2014). Statistical results from linear regression are shown on the figure with 95% confidence intervals (grey shading).

Figure 7 The effect of sea ice conditions on body condition (mean ± SE) of female polar bears in the Northern Beaufort Sea subpopulation (1999-2015). Statistical results from linear regression are shown on the figure with 95% confidence intervals (grey shading). Data from Stern and Laidre 2016.

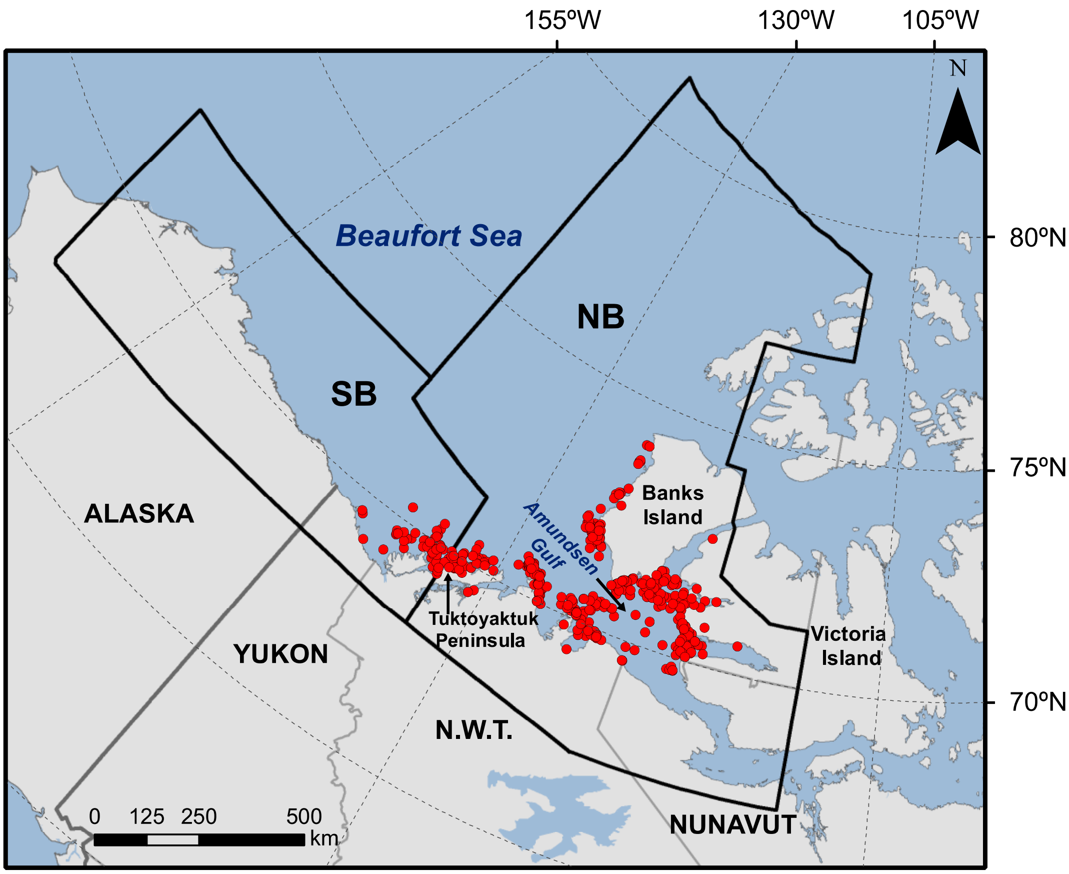

155ºW
130ºW
105ºW
N
80ºN
75ºN
70ºN
Beaufort Sea
NB
SB
ALASKA
YUKON
N.W.T.
NUNAVUT
Banks Island
Amundsen Gulf
Tuktoyaktuk Peninsula
Victoria Island
0 125 250 500
km

Figure 1

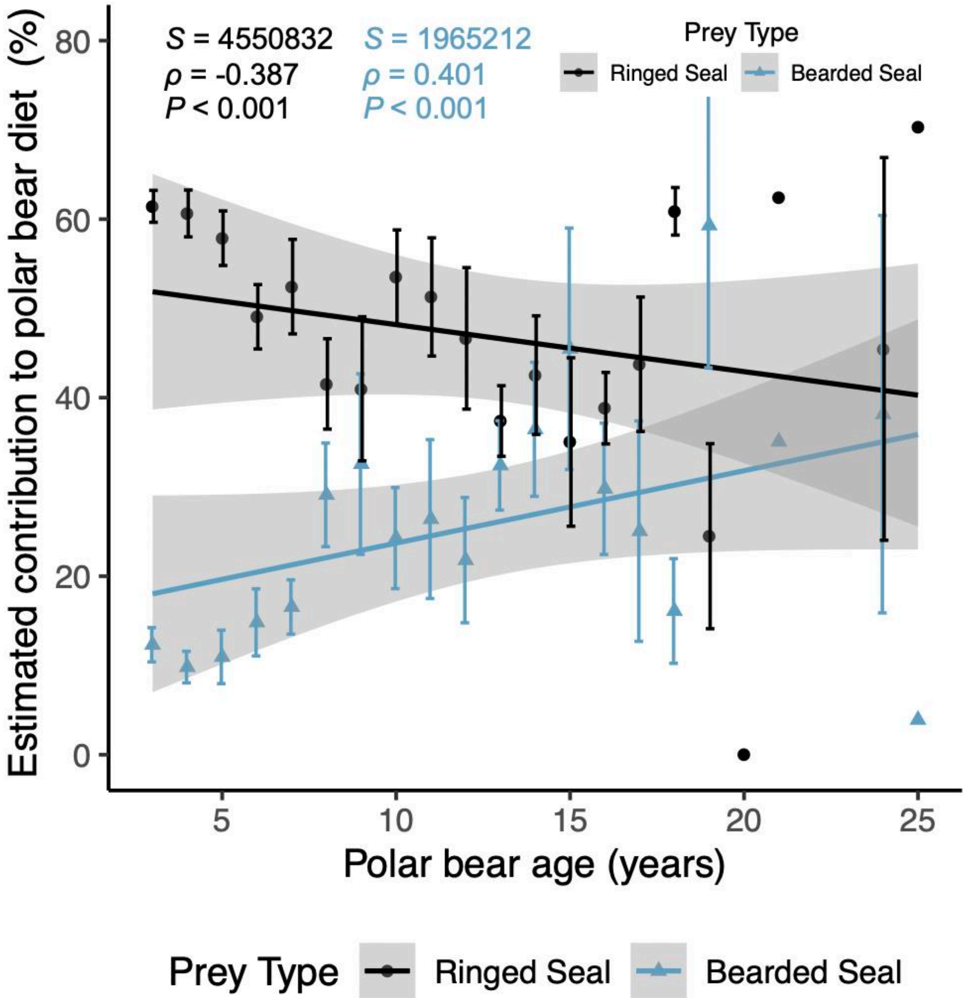

S = 4550832
ρ = -0.387
P < 0.001
S = 1965212
ρ = 0.401
P < 0.001
Prey Type
Ringed Seal
Bearded Seal
Estimated contribution to polar bear diet (%)
0
20
40
60
80
5
10
15
20
25
Polar bear age (years)
Prey Type
Ringed Seal
Bearded Seal

Figure 2

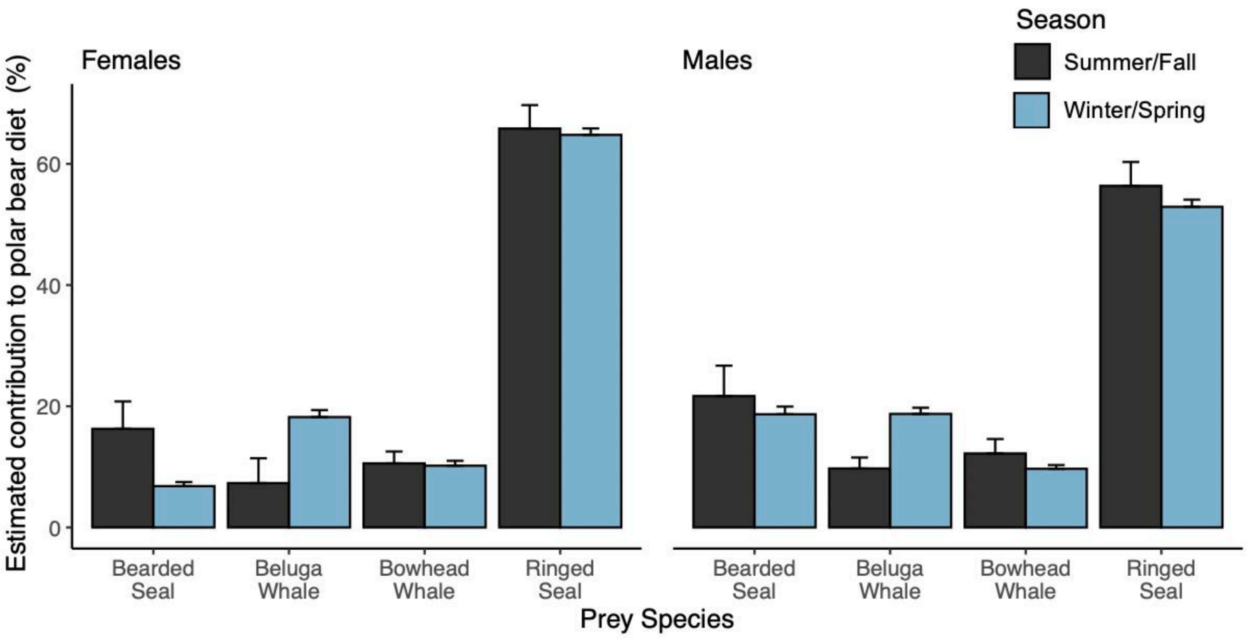
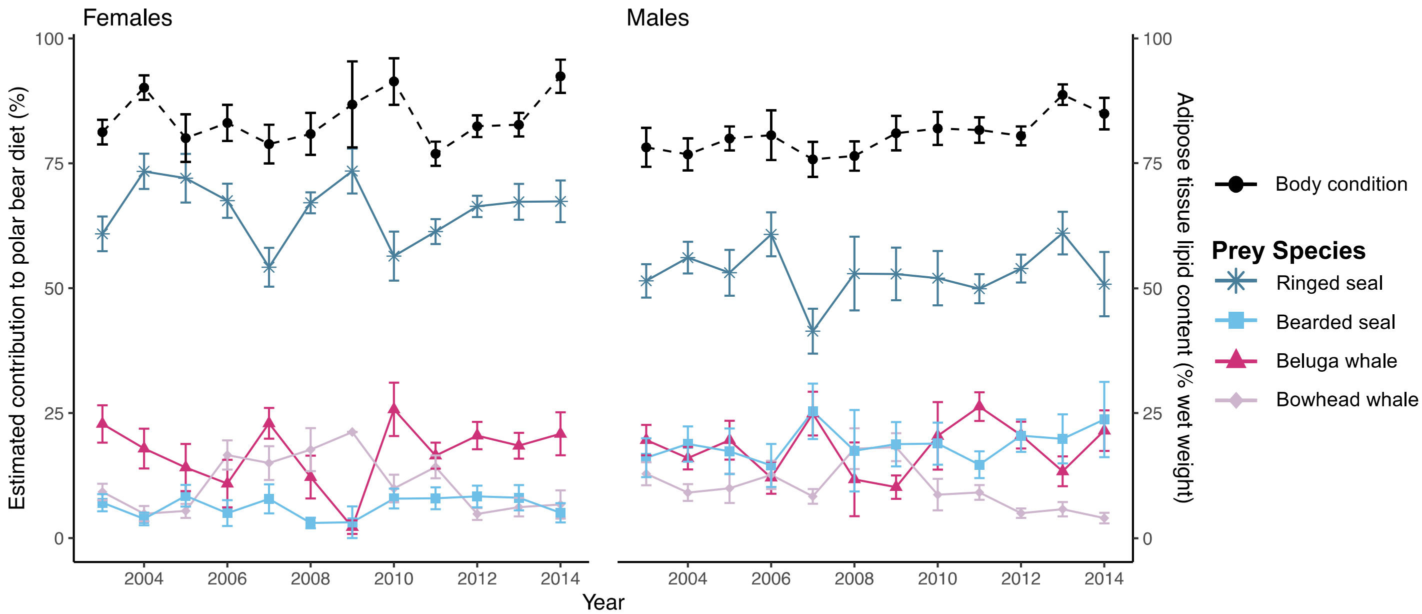
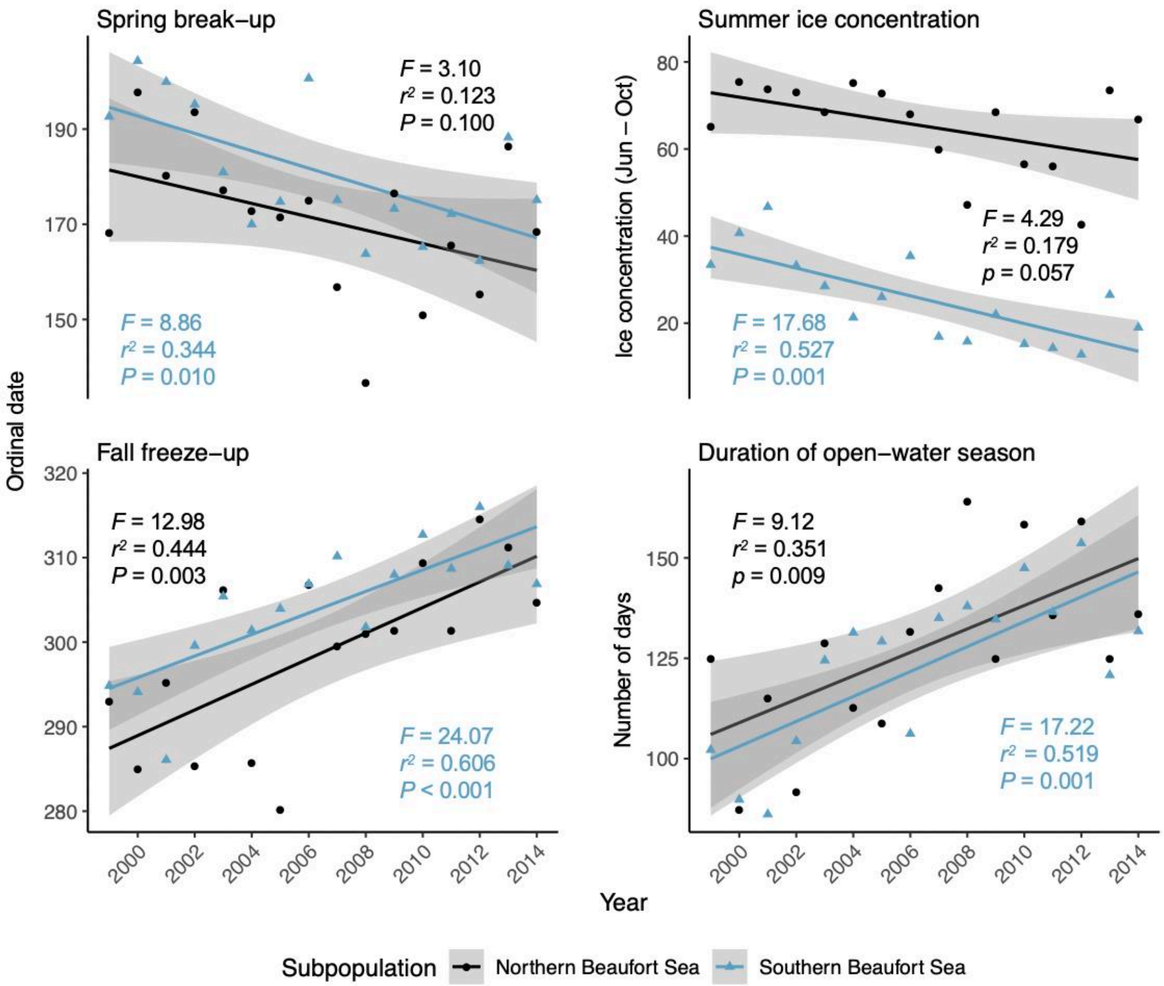

Season
Summer/Fall
Winter/Spring
Females
Males
Estimated contribution to polar bear diet (%)
0
20
40
60
Bearded Seal
Beluga Whale
Bowhead Whale
Ringed Seal
Bearded Seal
Beluga Whale
Bowhead Whale
Ringed Seal
Prey Species

Figure 3



Females
Males
100
75
50
25
0
2004
2006
2008
2010
2012
2014
Year
Estimated contribution to polar bear diet (%)
Adipose tissue lipid content (% wet weight)
Body condition
Prey Species
Ringed seal
Bearded seal
Beluga whale
Bowhead whale

Figure 4



Spring break–up
F = 3.10
r² = 0.123
P = 0.100
F = 8.86
r² = 0.344
P = 0.010
Summer ice concentration
F = 4.29
r² = 0.179
p = 0.057
F = 17.68
r² = 0.527
P = 0.001
Ice concentration (Jun – Oct)
Ordinal date
Fall freeze–up
F = 12.98
r² = 0.444
P = 0.003
F = 24.07
r² = 0.606
P < 0.001
Duration of open–water season
F = 9.12
r² = 0.351
p = 0.009
F = 17.22
r² = 0.519
P = 0.001
Number of days
Year
Subpopulation
Northern Beaufort Sea
Southern Beaufort Sea

Figure 5

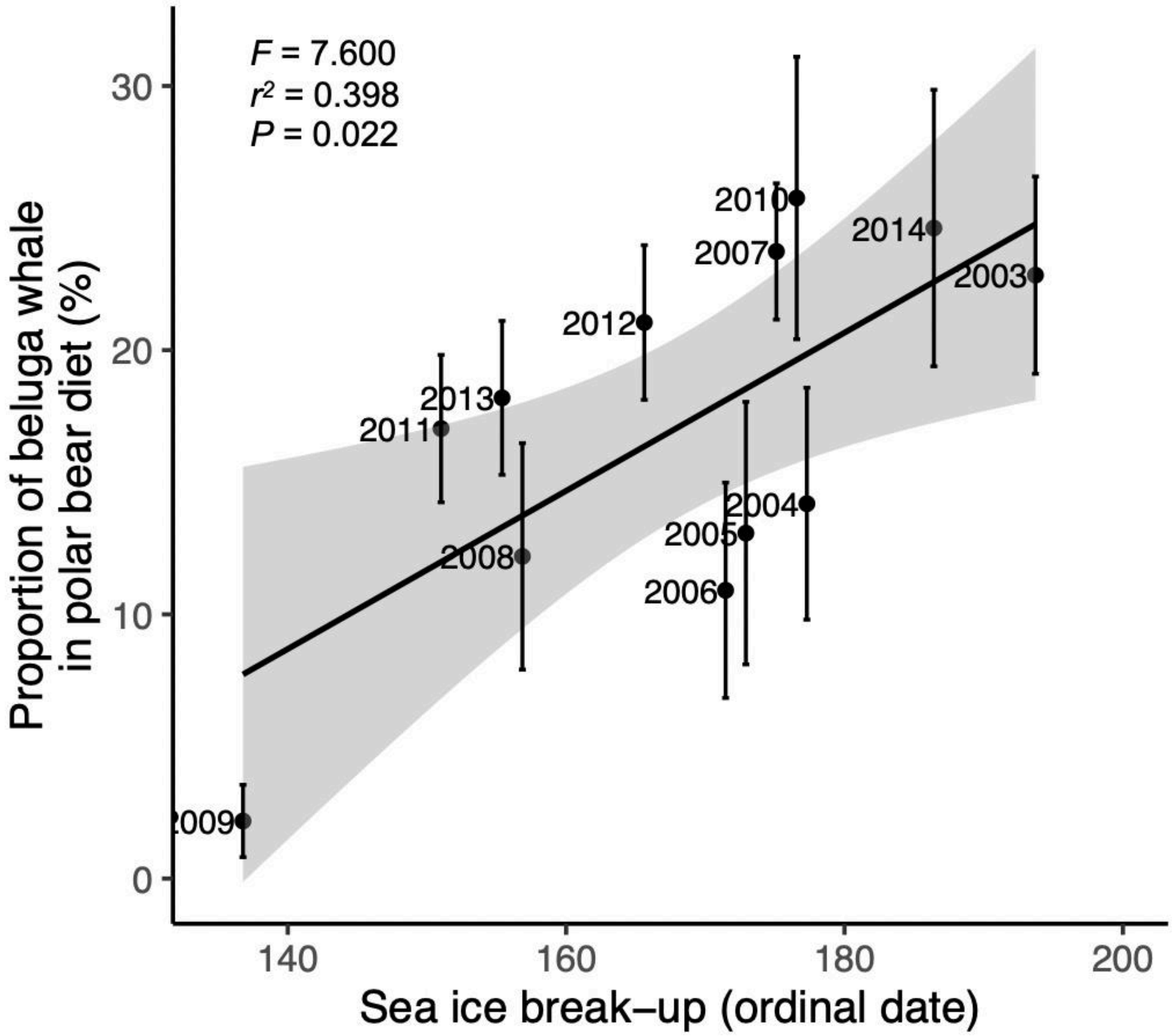

F = 7.600
r² = 0.398
P = 0.022
Proportion of beluga whale in polar bear diet (%)
Sea ice break–up (ordinal date)
0
10
20
30
140
160
180
200
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014

Figure 6

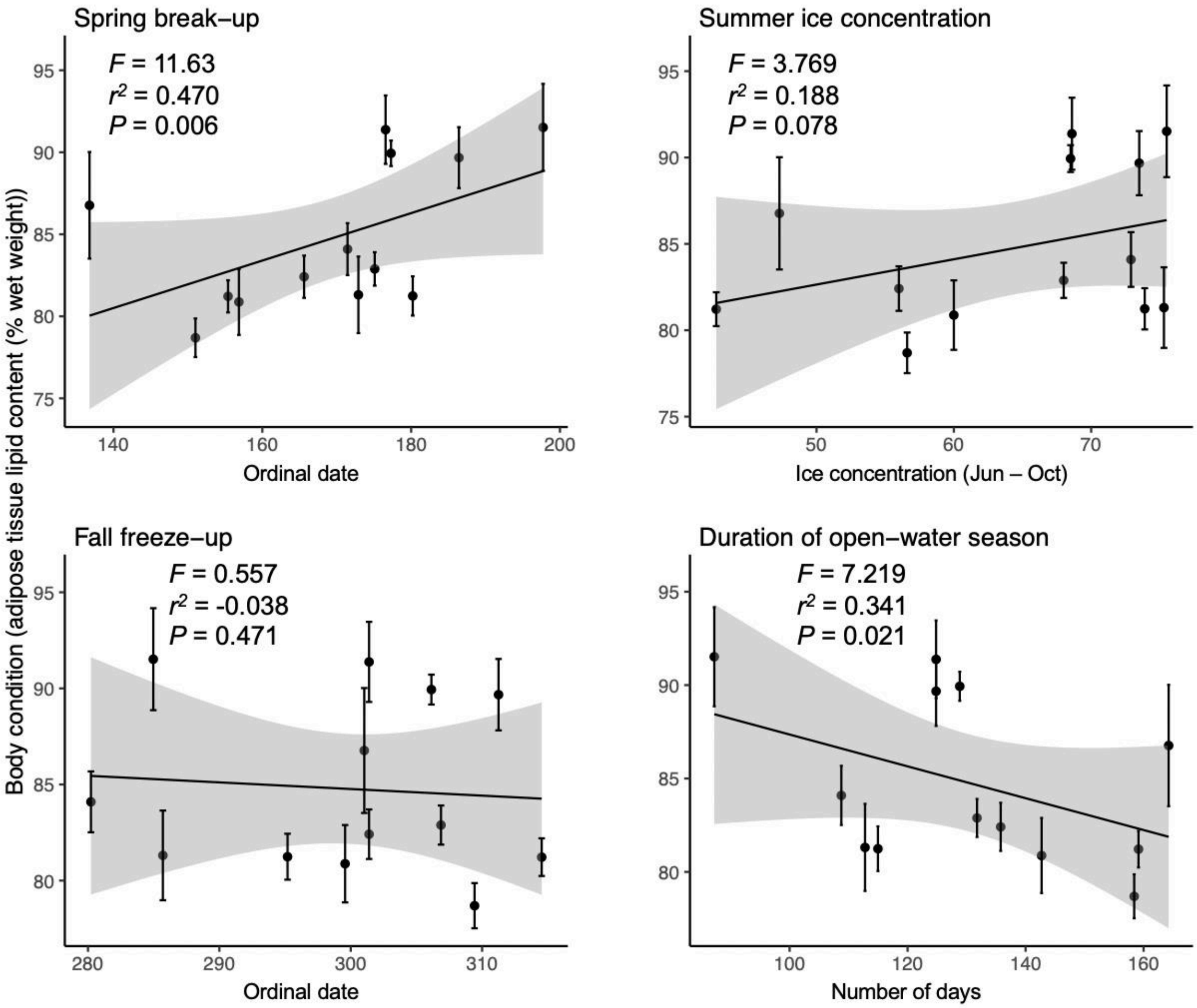

Spring break–up
F = 11.63
r2 = 0.470
P = 0.006
Summer ice concentration
F = 3.769
r2 = 0.188
P = 0.078
Fall freeze–up
F = 0.557
r2 = -0.038
P = 0.471
Duration of open–water season
F = 7.219
r2 = 0.341
P = 0.021
Body condition (adipose tissue lipid content (% wet weight))
Ordinal date
Ice concentration (Jun – Oct)
Number of days

Figure 7

Table 1 Redundancy analysis (RDA) candidate models evaluating the best-fitting model of factors influencing the diet of polar bears in the Canadian Beaufort Sea from 1999 to 2015. Akaike Information Criterion (AIC) was used as the main criteria for model selection. Variables: long = longitude; sif = date of sea ice freeze-up; sib = date of sea ice break-up.

Model	**RDA forward-selection model**				
	AIC	ΔAIC	*w*	F	*p*-value
long	-812.03	40.97	<0.001	21.108	0.002
long + sex	-828.98	24.02	<0.001	19.259	0.002
long + sex + age	-841.71	11.29	0.003	14.849	0.002
long + sex + age + sif	-845.48	7.52	0.018	5.741	0.006
long + sex + age + sif + sib	-850.54	2.46	0.222	7.020	0.002
long + sex + age + sif + sib + year	-853.00	0	0.758	4.408	0.006

w = AIC weight