Prey selection of polar bears in Foxe Basin, NU, Canada: evidence of dietary flexibility in a specialized predator

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ABSTRACT

Ecological flexibility of a species reflects its ability to cope with environmental change. Although polar bears (Ursus maritimus) are experiencing changes in foraging opportunities due to sea ice loss, regional prey availability and environmental conditions will influence the rate and severity of these effects. We examined changes in polar bear diet and the influence of sea ice characteristics in Foxe Basin over an 18-year period. We combined previous fatty acid data from bears harvested from 1999 to 2003 (n = 82) with additional data from 2010 to 2018 (n = 397). Polar bear diets were diverse; however, ringed seal (Pusa hispida) was the primary prey throughout the sample period. Prey contribution varied temporally and spatially, and by intrinsic factors, while the frequency of prey in diets varied over time suggesting that diet estimates reflect the variability in available prey. Bowhead whale (Balaena mysticetus), although still a minor dietary component, has more than doubled in frequency of occurrence in diets in recent years in association with increased scavenging opportunities. Higher dietary levels of beluga whale (Delphinapterus leucas) and harbour seal (Phoca vitulina) were linked to later breakup date suggesting heavier ice conditions may promote access to both prey species. The flexible foraging strategies of bears in Foxe Basin may help mitigate their vulnerability to changes in prey distribution and habitat conditions. Our results provide insights into the importance of alternative and supplemental food sources for polar bears during phenological changes in ice conditions that will likely have consequences to Arctic community structure as warming continues.

Key words: diet; feeding ecology; polar bear (Ursus maritimus); Arctic; quantitative fatty acid signature analysis (QFASA); sea ice
INTRODUCTION

Ecological flexibility refers to the ability of an animal to respond to shifts in environmental conditions through behavioural mechanisms [1–3]. Behavioural responses including changes in habitat use [4, 5], phenology (e.g. migration or reproduction [6, 7]), thermoregulation [8], predator avoidance [9] and foraging strategies [10, 11] are used by some animals to cope with variability within their habitat. A predictable environment, for example, when resources are temporally and spatially consistent, facilitates dietary specialization of individuals and populations [10, 12]. Specialists, however, can be constrained by dietary requirements and their lack of flexible foraging strategies may lead to increased sensitivity to environmental fluctuation [13, 14]. In contrast, a generalist foraging strategy may be favourable in more diverse and variable habitats with fluctuating or patchy resources [10]. Generalists are less constrained by the predictability of resources and environmental conditions, and flexibility in foraging behaviour may be advantageous for species that experience changes in their habitat [3].

Climatic warming in the Arctic has occurred two to three times faster than any other region [15]. The warmer climate has contributed to reduced sea ice extent (e.g. [16–18]), declining ice thickness (e.g. [19–21]) and reduced seasonal sea ice duration [22]. An earlier onset of spring melt has contributed to a thinner ice cover and reduced summer extent [23], and in combination with a later freeze-up has led to a longer ice-free season [24]. The rate of sea ice loss is expected to accelerate due to positive feedback mechanisms [25]. Substantial sea ice loss is projected to continue as temperatures warm, although there is uncertainty surrounding the exact timing of ice-free conditions and/or the first occurrence remains unclear. Recent studies have projected that if the mean global temperature rises to 2°C above pre-industrial levels, there is a very high probability (>99%) that the Arctic will become ice-free throughout August and September by 2100 [26–28].

Arctic warming has driven profound ecological change in biological productivity, species assemblages, resource availability and habitat conditions associated with sea ice loss [29–31]. Arctic species have adapted to seasonal pulses in habitat conditions and resource availability yet are reliant on the predictable year-to-year timing of ecological conditions [32–34]. Phenological changes in sea ice conditions will have significant effects across ecosystems [35]. However, flexible foraging strategies may enable individuals to meet their energetic needs by exploiting alternate prey [36] and increase their chances of persistence in a changing environment [3]. Understanding the limits to ecological flexibility of a species is essential for predicting its vulnerability to climate-driven changes in resource availability.

Polar bears (Ursus maritimus) across their range feed primarily on ringed seals (Pusa hispida) and secondarily on bearded seals (Erignathus barbatus; [37–39]). Extensive feeding by polar bears (i.e. hyperphagia period) occurs in the spring and early summer [38, 40] when newly weaned seal pups are most vulnerable and accessible to predators and adults are hauled out on the sea ice to moult [37, 41]. However, when alternate foraging opportunities are spatially and temporally available, polar bears can be opportunistic feeders and also prey on harp seals (Pagophilus groenlandicus; [42–44]), harbour seals (Phoca vitulina; [45, 46]), beluga whales (Delphinapterus leucas; [39, 47, 48]), narwhal (Monodon monoceros; [47]), walrus (Odobenus rosmarus; [49, 50]) and scavenge on large whale carcasses including bowhead whales (Balaena mysticetus; [50, 51]). The ability of an individual to facultatively switch between food types may help individuals meet their energetic needs, especially when preferred prey (i.e. ringed seal and to a lesser extent bearded seal) are less available.

Polar bears are reliant on sea ice habitat for travelling, mating and foraging [52, 53], and a decline in sea ice availability will negatively affect polar bears via reduced foraging opportunities. The mechanistic relationships between habitat conditions and polar bear demography are poorly understood [54], although some factors may help mitigate the negative effects of sea ice loss, at least in the near term [55, 56]. Prey availability, ecosystem productivity and variation in sea ice conditions may be important determinants of demographic decline in polar bears [55, 57]. In the Chukchi Sea, polar bear body condition and reproduction appear to be stable, despite reduced sea ice extent, likely because of the highly productive waters and diverse prey assemblage in the region [57]. Hamilton and Derocher [58] found that prey diversity was the strongest predictor of polar bear density across their global range and at the subpopulation level. Lower prey diversity may make polar bears more vulnerable to demographic decline.

Polar bears in Foxe Basin have experienced an overall loss of sea ice, increased fragmentation and shifts in timing of breakup and freeze-up [59]. From 1979 to 2008, the proportion of preferred habitat (defined as >60% ice cover; includes ‘good’ habitat: 61–85% ice cover and ‘best’ habitat: >86% ice cover) declined, especially during breakup and freeze-up. For example, in Foxe Basin preferred habitat was replaced with poor (31–60% ice cover) or non-habitat (<30% ice cover).
cover) in May–July and November. Similarly, in Hudson Strait, best habitat was replaced with poor and non-habitat in May and from January to March (winter months), there was an overall loss of best habitat [59]. Stern and Laidre [60] determined that average breakup in the Foxe Basin subpopulation occurred 5.3 days earlier per decade and freeze-up occurred 5.7 days later per decade from 1979 to 2014. These trends have extended the length of the ice-free season, when polar bears do not have access to marine mammal prey, by 38.5 days over the last 35 years [60].

Given the highly seasonal timing of polar bear feeding [40], even minor advances in breakup or declines in preferred habitat during spring could lead to reduced foraging opportunities, with negative consequences on body condition, energy expenditure, reproduction and survival. However, to date, Foxe Basin subpopulation estimates have remained stable despite changes to the sea ice habitat [61]. Improved understanding of the mechanistic relationship between polar bear habitat and demography would help reveal whether, and for how long, this stability may persist in the face of continued habitat decline. The current population stability may be attributed to the diversity of prey species and carcasses available for scavenging by bears in Foxe Basin [50]. With increased areas of open water, killer whales (Orcinus orca) have expanded their range and are now annually present in Foxe Basin [62]. Because killer whales feed selectively on parts of prey [63, 64], a large portion of a bowhead whale kill may be left to drift onshore where it becomes accessible to bears [65]. Laidre et al. [66] estimated that the consumable biomass of an adult bowhead was equal to approximately 1300 adult ringed seals, and bears can potentially feed on a carcass for two or more years. If bowhead carcasses appear in a reliable manner (i.e. predictable areas and times of the year), the substantial nutrition may help support portions of the population [66].

We measured changes in polar bear prey selection in response to changes in sea ice habitat in Foxe Basin over an 18-year period by assessing the diets of polar bears using fatty acid (FA) signature analysis [48, 50, 67]. Our objective was to assess possible temporal shifts in polar bear diet to test the hypothesis that prey selection has become more diverse over time in response to increased environmental variability. We also tested the influence of spatial and intraspecific (e.g. age class and sex) factors, and the effects of sea ice conditions on diet composition. A better understanding of the ability of polar bears to exploit diverse marine mammal prey will help to refine predictions of future climate- and habitat-driven changes in Arctic food webs.

MATERIALS AND METHODS
Sample collection and laboratory analysis
We used previously published FA data from polar bears harvested from 1999 to 2003 (n = 82; [39]) and analysed adipose tissue samples from polar bears harvested during the annual subsistence hunts from 2010 to 2018 (n = 397) from the Foxe Basin subpopulation. Samples were collected year-round from adults (5+ years old) and subadults (3–4 years old) from both male and female polar bears. Subcutaneous adipose tissue samples (ca. 6 cm × 6 cm) were taken from the rump of each bear, wrapped in aluminum foil, sealed in a labelled Whirl-Pak and stored at −20°C until analysis. Lipid was quantitatively extracted according to Iverson et al. [68] and sulphuric acid was used as a catalyst to derive FA methyl esters (FAMEs) from the extracted lipid [69]. FAME samples were analysed using gas-liquid chromatography and flame-ionization detection at the Canadian Institute for Fisheries Technology at Dalhousie University, Halifax, NS, Canada. Typically, over 70 FAs are identified in each adipose tissue sample and expressed as the mass percentage of total FA ± SEM. FAs are identified using the nomenclature A:Bn-X, where A is the carbon chain length, B is the number of double bonds and X is the position of the first double bond in relation to the terminal methyl group.

Sea ice data
Sea ice concentration data from 1998 to 2018 were downloaded in 25 km × 25 km grid cells from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data [70] available from the National Snow and Ice Data Center in Boulder, Boulder, Colorado, USA, for the Foxe Basin subpopulation. ArcGIS (Environmental Systems Research Institute) was used to extract daily sea ice concentration raster imagery, where each cell grid has an associated sea ice concentration value [70]. We used sea ice area defined as sea ice concentration multiplied by grid cell area to determine date of sea ice breakup and freeze-up according to Stern and Laidre [60]. Dates of 50% breakup and 50% freeze-up were defined as the date when area was below the 50% threshold and when the area above the 50% threshold, respectively (see [60]). Cherry et al. [71] recorded bears coming on shore in the spring when sea ice had a daily concentration of 30% indicating the end of the spring feeding period and bears leaving shore when daily concentrations were 10% indicating the resumption of foraging in the fall. Dates of 30% breakup and 10% freeze-up were also calculated using the 30% and 10% threshold, respectively. Rate of spring sea ice decay was expressed as the beta coefficient (slope) from the linear regression of daily sea ice concentration from 1 May to date ice concentration dropped below 30% [71, 72].

Diet estimation
Quantitative FA signature analysis (QFASA) was used to estimate diet composition of polar bears [67]. Briefly, individual predator FA profiles (or ‘signatures’) are modelled as a combination of average prey FA signatures and diet is estimated as the combination of prey that minimizes the distance between the observed and modelled predator. QFASA estimates the proportion of biomass each prey type contributes to a predator’s diet [73]. To account for FA-specific patterns of metabolism in the predator, we used calibration coefficients derived from a captive carnivore (mink, Neovison vison) fed a controlled marine-based diet [39, 74, 75]. In this study, we used the Aitchison distance measure to compare modelled and observed predator FA signatures [73, 76] and a set of 30 dietary FAs [48]. Diet estimates were produced using the qfassar package (version 1.2.1, [77]) in R (version 3.5.1, [78]).

An ecologically relevant prey library (i.e. the collection of prey FA profiles used in the QFASA model) is important to accurately quantify predator diet. When the FA signatures of prey types are distinct from each other, the model should perform better than when prey FA signatures are similar [79]. Thus, the analysis of prey library performance is an important step to accurately estimate diet. We used two diagnostic functions built into the qfassar package (version 1.2.1, [77]) to examine FA variability among and within prey types: leave-one-prey-out (LOPO) and divisive magnetic clustering (DIMAC). The LOPO function examines the distinctiveness and potential confounding of prey types within the library. The function temporarily removes an individual prey signature from the library, determines the mixture of remaining prey FA signatures that best approximate...
the removed prey (a process identical to diet estimation) and repeats for all prey in the library. The output provides the proportion of prey correctly (distinctiveness within library) and incorrectly identified (confounding within library). Variation in FA signatures within a prey type could be driven by spatial or temporal differences within a prey species, which can increase confounding and impair the accuracy of QFASA diet estimates. DIMAC is a clustering technique that identifies substructure within the prey library by partitioning prey samples into clusters that are potentially more similar than the original prey groups (based on species). The DIMAC function can reveal underlying ecological relationships such as spatial and temporal patterns within a prey species. Once a partitioned library was created using the DIMAC function, we simulated predator signatures using both the original prey library and partitioned prey library to examine the performance of the QFASA model (see Supplementary Material for details and results, Supplementary Table S1).

We used an established library of FA data from marine mammals \( (n=316) \) including bearded seals, beluga whales, bowhead whales, harbour seals, harp seals, ringed seals and Atlantic walrus sampled from 2000 to 2012 \[45, 50, 81\] to estimate predator diet. We also analysed additional blubber samples from bearded seal \( (n=5) \), harp seal \( (n=10) \) and ringed seal \( (n=24) \) from 2013 to 2015. All prey species were sampled from Foxe Basin and adjacent regions including Davis Strait, Gulf of Boothia and western Hudson Bay.

Statistical analysis

Prey selection

Zero-augmented beta regression models were used to analyse the influence of biological and environmental variables on diet composition. A zero-augmented beta model was used to account for the proportional data bound between 0 and 1, as well some prey that did not contribute to the overall diet composition of some individuals leading to exact zeros \[82\]. Models were run separately for each prey type in Foxe Basin. We used prey contribution to diet (i.e. the proportional biomass of prey in diet) as the response variable for each model and possible explanatory predictors included year, time period \( (1999–2003 \text{ or } 2010–2018) \), harvest date, sex, age class (adult or subadult), region (Hudson Strait, northern Foxe Basin and southern Foxe Basin; previously identified intrapopulation structure in Sahanatien et al. \[83\] and Galicia et al. \[50\], although Cape Dorset was removed from analysis due to small sample size; Supplementary Fig. S1) and/or season (defined as per Sahanatien et al. \[83\]). Seasons were defined as ice-free (August–October), freeze-up (November–December), winter (January–March), spring (April–May), and breakup (June–July). Sea ice variables included 50% breakup date, 30% breakup date, rate of sea ice decay, 50% freeze-up date and 10% freeze-up date. All sea ice variables were dependent on the harvest date of the individual. For example, if a bear was harvested from July to December, the current year’s breakup date was used; however, if a bear was harvested from January to June the previous year’s breakup date was used because breakup for the current year had not yet occurred at the time the bear was harvested.

We used AICc to select the model that best explained variation in prey selection from a set of ecologically relevant candidate models defined \( a \text{ priori} \) \[84\]. We calculated log-likelihood (LL), AICc values, ΔAICc, and AICc weights \( (w_\text{A}) \) relative likelihood of the model using MuMIn package in R (version 1.43.17, \[85\]). All continuous variables including harvest date (day of year), breakup date, freeze-up date and rate of decay were standardized. Collinearity among covariates was assessed using Pearson’s correlation coefficient and variance inflation factor (VIF). Covariates with a Pearson’s correlation coefficient \( r > 0.6 \) and/or VIF > 5.0 \[86\] were used in separate models. To assess uninformative parameters in top models, we investigated the relative importance of individual variables \( (i.e. \text{cumulative weights}) \) in top models AAIc < 2.00, by calculating the sum of Akaike model weights across all models that included the variable \[87\].

A generalized linear model with a binomial family distribution and logistic link was used to assess the relationship between frequency of prey occurrence in diets over time (count-based proportional data; \[86\]). The frequency of individual prey species in diet was defined as the frequency of events out of a total set of events, i.e. the number of bears with \( i \) prey in diet out of the total number of bears sampled each year. Models were also weighted to account for the unequal sample size of each year.

We used the Shannon–Wiener index \( (H'; \ [88]) \) to calculate niche breadth \( (i.e. \text{dietary diversity}) \) of polar bears in Foxe Basin:

\[
H' = - \sum_{j=1}^{S} p_j \ln p_j
\]

where \( p_j \) is the proportion of prey species \( j \) in the diet and \( S \) is the total number of prey species consumed by all individuals. Differences in dietary diversity across age class and sex were assessed using a two-way ANOVA.

Influence of sea ice metrics

Temporal trends in spring and fall sea ice metrics \( (i.e. \text{breakup and freeze-up date}) \) were tested using linear regressions. Although sea ice metrics were included as a predictor variable in prey consumption models, we also assessed the direct relationship between sea ice conditions and prey contribution to diet (beta regression models) and prey frequency of occurrence in diet \( (\text{generalized linear models}) \). All statistical analyses were conducted using R (version 3.5.1; \[78\]).

RESULTS

QFASA diagnostics

The LOPO function indicated that prey types in our library were well-separated by FA signatures. The mean proportion of prey correctly identified was 0.85 across prey types and 0.82 across all individuals. Proportions attributed to the correct prey were: 0.74 for bearded seal, 0.75 for ringed seal, 0.78 for harp seal, 0.83 for beluga whale, 0.94 for walrus, 0.95 for harbour seal and 1.00 for bowhead whale. The DIMAC function identified no substructure within prey species, indicating that spatial or temporal variability within prey species was minor relative to differences among prey species. Prey samples were thus pooled into species for diet estimation.

Prey selection

Ringed seal was the primary prey of polar bears during both sampling periods \( (45 \pm 2.68\% \text{ in } 1999–2003 \text{ and } 36 \pm 1.40\% \text{ in } 2010–2018) \). Bearded seal increased while beluga whale and harbour seal both declined between the two time periods (see model results below). Harp seal and walrus \( (<11\%) \) and bowhead whale consumption \( (<2\%) \) remained consistent over time (Fig. 1).

The top ranked model for bearded seal contribution to diet included bear age class, sex, and time period with a model weight of 0.92 \( (\text{Table 1}) \). Overall, bearded seal consumption was 18% higher in 2010–2018 than 1999–2003 with adult males having the highest contribution of bearded seal \( (1999–2003: \text{male} (0.75) \text{ vs. adult (1.00}); \text{female} (0.55) \text{ vs. adult (0.75)}) \). Differences in dietary diversity across age class and sex were assessed using a two-way ANOVA.
7 ± 1.67% and 2010–2018: 27 ± 1.36%), although subadult males had a similar proportion of bearded seal in their diets in 1999–2003 as adult males (6 ± 1.64%; Fig. 2a). The top ranked model for ringed seal included only intrinsic variables (i.e. age class and sex; Table 1), although there was less model certainty in ringed seal contribution where the top four models had an ΔAIC_c < 2.00 (Supplementary Table S2). Age class and sex had the highest cumulative weight of 0.97, whereas the other parameters found in the top models had lower cumulative weights (time period: 0.23; year: 0.19; 50% breakup date: 0.14 and 50% freeze-up date: 0.14). Adult and subadult females had the highest contribution of ringed seal to diet (47 ± 3.28% and 46 ± 2.87%, respectively), followed by subadult males (40 ± 2.79%) and the lowest contribution in adult males (28 ± 1.82%; Fig. 2b). Walrus consumption was also influenced by bear age class and sex, in addition to region (Table 1), and the top ranked model was 4.8 times more likely than the second ranked model which only included sex (Supplementary Table S2). Bears in northern Foxe Basin had the highest contribution of walrus to diet (22 ± 2.01%) driven by the high levels of walrus consumption by adult male bears (33 ± 3.72%; Fig. 2e) with 46% of adult males having over 35% walrus in diet and one individual with 80%. The top ranked model of bowhead whale contribution to diets included only age class. Although all other models had an ΔAIC_c > 2.00 (Supplementary Table S2), the overall model weight was only 0.29 leading to some model uncertainty (Table 1). Age class had the highest cumulative weight of 0.38 compared with 50% breakup (0.15) or sex (0.16). Adults had higher levels of bowhead whale in diets (1.7 ± 0.25%) compared with subadults (0.6 ± 0.13%; Fig. 2d). Although this trend was primarily driven by adult males (1.9 ± 0.31%), whereas adult females had lower levels (0.9 ± 0.43%).

A common predictor variable in harbour seal, harp seal and beluga whale contribution to diet was region. The top ranked model for harbour seal consumption included region and time period (Table 1) and was 4.5 times more likely than the second ranked model which included region and season (Supplementary Table S2). Harbour seal consumption was 5% higher in 1999–2003 than 2010–2018 with the highest contribution consistently found in southern Foxe Basin bears (1999–2003: 18 ± 2.14% and 2010–2018: 13 ± 0.81%; Fig. 3a and b). The top ranked model for beluga whale contribution also included region and period with a model weight of 0.77 (Table 1). Beluga whale consumption was higher in 1999–2003 (23 ± 0.89%) compared with 2010–2018 (7 ± 0.61%) and higher in southern Foxe Basin (12 ± 0.93%) than the other two regions (Hudson Strait: 7 ± 1.51% and northern Foxe Basin: 7 ± 1.7%; Fig. 3a and b). The top ranked model for harp seal contribution included region and was only 2.3 and 2.4 times more likely than the second (region and period) and third (region and year) ranked models, respectively, both with an ΔAIC_c < 2.00 (Supplementary Table S2). Of the variables found in the top models, region had a highest cumulative weight of 0.99 compared with period (0.22) and year (0.21). The highest contribution of harp seal to diets occurred in Hudson Strait bears (20 ± 1.92%) compared with northern Foxe Basin (11 ± 1.26%) and southern Foxe Basin (9 ± 0.81%; Fig. 3c).

Shannon–Wiener values (H’) significantly differed by sex (F_1,475 = 11.679, P = 0.001) and there was a significant interaction between age class and sex (F_3,475 = 4.201, P = 0.041), driven by the difference between adult males and females (P = 0.001). Adult males had the most diverse diet (1.17 ± 0.02) and adult females the least diverse (1.02 ± 0.04), whereas H’ values were consistent between males and females in the subadult age class (1.13 ± 0.03 and 1.09 ± 0.03, respectively). Adult males also showed the most variability within the group ranging in H’ values from 0.28 to 1.80 (difference of 1.52), whereas adult females had the least within-group variation ranging from 0.27 to 1.45 (difference of 1.18). Subadults showed similar sex-specific variability in dietary niche breadth (female subadults: 0.45–1.65, difference of 1.20 and male subadults: 0.37–1.62, difference of 1.25).

The frequency of occurrence of prey types in diet varied over time (Fig. 4a–g). Ringed seal and beluga whale significantly decreased in frequency over time, whereas bearded seal, harp seal and bowhead whale all significantly increased in frequency from 1999 to 2018. Harbour seal and walrus frequency remained consistent (Table 2). In 1999–2003, bearded seal appeared in the diets on an annual average of 51% of bears (ranging from 0 to 75%) and increased to 90% of bears (ranging from 84% to 95%) in 2010–2018 (Fig. 4a). Harp seal was found in 60% of bears (ranging from 33% to 83%) in 1999–2003 and 84% of bears (ranging from 73% to 95%) in 2010–2018 (Fig. 4c). Frequency of ringed seal in diets declined from 97% of bears (ranging from 88% to 100%) in 1999–2003 to 79% of bears (ranging from 54% to 95%) in 2010–

![Figure 1: Diet composition of polar bears across the Foxe Basin subpopulation separated by time period 1999–2003 and 2010–2018 as estimated from QFASA.](https://academic.oup.com/oocc/article/1/1/kgab002/6284233)

### Table 1: Model selection results identifying variables affecting prey contribution to polar bear diets in 1999–2003 and 2010–2018 in Foxe Basin as estimated from QFASA

| Prey species      | Model                          | k | LL   | ΔAIC_c | ΔAICc | w_i |
|-------------------|--------------------------------|---|------|-------|-------|-----|
| Bearded seal      | Age class * sex + time period  | 7 | 16.16| -18.04| 0.00  | 0.92|
| Harbour seal      | Time period + region           | 5 | 190.67| -371.19| 0.00  | 0.76|
| Harp seal         | Region                         | 4 | 82.93| -157.77| 0.00  | 0.51|
| Ringed seal       | Age class * sex                | 6 | -154.95| 322.10| 0.00  | 0.39|
| Walrus            | Age class * sex + region       | 7 | -8.50 | 31.27  | 0.00  | 0.53|
| Beluga whale      | Time period + region           | 5 | -83.78| 177.71 | 0.00  | 0.77|
| Bowhead whale     | Age class                       | 4 | 50.03| -91.96 | 0.00  | 0.29|

All prey species were modelled separately, and only the top ranked models are shown. Included in the table are number of estimated parameters (k), LL, Akaike’s information criterion corrected for small sample sizes (AIC_c) values, ΔAIC_c, and AIC_c weights (w_i) are shown for each model. Time period represents polar bears harvested in 1999–2003 and 2010–2018, region represents Hudson Strait, northern Foxe Basin and southern Foxe Basin.
2018 (Fig. 4d). Beluga whale had the largest decrease in frequency of occurrence in diets, decreasing from 86% of bears (ranging from 80% to 100%) in 1999–2003 to 52% of bears (ranging from 21% to 82%) in 2010–2018 (Fig. 4f). Bowhead whale frequency in diet had the second largest increase over the years with bowhead found in 10% of bears (ranging from 0 to 17%) in 1999–2003 and 42% of bears (30–54%) in 2010–2018 (Fig. 4g).

Influence of sea ice metrics

There was evidence of considerable inter-annual variability in sea ice metrics (breakup and freeze-up date), although no directional trend during our study period (Supplementary Table S3). Date of 50% sea ice breakup varied from 8 June to 29 June and 30% sea ice breakup varied from 20 June to 13 July. Date of 50% freeze-up varied from 18 November to 22 December and 10% freeze-up varied from 24 October to 1 December (Supplementary Fig. S2). Sea ice metrics were not included in any top ranked models for variation in prey contribution to polar bear diet (Supplementary Table S2) with relatively low cumulative weights in comparison to other variables. However, significant relationships with spring breakup were identified in beluga whale and harbour seal consumption when sea ice metrics were analysed separately. Beluga whale contribution to diet was significantly influenced by 50% breakup date ($\beta = 0.098 \pm 0.036$, pseudo-$R^2 = 0.419$, $P = 0.006$), where beluga whale consumption increased with a later breakup date (Fig. 5a). Harbour seal showed a similar trend to beluga whale, where consumption increased with a later 30% breakup date ($\beta = 0.047 \pm 0.024$, pseudo-$R^2 = 0.231$, $P = 0.046$; Fig. 5b). However, there was no significant relationship between 50% breakup date and any other prey species ($P > 0.101$), 30% breakup date and any other prey species ($P > 0.063$) or rate of sea ice decay and any prey species ($P > 0.307$). There was no significant relationship between 50% freeze-up date or 30% freeze-up date and any prey species ($P > 0.070$ and $P > 0.365$, respectively).

The frequency of bearded seal, harp seal and bowhead whale in bear diet was significantly influenced by 50% breakup date and 30% breakup date (Table 3), where the frequency of occurrence decreased with a later breakup date (Fig. 6a, c, and g). Beluga whale and harbour seal frequency significantly increased with a later 50% breakup date (Fig. 6d and e) and 30% breakup date (Table 3). Ringed seal and walrus frequency in diet showed no significant relationship to 50% or 30% breakup date (Table 3 and Fig. 6d and e). Rate of sea ice decay had no significant influence on the frequency of occurrence of any prey species ($P > 0.527$). The frequency of bearded seal and harp seal increased significantly with a later 50% freeze-up date ($\beta = 0.046 \pm 0.015$, $z = 3.071$, $P = 0.002$ and $\beta = 0.028 \pm 0.012$, respectively).

Figure 2: Prey contribution to polar bear diets across the Foxe Basin subpopulation in 1999–2003 and 2010–2018 from (a) bearded seal, (b) ringed seal, (c) walrus and (d) bowhead whale as estimated from QFASA. Data represent each prey species’ proportional biomass contribution to diet estimates shown as boxplots showing the 25th quartile, median, 75th quartile and outliers shown as solid circles. Mean proportion for each prey is represented by ‘x’. Plots include most influential variables determined by Akaike’s information criterion (corrected for small sample sizes) model selection.
Beluga whale frequency in diet was significantly influenced by freeze-up date, where frequency in diet decreased with a later 50% freeze-up date ($\beta = -0.038 \pm 0.010$, $z = -3.968$, $P < 0.001$) and 30% freeze-up date ($\beta = -0.022 \pm 0.010$, $z = -2.360$, $P = 0.018$). Date of 50% and 30% freeze-up did not significantly influence any other prey frequency in diets ($P > 0.062$ and $P > 0.100$, respectively).

**DISCUSSION**

Arctic species are dependent on predictable seasonal environmental conditions [32, 34] and populations may be negatively affected by climate-induced shifts in the spatiotemporal availability of resources and preferred habitat. Although polar bears are considered a specialized top predator [89], bears in Foxe
Basin make use of a relatively wide diversity of prey. Our results suggest that diet composition and the frequency of occurrence of prey varies with temporal and spatial fluctuations in prey availability. Intrinsic factors (e.g. the large body size of adult male bears) influenced the ability of bears to actively hunt larger bodied prey and thus exploit a greater diversity of prey species. Bowhead whale has become more frequent in polar bear diets suggesting an increase in encounter rates with carcasses. Our results provide new insights into patterns of prey selection by polar bears over a broad timescale and suggest that climate-driven changes in sea ice may be affecting polar bear diet composition and the structure and functioning of the Foxe Basin food web.

Prey selection

Ringed seal has been consistently identified as the primary prey of polar bears due to their small size, which makes them vulnerable to predation by bears of all sizes, and high abundance throughout their circumpolar range [37–39]. We found polar bear diet composition in Foxe Basin was largely consistent with previous studies (e.g. [50]) in that the overall diet was dominated by ringed seal and then bearded seal, followed by a varied consumption of harbour seal, harp seal, walrus and minor levels of bowhead whales. Beluga whale was a secondary prey species from 1999 to 2003 and then found in lower levels in more recent years (2010–2018), potentially due to a change in availability. Although overall contribution varied, the consistent occurrence of harbour seal and walrus indicates that these prey species have been relatively common and accessible to bears in Foxe Basin. Bearded seal and harp seal increased in frequency

Table 2: The results of a generalized linear model examining temporal trends in frequency of prey item in diets of polar bears harvested in Foxe Basin, in 1999–2003 and 2010–2018 as estimated from QFASA, showing the $\beta$ coefficient, standard error, $z$ and $P$ values for the predictor variable

| Prey            | $\beta$ coefficient | SE      | z       | $P$       |
|-----------------|---------------------|---------|---------|-----------|
| Bearded seal    | 0.143               | 0.020   | 7.270   | $<0.001^*$|
| Harbour seal    | −0.044              | 0.023   | −1.949  | 0.051     |
| Harp seal       | 0.086               | 0.018   | 4.810   | $<0.001^*$|
| Ringed seal     | −0.103              | 0.028   | −3.671  | $<0.001^*$|
| Walrus          | 0.018               | 0.016   | 1.081   | 0.280     |
| Beluga whale    | −0.089              | 0.018   | −0.507  | $<0.001^*$|
| Bowhead whale   | 0.114               | 0.021   | 5.459   | $<0.001^*$|

An asterisk beside $P$-values indicates statistical significance for prey species.

Table 3: The results of a generalized linear model examining trends in the frequency of prey item in diets of polar bears harvested in Foxe Basin, in 1999–2003 and 2010–2018 as estimated from QFASA and spring sea ice metrics, showing the $\beta$ coefficient, standard error, $z$ and $P$-values for the predictor variable

| Prey            | 50% breakup date | 30% breakup date |
|-----------------|------------------|------------------|
|                 | $\beta$ coefficient | SE      | z       | $P$       | $\beta$ coefficient | SE      | z       | $P$       |
| Bearded seal    | −0.089            | 0.026   | −3.393  | $<0.001^*$| −0.093            | 0.022   | −4.183  | $<0.001^*$|
| Harbour seal    | 0.089             | 0.025   | 3.586   | $<0.001^*$| 0.056             | 0.018   | 3.059   | 0.002*    |
| Harp seal       | −0.057            | 0.022   | −2.619  | 0.009*    | −0.046            | 0.018   | −2.652  | 0.008*    |
| Ringed seal     | 0.025             | 0.025   | 1.038   | 0.299     | 0.036             | 0.019   | 1.915   | 0.056     |
| Walrus          | 0.021             | 0.019   | 1.131   | 0.258     | −0.007            | 0.015   | −0.466  | 0.641     |
| Beluga whale    | 0.071             | 0.018   | 3.842   | $<0.001^*$| 0.028             | 0.014   | 2.011   | 0.044*    |
| Bowhead whale   | −0.067            | 0.019   | −3.533  | $<0.001^*$| −0.045            | 0.014   | −3.145  | 0.002*    |

An asterisk beside $P$-values indicates statistical significance for prey species.
in diet while ringed seal frequency declined, suggesting that bears may switch between prey types depending on availability as a function of fluctuating environmental conditions, recruitment and pup survival [90].

The wide diversity of prey available to polar bears in Foxe Basin may contribute to the demographic stability of the subpopulation despite declining sea ice conditions [59, 61] by facilitating resource partitioning and reducing intraspecific competition. Prey diversity may also contribute to the lower seasonal fluctuations in body condition experienced by bears in Foxe Basin [40]. Adult males have a broader dietary niche compared with adult females and subadults likely because of their ability to capture larger-bodied prey including bearded seal and walrus [39, 91]. The narrower dietary niche breadth of subadults and especially adult females, likely due to their smaller size [92], may suggest their dependence and potential specialization on fewer prey species, primarily ringed seals [91]. All groups showed evidence of within group variability, but it was particularly high in adult males. This suggests varying foraging strategies at the individual level, where some individuals may specialize on one or a few species and others may take advantage of the wide range of available prey or opportunistically scavenge. This variability may also be influenced by changes to prey distributions across years or sea ice conditions that either facilitates or limits access to prey. Decadal scale fluctuations in ringed seal density have also been observed as a function of ice regime shifts in Hudson Bay [90, 93]. The increase in bearded seal contribution in more recent years may be a consequence of declining abundance of the more numerically abundant ringed seal population leading to proportionally higher levels of bearded seal in the diet. It appears that alternate prey species play an important role in determining the dietary consequences of sea ice declines, however even individual bears and populations with wide niche breadths will eventually be limited by food availability resulting in population decline.

A large whale carcass can act as a substantial food source for a year or more in a cold environment, potentially supporting a large number of bears, in contrast to seals, walruses or smaller whales which are consumed rapidly by one or a few bears [66]. Our estimates of bowhead whale consumption (1999–2003: 0 ± 0% and 2010–2018: 2 ± 0%) were similar to previous studies in Foxe Basin [50]. However, bowhead dietary levels were lower than in the Southern Beaufort Sea where bears may derive 15% of their diet from bowhead whale [94]; a level of dietary intake facilitated by a high number of whales (≥18) harvested annually and recurring locations of unused tissue (known as ‘bone piles’) for bears to scavenge [51, 95]. Although mean dietary contribution of bowhead in Foxe Basin has remained low, we found evidence of increase in both consumption and frequency over time, suggesting an increase in encounter rates. Bowheads may become available to polar bears from a combination of sources including subsistence harvest, natural mortality and killer whale predation. Subsistence harvest levels are currently low (≤5 across Nunavut; [96]), however at least one bowhead was landed every year in Foxe Basin or Hudson Strait from 2010 to 2018 except for 2014 (DFO unpublished data). Nevertheless, carcass location in Foxe Basin is unpredictable, likely contributing to the low dietary levels estimated in our study. Given the increasing abundance of the Eastern Canada-West Greenland bowhead population [97, 98], a future increase in naturally stranded carcasses is a possibility. Declining sea ice has improved habitat conditions for killer whales in the Arctic and they appear to be increasingly depredating and affecting the behaviour of bowhead whales in a region closely associated with Foxe Basin [99]. Killer whales primarily target the mouthparts of bowheads, potentially leaving a largely intact carcass for polar

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**Figure 6:** Relationship between frequency of occurrence of prey in diets of polar bears harvested in Foxe Basin in 1999–2003 and 2010–2018 as estimated from QFASA and 50% breakup date, (a) bearded seal, (b) harbour seal, (c) harp seal, (d) ringed seal, (e) walrus, (f) beluga whale and (g) bowhead whale. Observed values (black dots) are shown in proportions (number of bears with prey present/number of bears sampled for breakup date), predicted values as a solid line and 95% confidence interval shaded in grey. Significant relationships are indicated with P-values for each prey species.
bears and other terrestrial scavengers. In October and November 2020, nine bowhead whales were found beached in central Nunavut [100], further suggesting increasing availability of this previously novel food resource.

Spatial differences in harbour seal, harp seal, walrus and beluga whale contribution to diets reflected the importance of locally available prey within Foxe Basin. For example, harp seal consumption was consistent with the spatial distribution of the prey, with the highest dietary levels in Hudson Strait which connects to Davis Strait where harp seal are found in abundance and consumed by polar bears in equal or at times greater proportions to ringed seals [39, 43]. Walrus are found year-round throughout most of Foxe Basin (Northern Hudson Bay–Davis Strait and Foxe Basin population) and in high concentrations in northern Foxe Basin [101, 102]. Areas with high concentrations of walrus may be avoided by ringed seals due to a risk of predation and contribute to a lower abundance of ringed seals in those areas [103, 104]. The high levels of walrus found in diets of some bears in northern Foxe Basin (e.g. 80% in one adult male) suggest some individuals may specialize and repeatedly target locally abundant walrus. Large adult male bears would be best equipped to hunt walrus, but successful kills could produce carrion for smaller bears.

Harbour seal and beluga whale consumption varied spatially and between the two sampling periods (1999–2003 and 2010–2018). Harbour seal made the highest contribution to diet in southern Foxe Basin which lies adjacent to the Western Hudson Bay subpopulation where harbour seal is increasingly important as an alternate prey species for polar bears [45, 46]. In western Hudson Bay, an increase in harbour seal abundance has been linked to longer periods of open water [105]. However, the lower contribution to diets in 2010–2018 suggests that even though abundance has increased in southwestern Hudson Bay, harbour seals remain less accessible to bears in Foxe Basin, at least partly due to their preference for open-water areas [106]. The high levels of beluga whale in diets, particularly in southern and northern Foxe Basin, could be the result of ice entrapment events or predation from the ice edge and around leads [47, 107–109]. Polar bears have been observed hunting beluga whales in open water and in river channels [66], although this is likely less common. Killer whale predation on beluga whales [62, 110] and the possibility of struck and lost beluga from the subsistence harvest (although estimates are lacking) may provide beluga carcass available to scavenge [111]. The lower proportional levels of harbour seal and beluga in 2010–2018 may be a consequence of lower abundance in southern Foxe Basin and possibly reduced accessibility of both prey items in more recent years.

Influence of sea ice metrics

Polar bears in Foxe Basin have experienced an overall decline in preferred sea ice conditions (ice cover >60% as defined by Sahanatien and Derocher [59]). However, we did not find a significant trend in the timing of breakup and freeze-up during our study period (1999–2018), likely due to the shorter time span of our study relative to the 35-year dataset of Stern and Laide [60]. Nevertheless, interannual variability in sea ice conditions has influenced overall diet composition in terms of prey contribution and frequency of occurrence. Bearded seal and harp seal frequency was highest when breakup was early and freeze-up was late, a pattern that may reflect the importance of prey other than ringed seal when habitat conditions are poor and access to ringed seal is limited (e.g. sea ice is more dynamic with increased areas of open water). Bearded and harp seal are also less reliant on a stable sea ice platform (land-fast ice or consolidated pack ice) than ringed seals; bearded seal prefers unconsolidated pack ice during breeding and to haul-out [103, 112]. Harp seals are primarily pelagic and thought to be largely inaccessible to polar bears except for the on-ice whelping patch in Davis Strait [39, 43]. More recently, polar bears in Svalbard have been observed hunting large aggregations of harp seals hauled out on drifting pack ice or feeding beneath the ice. Unlike ringed seals, harp seals lack a predator escape response which makes them particularly vulnerable to polar bears. If the bears can find them when they occur unpredictably in areas of seasonal pack ice [44], it may partially explain their greater occurrence in bear diets in recent years. The frequency of occurrence and proportion of beluga whales in polar bear diets increased with a later breakup date and frequency was higher with an earlier freeze-up date. Beluga whales migrate through Hudson Strait during the spring (mid-June) and fall (September and October; [108, 113, 114]). Heavier ice conditions may lead to more entrapment events when belugas are limited to leads or cracks in pack ice leading to higher levels in diets [115]. Harbour seal consumption also increased with a later breakup, consistent with the findings of Sciullo et al. [45] in Western Hudson Bay. Harbour seals remain offshore during the ice-covered periods, and access to summer coastal haul-out sites where the risk of polar bear predation is low may be limited in years with a later breakup [106]. Bowhead whale dietary levels were not influenced by breakup date; however, we found that when breakup occurred earlier frequency in diet was higher. Early breakup and long open water seasons would allow increased access to the region by killer whales and potentially increase predation on bowhead whales and subsequent access to carcasses to scavenge [62]. Although we found links between spring sea ice conditions and diet composition, it is likely that multiple interacting environmental conditions affect recruitment, survival and behaviour of prey, and in turn their availability to bears. However, our results suggest that bears in Foxe Basin may effectively switch to alternate food sources (e.g. secondary prey and bowhead carcasses) if access to ringed seal is impaired by environmental conditions.

Climate-driven shifts in resource availability will result in significant ecosystem effects across the Arctic [35]. For polar bears, the ecological consequences of sea ice loss may be buffered by the diverse prey assemblage within Foxe Basin, which provides alternatives to preferred prey in years of low abundance or accessibility, at least in the near term. In recent years, alternate prey have become more common and abundant in the diets of bears, and some individuals may be actively hunting, and perhaps specializing on, alternate prey (e.g. [91]). Although bowhead whale remains a minor component of polar bear diets to date, it is increasing in both frequency and amount consumed. In Foxe Basin, polar bears may be indirectly benefitting from the subsistence harvest of a naturally increasing bowhead whale population, and an ecological regime shift that may allow killer whales to become established as a new top predator. In the short term, this reconfiguration of the marine food web and availability of alternate food sources may mitigate the demographic effects of sea ice loss on polar bears. But their reliance on the sea ice as a platform for hunting seals makes the sea ice habitat critical and the long-term effects of continued habitat loss will be unavoidably negative. The results of this study provide a more comprehensive understanding of the importance of prey diversity to polar bears and reveal some of the complexities of food web responses to rapidly changing sea ice conditions.
SUPPLEMENTARY DATA
Supplementary data are available at Oxford Open Climate Change online.

ACKNOWLEDGEMENTS
The authors are especially grateful to the Hunters and Trappers Associations and Organizations of Nunavut for collecting fat samples from polar bears harvested during their subsistence hunts; A. Coxon, F. Piugattuk, F. Frame, M. Harte, J. Ware and C. Mutch (Government of Nunavut) who assisted with the collection, organization and shipment of polar bear adipose tissue samples; B. Dunn and B. Young (Fisheries and Oceans Canada), D. Muir and X. Wang (Environment and Climate Change Canada) provided additional marine mammal samples. They thank S. Budge, C. Barry and C. Green (Dalhousie University) for conducting gas chromatography. They also thank E. Richardson (Environment and Climate Change Canada) for the extraction and calculation of sea ice metrics.

STUDY FUNDING
This project was funded by the Natural Sciences and Engineering Research Council (NSERC) Discovery Grant, Environment and Climate Change Canada – Grants and Contributions, Fisheries and Oceans Canada, Kenneth M. Molson Foundation, Nunavut General Monitoring Plan, Nunavut Wildlife Research Trust Fund (grant no. 3-09-05), Northern Scientific Training Program, WWF Canada and York University, Faculty of Graduate Studies.

CONFLICT OF INTEREST STATEMENT
None declared.

AUTHORS’ CONTRIBUTIONS
M.P.G. and G.W.T. conceived the project. M.P.G. performed the analyses with input from G.W.T., S.H.F., and I.S. Funding acquisition for the project by G.W.T., M.G.D., and S.H.F. Original draft written by M.P.G. with review and input by G.W.T., M.G.D., S.H.F., and I.S. Final manuscript version was approved by all authors.

DATA AVAILABILITY
Data supporting our results for polar bear diet estimates is archived in the Dryad public archive (datadryad.org). Dryad Digital Repository. https://doi.org/10.5061/dryad.pzgmsbcm3. Sea ice concentration data is open access on the National Snow and Ice Data Center (https://nsidc.org/).

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