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Intraspecific and temporal variability in the diet composition of female polar bears in a seasonal sea ice regime

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Abstract

Predator foraging behaviour is influenced by a suite of intrinsic and extrinsic factors, including energetic requirements, resource availability, and habitat conditions. Polar bears (*Ursus maritimus*) are specialized predators of marine mammals and are adapted to a seasonal sea ice regime in much of their range. We used quantitative fatty acid signature analysis (QFASA) to estimate the diet composition of 374 female polar bears from 2004 to 2014 in western Hudson Bay, Canada. Ringed seal (*Pusa hispida*) was the dominant prey species, followed by bearded seal (*Erignathus barbatus*) and harbour seal (*Phoca vitulina*), with minimal consumption of beluga whale (*Delphinapterus leucas*), harp seal (*Pagophilus groenlandica*) and walrus (*Odobenus rosmarus*). Solitary adults and females supporting yearling cubs consumed more bearded seal than did subadults or females with cubs-of-the-year (COY). Subadults may be too small or inexperienced to capture bearded seals and females with COY may avoid offshore pack ice where densities of bearded seals, and potentially infanticidal adult male polar bears, may be highest. A relatively high dietary diversity in subadults and females supporting COY suggests less selective foraging and opportunistic scavenging. Overall, bears consumed more harbour seal and less ringed seal in congruent years suggesting variable local prey availability. Date of sea ice breakup influenced the diet of subadults and family groups more so than solitary females, suggesting differential sensitivity to sea ice conditions. Inter-annual variability in diet may be a consequence of differing responses of polar bears and multiple prey species to sea ice conditions in Hudson Bay.

**Keywords:** foraging ecology, polar bear (*Ursus maritimus*), quantitative fatty acid signature analysis, western Hudson Bay
Introduction

An organism's foraging behaviour is determined by intrinsic and extrinsic factors. Success in the capture and consumption of prey will be a function of individual traits (e.g., morphology, energetic state, life history) and environmental conditions (e.g., resource availability, competition) (Sih 2011). Foraging efficiency is optimized when net energy gain is maximized, translating into greater individual reproductive success and survival (Sih 2011; Stephens et al. 2007; Stephens and Krebs 1986). However, resources are often neither evenly distributed in an environment nor found in consistent seasonal or annual abundance (Drickamer et al. 2002). Consequently, foragers must modify behaviour by altering prey selection based on availability, or forage in an alternate habitat, both of which can influence net energy gain (Drickamer et al. 2002; Schoener 1971).

Intraspecific interactions among predators can affect both foraging success and prey selection. Such interactions can result in the diets of weaker competitors being broader, whereas more dominant individuals can specialize on high value prey (Sih 1993), thereby partitioning resources (prey type) among predators. Subordinate individuals may avoid dominant conspecifics while foraging, which may reduce foraging efficiency or alter diet composition (Lima and Dill 1990; Sih 1993). Such avoidance behaviour may stimulate individuals to broaden their dietary niche (Sih 1993), engage in scavenging behaviour, travel further distances for prey, or forage in less productive habitats. A growing body of evidence has documented resource partitioning across a broad range of environments and taxa, including invertebrates (Townsend and Hildrew 1979), fish (Grossman 1986; Matich et al. 2011), terrestrial carnivores (Karanth and Sunquist 1995), and marine mammals (Cooper et al. 2009; Weise et al. 2010). Divergence in prey selection can also occur as a function of age- or sex-specific differences in morphology,
breeding behaviour, and energetic demands (Bolnick et al. 2003). For example, sex differences in diet composition have been observed in birds (Lewis et al. 2002), primates (Boinski 1988) and marine mammals (Beck et al. 2005, 2007; Thiemann et al. 2007). Moreover, diet composition may vary across females of the same species based on social hierarchy (primates: Whitten, 1983), predation risk to females with offspring (ungulates: Bøving and Post 1997), and reproductive status of lactating females (pinnipeds: Merrick and Loughlin 1997).

Polar bears (*Ursus maritimus*) are marine top predators that use annual sea ice as their primary habitat for hunting marine mammal prey (Amstrup 2003; Stirling and Derocher 1993). The seasonal life history of polar bears is largely dependent upon consumption of high energy prey to support periods of fasting, migration, breeding and, for adult females, maternal care. Past studies have shown that polar bears feed primarily on ringed seal (*Pusa hispida*) and bearded seal (*Erignathus barbatus*), and to a lesser extent on harp seal (*Pagophilus groenlandica*), harbour seal (*Phoca vitulina*), walrus (*Odobenus rosmarus*) and beluga whale (*Delphinapterus leucas*) (Thiemann et al. 2008). In Hudson Bay, Canada, polar bears experience a seasonal sea ice regime, during which foraging is primarily limited to the ice-covered season (Ramsay and Hobson 1991; Stirling et al. 1977). Since marine mammals are unevenly distributed and densities can fluctuate both spatially and temporally (Kingsley et al. 1985; Stirling et al. 1982), bears often travel long distances while foraging (Amstrup et al. 2000, 2001; Ferguson et al. 1999).

On-ice foraging is particularly crucial for pregnant females who require substantial energy stores (i.e., fat) to support gestation, parturition, and lactation, which occurs during an 8-month onshore period following sea ice melt in late summer (Atkinson and Ramsay 1995; Stirling et al. 1977). Terrestrial feeding during the onshore period may be minimal and does not appear to provide energetic value to improve body condition (Pilfold et al. 2016; Rode et al.)
Moreover, females with dependent cubs require considerable energy to support the energetic demands of lactation through the approximately 2.5 year period of maternal care (Derocher and Stirling 1995). Aggressive interactions and infanticide by adult male bears (Taylor et al. 1985) can drive spatial separation during periods of foraging (Stirling et al. 1993) and may thus be reflected in diet composition.

Recent changes in sea ice, including progressively earlier breakup and later freeze-up, have been linked to declines in body condition, reproductive success, and survival of female bears in the Western Hudson Bay (WH) subpopulation (Lunn et al. 2016; Sciullo et al. 2016; Stirling et al. 1999). Progressively earlier ice breakup can shorten the period of polar bear hyperphagia that is associated with the peak of seal pupping in the spring (Stirling and Øritsland 1995). Sea ice cover and breakup have also been linked to changes in prey life history and survival. Declines in ringed seal pregnancy rate have been observed during years with earlier ice breakup, in conjunction with increased frequency of diseased seals (Ferguson et al. 2016). The behaviour and distribution of harbour seals vary with sea ice breakup and freeze-up date (Bajzak et al. 2013). Sea ice phenology may thus be associated with changes in prey distribution or availability, altering polar bear foraging behaviour and diet composition. Since the demographic effects of sea ice loss on polar bears are expected to be driven by changes in feeding opportunities, diet composition may reflect broader ecological trends relevant to the conservation and management of the species.

Our objective was to characterize the diet composition of WH female polar bears using quantitative fatty acid signature analysis (QFASA; see Iverson et al. 2004; Thiemann et al. 2008) and assess long-term temporal trends in diet potentially affected by sea ice conditions. We hypothesized that female diet composition would vary according to age and reproductive status,
as individuals would exploit resources differently based on foraging experience, energetic requirements, or avoidance of adult males. We further hypothesized that the dietary niche of females supporting dependent cubs would be broader in comparison to solitary females due to less selective foraging to offset higher energetic demands. Finally, we hypothesized that the diet composition of all females would be influenced by the timing of sea ice breakup, reflecting the effects of ongoing environmental changes in Hudson Bay (Gagnon and Gough 2005; Hochheim et al. 2010; Hochheim and Barber 2014).

Methods

Sample collection

Samples were collected during the fall (late August – September) 2004 to 2014 from free-ranging polar bears handled in northeastern Manitoba (Fig. 1) as part of a long-term study of the population ecology of WH polar bears (Lunn et al. 2016; Ramsay and Stirling 1988; Stirling et al. 1999). A vestigial premolar was extracted from previously unmarked bears older than one year for age determination (Calvert and Ramsay 1998). Adult bears were 5 years and older, and subadults were independent bears 2-4 years. Ages of cubs-of-the-year (COY; approximately 9 months old in fall) and yearling cubs (approximately 21 months old) were based on body size and dentition. Family groups consisted of an adult female with one or more dependent COY or yearlings. We collected a subcutaneous adipose tissue sample from each adult and subadult using an 8 mm disposable biopsy punch (Miltex Inc., York, PA, USA) inserted ca. 15 cm lateral to the base of the tail (Thiemann et al. 2006). Biopsies were stored in labelled cryogenic vials at -20°C until analysis. All capture and handling procedures were reviewed and approved annually by
Animal Care and Use Committees at Environment and Climate Change Canada, and York University.

We also collected 248 full-depth blubber samples from six potential polar bear prey species taken in Inuit subsistence hunts from 1994-1996 and 2001-2009. Prey samples were thought to be representative of those available to WH polar bears, and included ringed seal (~ 65 kg), bearded seal (300 kg), harbour seal (87 kg), harp seal (110 kg), walrus (1040 kg) and beluga whale (1500 kg) of all age and sex classes (Fig. 1). Blubber samples were wrapped in aluminum foil and stored in Whirl-Pak bags at -20°C until analysis.

**Laboratory analysis**

Lipid was extracted from adipose tissue biopsies after removing any attached skin or muscle. Prey blubber was subsampled (ca. 0.5 g) through the full depth of the sample, avoiding any exposed and potentially oxidized surfaces. We extracted lipid from all samples using methods outlined by Iverson, Lang and Cooper (2001). Fatty acid methyl esters (FAME) were prepared from extracted lipid using sulfuric acid as a catalyst (Budge et al. 2006). We analyzed each sample in duplicate and identified and quantified > 70 fatty acids (FA) via temperature-programmed gas-liquid chromatography using a Perkin Elmer Autosystem II capillary gas chromatograph and flame ionization detector (Agilent Technologies, Palo Alto, California, USA). FA were identified using the nomenclature A:Bn-X, indicating the length of the carbon chain (A), number of double bonds (B), and the position of the first double bond relative to the terminal methyl group (-X). Each FA was expressed as mass percent of total FA ± 1 SEM.
QFASA and diet modelling

We estimated polar bear diet composition using the QFASA model developed by Iverson et al. (2004) and applied to polar bears as described elsewhere (e.g., Thiemann et al. 2008; Galicia et al. 2016). Briefly, QFASA models the FA profile (or "signature") of a predator as a linear combination of mean prey signatures and then determines the proportional combination that minimizes the distance between the observed and modelled predator, after accounting for patterns of FA metabolism. To account for these metabolic patterns, we used calibration coefficients derived from captive mink (*Mustela vision*) fed a marine-based diet (Thiemann et al. 2008). We modified the original Iverson et al. (2004) QFASA model to use the Aitchison distance between modeled and observed predator signatures (Bromaghin et al. 2015, 2016). Diets of polar bears were estimated using 30 FA derived primarily from diet (Iverson et al. 2004). We excluded 20:1n-11 as this FA appeared to contribute to confounding among prey species (Galicia et al. 2015). Adipose FA profiles provide insight into the integrated diet composition of individuals over the weeks to months prior to sampling (Iverson et al. 2004). Our diet estimates therefore reflect foraging behaviour of females on the sea ice from late winter through early summer. Although the onshore period is associated with a metabolic fasting state in WH bears (Stirling et al. 1977), individuals were sampled early in the fall season (August - September) and any fasting-associated changes in FA stores would be minimal. All QFASA estimates were generated in R (version 3.2.4, The R Foundation for Statistical Computing, 2005) using the package QFASA.
Statistical analysis

We compared diet estimates of females across the following age and reproductive classes: (1) solitary adult; (2) adult with COY; (3) adult with yearlings; and (4) subadult. Since diet composition of individual bears did not necessarily include all prey species, diet data were not normally distributed. We therefore used randomization-permutation MANOVA to test for intraspecific differences in diet composition (randomly permuting factor levels 10 000 times) (Anderson 2001a, 2001b). We also used one-way permutation ANOVA to test post hoc differences in the proportion of each prey type across groups. We used simple linear regression to test for inter-annual changes in diet composition for each age and reproductive class. Adult females supporting either yearling or COY were pooled for inter-annual comparisons due to small sample sizes in each year. We used Spearman-rank correlations to assess the relationship between ringed seal and harbour seal consumption across all females and in each group. We used the Shannon-Wiener Index \( H' \) to estimate dietary diversity in females using the formula:

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

where \( p_j \) represents the proportion of prey type \( j \) in the diet, summed across all \( S \) prey types. Differences in dietary diversity across female groups were assessed using one-way ANOVA.

Following Lunn et al. (2016), we used ArcInfo (Environmental Systems Research Institute, California) to extract sea ice concentration from 25 x 25 km resolution passive microwave satellite raster imagery from the National Snow and Ice Data Center (NASA Team algorithm; Cavalieri et al. 1996, 2012) for 2003-2014. We calculated mean daily sea ice concentration from the fractional amount of sea ice covering each of 381 grid cells that provided
complete coverage of the WH management zone (PBSG, 2015). From these data, we determined spring sea ice breakup as the ordinal date when sea ice reached and remained below 50% concentration for a minimum of three consecutive days (Gagnon and Gough 2005; Stirling and Parkinson 2006). To assess if environmental factors influenced diet composition, we performed multiple linear regression using the current year’s sea ice breakup date \((\text{breakup})\), the previous year’s breakup date \((\text{lag breakup})\), and \(\text{year}\) for each prey species in each female group. Since the spring period of hyperphagia likely overlaps the period when sea ice melt is at 50% (May-June), we used the current year's sea ice breakup date as a predictor in determining diet composition, while \(\text{year}\) was included in the model to reflect potential cumulative effects of multiple environmental factors that may fluctuate over time. As abundance and availability of prey may be affected by seal reproductive success the previous year, we also used \(\text{lag breakup}\) as a covariate to assess prior-year habitat effects on diet composition. The assumption of non-collinearity among predictor variables was met using a variance inflation factor <2.5 and tolerance values >0.10, and correlation coefficients between independent variables remained <0.50. P-values for each predictor variable were used to determine the relationship between predictors and consumption of each prey species, while standardized \(\beta\) coefficients provided the strength of each predictor in the model. Statistical analyses were performed in R (Version 3.2.4, The R Foundation for Statistical Computing, 2005) and SPSS® version 22 for Windows® (IBM, Chicago, USA).

**Results**

**Diet composition**
Across all female polar bears, ringed seal contributed the most to polar bear FA signatures (mean ± SEM: 57.2 ± 0.8%) (Fig. 2a), and did not differ significantly across age class or reproductive status (one-way permutation ANOVA, p = 0.59) (Fig. 2b). Bearded seal was also consumed in relatively high proportion across all females (15.6 ± 0.8%) (Fig. 2a). Mean bearded seal consumption was higher among solitary adult females than subadults (p = 0.02) (Fig. 2b). Bearded seal was also found more frequently in the diets of solitary adults (82% of bears) compared to females supporting COY (74%), females supporting yearlings (66%) and subadults (63%).

Harbour seal was consumed in similar proportions to bearded seal across all females (15.4 ± 0.5%) (Fig. 2a), however this component of the diet did not differ across age class or reproductive status (p = 0.67). Similarly, beluga whale was consumed in minor proportions across all females (6.6 ± 0.4%) (Fig. 2a), and did not differ across female groups (p = 0.07). Harp seal and walrus were consumed in lowest proportions across all females (3.5 ± 0.4% and 1.3 ± 0.08%, respectively) (Fig. 2a), and significantly differed across age class and reproductive status (p < 0.01 and p = 0.03, respectively). Specifically, subadult females consumed more harp seal (6.1 ± 1.4%) than both solitary females (2.0 ± 0.3%) (p < 0.01) and females with yearlings (2.5 ± 0.5%) (p = 0.03). Walrus was found in higher proportions in solitary adult females compared to females supporting yearlings (p < 0.01), but not females supporting COY (p = 0.40) or subadults (p = 0.10) (Fig. 2b). Family groups only differed in their consumption of walrus with adults supporting COY consuming greater proportions than those supporting yearlings (p < 0.01).

Overall, walrus was found more often in the diets of solitary adult females (90% of bears) than subadults (72%).
Dietary diversity did not differ significantly across age and reproductive status (ANOVA, F = 1.57, p = 0.18). Dietary diversity, however, varied considerably among individual bears, both within and across age and reproductive status ($H'$ range: 0.25-1.43, Table 1) and was most variable in females with COY (Table 1).

**Temporal trends in diet**

Female diet composition varied over time across age and reproductive groups. Bearded seal consumption increased in solitary females (linear regression, $R^2 = 0.16$, p < 0.01), females with dependents ($R^2 = 0.21$, p < 0.01) and subadults ($R^2 = 0.17$, p < 0.01) (Fig. 3). Conversely, beluga whale decreased over time in solitary females ($R^2 = 0.27$, p < 0.01), females with dependents ($R^2 = 0.38$, p < 0.01) and subadults ($R^2 = 0.20$, p < 0.01). Harp seals remained relatively low in proportion throughout the study, and consumption increased over time in solitary females ($R^2 = 0.06$, p < 0.01), but not in females with dependents (p = 0.21) or subadults (p = 0.71). Similarly, walrus contributed minimally to female polar bear diet and only increased over time in subadult females ($R^2 = 0.08$, p < 0.01) (Fig. 3).

Ringed seal consumption showed no directional trend in solitary females (p = 0.21), females with dependents (p = 0.14) or subadults (p = 0.94), however consumption ranged from 48.4% (2009) to 64.8% (2014) (Fig. 3). Consumption of harbour seal declined in solitary females ($R^2 = 0.26$, p < 0.01), females with dependents ($R^2 = 0.20$, p < 0.01) and subadults ($R^2 = 0.05$, p = 0.01), with the lowest proportion observed in 2013 (solitary 4.8%, family 4.5%, and subadult 3.8%). Years in which harbour seal consumption was greatest (for example, 2005 and 2009), were paralleled with declines in ringed seal consumption (Fig. 3). Consumption of ringed seal and harbour seal were inversely related across the entire study period (2004-2014) ($r_s = -0.29$, p
< 0.001) although the relationship appeared to get weaker after 2009. In 2004-2009, ringed seal and harbour seal consumption were negatively correlated in solitary females (Spearman-rank correlation, $r_s = -0.39, p = 0.01$), females with dependents ($r_s = -0.35, p < 0.01$), and subadults ($r_s = -0.43, p < 0.01$) (Fig. 4a). Consumption of ringed and harbour seal during the last stage of the study (2010 - 2014) was not significantly correlated across females in any group ($p > 0.05$) (Fig. 4b).

**Diet composition and timing of sea ice breakup**

Although date of sea ice breakup varied from 5 June to 2 July (ordinal date: 156 - 183) over the period 2004 - 2014, there was no directional trend (linear regression, $F = 0.75, p = 0.40$) (Fig. 5). Overall, only year affected diet composition of solitary females, specifically in their consumption of harbour seal, bearded seal, beluga whale and harp seal (Table 2). For adult females accompanied by dependent offspring, breakup date, lag breakup and year had a significant effect on both harbour seal and beluga whale consumption, while only year influenced consumption of bearded seal (Table 2). Among females with dependents, breakup date and lag breakup was negatively related to ringed seal consumption (Table 2). Subadults were similarly influenced by breakup date, lag breakup and year in beluga whale consumption, while harbour seal was affected by breakup date and lag breakup (Table 2).

**Discussion**

Our results suggest that the diets of WH female polar bears are dependent on age and reproductive status and that ongoing ecological change in the region has potentially contributed to long-term variability in foraging habits. Dietary differences among age and reproductive classes of females may be a function of alternate space-use strategies, prey selection, or both.
Our results reveal intra-population variability in WH polar bears and suggest a complex interaction between sea ice habitat and predator-prey dynamics.

**Diet composition**

Our results are consistent with past studies that have identified ringed and bearded seals as the most common prey of polar bears in WH and throughout most of their circumpolar range (Derocher et al. 2002; Galicia et al. 2015; Iverson et al. 2006; Thiemann et al. 2008). Ringed seals are likely the primary prey because of their ubiquitous distribution across the Arctic, high abundance, and relative ease of capture (Stirling and McEwan 1975). The highest consumption of bearded seal by solitary adult females and the lowest consumption by subadults (Fig. 2) is consistent with the use of offshore pack ice by these large-bodied seals (Chambellant et al. 2012a; Kovacs et al. 1996; Pilfold et al. 2014). Subadult female bears may be too small or inexperienced to hunt even juvenile bearded seals. Pack ice is frequented by adult male polar bears (Stirling et al. 1993) and females with dependent cubs may avoid adult males to minimize the risk of infanticide (Derocher and Stirling 1990; Pilfold et al. 2014; Taylor et al. 1985). Stirling et al. (1993) found that solitary adult females and females with older dependents (two year old cubs) foraged along the floe edge adjacent to adult males, consistent with our observation of higher bearded seal consumption among solitary females and females with yearlings (Fig. 2).

The consumption of other prey species, including harp seal, beluga whale and walrus, suggests opportunistic foraging and locally variable availability. Scavenging on beluga whales, for example, has been recorded across the Arctic (Freeman 1973; Heyland and Hay 1976; Rugh and Shelden 1993). Similarly, walrus has been detected in the diets of polar bears in Foxe Basin
and Gulf of Boothia (Galicia et al. 2016; Thiemann et al. 2007, 2008) and bears have been observed both scavenging and actively hunting walrus throughout the High Arctic and Chukchi Sea (Calvert and Stirling 1990; Kochnev 2006). Polar bears are sexually size dimorphic (Derocher et al. 2005) and the female bears in our study were presumably limited to scavenging walrus, which have only been observed to be successfully hunted by adult male polar bears (Calvert and Stirling 1990) and walrus consumption is positively correlated with adult male body size (Thiemann et al. 2007). WH polar bears have large home ranges (Mauritzen et al. 2003a; McCall et al. 2015; Parks et al. 2006) and can access walrus colonies in northern and eastern parts of Hudson Bay. Overlapping use of prey resources by bears in adjacent subpopulations is reflected in similar diet composition of bears (specifically, ringed seal and walrus proportions) from western Hudson Bay and southern Foxe Basin (Galicia et al. 2016).

The large range we observed in female dietary diversity implies substantial individual variation in prey selection or space-use strategies. Females with COY and subadults had a higher than expected diet diversity and are likely scavenging on a broader range of prey types (Thiemann et al. 2011). Parks et al. (2006) and McCall et al. (2015) found that family groups travel further on the sea ice compared to solitary females, which is consistent with less selective foraging habits. Females supporting COY may be in an energy deficit in spring following the maternal denning period and thus be motivated to forage widely (Parks et al. 2006; Ricklefs et al. 1996). As long distance migration can be energetically expensive in polar bears (Hurst et al. 1982a, 1982b) and can fluctuate with sea ice dynamics (Mauritzen et al. 2003b), females with dependents may experience a trade-off between the need to forage widely and the need to avoid potentially infanticidal males.
Temporal trends in diet

We documented long term variability in diet composition among female WH polar bears. Ringed seal consumption varied over time, consistent with documented changes in seal density in our study area (Chambellant et al. 2012a; Ferguson et al. 2016; Young et al. 2015). Spring aerial surveys in WH showed an overall decline in ringed seal density from 2007 to 2009 (Young et al. 2015) and the lowest seal densities in 2009 and 2013 (Chambellant et al. 2012a), matching our results of reduced ringed seal consumption during these years (Fig. 3). Moreover, although we found bearded seal consumption to increase over time, reduced consumption was observed from 2007 to 2008 across all groups, consistent with a decline in density observed in 2008 (Chambellant et al. 2012a). The distribution of ringed and bearded seals, and thus their availability to polar bears, is influenced by timing of ice breakup, snow depth, and ice cover and habitat conditions were notably poor in 2008 (Chambellant et al. 2012a).

We detected an inverse relationship in the consumption of harbour seal and ringed seal: years marked with a decline in the proportion of ringed seal (2005, 2009) were matched by an increase in the proportion of harbour seal (Fig. 3; Fig. 4a). Both ringed and harbour seals coexist along the western and southern shore of Hudson Bay (Stirling 2005), and both are available to WH polar bears. However, timing of ice breakup can dictate when female bears begin moving into coastal habitat (Bajzak et al. 2013; Cherry et al. 2013; Derocher and Stirling 1990; McCall et al. 2016; Stirling et al. 1999) allowing them access to harbour seals concentrated in coastal habitat with shallow, nutrient rich rivers and estuaries (Bajzak et al. 2013; Derocher et al. 2004; Mansfield 1967; Stewart and Barber 2010; Stirling 1997). Ringed and harbour seal consumption, however, uncoupled during the final years of the study (2010 - 2014) (Fig. 4a), when timing of sea ice breakup exhibited greater inter-annual variability (Fig. 5). Even during years of later sea
ice breakup, harbour seal consumption was high while ringed seal declined (Table 2), suggesting that sea ice dynamics such as proportion of land fast ice along the coast, changes in the shore lead system, and timing of ice breakup may influence harbour seal presence along the coast and affect availability to polar bears (Bajzak et al. 2013).

Sporadic dietary shifts in polar bears may be a consequence of ephemeral prey availability and opportunistic foraging (e.g. Galicia et al. 2016). For instance, the observed decrease in bearded seal and increase in beluga consumption in 2004 and 2005 may be related to local entrapment of beluga whales (Freeman 1973; Heide-Jørgensen et al. 2002) that overwinter in parts of Hudson Bay (S. Ferguson, unpublished data) (Luque and Ferguson 2010). The expansion of killer whale (*Orcinus orca*) distribution in response to reduced sea ice cover has been associated with increased predation of beluga whales in both northwestern and western Hudson Bay (Higdon and Ferguson 2009; Westdal et al. 2016). Killer whale presence can drive beluga into shallow waters, making them more accessible to polar bears (Smith and Sjare 1990; Westdal et al. 2016). In 2004 and 2005, an increase in the number of killer whales in WH (see Higdon and Ferguson 2009; Richard 2005) may have resulted in increased beluga whale predation and, as a consequence, increased carrion for polar bears.

**Diet composition and timing of sea ice breakup**

Timing of sea ice breakup has been found to predict overall body condition in polar bears (Sciullo et al. 2016), suggesting a decrease in foraging success associated with reduced feeding time. Our results suggest the effects of sea ice on diet composition are more variable. Date of *breakup*, *lag breakup* and *year* influenced diet composition of subadult females and females with young, while only *year* influenced the diet of solitary females (Table 2). Subadult females and
females with dependents may be especially sensitive to habitat conditions because of their smaller absolute energy stores and higher energetic requirements, respectively, relative to solitary adult females. Responses to changes in sea ice availability will also differ across prey species (Chambellant et al. 2012a, 2012b; Johnston et al. 2005; Smith and Harwood 2001). Earlier ice breakup, for example, can negatively affect ringed seal recruitment and pup survival with negative consequences for abundance the following year (Ferguson et al. 2005). Numerical responses of prey to sea ice conditions may explain the effect of lag breakup on subadult and family group diet composition. Year was found to significantly influence diet composition across all groups, which suggests that unidentified habitat conditions contributing to the variability in prey selection are not completely reflected in the timing of breakup. Long term trends suggest that consumption of ringed seal may be less variable over time relative to other prey, including bearded seal, harbour seal, and beluga whale. The reasons for the apparent constraint on ringed seal consumption are not immediately clear, but the ubiquitous distribution and relatively high abundance of ringed seal in Hudson Bay may maintain this species as the primary polar bear prey. Proportional consumption of alternative prey species, however, may be more strongly related to sea ice conditions and prey availability (Thiemann et al. 2008).

Ongoing changes in sea ice habitat may alter predator-prey interactions in complex ways, including functional and numerical responses in polar bears across the Arctic (Ferguson et al. 2000; Mauritzen et al. 2003a). Our results suggest that prey selection in females is influenced by age and reproductive status, and the avoidance of potentially predatory adult males. Polar bears use sea ice as foraging habitat and sea ice conditions are thus likely to affect foraging success and diet composition. The inter-annual variability in diet composition we detected may be driven by habitat-mediated changes in prey availability, polar bear behaviour, or both. Understanding
how prey density and polar bear foraging are linked to sea ice characteristics will be essential to understanding and predicting how Arctic marine food webs will respond to long term climate warming.

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List of Figure and Table Captions

**Figure 1.** Hudson Bay, Canada showing the location where polar bears (n=374) were captured south of Churchill, Manitoba, 2004-2014. The management boundary of the Western Hudson Bay polar bear subpopulation is shown as a dashed line. Prey samples were collected from community subsistence harvests: Arviat - ringed seal (n = 98), bearded seal (n = 33), harbour seal (n = 17); Pangnirtung - harp seal (n = 42); Hall Beach and Igloolik - walrus (n = 21); and, Inukjuak, Sanikiluaq, Repulse Bay, and Whale Cove - beluga whale (n = 37).

**Figure 2.** Diet composition of Western Hudson Bay female polar bears captured in fall, 2004-2014 (a) pooled and (b) by age and reproductive status. Each prey species' biomass contribution to individual diet composition is represented as a mean ± SEM. Different letters indicate statistical differences between age and reproductive status within each prey species.

**Figure 3.** Diet composition of Western Hudson Bay female polar bears captured in fall, 2004-2014 (a) pooled and (b-d) by age and reproductive status. Prey species contributing to overall diet composition include ringed seal and harbour seal (left panel), bearded seal and beluga whale (middle panel), and harp seal and walrus (right panel). Note differing scales across y-axis. Diet estimates are expressed as mean ± SEM. Significant linear regression equations are indicated for each prey species.
**Figure 4.** Relationship between consumption of ringed seal versus harbour seal of solitary females (▲), females with dependent offspring (○) and subadults (●) captured in the fall, (a) 2004 - 2009 and (b) 2010 - 2014 in western Hudson Bay. Consumption of harbour seal and ringed seal across all females during the entire study period (2004 - 2014): \( r_s = -0.29, p < 0.001 \).

**Figure 5.** Timing of sea ice breakup (50% sea ice concentration) in the Western Hudson Bay management zone (PBSG, 2015), 2004 to 2014.

**Table 1.** Shannon-Wiener Diversity Index \((H')\) values (mean ± SEM) for 374 female polar bears captured in western Hudson Bay in fall 2004 - 2014. Minimum and maximum individual observations of diet diversity are indicated as well as absolute differences in diversity index.

**Table 2.** Multiple linear regression models examining the effect of ice breakup date, lag breakup date and year on consumption of prey species for female polar bears including solitary adults, family groups (adult females supporting dependents), and subadults captured between 2004 - 2014 in western Hudson Bay. * represents the significant predictor variable in each model.
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<table>
<thead>
<tr>
<th>Age and Reproductive Status</th>
<th>$H'$ Mean ± SE</th>
<th>Range [absolute difference in range]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solitary adult female (n=102)</td>
<td>0.97 ± 0.017</td>
<td>0.50 - 1.28 [0.78]</td>
</tr>
<tr>
<td>Adult female with yearling cubs (n=62)</td>
<td>1.04 ± 0.019</td>
<td>0.63 - 1.42 [0.79]</td>
</tr>
<tr>
<td>Adult female with cubs-of-the-year (n=120)</td>
<td>0.98 ± 0.018</td>
<td>0.25 - 1.40 [1.15]</td>
</tr>
<tr>
<td>Subadult female (n=90)</td>
<td>0.97 ± 0.021</td>
<td>0.40 - 1.43 [1.03]</td>
</tr>
</tbody>
</table>
Table 2. Multiple linear regression models examining the effect of ice breakup date, lag breakup date and year on consumption of prey species for female polar bears including solitary adults, family groups (adult females supporting dependents), and subadults captured between 2004 - 2014 in western Hudson Bay. * represents the significant predictor variable in each model.

<table>
<thead>
<tr>
<th>Solitary</th>
<th>Multiple Regression Model</th>
<th>β Coefficient (p significance)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solitary</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 102</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ringed seal</td>
<td>2.40</td>
<td>0.07</td>
</tr>
<tr>
<td>Harbour seal</td>
<td>13.63</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bearded seal</td>
<td>7.82</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Beluga whale</td>
<td>13.59</td>
<td>&lt;0.001</td>
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<tr>
<td>Harp seal</td>
<td>2.83</td>
<td>0.04</td>
</tr>
<tr>
<td>Walrus</td>
<td>1.06</td>
<td>0.36</td>
</tr>
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</table>

Family n = 182

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<th>Multiple Regression Model</th>
<th>β Coefficient (p significance)</th>
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<tr>
<td>Ringed seal</td>
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<td>Bearded seal</td>
<td>17.73</td>
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<tr>
<td>Beluga whale</td>
<td>40.73</td>
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<tr>
<td>Harp seal</td>
<td>1.25</td>
<td>0.29</td>
</tr>
<tr>
<td>Walrus</td>
<td>3.79</td>
<td>0.01</td>
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Subadult n = 90

<table>
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<th>β Coefficient (p significance)</th>
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<tr>
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</tr>
<tr>
<td>Ringed seal</td>
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<tr>
<td>Harbour seal</td>
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<td>Bearded seal</td>
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<tr>
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<td>&lt;0.001</td>
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<tr>
<td>Harp seal</td>
<td>1.10</td>
<td>0.35</td>
</tr>
<tr>
<td>Walrus</td>
<td>2.84</td>
<td>0.04</td>
</tr>
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