FORAGING PATTERNS OF POLAR BEARS (*URSUS MARITIMUS*) IN A RAPIDLY CHANGING ARCTIC: INSIGHTS FROM HARVEST-BASED SAMPLING IN NUNAVUT, CANADA

MELISSA P. GALICIA

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Abstract

Arctic species are adapted to the seasonal changes in habitat conditions and resource availability; however, anthropogenic climate warming and associated sea ice loss are having widespread ecological consequences. Polar bears (*Ursus maritimus*) are top predators across their circumpolar range, where they rely on predictable sea ice patterns for life history characteristics. Thus, polar bears may be sensitive indicators of environmental change and their dietary patterns may reflect prey availability. Continued changes in environmental conditions are predicted to reduce foraging opportunities, however the mechanistic relationship between bear demography and habitat change are poorly understood. The objective of this dissertation was to identify patterns of polar bear diet composition and foraging success and examine how polar bears are responding to shifting environmental conditions in the Canadian Arctic.

To examine the foraging ecology of polar bears, I used adipose tissue samples from harvested and remote biopsied bears across Nunavut, Canada from 2010-2018 with additional samples from 1999-2003 for the Foxe Basin subpopulation. I used quantitative fatty acid signature analysis to estimate diet composition and the relative lipid content of adipose tissue was used as an index of body condition. I found that seasonal fluctuations in the body condition of polar bears was correlated with seasonal changes in sea ice conditions. Polar bear diet composition varied spatially and temporally based on local prey availability. In some cases, the dietary proportion, and frequency of prey occurrence in diets was influenced by sea ice conditions that promote prey susceptibility to predation or an increase in the availability of supplemental food (i.e., marine mammal carcasses). Age- and sex-specific variation in diet was associated with the broader dietary niche of adult male bears. This dissertation provides a more comprehensive understanding of the mechanisms affecting the responses and resilience of polar

bears to climate-driven environmental change. Adipose tissue samples collected during subsistence harvests of polar bears have provided unprecedented insight into the foraging ecology of polar bears. Continued monitoring of polar bear body condition and diet will help inform effective management and conservation action.

Dedicated to my mother, Suzanne Hunter-Galicia

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Chapter 1: Introduction

Food web ecology

An ecosystem consists of a biotic community, in addition to the physical and chemical processes necessary for the persistence of organisms within a given space and time (Tansley 1935, Lindeman 1942). The assemblage of organisms and the factors that contribute to their presence forms the structure, whereas ecological interactions within the environment forms the functioning of an ecosystem (Odum 1971). Food webs represent the feeding relationships among species and energy pathways within an ecological community (Elton 1927, Lindeman 1942). Organisms are grouped into relatively discrete trophic levels (e.g., primary producers, primary consumers, etc.), where each trophic level depends on the preceding level as a source of energy, with primary producers depending on solar radiation (Lindeman 1942). Linear trophic interactions form a food chain typically limited by 5 levels which then combine to form a larger interconnected food web (or "food cycle"; Elton 1927).

It was thought that resources and habitat limit populations, however in some communities, biotic interactions (e.g., predation and grazing) play an equally important role in regulating populations (Hairston et al. 1960). Communities can be structured via a bottom-up system, where populations are limited by resources or a top-down system, where populations are controlled by predators (Hairston et al. 1960, Power 1992). In a bottom-up regulation, higher trophic level species respond to fluctuations in food supply (e.g., primary productivity). For example, the abundance of Raitt's sand eel (*Ammodytes marinus*), a mid-trophic position fish, was primarily influenced by climatic-driven fluctuations in plankton abundance as opposed to predation or fisheries, in turn affecting breeding success of higher trophic levels such as seabirds (Frederiksen et al. 2006). On the other hand, in a top-down system, the influence of a predator cascades down trophic levels, with measurable effects on prey populations (Carpenter et al.

1985, Hunter and Price 1992). Worm and Myers (2003) suggested a top-down system in the North Atlantic Ocean where predators suppress prey abundance. Atlantic cod (*Gadus morhua*; predatory fish) was inversely correlated with abundance of northern shrimp (*Pandalus borealis*; prey) but showed no relation to fluctuating ocean temperatures. The prevalence of top-down versus bottom-up forces has been debated in the literature and may differ across ecosystems (Power 1992). However, ecologists have suggested the two are likely not mutually exclusive with a possibility of both forms simultaneously or alternatively regulating populations and shaping communities (Hunter and Price 1992) with examples from terrestrial (Krebs et al. 1995, Meserve et al. 2003), freshwater (McQueen et al. 1989), and marine ecosystems (Hunt et al. 2002).

Predation and the ecological role of top predators

In simplest terms, predation is when all or part of an organism (prey) is consumed by another organism (predator) in which the prey was initially alive at the time of the predator's attack (Begon et al. 2006). Predation is harmful to the individual prey being eaten; however, the effects of predators may not be necessarily harmful to the entire population if: (1) predation occurs on individuals less likely to contribute to the population (young, old or in poorer condition, e.g., FitzGibbon and Fanshawe 1989, Begon et al. 2006, Tucker et al. 2016); or (2) intraspecific competition in prey is reduced (e.g., Oedekoven and Joern 2000, Begon et al. 2006). Although, in some cases there are factors mitigating the impact of predation, many predators will limit prey abundance and shape communities either through direct effects (i.e., the removal of prey; Estes and Palmisano 1974, Pace et al. 1999) or indirect effects (i.e., risk of predation; Schmitz et al. 1997, Creel and Christianson 2007).

Direct effects include the removal of an individual from a population via predation with direct influences on prey abundance. Robinson et al. (2002) found that cougar (*Puma concolor*) predation was the primary cause of adult mule deer (*Odocoileus hemionus*) mortality leading to a population decline in south-central British Columbia. However, in natural communities direct and indirect effects may act together to influence populations (Creel and Christianson 2007). Indirect effects may induce behavioural responses in prey such as shifts in habitat use (e.g., Creel et al. 2005, Breed et al. 2017, Palmer et al. 2021), vigilance (e.g., Armitage 2004), foraging (e.g., Barnier et al. 2014), or movement (e.g., Sih and McCarthy 2002) to reduce risk of predation. Laundré et al. (2001) proposed the term 'landscape of fear' suggesting that habitat features are associated with varying levels of predation risk which can induce increased vigilance by prey to reduce vulnerability to predation. Antipredator responses may be energetically costly and ultimately influence population and community dynamics (Lima and Dill 1990, Creel and Christianson 2007). For example, Fortin et al. (2005) identified mechanisms of the trophic interactions in the wolf (*Canis lupus*)-elk (*Cervus canadensis*)-trembling aspen (*Populus temuloides*) system that occurred due to behavioural responses by elk linked to predation risk. Specifically, areas with increased wolf presence resulted in avoidance by elk, and consequently higher aspen biomass, whereas the absence of wolves led to increased use of aspen by elk. Indirect interactions between predator and prey leading to a trade-off between food and safety has also been identified in marine systems. For example, Heithaus and Dill (2002) found when tiger sharks (*Galeocerdo cuvier*) were present, bottlenose dolphins (*Tursiops aduncus*) foraged in deeper waters with less energetic return but avoided shallower areas with higher food availability where predation risk was high.

Top predators (also known as apex predators) are found at the highest trophic level of a food chain; their prey selection can thus influence population abundance and exert top-down effects across multiple trophic levels (Krebs 2009, Baum and Worm 2009). Consequently, top predators can play a significant role in shaping communities. Top predators are typically large-bodied animals with wide-ranging distributions adding to the difficulty of empirical studies and often, the impacts of top predator abundance are not observed until years to decades after reductions (Estes et al. 2011). Despite these challenges, the loss of top predators has led to observed trophic cascades of varying degrees in terrestrial (e.g., Terborgh et al. 2001), freshwater (e.g., Carpenter et al. 2001), and marine systems (e.g., Estes and Duggins 1995) with broader ecosystem degradation. Myers et al. (2007) found the reduction of great sharks (apex predators) resulted in the release of mesopredators from top predator control, in turn an increase in mesopredator abundance. This led to a decrease in bay scallop (*Argopecten irradians*) abundance from increased predation pressure by mesopredators to the eventual closure of the scallop fishery in the northwest Atlantic Ocean. The response of upper trophic level species to environmental change and the effects that may cascade through the ecosystem remains unclear, and ecosystem sentinels (or indicator species) may help identify and predict the timing and spatial extent of broad-scale changes (Hazen et al. 2019).

Given their wide geographic distribution, predatory role, and long lifespan, and in some cases sensitivity to fluctuating habitat conditions, top predators can serve as indicator (or sentinel) species reflecting local- and broad-scale change in the functioning of an ecosystem over time and space (Bowen 1997, Sergio et al. 2008). Ecosystem change can be reflected in top predator ecology through their diet, movement, life history characteristics, distribution, and abundance (Hazen et al. 2019). Sentinel species can also be used in a predictive manner. For

example, proportions of prey (Pacific sardines; *Sardinops sagax* and northern anchovies; *Engraulis mordax*) in the diet of piscivorous seabirds can be a useful index to predict availability for fisheries (i.e., catch per unit effort) months later in the Gulf of California (Velarde et al. 2015). Understanding a top predator's role within a system and underlying mechanisms that influence population dynamics can be useful for predicting climate-mediated change and the resilience of an ecosystem, subsequently leading to improved management and conservation strategies.

Foraging ecology

Foraging is the ecological process of a predator searching for, capturing, and consuming prey that influences life history characteristics, and consequently individual fitness and population dynamics (Krebs 2009). The foraging behaviour of predators can provide important insight into predator-prey interactions, nutrition, competition, and habitat use which are essential components influencing the structure and functioning of a community. Predator foraging behaviour is based on the principle that an individual will attempt to maximize their energetic return while reducing foraging costs (e.g., encounter rate, probability of attack, success of capture and probability of consumption), also known as optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966, Pyke et al. 1977). Predators should show a preference for the most profitable prey (i.e., highest energetic return per unit of time) when in high abundance (Schluter 1981, Pyke 1984). For example, Hayward et al. (2006) found that leopards (*Panthera pardus*) preferred prey within a specific weight range associated with high encounter rates and a minimal risk of injury. Leopards tended to avoid prey that had a smaller or larger body mass, were found in open areas, or had effective defense strategies that would reduce a leopard's energetic gain.

Some predators may be able to alter their foraging strategies based on prey availability and may switch to less profitable prey if the abundance of the preferred prey is reduced.

Resources can fluctuate seasonally or annually, and predators may need to shift their foraging behaviour or broaden their prey selection in response to changing habitat conditions or prey availability (Schoener 1971, Schluter 1981). A predictable environment with less seasonal and/or resource variability will enable predator specialization. Conversely, an environment with patchy resources or variable environmental conditions may favour a generalist foraging strategy (Gilmour et al. 2018). Predators with a flexible foraging behaviour can act opportunistically to exploit diverse prey. The ability of a predator to switch between prey that may be seasonally or spatially available while still meeting their energetic needs may reduce a predator's vulnerability to environmental change (Bolnick et al. 2007). For example, marine seabirds such as Northern gannets (*Sula bassana*) exhibit flexible foraging behaviour in response to changing prey distribution and abundance. Northern gannets switched between a higher consumption of capelin (*Mallotus villosus*) and Atlantic salmon (*Salmo salar*) that was linked to prey abundance during a given year, and this switch between prey species had no effect on the breeding success of the Northern gannet population (Montevecchi et al. 2009). Thus, monitoring diet can provide insight on the ecological flexibility of species in response to shifting environmental conditions.

Polar bear ecology

Polar bears are top predators across their circumpolar distribution which extends throughout five nations: Canada, Denmark (Greenland), Norway (Svalbard), Russia, and the United States of America (Alaska; Prestrud and Stirling 1994). There are approximately 26,000 polar bears globally with two thirds inhabiting the Canadian Arctic (Vongraven and Peacock 2011, Wiig et al. 2015). Polar bears are separated into 19 discrete subpopulations, in which the name refers to

the subpopulation and not directly to the body of water for which they are named (Obbard et al. 2010; Figure 1.1). Polar bears have different life history characteristics and foraging strategies in relation to their environment and sea ice patterns across geographic areas (Stirling 2002). For example, Amstrup et al. (2008) combined the 19 subpopulations into 4 ecoregions based on sea ice regime including seasonal sea ice (ice melts completely and bears are forced on land; e.g., Stirling et al. 1977, Cherry et al. 2013), archipelago (comprised of interisland channels that historically filled with multiyear ice, although with shifts towards seasonal ice in more recent years; Hamilton et al. 2014), divergent ice (formation of sea ice that retreats towards the polar basin during the summer and bears either remain with sea ice or move onto land; Atwood et al. 2016a), and convergent ice (sea ice from other regions moves towards coastline acting as a platform for bears; Atwood et al. 2016a; Figure 1.1).

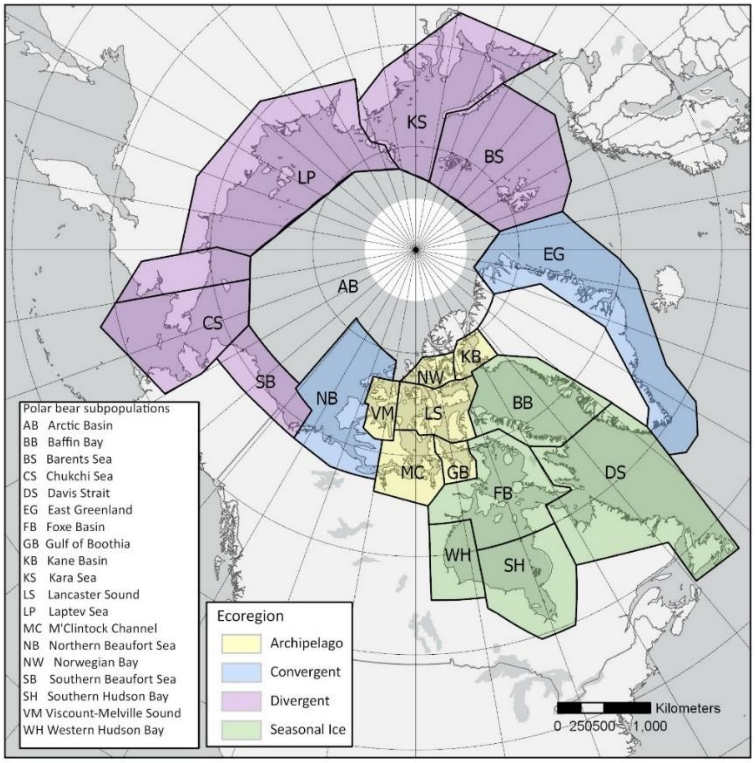

Figure 1.1 Circumpolar distribution of the 19 polar bear subpopulations and the four ecoregions.

Body condition can serve as an indicator of physiological/nutritional stress, reproductive potential, and overall health of an individual in relation to food resources and environmental conditions (Peig and Green 2009). Polar bears experience fluctuations in their body condition (i.e., overall fatness) throughout the year. During times when prey are abundant, polar bears can shift to a phase of hyperphagia, and conversely switch to fasting when accessibility of prey is limited (Stirling and McEwan 1975, Messier et al. 1992, Stirling and Øritsland 1995). During hyperphagia, polar bears accumulate subcutaneous fat (Pond et al. 1992) to rely on during periods of fasting (Derocher and Stirling 1990, Atkinson et al. 1996), and then supports maintenance, growth, or reproduction when energy intake is greater than expenditure (Parker et al. 2009, Molnár et al. 2009).

Polar bears have a high fat diet, feeding extensively on the blubber of marine mammals (Stirling and McEwan 1975, Stirling and Øritsland 1995). Across their distribution, polar bears feed primarily on ringed seals (*Pusa hispida;* e.g. Stirling and Øritsland 1995, Iverson et al. 2006, Thiemann et al. 2008), while bearded seal (*Erignaathus barbatus*) are important alternate prey species throughout the Arctic (e.g., Stirling and Archibald 1977, Smith 1980, Stirling and Øritsland 1995). Polar bears have developed a close predator-prey relationship with ringed seal in which timing of the spring hyperphagia period coincides with the pupping season of ringed seals, when newly weaned pups are most vulnerable to predation (Stirling and Øritsland 1995). Ringed seals, in turn have evolved behavioural adaptations in response to predation risk from surface predators such as polar bears. Ringed seals create and maintain multiple breathing holes 200 m or more apart (Smith and Stirling 1975) in case one is discovered by a bear, display vigilance when hauled out on the sea ice by continuously looking around for predators and make use of subnivean birth lairs to hide from predators during parturition and weaning (Stirling

1977). Past studies have also identified opportunistic feeding on other marine mammals, including beluga whales (*Delphinapterus leucas*; e.g., Smith and Sjare 1990, Thiemann et al. 2008, Galicia et al. 2015), harp seals (*Pagophilus groenlandicus*; Derocher et al. 2002, McKinney et al. 2013, Galicia et al. 2016), narwhals (*Monodon monoceros*; Smith and Sjare 1990), and walrus (*Odobenus rosmarus*; Kiliaan and Stirling 1978, Calvert and Stirling 1990, Thiemann et al. 2007, Galicia et al. 2016). Polar bears have also been found scavenging on bowhead whale (*Balaena mysticetus*) carcasses (Bentzen et al. 2007, Herreman and Peacock 2013, Galicia et al. 2016). Prey availability and environmental conditions (such as sea ice dynamics) can strongly influence Arctic food webs. Short-term studies have indicated the importance of locally and seasonally available prey species to the diet selection of polar bears (Galicia et al. 2015, 2016). However, long-term dietary habits of polar bears and potential dietary shifts in relation to changing sea ice are largely unknown throughout the species' range.

Several methods have been previously used to study polar bear diets such as kill remains (e.g., Stirling and Archibald 1977, Lowry et al. 1987, Smith 1980, Calvert and Stirling 1990, Pilfold et al. 2012) and scat analysis (e.g., Iversen et al. 2013, Gormezano and Rockwell 2013). Although these past studies provide insight into predator-prey dynamics, they are largely opportunistic providing only a snapshot of the most recent meal and potentially underrepresenting rare prey species (Dellinger and Trillmich 1988, Spaulding et al. 2014). Fatty acids (FA) are the primary component of most lipids and can predictably reflect a predator's diet because FA with a carbon chain length of 14 or more are predictably deposited into the adipose tissue of predators with little or no modification (Iverson et al. 2004, Budge et al. 2006, Iverson 2009). Individual predators and prey will have a unique FA profile (or signature) reflecting diet over weeks to months (Budge et al. 2006). Quantitative fatty acid signature analysis (QFASA;

developed by Iverson et al. 2004) can be used to estimate the proportional biomass of each potential prey species in an individual predator's diet, thus indicating both population- and individual-level dietary shifts (Iverson et al. 2004, Budge et al. 2006, Bromaghin et al. 2016).

Impacts of climate change

Throughout their range, polar bears rely on the sea ice as a platform for hunting, travelling, and mating (Stirling and Derocher 1993, Amstrup 2003). The Arctic ecosystem is undergoing climatic-driven change faster than any other region (AMAP 2021), and changes are projected to accelerate in the future (Stroeve and Notz 2015). Significant trends towards earlier break-up and later freeze-up have been observed ranging from -/+3 to -/+9 days per decade, consequently lengthening the ice-free season by 3 to 9 weeks in most polar bear subpopulations (17 out of 19; Stern and Laidre 2016). The timing and response of climate change varies throughout the Arctic (Crawford et al. 2021) and thus the impact on polar bears and their marine mammal prey varies spatially and temporally (e.g., Stirling and Derocher 2012, Rode et al. 2014, Stern and Laidre 2016). However, continued unidirectional warming and sea ice loss will have profound negative consequences for polar bears, in addition to cascading ecological effects across the Arctic ecosystem.

With continued habitat degradation (e.g., thinning and fragmentation) polar bears may use more energy attempting to remain with their preferred sea ice habitat (Derocher et al. 2004). Sea ice conditions and limited access to preferred prey species can impact the foraging opportunities of polar bears, and ultimately body condition at the individual and population-level. Reduced polar bear body condition and increased energetic demands in relation to changes in sea ice habitat have been observed in Western Hudson Bay (e.g., Stirling et al. 1999, Sciullo et al. 2016), Southern Hudson Bay (e.g., Obbard et al. 2016), Baffin Bay (e.g., Rode et al. 2012), and

Beaufort Sea (e.g., Rode et al. 2018). Similarly, increased fragmentation in sea ice habitat during the hyperphagia period of polar bears is linked to increased energetic expenditure coupled with reduced foraging success (Durner et al. 2017, Pagano et al. 2018). Sea ice loss has led to population-level effects including reduced reproductive success, survival, in addition to observed and projected declines in abundance in the Beaufort Sea (e.g., Regehr et al. 2010, Rode et al. 2010, Bromaghin et al. 2015), Western Hudson Bay (e.g., Stirling et al. 1999, Regehr et al. 2007, Lunn et al. 2016), and Southern Hudson Bay (Obbard et al. 2018).

In the near term, some factors (e.g., prey availability, dietary flexibility, and ecosystem productivity) may help mitigate the negative impacts of habitat loss (Bromaghin et al. 2015, Atwood et al. 2016b, Rode et al. 2014). For instance, an increase in polar bear abundance in Davis Strait was associated with an increase in harp seal abundance (Peacock et al. 2013). Hamilton and Derocher (2019) suggested polar bears in regions with higher prey diversity will be less vulnerable to sea ice loss. Similarly, in the Chukchi Sea high biological productivity and diverse prey availability contributed to population stability despite reductions in sea ice extent (Rode et al. 2014, Regehr et al. 2018). Land use by bears during the ice-free season has become more common (Rode et al. 2015). However, in some regions, for example Southern Beaufort Sea, there is currently a predictable source of harvested bowhead whale remains that acts as supplemental food for bears when prey are less accessible (Atwood et al. 2016b). These mechanisms are unlikely to completely offset projected sea ice loss and continued research is necessary to help reveal important spatiotemporal patterns in the foraging habits and to refine predictions of future climate- and habitat-driven changes in Arctic food webs.

Polar bears can act as indicators of ecosystem change due to their sensitivity to fluctuations in their sea ice habitat, wide geographic distribution, and top trophic level position (Laidre et al.

2008, Moore and Huntington 2008). However, polar bears, like all species, have a level of resilience and tolerance for environmental change (Molnár et al. 2020). Further insight into temporal, regional, and broad-scale patterns of polar bear foraging ecology (i.e., body condition and diet composition) is crucial to better understanding and predicting how bears will respond to habitat change and shifts in the functioning of the Arctic ecosystem.

Dissertation outline

Climate change is expected to negatively affect polar bears via habitat loss and reduced foraging opportunities, yet the mechanistic relationships between sea ice habitat and polar bear demography are poorly understood. The overall objective of this research was to explore these relationships by quantifying the effects of changing environmental conditions and underlying mechanisms that influence multiple aspects of polar bear foraging ecology including spatiotemporal variation in prey selection and foraging success. Samples and data collected in collaboration with the Government of Nunavut and Inuit subsistence hunters provide unprecedented insights into the foraging ecology of an Arctic top predator and the potential effects of climate warming on marine ecosystems across the Canadian Arctic. This dissertation is formatted as four independent studies (Chapter 2 – 5) with a general introduction (Chapter 1), and discussion of main findings and conclusions (Chapter 6).

In Chapter 2, I investigate the seasonal body condition of polar bears in relation to the timing of spring sea ice break-up. Polar bears undergo seasonal changes in energy stores, feeding extensively in the spring when seal pups are vulnerable and accessible, and then fasting during the ice-free period when access to prey is low (Stirling and Øritsland 1995, Pilfold et al. 2012). In some subpopulations, reduced body condition has been associated with declines in sea ice (e.g., Rode et al. 2012, Bromaghin et al. 2015, Obbard et al. 2016), however, the seasonal timing

of acquiring energy stores in relation to sea ice conditions is poorly understood. This study provides new knowledge on the timing of the hyperphagia period of polar bears in relation to sea ice break-up to help inform predictive models on the effects of continued sea ice loss.

In Chapter 3, I evaluate the utility of polar bear adipose tissue obtained from remote biopsy darts used in genetic mark-recapture studies to generate reliable FA data and estimates of diet composition. There has been an increased emphasis on less invasive methods including genetic marking, either through passive hair snags (Lillie et al. 2019) or remote biopsy darting (Pagano et al. 2014, Aars et al. 2017). Biopsy darting is primarily used to collect skin for DNA extraction; however, a small amount of subcutaneous adipose tissue is often included in the sample (Pagano et al. 2014, McKinney et al. 2014). If the same samples collected for genetic analysis could also be used to infer the dietary habits on individual animals, a potentially large amount of ecological information could be obtained with no additional sampling effort or cost and in a minimally invasive manner in line with northern research priorities. This study validates the use of remote biopsy tissue samples to estimate diet of polar bears via fatty acid analyses.

In Chapter 4, I investigate polar bear prey selection over an 18-year period in Foxe Basin. Sea ice loss will reduce foraging opportunities for polar bears, but the availability of a diverse prey base and local environmental conditions may help buffer the negative impacts (Rode et al. 2014). The abundance of the Foxe Basin subpopulation has remained stable despite declines in sea ice quality and increased fragmentation (Sahanatien and Derocher 2012, Stapleton et al. 2016). The ability of polar bears to exploit diverse marine mammal prey may help reduce the subpopulation's vulnerability to environmental change. This study provides more insight into potential ecological regime shifts occurring in Foxe Basin and the increasing importance of alternate food sources for maintaining population dynamics.

In Chapter 5, I examine the spatiotemporal dietary patterns of polar bears across Nunavut. Seasonal and spatial fluctuations in prey availability have been previously reflected in polar bear diet composition (Iverson et al. 2006). Information on marine mammal distribution across the Arctic is limited (Laidre et al. 2015) and tracking marine mammals is logistically challenging. However, monitoring spatial patterns of predator diet may infer localized areas of prey availability and provide early signals of change in the distribution and relative abundance of prey populations. This study provides a better understanding of the ability for polar bears to be used as ecological indicators in predicting underlying climatic-driven changes in ecosystem structure and function.

Top predators, such as polar bears are influenced by species composition and habitat conditions within a given space and time, however top predators can also influence the structure and functioning of their ecosystem. In this dissertation, I use adipose tissue to investigate the foraging habits of an Arctic top predator with links to shifting ecological conditions. Chapters 2, 4, and 5 collectively highlight the valuable information on foraging ecology that can be obtained via analyses of adipose lipid content and fatty acids of harvested polar bears. Chapter 3 provides evidence that adipose tissue obtained through less invasive methods can provide a similar ecological understanding and may help increase knowledge across demographic classes, where harvested samples may be limited. A better understanding of the foraging behaviour of polar bears, in combination with prey distribution, body condition, and environmental drivers, can ultimately aid in assessing population dynamics to improve conservation and management strategies. In chapter 6, I discuss the significance of this research, relevance and applicability for management and conservation, and suggest future directions for improved understanding of an Arctic top predator currently experiencing shifts in environmental conditions.

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Chapter 2: Correlates of seasonal change in the body condition of an Arctic top predator

Melissa P. Galicia*, Gregory W. Thiemann, and Markus G. Dyck

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Abstract

Climate-driven sea ice loss has led to changes in the timing of key biological events in the Arctic, however the consequences and rate of these changes remain largely unknown. Polar bears (*Ursus maritimus*) undergo seasonal changes in energy stores in relation to foraging opportunities and habitat conditions. Declining sea ice has been linked to reduced body condition in some subpopulations, however, the specific timing and duration of the feeding period when bears acquire most of their energy stores and its relationship to timing of ice break-up is poorly understood. We used community-based sampling to investigate seasonality in body condition (energy stores) of polar bears in Nunavut, Canada, and examined the influence of sea ice variables. We used adipose tissue lipid content as an index of body condition for 1206 polar bears harvested from 2010-2017 across five subpopulations with varying seasonal ice conditions: Baffin Bay (October-August), Davis Strait and Foxe Basin (year-round), Gulf of Boothia and Lancaster Sound (August-May). Similar seasonal patterns were found in body condition across subpopulations with bears at their nadir of condition in the spring, followed by fat accumulation past break-up date and subsequent peak body condition in autumn, indicating that bears are actively foraging in late spring and early summer. Late season feeding implies that even minor advances in the timing of break-up may have detrimental effects on foraging opportunities, body condition, and subsequent reproduction and survival. The magnitude of seasonal changes in body condition varied across the study area, presumably driven by local environmental conditions. Our results demonstrate how community-based monitoring of polar bears can reveal population-level responses to climate warming in advance of detectable demographic change. Our data on the seasonal timing of polar bear foraging and energy storage should inform predictive models of the effects of climate-mediated sea ice loss.

Introduction

Arctic ecosystems are characterized by dramatic seasonal changes in ambient temperature, photoperiod, biological productivity, species assemblage, and resource availability (Gosselin et al. 1997, Walsh 2008, Serreze and Barry 2011, Ernakovich et al. 2014). The life history characteristics of Arctic species are adapted to this pronounced seasonality but are often dependent on predictable spatiotemporal patterns of seasonal change (e.g. Thomas and Dieckmann 2003, Post and Forchhammer 2008, Daase et al. 2013). Arctic climate warming has disrupted seasonal patterns of resource availability and habitat conditions, with important consequences for individual fitness and community dynamics. In marine ecosystems, for example, ice thinning and accelerated melt has led to a mismatch in the timing of primary and secondary production (Søreide et al. 2010, Leu et al. 2011), with consequences for higher trophic levels (Ramírez et al. 2017). In terrestrial systems, earlier plant emergence has led to a trophic mismatch with migratory caribou (*Rangifer tarandus*) resulting in reduced reproduction (Post and Forchhammer 2008, Kerby and Post 2013). Understanding the consequences of changes in seasonal timing is essential for predicting the ecological effects of future climate warming.

Arctic species take advantage of seasonally abundant resources to accumulate energy stores for survival and subsequent reproduction (Lepage et al. 1998, Bouchard and Fortier 2008, Miller-Rushing et al. 2010, McKinnon et al. 2012). For mammals, body condition thus reflects the energetic state of an individual and acts as an indicator of physiological/nutritional stress and reproductive potential in relation to food resources and environmental conditions (Millar and Hickling 1990, Schulte-Hostedde et al. 2005, Peig and Green 2009). Polar bears (*Ursus maritimus*) are wide-ranging Arctic top predators that use the seasonal sea ice platform as their primary habitat (DeMaster and Stirling 1981, Amstrup 2003). Peak feeding occurs in the spring,

when seal pups are vulnerable to predation and mature seals haul out to molt (Stirling and Archibald 1977, Smith 1980, Pilfold et al. 2012). In parts of their range where the sea ice melts completely, polar bears are forced to migrate to land, where they remain without access to their primary prey until the ice re-forms in the autumn (Stirling and Øritsland 1995, Stirling 2002). Although most of the subpopulation returns to the sea ice in the autumn, pregnant females enter maternity dens where they remain until late winter (Derocher and Stirling 1990, Atkinson and Ramsay 1995, Atkinson et al. 1996). Thus, the energy (i.e., fat) accumulated in the spring is crucial to polar bear survival and reproduction during the onshore period (Molnár et al. 2009, 2010, 2011).

The specific factors affecting polar bear energy stores are poorly understood in most regions of the Arctic. Individual- and population-level responses to habitat changes vary across the species' range (e.g. Stirling and Derocher 2012, Rode et al. 2014, Stapleton et al. 2016), likely as a function of life history characteristics, local ecological conditions, and the rate of change in sea ice (Rode et al. 2014, Stern and Laidre 2016). However, reduced body condition, reproduction, survival, and abundance associated with declines in habitat quality have been identified in Baffin Bay, Southern Hudson Bay, Southern Beaufort Sea, and Western Hudson Bay subpopulations (e.g. Regehr et al. 2007, Rode et al. 2010, 2012, Bromaghin et al. 2015, Obbard et al. 2016). Changes in body condition, however, may be one of the first indicators of the effects of habitat loss and may appear in advance of measurable demographic declines (Derocher et al. 2004, Obbard et al. 2016).

A variety of methods have been used to assess body condition in polar bears, including body mass and morphometric measurements (body length, axillary girth, and skull width; Cattet et al. 2002, Rode et al. 2010, 2012, McKinney et al. 2014), body composition models (Molnár et

al. 2009), and bioelectrical impedance analysis (Sciullo et al. 2016, Pagano et al. 2017). These methods, however, are reliant on the capture of free-ranging animals and are thus limited, in both time and space, to the areas and seasons where bears are accessible. Subcutaneous adipose tissue acts as the primary site for energy storage in polar bears (Pond et al. 1992) and adipocytes (fat cells) swell and shrink as lipid is stored and mobilized, respectively (Schemmel 1976). The lipid content of adipose tissue, relative to water and other cellular components has been shown to be correlated with overall fatness in a range of taxa (Lockyer 1986, Moreau-Hamsany et al. 1988, Martin et al. 1994), and has served as a useful indicator of body condition in polar bears (Thiemann et al. 2006, McKinney et al. 2014, Sciullo et al. 2016). To date, body condition studies on polar bears have been limited to autumn and spring, and little is known about body condition during the winter and summer. In Nunavut, samples from subsistence harvest are available over much of the year and may provide an opportunity to track fluctuations in fatness relative to seasonal changes in sea ice conditions.

Our objective was to use adipose tissue lipid content as an index of body condition and examine the seasonal timing of energy storage in relation to sea ice conditions. We investigated seasonality in body condition of polar bears in Nunavut, Canada, as well as the influence of age class, sex, and sea ice variables on body condition. We tested the hypothesis that polar bear body condition changes in response to shifts in food resources linked to seasonal changes in sea ice habitat. Specifically, we predicted that body condition would reflect an annual cyclical pattern, peaking concomitantly with the seal pupping season (May-July), and then declining throughout much, or all, of the rest of the year. This study also explored the utility of using community-based sampling to monitor the body condition of polar bears in a changing Arctic environment.

Materials and Methods

Sample collection and laboratory analysis

We analyzed adipose tissue samples from 1206 polar bears harvested from 2010 to 2017 across 5 subpopulations: Baffin Bay (n = 154 from October to August), Davis Strait (n = 174 year-round), Foxe Basin (n = 305 year-round), Gulf of Boothia (n = 231 from August to May), and Lancaster Sound (n = 342 from August to May; Figure 2.1). Samples were collected by Inuit hunters throughout the year and bears were harvested largely non-selectively (Lee and Taylor 1994), although harvest regulations targeted a 2:1 male:female sex ratio and prohibited taking females with dependent cubs. Hunters recorded biological characteristics such as sex and age class (adult, 5+ years old; subadult, 3-4 years old; independent 2-year old), as well as harvest date. Subcutaneous adipose tissue samples (ca. 6 cm x 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. A subsample of approximately 0.5 g was taken from the interior of each adipose tissue sample to avoid any desiccated or oxidized surfaces. Lipid was quantitatively extracted according to Iverson et al. (2001) and lipid content was expressed as percent total sample wet weight.

Sea ice data

Daily sea ice concentrations from 2006 to 2016 were downloaded in 25 km x 25 km grid cells from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data (Cavalieri et al. 1996) available from the National Snow and Ice Data Center in Boulder, CO, USA. We used ArcGIS version 10.4 (Environmental Systems Research Institute, Redlands, California, USA) to extract sea ice concentration raster imagery, where each cell grid has an associated sea ice concentration value (estimate of the fractional amount of sea ice covering that cell, Cavalieri et al. 1996).

We used sea ice area to determine date of break-up and freeze-up according to Stern and Laidre (2016). Area was defined as sea ice concentration multiplied by grid cell area then summed over all cells with a sea ice concentration >15%. A 50% threshold was calculated for each subpopulation as the mid-point between the mean area in March (annual maximum) and mean area in September (annual minimum) from 2006 to 2016 (see Stern and Laidre 2016). Dates of break-up and freeze-up were defined as the date when area was below the 50% threshold and when the area was above the 50% threshold, respectively, for each subpopulation (Figure 2.1).

The Davis Strait subpopulation spans a large geographic area (2.62 million km^2; (Vongraven and Peacock 2011) and includes parts of Nunavut, northern Quebec, and Newfoundland and Labrador. However, only bears harvested by Nunavut residents were included in the study. Moreover, bears have been rarely observed along the Greenland coast due to the persistence of year-round open water (Taylor et al. 2001). An additional polygon was created in ArcGIS to reflect sea ice conditions experienced by bears specific to our study area (north-western portion of the Davis Strait subpopulation boundaries; Figure 2.1). The polygon approximated the 95% population kernel contours estimated by Taylor et al. (2001).

Polar bears prefer ice over the continental shelf (≤ 300 m depth; e.g. Derocher et al. 2004, Durner et al. 2009, Rode et al. 2014, Laidre et al. 2018), which accounts for less than 30% of the Baffin Bay and Davis Strait subpopulations area (Figure 2.1). Therefore, to determine if the availability of preferred habitat affected polar bear body condition, we tested the date of break-up and freeze-up over the continental shelf as additional predictor variables for Baffin Bay and Davis Strait. Although the Baffin Bay subpopulation area includes the continental shelves of both Canada and Greenland, since all bears in our study were harvested in Nunavut, we only

used the Canadian continental shelf to determine break-up and freeze-up date. We used bathymetry data from the ETOPO1 1 Arc-Minute Global Relief Model (Amante and Eakins 2009) and followed the methods of Stern and Laidre (2016) to calculate dates of freeze-up and break-up. The 50% threshold for each polygon was calculated according to Stern and Laidre (2016) using the mean March and mean September sea ice area from 2006 to 2016.

Statistical analysis

We used monthly mean values (± SEM) of adipose tissue lipid content for each subpopulation to explore seasonal patterns in body condition of polar bears in relation to sea ice break-up and freeze-up. We used Mann-Whitney U tests to compare maximum and minimum monthly values in adipose tissue lipid content for each subpopulation. Generalized additive models (GAM) and Akaike's information criterion corrected for small sample size (AIC_c) were used to analyze the influence of biological and environmental variables on body condition. Separate models were run for each subpopulation. Generalized linear models were first run for data exploration and AIC_c was used to determine if a predictor variable should be included as a smooth term (non-linear) or linear term. In each GAM, the response variable (adipose tissue lipid content) was run using a gamma family distribution and logistic link (Wood 2017). Model validation followed Zuur et al. (2009). All statistical analyses were performed in R (version 3.5.1; R Development Core Team 2018). GAMs were analyzed using the mgcv package in R (version 1.8.24; Wood 2015).

Possible predictor variables included in models were harvest date (smooth term); categorical variables were sex, age class (subadult or adult), year, and season (autumn, winter, spring, and summer); and continuous variables (linear) included were date of break-up, freeze-up, lag break-up (break-up date in previous year), and lag freeze-up (freeze-up date in previous

year). Additional continuous variables (linear) included in Baffin Bay and Davis Strait models were date of break-up, freeze-up, lag break-up, and lag freeze-up over the continental shelf. Break-up and freeze-up date included for each bear was dependent on both harvest date and the subpopulation where the bear was harvested. For example, if break-up occurred in June, the previous year's break-up date was used for bears harvested from January to June, since break-up for the current year had not yet occurred at time of harvest. In contrast, the current break-up date was used for bears harvested from July to December. Seasons were defined as per Ferguson et al. (1997) based on sea ice dynamics and activity level of bears: autumn (August 16-October 31); winter (November 1-March 15); spring (March 16-May 31); and summer (June 1-August 15).

We used AIC_c to select from a set of ecologically relevant candidate models defined *a priori* (Burnham and Anderson 2002). AIC_c values, ΔAIC_c, and Akaike weights (w_i – relative likelihood of the model) were calculated using MuMIn package in R (version 1.42.1; Barton 2018). Collinearity among covariates was assessed using Pearson's correlation coefficient and variance inflation factor (VIF). Covariates with a Pearson's correlation coefficient > 0.6 and/or VIF > 5.0 (Zuur et al. 2009) were used in separate models.

Results

Seasonal trends in body condition

Polar bears in all subpopulations showed a general decline in body condition during autumn and winter, followed by increasing condition in spring and summer (Figure 2.2). In Baffin Bay, the largest increase in adipose tissue lipid (7.9%) occurred from April (73.6 ± 2.0%) to August (81.5 ± 6.4%; Mann-Whitney U test: $p = 0.027$). The largest decrease (10.2%) occurred from February (83.8 ± 1.4%) to April ($p = 0.001$; Figure 2.2a). Bears in Davis Strait experienced a decline of 10.4% from October/November (85.0 ± 1.2%) to April (74.6 ± 1.2%; $p < 0.001$). Adipose tissue

lipid content increased by 11.5% from April to October (86.0 ± 3.4%; Figure 2.2b). The small sample size (3 bears) in October, however, may not represent the larger subpopulation. All 3 bears were harvested in 2013 and break-up occurred later than average (June 21) that year which likely influenced the higher adipose tissue lipid content in October. Bears in Foxe Basin experienced the smallest winter decrease of 5.9% from December (82.7 ± 0.9%) to April (76.8 ± 0.9%), a trend that was not significant ($p = 0.586$). Foxe Basin also had the smallest spring increase of 5.6% from April to August (82.4 ± 1.2%; $p = 0.004$; Figure 2.2c). Adipose tissue lipid content in bears harvested in Gulf of Boothia decreased by 10.5% from February (82.9 ± 0.9%) to April (72.4 ± 1.4%; $p < 0.001$). There was a lack of samples in August and September (1 bear harvested in each month), however adipose tissue lipid content in October (82.0 ± 1.4%) was significantly higher by 9.6% than April ($p < 0.001$; Figure 2.2d). Bears in Lancaster Sound experienced the largest fluctuation in adipose tissue lipid content of all subpopulations, with an increase of 14.1% from May (68.9 ± 2.5%) to October (83.0 ± 1.0%; $p <0.001$). The largest decrease of 11.4% occurred from March (80.3 ± 1.0%) to May in Lancaster Sound ($p < 0.001$; Figure 2.2e).

The body condition of polar bears in all subpopulations continued to increase beyond the date of break-up (Figure 2.2). Small fluctuations in adipose tissue lipid content occurred in all subpopulations throughout autumn and winter, however in Baffin Bay adipose tissue lipid content increased during the freeze-up period, improving from 77.2 ± 4.7% in November to 83.8 ± 1.4% in January.

Factors affecting adipose tissue lipid content

Harvest date influenced body condition across all subpopulations. However, environmental variables only appeared as correlates of variation in adipose lipid content in the top ranked

models for Davis Strait and Lancaster Sound, whereas sex influenced lipid content in Baffin Bay, and Foxe Basin was influenced by a combination of environmental and biological variables.

Gulf of Boothia was the sole subpopulation where the top ranked model only included harvest date and was 1.62 times more likely than the next ranked model (Table 2.1). Bears in Gulf of Boothia reached their lowest body condition mid-May and their peak body condition mid- to end of November (Figure 2.3).

In Davis Strait, the top ranked model included harvest date and lagged break-up date over continental shelf and was only 1.20 times more likely than the second ranked model which included only lagged break-up (Table 2.1). Adipose tissue lipid content was lower with earlier break-up over the continental shelf in the previous year in Davis Strait (Table 2.2). Bears in Davis Strait experienced their lowest body condition mid-May and their highest adipose lipid content end of October (Figure 2.3).

Polar bears in Lancaster Sound experienced the largest change in adipose tissue lipid content of the subpopulations that were not influenced by a biological variable (i.e., sex or age; Figure 2.3), indicated by a more complex GAM smooth function (edf = 4.065) compared to Davis Strait (edf = 3.091) and Gulf of Boothia (edf = 3.273; Table 2.2). In Lancaster Sound, bears experienced their lowest body condition mid-May and their peak in early October. An additional point of change occurred mid-December when adipose lipid began to increase to mid- to end of February (Figure 2.3).

In Baffin Bay, the top ranked model included harvest date and sex which was 1.63 times more likely than the second ranked model which included sex and freeze-up date over the continental shelf (Table 2.1). Males experienced larger seasonal fluctuations in lipid content than

females (edf = 1.581 and 0.592, respectively; Table 2.2). Adipose tissue lipid content in females peaked earlier than males (mid-November and early December). Both females and males lost lipid throughout the winter, reaching their lowest lipid content by mid- to end of March and end of May (Figure 2.4a), respectively.

The top ranked model for Foxe Basin included harvest date, sex, and sea ice freeze-up and was 2.46 times more likely than the second ranked model which included only harvest date and sex (Table 2.1). In Foxe Basin, adipose lipid increased with later freeze-up (Table 2.2). Females in Foxe Basin had larger fluctuations in body condition than males (edf = 1.556 and 0.959, respectively). Female adipose tissue lipid content peaked at the end of August and decreased to mid-March. In contrast, males showed little seasonal variation in our measure of body condition, with adipose lipid peaking at the end of November and reaching their lowest point end of May. Both increases and decreases in adipose tissue lipid content occurred later in males than in females (Figure 2.4b).

Discussion

Arctic species are reliant on the seasonality of resources and habitat conditions. Changes in the timing of key biological processes may have cascading effects across trophic levels (Post et al. 2013). For polar bears, the precise timing of feeding in relation to sea ice conditions may substantially affect the degree to which subpopulation dynamics are influenced by environmental change. Our study provides insights into the seasonal patterns of energy storage and depletion in polar bears in relation to sea ice dynamics. We found evidence that bears continued to forage into early summer across all 5 subpopulations, implying that any significant advance in break-up date may directly reduce foraging opportunities and have negative effects on body condition and reproductive rates (see below). Regional differences in sea ice patterns, and presumably food

availability, were related to subpopulation differences in the seasonality of body condition. The seasonal patterns of energy accumulation and mobilization that are apparent in our data have important implications for predicting the responses of polar bears to widespread sea ice decline.

Harvest date was the most common predictor of body condition in our study and suggests that fluctuations were related to seasonal resource availability across all subpopulations. In contrast, sea ice had variable effects likely due to variability in the timing and magnitude of shifts in local sea ice patterns. Bears in our study reached their lowest body condition in April or May. The highest adipose tissue lipid content was in the autumn (August-October), except in Baffin Bay where bears reached their highest body condition in January. The observed seasonal trends in body condition suggest that polar bears are actively feeding throughout late spring and early summer, corresponding with the availability of seal pups (e.g. Stirling and McEwan 1975, Stirling and Øritsland 1995, Pagano et al. 2018) and mature seals hauling out on the ice to moult (Stirling and Øritsland 1995, Stirling 2002, Kelly et al. 2010).

The increase in body condition after break-up date was somewhat unexpected and suggests that polar bears may continue to feed as sea ice deteriorates to maximize energy gain. In Baffin Bay, Laidre et al. (2018) suggested that bears remain on sea ice over the continental shelf into July and early August to increase hunting opportunities. Our results suggest late-season foraging effort was energetically profitable for bears. Forecasted advances in the timing of break-up are expected to have negative consequences for bears (e.g. Castro de la Guardia et al. 2013, Hamilton et al. 2014). However, the exact responses have been difficult to predict because of limited information on the timing of spring feeding. Molnár et al. (2011) projected reproductive success based on two feeding scenarios: early feeding (bears gained most of their energy stores by the end of May) and late feeding (bears gained most of their stored energy by June and July).

The study concluded that progressively earlier break-up would most acutely affect reproductive rates under a late feeding scenario, with projected reproductive collapse if break-up date advanced by 8 weeks relative to the 1990s. Our results support a late feeding scenario, suggesting earlier break-up will reduce hunting opportunities, with potentially profound consequences on polar bear reproductive success and demographic viability.

The Davis Strait subpopulation experienced the earliest break-up in our study and was the only subpopulation influenced by the timing of break-up, specifically break-up over the continental shelf in the previous year. Our results provide further support that ice over the continental shelf is an important variable that may better predict future shifts in feeding ecology of polar bears. This is particularly the case in Davis Strait and Baffin Bay where most of the subpopulation is comprised of deeper, less productive waters (Stern and Laidre 2016).

Our findings provide insights into the importance of late spring/summer feeding in supplying energy for much of the rest of the year. Bears appeared to be in a negative energy balance through the autumn and winter as we found decreasing adipose tissue lipid content from August (Baffin Bay), September (Foxe Basin), and October (Davis Strait, Gulf of Boothia, and Lancaster Sound) through to February. The largest decrease occurred during late winter – early spring (February/March – April/May) in all subpopulations and was likely a result of low prey availability (Stirling and Øritsland 1995). Consistent with reduced foraging success, polar bears significantly reduce movement rates and activity levels from late summer through to winter (Messier et al. 1992, Ferguson et al. 1997, Ware et al. 2017, Laidre et al. 2018), which may help conserve stored energy during periods of low prey accessibility.

Bears in Davis Strait, Foxe Basin, and Gulf of Boothia showed an overall decline in body condition during autumn and winter, suggesting prey availability was not sufficient to meet

energetic demands. However, in Baffin Bay and Lancaster Sound, bears experienced slight increases in body condition during and after the freeze-up period, suggesting feeding opportunities in late autumn/early winter. In Hudson Bay, bears migrated from shore after autumn sea ice concentration reached 10% (Cherry et al. 2013). These bears travel along the advancing ice edge, presumably searching for prey (McCall et al. 2016). Laidre et al. (2018) suggested bears in Baffin Bay follow the ice edge eastward towards Greenland with access to feeding areas off west Greenland during the winter months. Winter feeding may explain the increase in body condition from November to January in Baffin Bay bears.

The ecological and environmental factors influencing seasonal changes in polar bear body condition appeared to differ regionally. Obbard et al. (2016) suggested that later freeze-up may have a stronger impact on polar bear body condition than earlier break-up because the fasting period was extended. Although we found evidence of this trend in Lancaster Sound, bears in Foxe Basin showed improved body condition with later freeze-up. The effect of freeze-up on body condition may be a function of the rate of ice formation rather than specific freeze-up date. For example, the rate of ice formation is slower in Foxe Basin than Lancaster Sound (Stern and Laidre 2016), perhaps providing more encounters with prey along the expanding floe edge during freeze-up. A slight increase in adipose tissue lipid content in Foxe Basin bears from October through to December, suggests bears in Foxe Basin are taking advantage of late autumn/early winter hunting opportunities. Seasonal patterns in body condition of bears in Foxe Basin may also be influenced by the opportunistic availability of bowhead whale (*Balaena mysticetus*) carcasses (Galicia et al. 2016). Supplemental, year-round food sources may have also contributed to the relative stability in seasonal body condition of Foxe Basin bears (see Figures 2.2 and 2.3).

Sex was the only intrinsic (non-environmental) correlate of variation in body condition and was only identified in models for Baffin Bay and Foxe Basin. Studies have found higher autumn body condition in females than males, presumably as a result of higher reproductive demands (Thiemann et al. 2006, Sciullo et al. 2016). Males in Baffin Bay showed larger fluctuations in body condition than did females, whereas the opposite occurred in Foxe Basin. In both subpopulations, female bears reached their lowest body condition earlier in the spring and highest body condition earlier in the autumn compared to male bears. These patterns may be a result of males reducing their foraging effort during breeding (Stirling et al. 1993, Cherry et al. 2009, Rode et al. 2018), which overlaps with the start of the spring feeding period (Stirling et al. 1993, Amstrup 2003). It is worth noting that all bears in this study were solitary at the time of harvest (i.e., no females with dependent cubs) and adults may have been engaged in mating during April-June (Amstrup, 2003). Since both males and females reduce foraging activity during breeding (Pilfold et al. 2015, Stirling et al. 2016, Rode et al. 2018), spring body condition in our samples might have been lower than in the population as a whole.

Seasonal resource pulses are crucial to the life history of virtually all Arctic species, and even subtle changes in the timing of seasonal resources can have dramatic ecological consequences (Post and Forchhammer 2008, Post et al. 2013). For polar bears, the link between progressively earlier sea ice break-up and declining body condition and reproduction is well-established (e.g. Stirling et al. 1999, Regehr et al. 2007, Lunn et al. 2016). However, predicting the consequences of future sea ice decline is complicated by a lack of understanding of the timing of polar bear feeding and energy gain (Molnár et al. 2011). Our findings suggest that polar bears continue to increase body condition through late-spring and early summer and remain in negative energy balance though much of the rest of the year. The results of this study provide

a more comprehensive understanding of the seasonal foraging behaviour of polar bears and will help inform models predicting the ecological consequences of future sea ice loss. Our results also illustrate how community-based sampling and monitoring can provide information on a wide-ranging, long-lived species in a manner that does not require live capture and is thus compatible with the research priorities of northern Indigenous communities. The results of such sampling efforts can provide insights into ecological changes before demographic shifts are detectable.

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Table 2.1 Model selection for the variation in body condition of polar bears harvested in Nunavut, Canada from 2010 to 2017. Each subpopulation was modelled separately, and the top five ranked models are shown with the top ranked model in bold. Number of estimated parameters (K), Akaike's information criterion corrected for small sample size (AIC_c) values, ΔAIC_c, and AIC_c weights (w_i) are shown for each model. Harvest date of bear is represented as date and the s(date) indicates the variable was included as a smooth term in the model.

Subpopulation	**Model**	***K***	**AICc**	**ΔAICc**	**AIC w_i**
Baffin Bay	**s(date, by = sex) + sex**	**6**	**945.48**	**0.00**	**0.26**
	s(date, by = sex) + sex + freeze-up 300 m	6	946.43	0.95	0.16
	s(date) + sex*age class	7	947.20	1.72	0.11
	s(date)	4	947.68	2.20	0.09
	s(date) + retreat	7	948.47	2.99	0.06
Davis Strait	**s(date) + lag break-up 300 m**	**6**	**1073.90**	**0.00**	**0.30**
	s(date) + lag break-up	6	1074.25	0.35	0.25
	s(date) + break-up 300 m*lag break-up 300 m	8	1074.80	0.89	0.19
	s(date) + break-up* lag break-up	8	1075.38	1.48	0.14
	s(date, by = age class) + age class + break-up 300 m	9	1078.58	4.67	0.02
Foxe Basin	**s(date, by = sex) + sex + freeze-up**	**7**	**1983.84**	**0.00**	**0.32**
	s(date, by = sex) + sex	8	1985.68	1.84	0.13
	s(date, by = sex) + sex + break-up + freeze-up	8	1985.74	1.90	0.13
	s(date, by = sex) + sex + break-up	6	1985.89	2.05	0.12
	s(date, by = sex) + sex + freeze-up + lag freeze-up	7	1985.90	2.07	0.12
Gulf of Boothia	**s(date)**	**5**	**1358.00**	**0.00**	**0.34**
	s(date) + break-up	7	1358.95	0.95	0.21
	s(date) + freeze-up	6	1359.97	1.97	0.13
	s(date) + break-up + lag break-up	8	1360.53	2.53	0.10
	s(date) + break-up + freeze-up	8	1361.06	3.07	0.07
Lancaster Sound	**s(date) + freeze-up**	**7**	**2127.45**	**0.00**	**0.38**
	s(date) + freeze-up + lag freeze-up	8	2128.31	0.86	0.24
	s(date) + break-up + freeze-up	8	2129.41	1.97	0.14
	s(date)	6	2130.21	2.76	0.09
	s(date, by = sex) + sex + freeze-up + lag freeze-up	11	2131.79	4.34	0.04

Table 2.2 Parameter estimates of the top ranked models for factors affecting body condition of polar bears harvested in Nunavut, Canada from 2010 to 2017. Harvest date of bear is represented as date. The estimate (β), standard error (SE), and p value are shown for linear predictor variables and the estimated degrees of freedom (edf) and p value are shown for predictor variables with a smooth function in each model.

Subpopulation	**Variable**	**Parameter estimates**			
		β	**edf**	**SE**	**p**
Baffin Bay	Intercept	4.419	-	0.021	<0.001
	Date by female	-	0.592	-	0.151
	Date by male	-	1.581	-	0.023
Davis Strait	Intercept	4.207	-	0.055	<0.001
	Lag break-up 300 m	0.000	-	0.000	0.004
	Date	-	3.091		<0.001
Foxe Basin	Intercept	3.574	-	0.299	<0.001
	Freeze-up	0.003	-	0.001	0.006
	Date by female	-	1.556	-	0.027
	Date by male	-	0.959	-	0.117
Gulf of Boothia	Intercept	4.352	-	0.007	<0.001
	Date	-	3.273	-	<0.001
Lancaster Sound	Intercept	5.098	-	0.315	<0.001
	Freeze-up	-0.003	-	0.001	0.019
	Date	-	4.065	-	<0.001

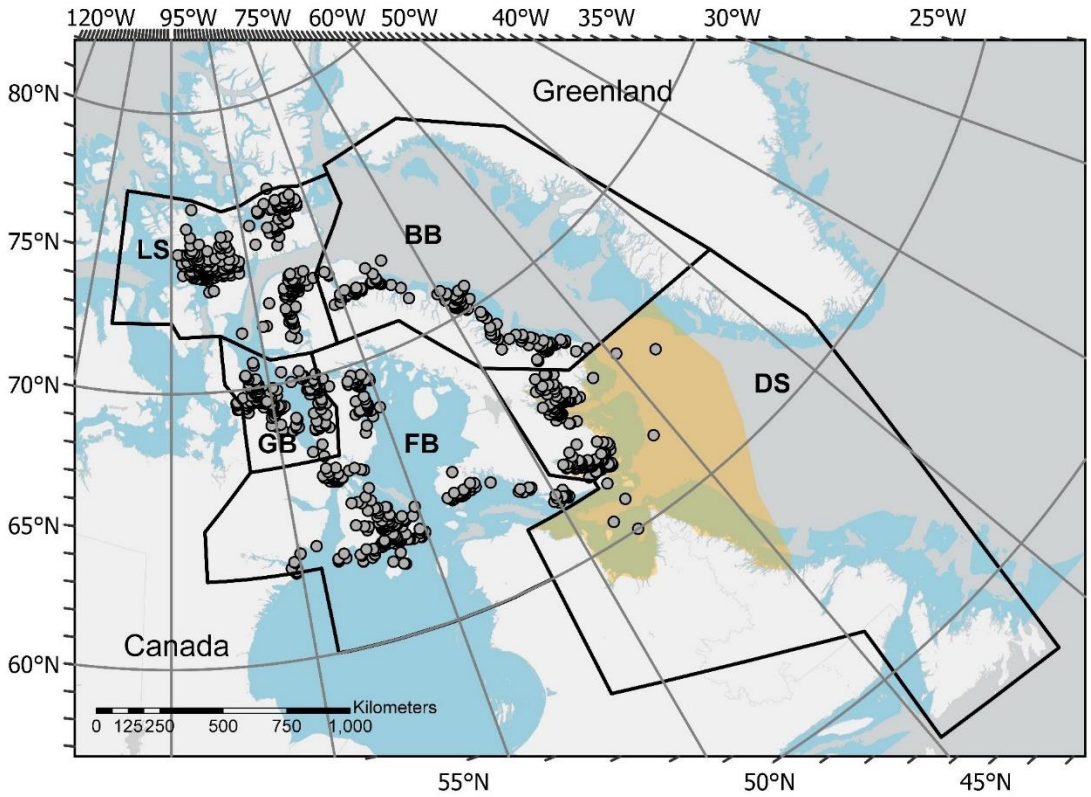

Figure 2.1 Location of polar bears (n = 1206) harvested by local Inuit hunters from 2010 to 2017 in 5 Canadian subpopulations: Baffin Bay (BB), Davis Strait (DS), Foxe Basin (FB), Gulf of Boothia (GB), and Lancaster Sound (LS) represented by grey dots. The black outline represents the subpopulation boundaries, shaded orange area represents the area most likely used by bears harvested in Davis Strait (approximated from 95% kernel contours from Taylor et al. 2001), and the blue shaded area represents the continental shelf (≤ 300 m depth).

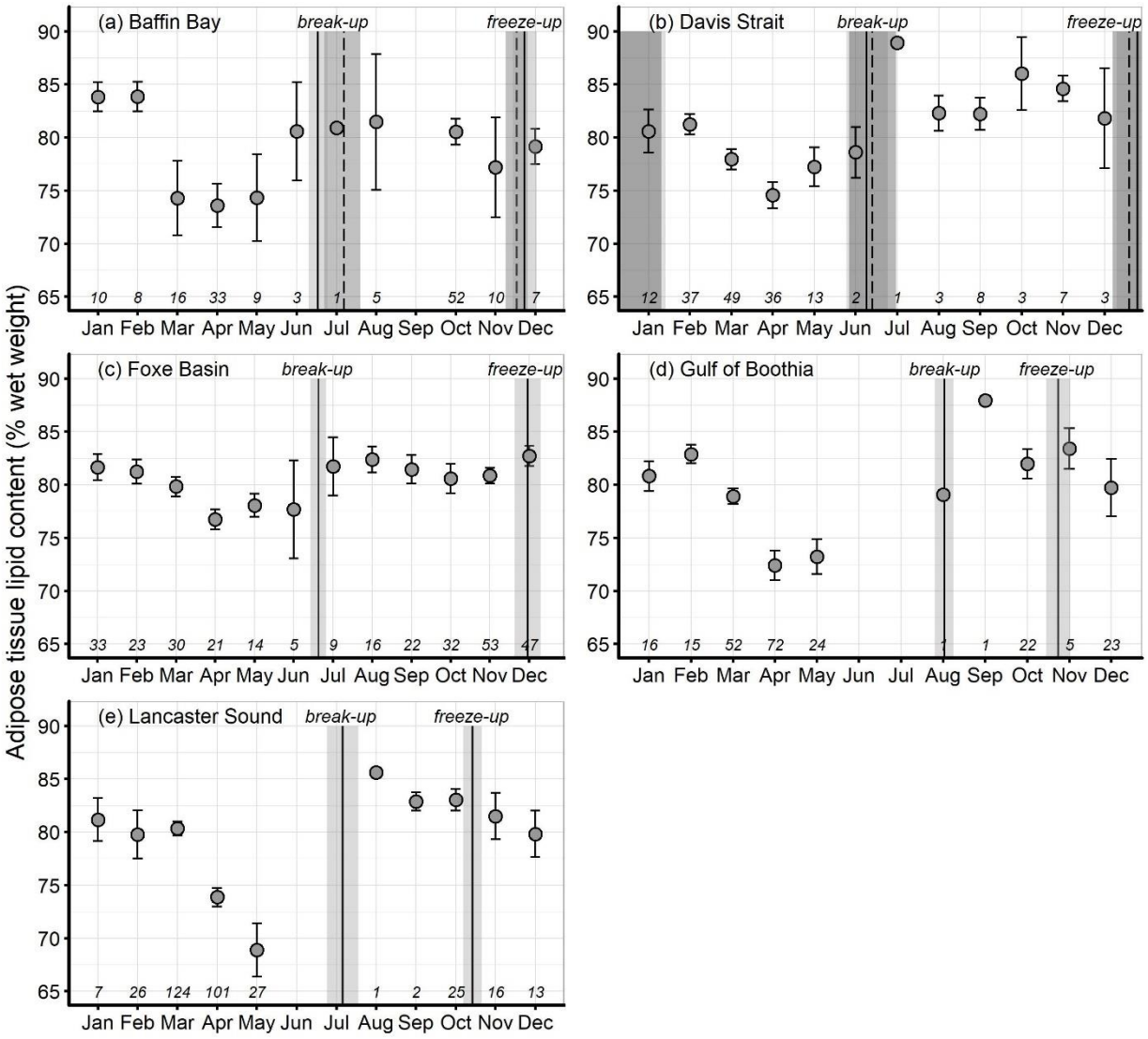

Figure 2.2 Monthly body condition (expressed as adipose tissue lipid content; mean ± SEM) for (a) Baffin Bay, (b) Davis Strait, (c) Foxe Basin, (d) Gulf of Boothia, and (e) Lancaster Sound polar bears harvested from 2010 to 2017. The values at the bottom of the plots indicate the number of polar bears harvested each month for the respective subpopulation. Mean break-up and freeze-up dates are shown as a solid black vertical line and the standard deviation for break-up and freeze-up dates are shown as grey shaded area for each subpopulation. Additionally, mean break-up and freeze-up dates for Baffin Bay and Davis Strait over the continental shelf (≤ 300 m depth) area are shown as a dashed black vertical line and the standard deviation shown as darker grey shaded area.

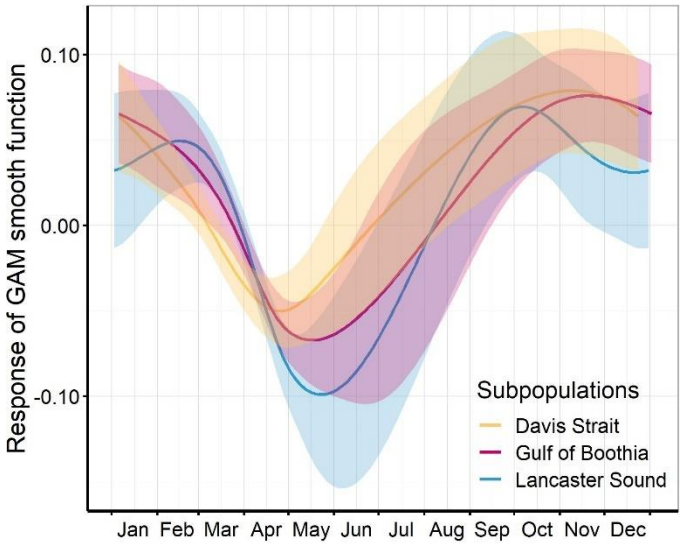

Figure 2.3 Response of generalized additive models' smooth curves to harvest date for body condition of polar bears from 2010 to 2017 in Davis Strait, Gulf of Boothia, and Lancaster Sound.

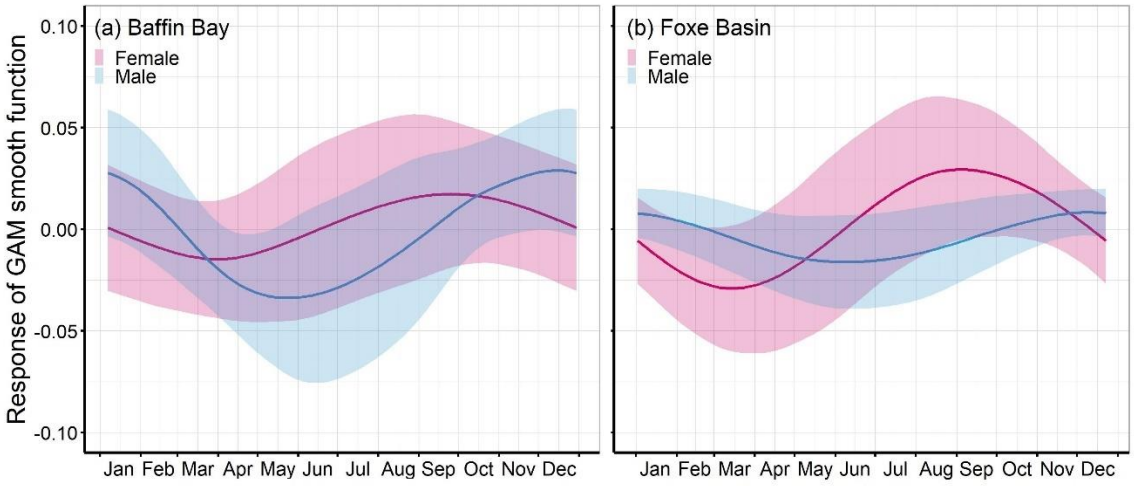

Figure 2.4 Response of generalized additive models' smooth curves to harvest date for body condition of polar bears from 2010 to 2017 in (a) Baffin Bay separated by sex and (b) Foxe Basin separated by sex.

Chapter 3: Are tissue samples obtained via remote biopsy useful for fatty acid-based diet analyses in a free-ranging carnivore?

Melissa P. Galicia*, Gregory W. Thiemann, Markus G. Dyck, and Steven H. Ferguson

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Abstract

Fundamental knowledge on free-ranging animals has been obtained through capture-based studies; however, these may be logistically intensive, financially expensive, and potentially inconsistent with local cultural values. Genetic mark-recapture using remote tissue sampling has emerged as a less invasive alternative to capture-based population surveys but provides fewer opportunities to collect samples and measurements for broader ecological studies. We compared lipid content, fatty acid (FA) composition, and diet estimates from adipose tissue of polar bears (*Ursus maritimus*) obtained from two collection methods: remote biopsies (n = 138) sampled from helicopters and hunter-collected tissue (n = 499) from bears harvested in Davis Strait and Gulf of Boothia, Nunavut, 2010-2018. Lipid content of adipose tissue was lower in remote biopsies than harvest samples likely because remote biopsies removed only the outermost layer of subcutaneous tissue, rather than the more metabolically dynamic innermost tissue obtained from harvest samples. In contrast, FA composition was similar between the two collection methods with relatively small proportional differences in individual FAs. For diet estimates in Davis Strait, collection method was not a predictor of prey contribution to diet. In Gulf of Boothia, collection method was a predictor for some prey types, but the differences were relatively minor; the rank order of prey types was similar (e.g., ringed seal was consistently the primary prey in diets) and prey proportions differed by < 6% between the collection methods. Results from both methods showed that diets varied by geographic area, season, year, age class, and sex. Our study indicates that adipose tissue from remote biopsy provides reliable estimates of polar bear diet based on FA analysis and can be used to monitor underlying ecological changes in Arctic marine food webs.

Introduction

The Arctic has experienced profound climate change and rapid sea ice loss leading to ecosystem-wide impacts (Walsh 2008, Post et al. 2013). Monitoring wildlife populations in association with environmental conditions is essential to understanding how individuals, and in turn populations, will respond to continued environmental change. However, untangling the mechanistic relationships between Arctic wildlife and their habitat at times requires the capture and handling of free-ranging animals. Live capture of large mammals is logistically complex, invasive, expensive and does not always coincide with research priorities of northern Indigenous people (Henri et al. 2010, Wong et al. 2017).

Capture of free-ranging polar bears (*Ursus maritimus*) involves chemical immobilization via remote injection, typically a dart fired from a helicopter (Stirling et al. 1989). Capture-based studies have been essential in addressing important questions about polar bear ecology, including population size (Regehr et al. 2007, Lunn et al. 2016), vital rates (Regehr et al. 2010), movement and habitat use (Durner et al. 2009, Laidre et al. 2018), body condition (Rode et al. 2012, Sciullo et al. 2016), energetic demand (Durner et al. 2017, Pagano et al. 2018), diet (Thiemann et al. 2008a, Sciullo et al. 2017), and genetic structure (Paetkau et al. 1999, Viengkone et al. 2016). However, live-capture population surveys are expensive and complex, and may not be feasible on the spatial and temporal scales necessary to detect rapid demographic change in polar bears (Vongraven et al. 2012). Although studies have found no evidence of long-term negative effects from chemical immobilization and handling (Thiemann et al. 2013, Rode et al. 2014), Inuit have nonetheless expressed concerns about live-capture studies (Henri et al. 2010, Peacock et al. 2011, Wong et al. 2017).

Polar bear research has increasingly emphasised less invasive methods, including aerial surveys (Stapleton et al. 2016, Obbard et al. 2018), scat collection (Iversen et al. 2013, Gormezano and Rockwell 2013), and genetic mark-recapture, either through passive hair snags (Lillie et al. 2019) or remote biopsy darting (Pagano et al. 2014, Aars et al. 2017). Tissue samples from harvested polar bears have provided important ecological insights (e.g., Galicia et al. 2020) without additional capture or handling, but harvest may be subject to seasonal or demographic restrictions. For instance, polar bear family groups cannot legally be hunted, and females with dependent cubs thus are excluded from harvest samples. Harvest-based sampling also may be biased towards bears that are closer to human settlements. Although remote biopsies are primarily intended to collect skin for DNA extraction, samples often include a small amount of subcutaneous adipose tissue (Pagano et al. 2014, McKinney et al. 2014). Analysis of adipose tissue of polar bears has provided data on diet composition (Thiemann et al. 2008a, Galicia et al. 2015) and body condition (Thiemann et al. 2006, Sciullo et al. 2016, Galicia et al. 2020). Thus, tissue samples obtained from remote biopsies may provide important information on foraging ecology of polar bears, without seasonal or demographic constraints, if the composition of this tissue: 1) can be accurately determined; and 2) is representative of overall subcutaneous fat stores.

The fatty acid (FA) composition of adipose tissue can be used to infer the feeding patterns of free-ranging animals based on the knowledge that ingested FA are predictably incorporated into the fat stores of a consumer and reflect integrated diet composition over the preceding weeks to months (Iverson et al. 1997, 2004, Budge et al. 2008). The relative lipid content of adipose tissue can provide insight into overall fatness because adipocytes (fat cells) shrink and swell as lipid is mobilized and deposited, respectively (Schemmel 1976, Pond et al.

1992). In polar bears, FAs were uniformly distributed across the depth of subcutaneous adipose tissue, whereas relative lipid increased with distance from the skin (Thiemann et al. 2006). The uniform distribution of FA in adipose tissue of polar bears contrasts with pinnipeds and cetaceans, which show vertical stratification in their FA across blubber depth (e.g., Koopman et al. 1996, Strandberg et al. 2008, Waugh et al. 2014). Pagano et al. (2014) found that FAs could be identified in most remote biopsy samples from polar bears but did not compare the results to bears sampled contemporaneously via other methods. There have been no attempts to date to quantitatively estimate diet composition via FA analysis of a free-ranging carnivore from remote biopsy samples.

The objective of our study was to evaluate the utility of adipose tissue obtained from remote biopsies used in genetic mark-recapture studies of polar bears. We hypothesized that lipid content in adipose tissue would be low in remote biopsies compared with harvest samples, and thus be unreliable in measuring body condition (see Thiemann et al. 2006, Pagano et al. 2014, McKinney et al. 2014). However, given evidence that FAs remain uniform across the depth of adipose tissue, we hypothesized that remote biopsy samples would accurately reflect total FA composition and thus diet estimates of biopsied bears, and would be comparable to those from bears harvested contemporaneously in the same subpopulation. Remote biopsy darting has become increasingly common in population surveys of polar bears (SWG 2016, Aars et al. 2017) and other species (e.g., Beausoleil et al. 2016, Frasier et al. 2020). If remote sampling can generate accurate estimates of diet, then genetic mark-recapture surveys could yield additional ecological data and reveal relationships between wildlife and their habitat in a manner that is cost-effective, minimally invasive, and more compatible with Inuit perspectives.

Materials and Methods

Sample collection

We compared adipose tissue samples collected from remote biopsy darts and harvest samples (Figure 3.1). We collected remote biopsies during the fall (late August-September) of 2017 in Davis Strait (n = 64) and the spring (April-May) of 2015-2016 in Gulf of Boothia (n = 74) as part of a genetic mark-recapture population survey. Once a bear was located, a small sample of tissue (< 5 mm diameter), mostly skin with some attached adipose tissue (Pagano et al. 2014), was taken using a biopsy dart (5CC Polar Bear Biopsy DNA Dart, Pneu-Dart Inc., Williamsport, PA). All sampled bears were darted in the rump area from inside a helicopter at an approximate distance (or altitude) of 3-7 m. Biopsy darts are designed to fall to the ground after impact and are retrieved without physically handling a bear. The effectiveness of these darts for sampling polar bears has been previously demonstrated in Pagano et al. (2014) and SWG (2016). On average, it takes < 4 minutes from when a bear is initially spotted to the time when the dart is retrieved. The design and relatively low velocity of the dart means that risk of injury to an individual is minimal. Typically, bears show no or very little response to the impact of the dart and are left with no visible marks. To facilitate dart recovery, we tied a 10-15 cm long and ~2 cm wide strip of brightly colored flagging tape (C.H. Hanson, Naperville, IL; or Johnson, Montreal, PQ) around the distal end of the dart. We stored collected skin and adipose tissue (ca. 1 cm in length) in 2-ml cryovials kept frozen at -20ºC until analysis.

Harvest samples were collected by Inuit hunters from 2010-2018 in Davis Strait (n = 221) and in Gulf of Boothia (n = 278). Samples were collected year-round from adult (5+ years old) and subadult (3-4 years old) polar bears of both sexes. Subcutaneous adipose tissue samples (ca. 6 cm x 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.

Laboratory analysis

We weighed remote adipose tissue biopsies after removing the epidermis. For harvest samples, we took a subsample of approximately 0.5 g from the interior of each sample to avoid any desiccated or oxidized surfaces. Lipid was quantitatively extracted following Iverson et al. (2001) and lipid content expressed as percent total wet weight. We used sulfuric acid as a catalyst to derive FA methyl esters (FAME) from the extracted lipid (Budge et al. 2006). FAME samples were analyzed using gas-liquid chromatography and flame-ionization detection at the Canadian Institute for Fisheries Technology at Dalhousie University, Halifax. Typically, over 70 FAs are identified in each adipose tissue sample and expressed as the mass percentage of the 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.

Diet estimation

We used quantitative FA signature analysis (QFASA) to estimate diet composition of polar bears both for remote biopsies and harvest samples (Iverson et al. 2004). Briefly, QFASA models a predator FA profile (or "signature") as a linear combination of average prey signatures and estimates diet as the proportional combination of prey that minimizes the distance between the observed and modeled predator (Bromaghin et al. 2015). For Davis Strait diet estimates, we used existing FA data from 144 marine mammals including bearded seals (*Erignathus barbatus*), harbor seals (*Phoca vitulina*), harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), ringed seals (*Pusa hispida*), and Atlantic walrus (*Odobenus rosmarus rosmarus*), sampled across Nunavut from 1994-2015 (Thiemann et al. 2008b, Galicia et al. 2016). For Gulf of Boothia diet estimates, we used existing FA data from 243 marine mammals including bearded seals, beluga whales (*Delphinapterus leucas*), harp seals, narwhal (*Monodon*

monoceros), ringed seals, and Atlantic walrus sampled from 2005-2016 across Nunavut (Galicia et al. 2015).

A combination of prey species that are most ecologically relevant to each subpopulation (i.e., prey library) is important to accurately quantify predator diet (Iverson et al. 2004). Thus, the analysis of prey library performance is a necessary step for reliable diet estimation. For instance, the more distinct prey species' signatures are from each other, the better the model should perform. The performance of the prey library was analyzed using two diagnostic functions in the qfasar package (version 1.2.0, Bromaghin 2017) in R (version 3.5.1; R Development Core Team 2018): 'leave-one-prey-out' analyses, and divisive magnetic clustering (DIMAC). The 'leave-one-prey-out' function temporarily removes a single prey FA signature from the prey library, then computes the mixture of the remaining prey FA signatures that best represents the signature of the removed prey, and subsequently repeats this for each prey sample. The output reflects the proportion of samples attributed to the correct species (distinctiveness within library), and the proportion that was misidentified (confounding within library; Bromaghin et al. 2017). DIMAC is a clustering technique that identifies substructure across FA signatures within a prey type. It partitions the prey library into clusters that are more similar than the original prey groups (i.e., species) with the goal of minimizing confounding and maximizing distinctiveness within the library (Bromaghin et al. 2017a).

Calibration coefficients derived from a captive carnivore with a controlled marine-based diet (mink, *Neovison vison*) were used to account for FA metabolism in the predator (Iverson et al. 2004, Thiemann 2006, Thiemann et al. 2008b, Bromaghin et al. 2017b). We used the Aitchison distance to compare modelled and observed predator signatures (Bromaghin 2015, Bromaghin et al. 2016) and a set of 30 dietary FAs (Galicia et al. 2015). All diet estimates were

produced using the qfasar package (version 1.2.0, Bromaghin 2017) in R (version 3.5.1; R Development Core Team 2018).

Statistical analysis

We compared adipose lipid content from remote-biopsied and harvested polar bears using Mann-Whitney *U* tests. Because polar bears undergo known seasonal changes in food intake and body condition (Galicia et al. 2020), adipose lipid content of harvest and biopsy samples were limited to the same sampling season. This would result in a more seasonally relevant comparison between collection methods. Thus, we limited Davis Strait harvest samples to August and September (n = 21) and Gulf of Boothia harvest samples to April and May (n = 108) for adipose tissue lipid analysis. We included season as a predictor variable in the model to test collection method, intraspecific (sex and age class), and spatiotemporal effects on FA composition and diet estimates (see below).

We used principal component analysis (PCA) and Akaike's information criterion for small sample size (AIC_c) to test whether there was a difference in FA composition between collection method (i.e., remote biopsy and harvest samples) while controlling for other covariates. We used a set of 18 of the most abundant FAs transformed by calculating the log of the ratio of each FA to 18:0 to improve normality (Budge et al. 2002, 2006). Broken stick models revealed PC1 and PC2 were significant axes in both subpopulations, PC1 accounted for 55% and 47% and PC2 accounted for 47% and 36% of the variation in FA signatures in Davis Strait and Gulf of Boothia, respectively. We used linear models with PC1 and PC2 scores to encompass variation of all 18 FAs into two parameters. Separate models were used for each PC axis and subpopulation. We included collection method (remote biopsy or harvest), year, sex, age class (adult or subadult), and season (defined as per Sahanatien et al. 2015), as possible predictors in

models. In Davis Strait, seasons were defined as ice-free (August-November), freeze-up (December-January), winter (February-March), spring (April-May), and break-up (June-July). In Gulf of Boothia, seasons were defined as ice-free (September), freeze-up (October-November), winter (December-March), spring (April-May), and break-up (June-August). In Davis Strait, remote biopsy and harvest samples were not evenly distributed across the subpopulation, with more remote biopsies collected in the southern portion and more harvest samples in the northern portion. The two collection methods were more evenly distributed in Gulf of Boothia (Figure 3.1). Moreover, FA composition and diet estimates have been found to vary spatially within Davis Strait (Iverson et al. 2006). We separated the subpopulation by latitude into northern (above 61°N) and southern (below 61°N) areas and included geographic area as a predictor in the Davis Strait models. We used AIC_c to select from a set of ecologically relevant candidate models defined a priori (Burnham and Anderson 2002). Log-likelihood (LL), AIC_c values, ΔAIC_c, and AIC_c weights (w_i – relative likelihood of the model) were calculated using MuMIn package in R (version 1.43.17, Bartoń 2018). To evaluate the relative importance (i.e., strength of evidence) of individual model parameters, we computed cumulative AIC_c weights by calculating the sum of Akaike model weights across all models that included the variable (Arnold 2010).

We used AIC_c to analyze variation associated with collection method in estimates of polar bear diet while controlling for other covariates (Burnham and Anderson 2002). Separate models were used for each prey type within Davis Strait and Gulf of Boothia. We used prey contribution to diet as the response variable for each generalized additive model with a zero-inflated beta distribution (Douma and Weedon 2019) and used the same possible explanatory predictors as in the FA signature models. Again, log-likelihood (LL), AIC_c values, ΔAIC_c, and AIC_c weights (w_i – relative likelihood of the model) were calculated using MuMIn package in R

(version 1.43.17, Bartoń 2018). We also computed the cumulative AIC_c weight of each parameter to evaluate its relative importance within the model set (Arnold 2010).

Results

Adipose lipid content

Remote biopsies of adipose tissue weighed 0.015 ± 0.002 g (mean ± SEM) and 0.013 ± 0.001 g for Davis Strait and Gulf of Boothia, respectively. Harvest subsamples weighed 0.423 ± 0.007 g and 0.439 ± 0.006 g for Davis Strait and Gulf of Boothia, respectively. Adipose lipid content was significantly higher (Mann-Whitney U, $p < 0.001$) in harvest samples in both Davis Strait (83.7 ± 1.0%) and Gulf of Boothia (68.6 ± 4.0%) than in biopsies from either region (51.6 ± 2.6% and 54.9 ± 2.6%, respectively; Figure 3.2). There was a seasonal/regional difference within harvest samples; Davis Strait (August-September) had a higher adipose lipid content than Gulf of Boothia (April-May), however this trend was not observed in remote biopsy samples.

FA composition

In Davis Strait and Gulf of Boothia, the top ranked models explaining variation in FA composition included a combination of predictor variables. In Davis Strait, none of the top models included collection method. The top ranked model for FA composition included geographic area and season for PC1, and sex and season for PC2 (Supplementary Table S3.1). In addition, collection method had a relatively low cumulative AIC_c weight compared with geographic area (PC1), season (PC1 and PC2), and sex (PC2; Table 3.1). In Gulf of Boothia, the top ranked model for variation in FA composition included sample collection method, sex, and season for PC1, and collection method, sex, and year for PC2 (Supplementary Table S3.1). Both collection method and sex had high cumulative AIC_c weights for both PC1 and PC2 (Table 3.1).

Remote biopsies contained the same number of FAs (> 70) in adipose tissue as harvest samples, although there was variability between collection method in the proportion of specific FAs. In Davis Strait and Gulf of Boothia bears, the largest differences between collection method occurred in 16:0 and 16:1n-7, which were consistently higher in biopsies (by 2.8% and 4.2%, respectively in Davis Strait; 1.0% and 1.5%, respectively in Gulf of Boothia), and 20:1n-9 which was consistently higher in harvest samples (by 5.3% in Davis Strait and 1.4% in Gulf of Boothia; Figure 3.3, Supplementary Table S3.2).

Diet composition

The leave-one-prey-out function indicated that prey types were distinguishable within prey libraries used for diet estimates (see Supplementary Table S3.3) and DIMAC indicated no significant substructure within prey types. In both Davis Strait and Gulf of Boothia, the variables that explained the contribution of a given prey to polar bear diet varied across prey types.

In Davis Strait, both collection methods identified harp seal as the primary prey of polar bears (biopsy: 25 ± 2.78% and harvest: 37 ± 1.42%; Figure 3.4a). Bearded seal, hooded seal, and ringed seal had the next largest contributions to diet, however the order of contribution varied between collection methods. Bearded seal contributed the second most to diet in biopsies but was fourth in harvest samples, whereas ringed seal contributed the second most to diet in harvest samples. The second largest difference in contribution between biopsy and harvest samples after harp seal occurred in bearded seal, which differed by 11% (biopsy: 23 ± 2.39% and harvest 12 ± 2.39%), whereas hooded seal differed by 2%, and ringed seal by 4% between the two collection methods (Figure 3.4a). Harbor seal and walrus consumption was lowest in both biopsy and harvest samples with a difference of 4% and 3% between collection methods, respectively (Figure 3.4a).

Collection method was not included in any top ranked models for bearded seal, harbor seal, harp seal, or hooded seal (Supplementary Table S3.4) with a low cumulative AIC_c weight across all prey types in Davis Strait (Table 3.2). Although collection method was included in the fifth-ranked model ($\Delta AIC_c < 2.00$) for ringed seal, it also included year and sex (Supplementary Table S3.4). The beta coefficient suggested no relationship between ringed seal dietary levels and collection method with a confidence interval that overlapped zero ($\beta = 0.15$, 95% CI = -0.17-0.48 from fifth-ranked model), regardless of year and sex. The cumulative weight of collection method was also relatively low compared with sex, geographic area, age class, and year (Table 3.2) and thus collection method likely was an uninformative parameter in the model. The top ranked model for walrus included only season with a low overall model weight of 0.11 and 9 models for walrus had a $\Delta AIC_c < 2.00$ with 4 of those models containing collection method as a predictor variable (Supplementary Table S3.4). Model uncertainty was apparent in the relatively low cumulative weights of all model parameters (Table 3.2) and proportional differences in walrus contribution remained low (by 3%). Season and sex were the most important explanatory variables in harp seal contribution to diet (Table 3.2) and by limiting the comparison to the ice-free season (July-November) and by sex, the difference between remote biopsy and harvest samples was reduced to 1% in females (biopsy: 24 ± 3.77% and harvest: 25 ± 11%) and 4% in males (biopsy: 26 ± 4.17% and harvest: 30 ± 4.42%).

Variation in contribution of bearded seal, harbor seal, and hooded seal, to diet between the two collection methods can be attributed to spatial variation in sampling within the Davis Strait subpopulation because geographic area was common in all top-ranked models with a high cumulative AIC_c weight > 0.76 (Supplementary Table S3.4; Table 3.2). While geographic area was included in the top ranked model for ringed seal, the variation in contribution was driven by

sex, because geographic area had a relatively lower cumulative AIC_c weight compared with sex (Table 3.2). Geographic area, year, and sex were important explanatory variables for bearded seal contribution to diet (Table 3.2). By limiting the comparison to the northern portion within 2017 and sex, the difference between collection methods was reduced from 11% to 1% in females (biopsy: 5 ± 1.61% and harvest: 6 ± 1.52%) and 2% in males (biopsy: 11 ± 3.70% and harvest: 9 ± 1.79%). Sample size of harvested bears in the southern portion of Davis Strait was too low for further comparison. While controlling for variables with high cumulative AIC_c weights for harbor seal (geographic area) and hooded seal (geographic area and year; Table 3.2), proportional differences between sample types remained low, differing by 2% (biopsy: 5 ± 1.61% and harvest: 4 ± 0.37%) and by 3% (biopsy: 22 ± 2.38% and harvest: 19 ± 1.92%), respectively.

In Gulf of Boothia, ringed seal made the highest contribution to polar bear diets in biopsy (52 ± 1.93%) and harvest samples (54 ± 1.21%). Bearded seal consistently had the second-highest biomass and varied by 4% between collection methods (biopsy: 19 ± 1.35% and harvest: 15 ± 0.74%; Figure 3.4b). Cumulative AIC_c weights indicated that collection method had little or no influence on bearded seal or ringed seal contribution to diets (Table 3.2). The top ranked model for bearded seal included only age class, and ringed seal included sex, age class, and season (Supplementary Table S3.5). Walrus had the lowest contribution to diets with no difference between collection methods. The largest difference in contribution to diets occurred in harp seals by 6% between biopsy (5 ± 1.06%) and harvest (11 ± 0.58%) samples, whereas beluga whale differed by 3% and narwhal by 2% between the two collection methods (Figure 3.4b). Collection method was common in all top ranked models for beluga whale, harp seal, narwhal, and walrus with high cumulative AIC_c weights (Table 3.2). However, sex also was included in

top ranked models for beluga whale, narwhal, and walrus (Supplementary Table S3.5), with high cumulative AIC_c weights (> 0.78) for beluga whale and walrus (Table 3.2). Sex and age class had similar importance values for narwhal contribution but were lower than collection method (Table 3.2). The variation in collection method for beluga was attributed to the difference (5%) within females, whereas contribution in males remained consistent between biopsy and harvest samples (Table 3.3). Conversely, male bears had the largest difference in contribution of narwhal (7% between collection methods compared to females with a difference of 1%; Table 3.3). Males consistently had higher levels of walrus in diets than females, although within both sexes, the contribution only varied by 1% between collection methods (Table 3.3). The top-ranked model for harp seal included collection method, year, and sex (Supplementary Table S3.5), and all three parameters had high cumulative weights in models (Table 3.2). Harp seal consistently varied by 4-5% in contribution to diets within year and sex across the two collection methods (Table 3.3).

Discussion

Remote biopsy darting is increasingly common in wildlife research, typically in the context of genetic mark-recapture surveys (e.g., Mijele et al. 2016, Aars et al. 2017, Frasier et al. 2020). Our study assessed the feasibility of using remote biopsy samples from genetic mark-recapture studies to generate reliable estimates of adipose lipid content, FA data, and diet composition, in free-ranging polar bears. Remote biopsies did not provide comparable estimates of lipid content in adipose tissue to harvest samples and therefore currently are not useful for estimating body condition of polar bears. Collection method had no effect or a minor effect on FA composition. In Davis Strait, collection method was not an informative predictor of diet estimates. Although collection method was a significant predictor of diet estimates in Gulf of Boothia, the proportional differences were low across prey types (< 6%). Overall, variation in FA

composition and diet estimation was primarily attributable to a combination of intraspecific (e.g., sex) and spatiotemporal factors, rather than sampling technique *per se*.

Adipose lipid content

Adipose tissue lipid was lower in remote biopsies relative to harvest samples both in Davis Strait and Gulf of Boothia even though comparison was restricted to the same sampling season. Live-capture biopsies of adipose tissue (Thiemann et al. 2006) and harvest samples (Galicia et al. 2020) are taken through the entire depth of the subcutaneous fat layer, whereas remote biopsies are collected superficially, close to the skin (Pagano et al. 2014, McKinney et al. 2014). For example, the average weight of a full-layer adipose tissue biopsy from a captured bear was 20 × greater (0.270 ± 0.010 g; Thiemann 2006) than the average weight from a remote biopsy (0.014 ± 0.001 g) in our study. Thiemann et al. (2006) also found that lipid content of subcutaneous adipose tissue was strongly related to tissue depth, with the outermost tissue having the lowest lipid content. Moreover, remote biopsies may have contained some non-adipose tissue (e.g., epidermis and connective tissue) generating negative bias in lipid content (Ylitalo et al. 2001, Thiemann et al. 2006). Finally, although the strong seasonal variation in polar bear body condition (Galicia et al. 2020) was evident within our harvest samples, remote biopsy samples showed consistent lipid values between April/May and August/September. Our results therefore indicate that remote biopsies are not a reliable technique to measure body condition, a finding consistent with other studies (Pagano et al. 2014, McKinney et al. 2014).

FA composition

The overall distribution of individual FAs between remote biopsy and harvest samples was similar, such that composition was dominated by monounsaturated and polyunsaturated FAs. Pagano et al. (2014) also found that remote biopsies provided similar proportions of routinely

identified FAs in polar bears, although they did not undertake statistical comparisons. Although vertical stratification of blubber FA has been identified in pinnipeds (Strandberg et al. 2008, Guerrero et al. 2016, Tverin et al. 2019) and cetaceans (e.g., Krahn et al. 2004, Waugh et al. 2014), the composition of subcutaneous adipose tissue in polar bears is considered uniform through its depth (Thiemann et al. 2006). Thus, the FA differences we detected between remote biopsy (adipose tissue close to the skin) and harvest samples (full depth of adipose layer) likely reflect regional, intraspecific, and temporal, differences as opposed to vertical stratification (i.e., collection method difference *per se*).

Fatty acid composition has been found to vary geographically within our study area, particularly between southern Davis Strait (south of 61°N – Northern Labrador) and northern Davis Strait (Frobisher Bay—63°N, and Cumberland Sound—65°N; Iverson et al. 2006). The majority (69%) of remotely darted bears were sampled in the southern portion of the subpopulation with the remaining samples taken in the northern region (see Figure 3.1). This spatial bias in sampling likely contributed to some of the collection method effect (biopsy vs. harvest) we found in individual FA proportions. For example, of the three most abundant FAs, 16:0 and 16:1n-7 were found in higher and 20:1n-9 in lower proportions in southern areas relative to northern areas of Davis Strait, consistent with a trend found by Iverson et al. (2006). FA composition in Gulf of Boothia was influenced by collection method and sex; however, the overall magnitude of differences across individual FAs was small (less than 2%; see Supplementary Table S3.2) between remote biopsy and harvest samples. The high surface-area-to-volume ratio of remote biopsy samples could promote surface oxidation (Budge et al. 2006), but the similarity of FA composition across collection methods suggests oxidation was not a significant factor in our study. Our results suggest that remote biopsy samples provide reliable

information on overall FA stores in polar bears, and thus could be used to infer general dietary differences between groups of bears (e.g., Tartu et al. 2016, 2017) or potentially be used in quantitative estimates of diet composition (see below).

Diet composition

Overall diet composition of bears both in Davis Strait and Gulf of Boothia was similar between remote biopsy and harvest samples. Although collection method was a significant predictor primarily in Gulf of Boothia, variability in diet composition was influenced by geographic area (in Davis Strait), sex, age class, and annual and seasonal variability. Sex and age class differences in polar bear diet composition are well-documented and may be due to larger more experienced adult male bears having more success catching larger-bodied prey (Thiemann et al. 2008b, Galicia et al. 2015, 2016). Interannual variability in polar bear diet composition previously has been attributed to interannual shifts in environmental conditions and local prey availability (Thiemann et al. 2008a, Sciullo et al. 2017).

Despite potential spatial and seasonal effects, Davis Strait diet estimates were broadly similar in both collection methods: harp seal contribution was highest in bear diets, followed by lower proportions of bearded, hooded, and ringed seal, a pattern consistent with Iverson et al. (2006). In Davis Strait, bearded, hooded, and ringed seal dietary contribution varied by intraspecific factors and interannually. However, dietary contributions of these three prey species also varied spatially, which is consistent with Iverson et al. (2006), who found that ringed and hooded seal consumption was higher in northern Davis Strait whereas bearded seal consumption was higher in southern Davis Strait. In addition, when we controlled specific model parameters with high AIC_c cumulative weights, differences between collection methods were reduced. For example, the proportional differences between collections methods were low for harp seal (<

4%) while controlling for season and sex, and low for bearded seal (< 2%) while controlling geographic area, year, and sex. The proportional differences to diets between collection method was < 4% in other prey. Our results suggest that differences in prey contribution was a function of geographic area where the bear was sampled, or variability between sexes, year or season as opposed to collection method.

In Gulf of Boothia, both collection methods identified ringed seal as the dominant prey followed by bearded seal, with similarly lower proportions of beluga whale, harp seal, narwhal, and walrus. These results also are consistent with previous studies (Galicia et al. 2015). Differences in ringed seal and bearded seal were attributable to intraspecific (sex and age class) and seasonal effects, with relatively low (< 4%) proportional differences between remote biopsy and harvest samples. The proportional differences between collection methods were similarly low for harp seal, beluga whale, narwhal, and walrus, ranging from 1% to 7% after controlling for variables with high cumulative AIC_c weights (sex and year). The remaining variation between collection methods may be explained by spatial differences (e.g., harvested bears closer to shore) or other ecological factors. For example, females with dependent offspring were included in biopsy samples but not subject to harvest (hunting of family groups is prohibited). Mothers with cubs are known to have different habitat preferences and target different prey than solitary females (Stirling et al. 1993, Sciullo et al. 2017, Johnson and Derocher 2020). Overall, the relatively low proportional differences in prey contribution between collection methods both in Davis Strait and Gulf of Boothia suggests remote biopsies accurately reflected the FA stores of polar bears and thus, can be used to estimate diet.

Capture-based studies have provided a wide breadth of knowledge on polar bear population dynamics and life history. However, less invasive methods of sample collection are

becoming increasingly important in wildlife research (e.g., Miller et al. 2005, Stansbury et al. 2014, Sittenthaler et al. 2020). Genetic mark-recapture has emerged as a key method of estimating polar bear abundance (SWG 2016, Aars et al. 2017), at least partly because it is more compatible with Inuit research perspectives and acceptance of research techniques (Henri et al. 2010, Wong et al. 2017). Our study validates the utility of remote biopsies to investigate the feeding patterns of polar bears but does not support the use of remote biopsies for quantifying body condition. Moreover, the diets of bears not typically subject to harvest (e.g., females with dependent offspring) can be estimated with remote biopsies. Declines in sea ice habitat are having complex effects on Arctic ecosystems (Leu et al. 2011, Stirling and Derocher 2012, Post et al. 2013, Ramírez et al. 2017). Ongoing remote biopsy darting could provide important insights into how food webs are responding to environmental change, in a manner that requires no additional sampling effort and is congruent with emerging Inuit contributions to northern research methodologies and priorities.

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Table 3.1 Cumulative Akaike's Information Criterion for small sample size (AIC_c) weights of fatty acid composition (PC1 and PC2) model parameters for polar bears harvested and remote biopsied in Davis Strait and Gulf of Boothia, 2010 to 2018. PC = principal component.

	Davis Strait		Gulf of Boothia	
Model parameter	PC1	PC2	PC1	PC2
Collection method	<0.01	0.08	0.98	1.00
Geographic area	1.00	0.15	-	-
Sex	0.04	0.47	0.97	0.99
Age class	0.23	0.21	<0.01	<0.01
Year	0.35	0.13	0.08	0.46
Season	0.77	1.00	0.75	0.01

Table 3.2 Cumulative Akaike's Information Criterion for small sample size (AIC_c) weights of diet composition model parameters for polar bears harvested and remote-biopsied in Davis Strait and Gulf of Boothia, 2010 to 2018.

Model Parameter	Prey					
Davis Strait	Bearded seal	Harbor seal	Harp seal	Hooded seal	Ringed seal	Walrus
Collection method	0.17	0.24	0.10	0.20	0.24	0.44
Geographic area	0.83	0.76	0.07	0.80	0.53	0.28
Sex	0.81	0.32	0.78	0.19	1.00	0.29
Age class	0.01	0.47	0.32	0.21	0.40	0.22
Year	1.00	0.24	0.11	1.00	0.35	0.22
Season	0.17	0.04	0.92	0.06	0.03	0.48
Gulf of Boothia	Bearded seal	Beluga whale	Harp seal	Narwhal	Ringed seal	Walrus
Collection method	0.12	1.00	1.00	1.00	<0.01	1.00
Sex	0.32	0.83	1.00	0.49	0.96	0.78
Age class	0.75	<0.01	<0.01	<0.01	0.96	0.17
Year	0.20	0.23	0.97	0.45	0.02	0.15
Season	0.14	<0.01	<0.01	0.17	1.00	<0.01

Table 3.3 Mean (± SEM) contribution of beluga whale, harp seal, narwhal, and walrus to diets of polar bears sampled in Gulf of Boothia. Estimated contribution (%) are separated by top ranked model variables for each prey type.

Prey		Collection method	Estimated contribution (%)
Beluga whale	female	biopsy	13 ± 1.38
Model: collection method + sex		harvest	8 ± 0.83
	male	biopsy	7 ± 1.53
		harvest	7 ± 0.59
Harp seal	2015, female	biopsy	1 ± 0.37
Model: collection method + year + sex		harvest	5 ± 1.46
	2016, female	biopsy	1 ± 0.82
		harvest	6 ± 3.33
	2015, male	biopsy	5 ± 1.18
		harvest	10 ± 1.17
	2015, male	biopsy	13 ± 3.03
		harvest	9 ± 2.39
Narwhal	female	biopsy	7 ± 2.29
Model: collection method + sex		harvest	8 ± 1.71
	male	biopsy	16 ± 2.76
		harvest	9 ± 1.16
Walrus	female	biopsy	1 ± 0.47
Model: collection method + sex		harvest	2 ± 0.51
	male	biopsy	5 ± 0.91
		harvest	6 ± 0.42

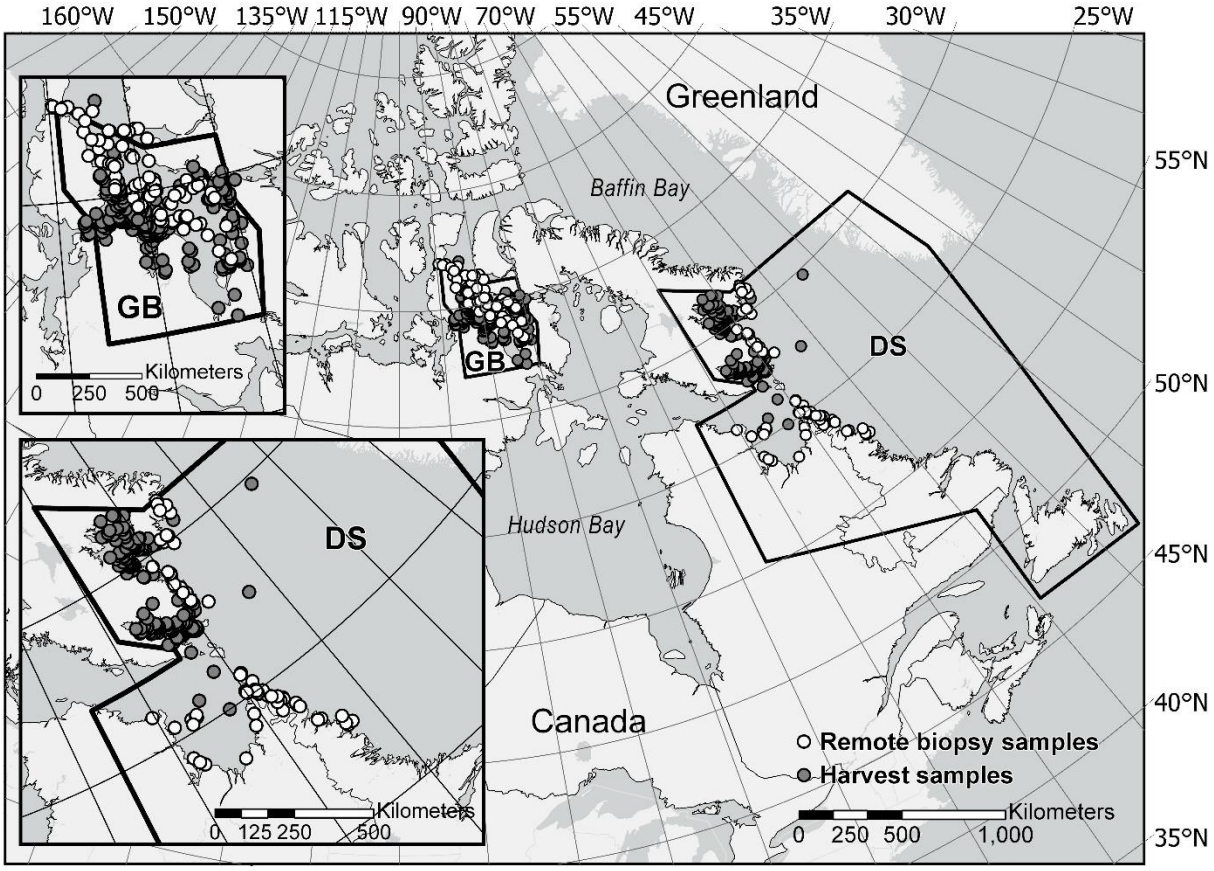

Figure 3.1 Location of polar bear adipose tissue samples collected from remote biopsy darts (n = 138) and harvest samples (n = 499) in Davis Strait (DS) and Gulf of Boothia (GB). The black outline represents the subpopulation boundaries.

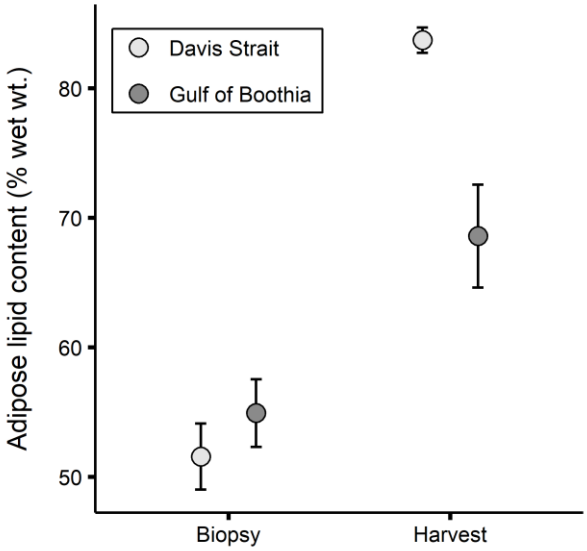

Figure 3.2 Body condition (expressed as lipid content of adipose tissue; mean ± SEM) for polar bears sampled in Davis Strait and Gulf of Boothia. Davis Strait polar bears sampled (harvest 2010 to 2017, n = 21 and remote biopsy 2017, n = 64) in August and September. Gulf of Boothia polar bears sampled (harvest 2011 to 2018, n = 108, remote biopsy 2015 to 2016, n = 74) in April and May.

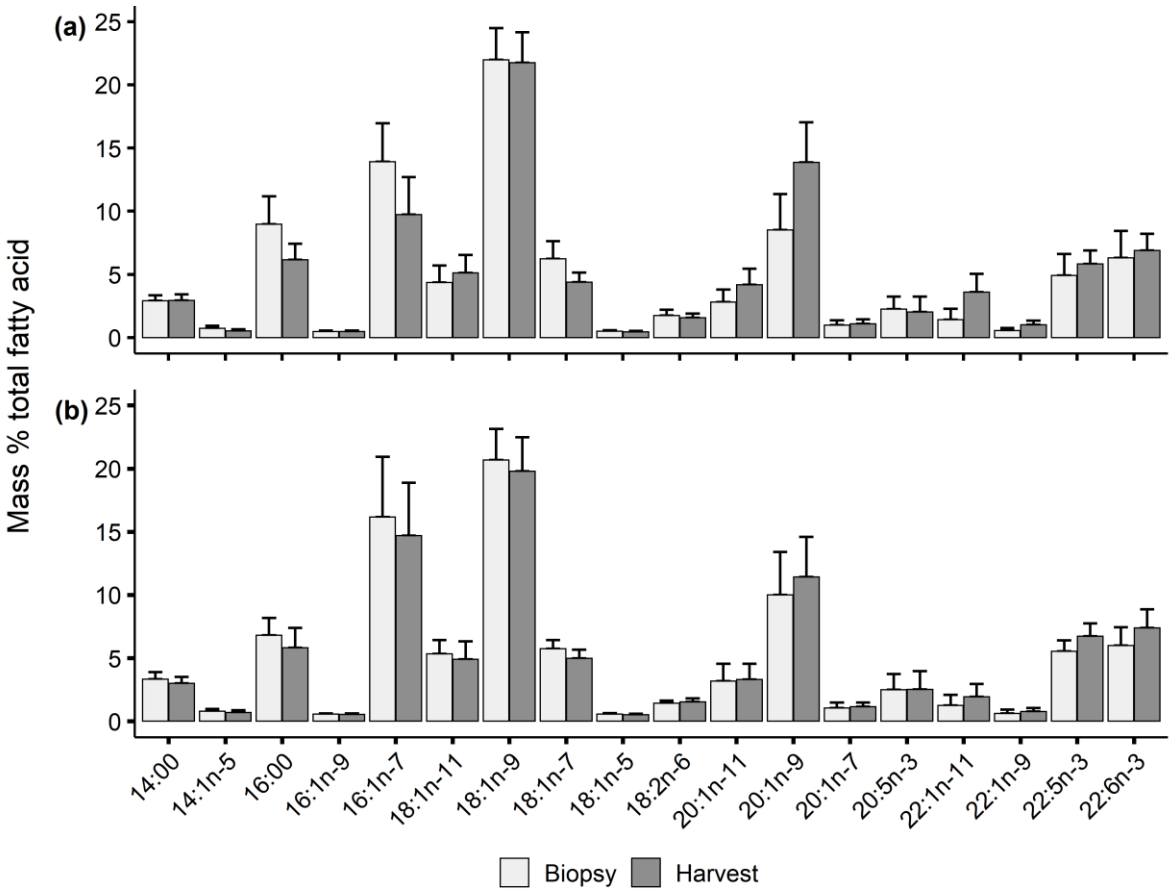

Figure 3.3 The 18 most abundant fatty acids (mass % of total ± SEM) of (a) Davis Strait polar bears from remote biopsy (2017, n = 64) and harvest (2010 to 2018, n = 221) samples; (b) Gulf of Boothia polar bears from remote biopsy (2015 to 2016, n = 74) and harvest (2010 to 2018, n = 278) samples.

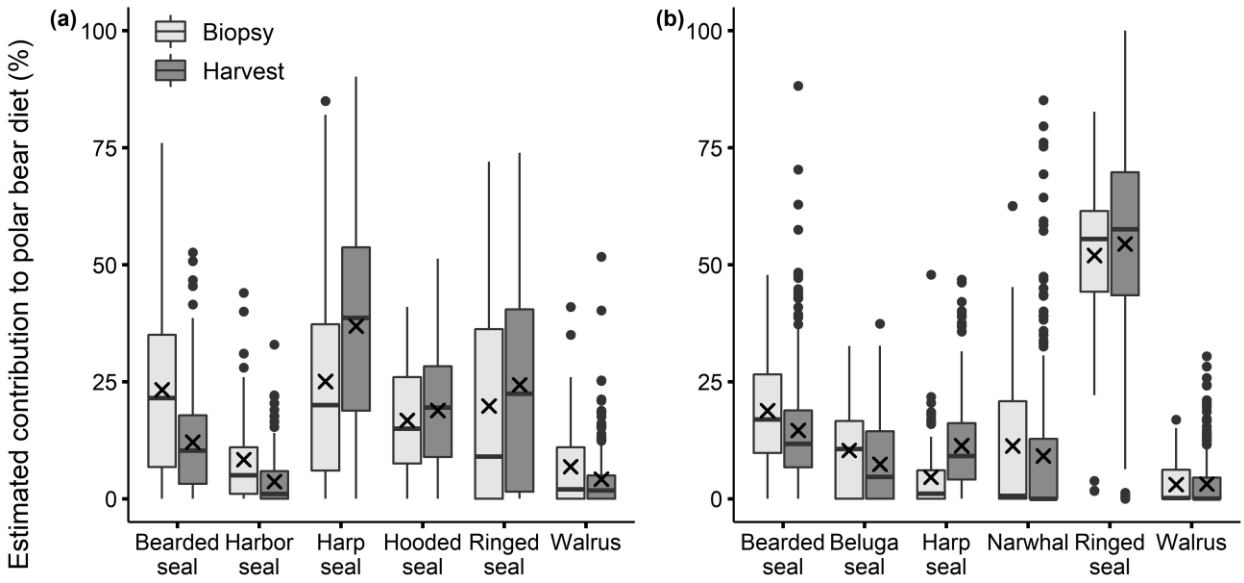

Figure 3.4 Diet composition of polar bears from (a) Davis Strait subpopulation (remote biopsy, n = 64 and harvest, n = 221) and (b) Gulf of Boothia subpopulation (remote biopsy, n = 74 and harvest, n = 278). Data represent each prey species' biomass contribution to diet estimates shown as boxplots showing the 25th quartile, median, 75th quartile, and outliers shown as solid circles. Mean proportion for each prey is represented by "x".

Supplemental Material

Table S3.1 Model selection for the variation in fatty acid composition of polar bears harvested and remote biopsied in Davis Strait and Gulf of Boothia, 2010 to 2018. The two subpopulations and principal component (PC) axes were modelled separately, and the top four ranked models are shown with the top ranked model in bold. Included in the table are number of estimated parameters (K), log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c) values, ΔAIC_c, and AIC_c weights (w_i), and are shown for each model. Geographic area (i.e. north and south Davis Strait) is represented by lat in model.

Subpopulation	Axes	Model selection	K	LL	AIC_c	ΔAIC_c	w_i
Davis Strait	**PC1**	**lat + season**	**7**	**-407.93**	**830.27**	**0.00**	**0.50**
		lat + year + season	8	-407.49	831.51	1.24	0.27
		lat + age class	4	-412.57	833.28	3.01	0.11
		lat + year + age class	5	-411.89	834.00	3.73	0.08
	PC2	**sex + season**	**7**	**-397.13**	**808.67**	**0.00**	**0.34**
		season	6	-398.96	810.23	1.55	0.15
		sex + age class + season	8	-396.99	810.50	1.83	0.13
		lat + season	7	-398.25	810.90	2.22	0.11
Gulf of Boothia	**PC1**	**collection method + sex + season**	**8**	**-526.41**	**1069.25**	**0.00**	**0.73**
		collection method + sex	4	-532.01	1072.14	2.89	0.17
		collection method + year + sex	5	-531.89	1073.95	4.70	0.07
		season	6	-532.58	1077.41	8.16	0.01
	PC2	**collection method + sex + year**	**5**	**-424.30**	**858.78**	**0.00**	**0.46**
		collection method + sex	4	-425.53	859.18	0.40	0.38
		collection method	3	-427.50	861.07	2.29	0.15
		collection method + sex + season	8	-424.79	866.00	7.22	0.01

Table S3.2 The 18 most abundant fatty acids in polar bear adipose tissue (by major lipid class; % mass of total fatty acid [FA] ± SEM).

	Davis Strait		Gulf of Boothia	
Fatty acid	**Biopsy (n = 64)**	**Harvest (n = 224)**	**Biopsy (n = 74)**	**Harvest (n = 293)**
Saturated fat				
14:0	2.90 ± 0.06	2.94 ± 0.03	3.32 ± 0.06	3.00 ± 0.03
16:0	8.97 ± 0.27	6.14 ± 0.09	6.81 ± 0.16	5.81 ± 0.09
Monounsaturated fat				
14:1n-5	0.73 ± 0.02	0.52 ± 0.01	0.80 ± 0.02	0.70 ± 0.01
16:1n-9	0.48 ± 0.01	0.47 ± 0.01	0.56 ± 0.01	0.53 ± 0.01
16:1n-7	13.92 ± 0.38	9.74 ± 0.20	16.15 ± 0.55	14.70 ± 0.24
18:1n-11	4.35 ± 0.17	5.10 ± 0.10	5.34 ± 0.13	4.91 ± 0.08
18:1n-9	21.98 ± 0.31	21.75 ± 0.16	20.66 ± 0.29	19.78 ± 0.16
18:1n-7	6.23 ± 0.18	4.37 ± 0.05	5.73 ± 0.08	4.97 ± 0.04
18:1n-5	0.51 ± 0.01	0.46 ± 0.00	0.56 ± 0.01	0.52 ± 0.00
18:2n-6	1.75 ± 0.06	1.56 ± 0.02	1.43 ± 0.02	1.54 ± 0.02
20:1n-11	2.80 ± 0.12	4.17 ± 0.08	3.17 ± 0.16	3.31 ± 0.07
20:1n-9	8.52 ± 0.35	13.86 ± 0.21	9.99 ± 0.40	11.43 ± 0.19
20:1n-7	0.98 ± 0.05	1.09 ± 0.02	1.06 ± 0.05	1.14 ± 0.02
22:1n-11	1.42 ± 0.11	3.59 ± 0.10	1.25 ± 0.10	1.94 ± 0.06
22:1n-9	0.55 ± 0.03	1.00 ± 0.02	0.62 ± 0.03	0.78 ± 0.02
Polyunsaturated fat				
20:5n-3	2.26 ± 0.12	2.03 ± 0.08	2.49 ± 0.14	2.52 ± 0.08
22:5n-3	4.92 ± 0.21	5.82 ± 0.07	5.54 ± 0.10	6.72 ± 0.06
22:6n-3	6.30 ± 0.27	6.90 ± 0.09	5.99 ± 0.17	7.38 ± 0.09

Table S3.3 Proportion of leave-one-prey-out estimates attributed to the correct prey type within the prey library in Davis Strait and Gulf of Boothia.

Davis Strait		**Bearded**	**Harbour**	**Harp**	**Hooded**	**Ringed**	**Walrus**
	Bearded	0.74	0.11	0.00	0.00	0.06	0.09
	Harbour	0.02	0.95	0.01	0.01	0.01	0.01
	Harp	0.01	0.01	0.76	0.04	0.16	0.01
	Hooded	0.00	0.05	0.11	0.83	0.00	0.01
	Ringed	0.03	0.01	0.06	0.01	0.86	0.03
	Walrus	0.02	0.02	0.00	0.00	0.03	0.94
Gulf of Boothia		**Bearded**	**Beluga**	**Harp**	**Narwhal**	**Ringed**	**Walrus**
	Bearded	0.82	0.03	0.01	0.01	0.05	0.09
	Beluga	0.01	0.72	0.03	0.18	0.06	0.00
	Harp	0.01	0.03	0.84	0.02	0.07	0.03
	Narwhal	0.05	0.04	0.02	0.86	0.02	0.01
	Ringed	0.03	0.01	0.07	0.01	0.85	0.03
	Walrus	0.01	0.00	0.00	0.00	0.01	0.99

Table S3.4 Model selection for the variation in contribution of prey to polar bear diet in Davis Strait. Contribution of each prey species was modelled separately, and the top five ranked models are shown with the top ranked model in bold. Included in the table are number of estimated parameters (K), log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c) values, ΔAIC_c, and AIC_c weights (w_i), and are shown for each model.

Prey	Model selection	K	LL	AIC_c	ΔAIC_c	w_i
Bearded seal	**lat + year + sex**	**6**	**109.78**	**-207.26**	**0.00**	**0.63**
	lat + year + season	9	111.67	-204.68	2.58	0.17
	collection method + year + sex	6	108.48	-204.65	2.61	0.17
	lat + year + age class	6	105.70	-199.10	8.15	0.01
	lat + year	5	104.52	-198.82	8.43	0.01
Harbour seal	**lat + age class**	**5**	**96.01**	**-181.80**	**0.00**	**0.21**
	lat	4	94.65	-181.15	0.65	0.15
	lat + sex + age class	6	96.30	-180.30	1.51	0.10
	lat + sex	5	95.20	-180.19	1.61	0.09
	lat + year + age class	6	96.07	-179.84	1.96	0.08
Harp seal	**sex + season**	**8**	**35.97**	**-55.41**	**0.00**	**0.43**
	sex + age class + season	9	36.57	-54.48	0.93	0.27
	year + season	8	33.88	-51.23	4.18	0.05
	season	7	32.80	-51.19	4.22	0.05
	collection method + season	8	33.12	-49.73	5.68	0.03
Hooded seal	**lat + year**	**5**	**121.35**	**-232.48**	**0.00**	**0.44**
	lat + year + age class	6	121.40	-230.50	1.97	0.17
	lat + year + sex	6	121.37	-230.44	2.03	0.16
	collection method + year	5	119.82	-229.42	3.06	0.10
	collection method + year + age class	6	120.06	-227.82	4.65	0.04
Ringed seal	**lat + year + sex**	**6**	**-82.36**	**177.01**	**0.00**	**0.25**
	sex + age class	5	-83.68	177.57	0.56	0.19
	lat + sex	5	-83.89	177.99	0.97	0.15
	lat + sex + age class	6	-82.99	178.28	1.27	0.13
	collection method + year + sex	6	-83.29	178.89	1.87	0.10
Walrus	**season**	**7**	**194.58**	**-374.76**	**0.00**	**0.11**
	collection method	4	191.36	-374.59	0.17	0.10
	collection method + sex	5	192.10	-373.99	0.77	0.08
	collection method + season	8	195.24	-373.95	0.81	0.07
	lat + season	8	195.13	-373.87	0.89	0.07

Table S3.5 Model selection for the variation in contribution of prey to polar bear diet in Gulf of Boothia. Contribution of each prey species was modelled separately, and the top five ranked models are shown with the top ranked model in bold. Included in the table are number of estimated parameters (K), log-likelihood (LL), Akaike's information criterion corrected for small sample sizes (AIC_c) values, ΔAIC_c, and AIC_c weights (w_i), and are shown for each model.

Prey	Model selection	K	LL	AIC_c	ΔAIC_c	w_i
Bearded seal	**age class**	**4**	**196.77**	**-385.42**	**0.00**	**0.38**
	year + age class	5	196.85	-383.54	1.88	0.15
	sex + age class	5	196.84	-383.51	1.91	0.14
	sex + age class + season	9	200.40	-382.27	3.15	0.08
	sex	4	195.12	-382.13	3.29	0.07
Beluga whale	**collection method + sex**	**5**	**283.74**	**-557.30**	**0.00**	**0.60**
	collection method + year + sex	6	283.83	-555.41	1.89	0.23
	collection method	4	281.44	-554.76	2.54	0.17
	collection method + year + season	9	282.05	-545.58	11.72	0.00
	age class + season	8	244.48	-472.54	84.76	0.00
Harp seal	**collection method + year + sex**	**6**	**717.15**	**-1422.05**	**0.00**	**0.97**
	collection method + sex	5	712.76	-1415.34	6.71	0.03
	collection method + year + season	9	712.83	-1407.14	14.91	0.00
	collection method	4	703.33	-1398.54	23.51	0.00
	sex + age class	5	614.67	-1219.17	202.88	0.00
Narwhal	**collection method + sex**	**5**	**250.31**	**-490.44**	**0.00**	**0.49**
	collection method + year	5	249.76	-489.35	1.09	0.28
	collection method + year + season	9	253.40	-488.28	2.16	0.17
	collection method	4	247.12	-486.13	4.31	0.06
	sex + age class + season	9	229.60	-440.67	49.77	0.00
Ringed seal	**sex + age class + season**	**9**	**55.38**	**-92.24**	**0.00**	**0.96**
	season	7	49.79	-85.25	7.00	0.03
	year + season	8	49.84	-83.25	8.99	0.01
	collection method + year + season	9	50.13	-81.74	10.50	0.01
	sex + age class	5	32.34	-54.50	37.74	0.00
Walrus	**collection method + sex**	**5**	**566.80**	**-1123.43**	**0.00**	**0.78**
	collection method + year + season	9	569.36	-1120.19	3.24	0.15
	collection method	4	562.94	-1117.77	5.66	0.05
	collection method + year	5	563.06	-1115.96	7.47	0.02
	sex + age class + season	9	536.47	-1054.41	69.02	0.00

Chapter 4: Prey selection of polar bears in Foxe Basin, Nunavut, Canada: evidence of dietary flexibility in a specialized predator

Melissa P. Galicia*, Gregory W. Thiemann, Markus G. Dyck, Steven H. Ferguson, and Ian Stirling

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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 1999-2003 (n = 82) with additional data from 2010-2018 (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.

Introduction

Ecological flexibility refers to the ability of an animal to respond to shifts in environmental conditions through behavioural mechanisms (Gordon 1991, Hadfield and Strathmann 1996, Beever et al. 2017). Behavioural responses including changes in habitat use (Righton et al. 2010, Van Daele et al. 2012), phenology (e.g., migration or reproduction; Tøttrup et al. 2010,

Mazerolle et al. 2011), thermoregulation (Murray and Smith 2012), predator avoidance (Chalfoun and Martin 2010), and foraging strategies (Gilmour et al. 2018, Mangipane et al. 2020) 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 (Forister et al. 2012, Gilmour et al. 2018). Specialists, however, can be constrained by dietary requirements and their lack of flexible foraging strategies may lead to increased sensitivity to environmental fluctuation (Colles et al. 2009, Gilg et al. 2012). In contrast, a generalist foraging strategy may be favourable in more diverse and variable habitats with fluctuating or patchy resources (Gilmour et al. 2018). 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 (Beever et al. 2017).

Climatic warming in the Arctic has occurred 2-3 times faster than any other region (IPCC 2018). The warmer climate has contributed to reduced sea ice extent (e.g., Serreze et al. 2007, Comiso et al. 2008, Stroeve et al. 2012), declining ice thickness (e.g., Kwok and Rothrock 2009, Lindsay and Schweiger 2015, Haas et al. 2017) and reduced seasonal sea ice duration (Parkinson 2014). An earlier onset of spring melt has contributed to a thinner ice cover and reduced summer extent (Meier et al. 2014), and in combination with a later freeze-up has led to a longer ice-free season (Stroeve and Notz 2018). The rate of sea ice loss is expected to accelerate due to positive feedback mechanisms (Stroeve and Notz 2015). 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 (Jahn 2018, Niederdrenk and Notz 2018, Sigmond et al. 2018).

Arctic warming has driven profound ecological change in biological productivity, species assemblages, resource availability, and habitat conditions associated with sea ice loss (Gosselin et al. 1997, Walsh 2008, Post et al. 2009). 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 (Post and Forchhammer 2008, Søreide et al. 2010, Daase et al. 2013). Phenological changes in sea ice conditions will have significant effects across ecosystems (Post et al. 2013). However, flexible foraging strategies may enable individuals to meet their energetic needs by exploiting alternate prey (Bolnick et al. 2007) and increase their chances of persistence in a changing environment (Beever et al. 2017). 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*; Stirling and Archibald 1977, Stirling and Øritsland 1995, Thiemann et al. 2008a). Extensive feeding by polar bears (i.e., hyperphagia period) occurs in the spring and early summer (Stirling and Øritsland 1995, Galicia et al. 2020) when newly-weaned seal pups are most vulnerable and accessible to predators and adults are hauled out on the sea ice to moult (Stirling and Archibald 1977, Pilfold et al. 2012). However, when alternate foraging opportunities are spatially and temporally available, polar bears can be opportunistic feeders and also prey on harp seals (*Pagophilus groenlandicus;* (Derocher et al. 2002, Iverson et al. 2006, Smith and Stirling 2019), harbour seals (*Phoca vitulina;* Sciullo et al. 2017, Johnson et al. 2019), beluga whales (*Delphinapterus leucas;* Smith

and Sjare 1990, Thiemann et al. 2008a, Galicia et al. 2015), narwhal (*Monodon monoceros;* Smith and Sjare 1990), Atlantic walrus (*Odobenus rosmarus rosmarus;* Calvert and Stirling 1990, Galicia et al. 2016), and scavenge on large whale carcasses including bowhead whales (*Balaena mysticetus;* Schliebe et al. 2008, Galicia et al. 2016). 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 (DeMaster and Stirling 1981, Amstrup 2003), 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 (Regehr et al. 2016), although some factors may help mitigate the negative effects of sea ice loss, at least in the near term (Bromaghin et al. 2015a, Atwood et al. 2016). Prey availability, ecosystem productivity, and variation in sea ice conditions may be important determinants of demographic decline in polar bears (Rode et al. 2014, Bromaghin et al. 2015a). 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 (Rode et al. 2014). Hamilton and Derocher (2019) 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 (Sahanatien and Derocher 2012). From 1979-2008, 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) in May-July and November. Similarly, in Hudson Strait, best habitat was replaced with poor and non-habitat in May, and from January-March (winter months), there was an overall loss of best habitat (Sahanatien and Derocher 2012). Stern and Laidre (2016) 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 1979-2014. 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 (Stern and Laidre 2016).

Given the highly seasonal timing of polar bear feeding (Galicia et al. 2020), 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 (Stapleton et al. 2016). 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 (Galicia et al. 2016). With increased areas of open water, killer whales (*Orcinus orca*) have expanded their range and are now annually present in Foxe Basin (Higdon and Ferguson 2009). Because killer whales feed selectively on parts of prey (Jefferson et al. 1991, Ford et al. 2005), a large portion of a bowhead whale kill, may be left to drift onshore where it becomes accessible to bears (Young et al. 2020). Laidre et al. (2018) 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 (Laidre et al. 2018).

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 (Iverson et al. 2004, Galicia et al. 2015, 2016). 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.

Material and Methods

Sample collection and laboratory analysis

We used previously published FA data from polar bears harvested from 1999-2003 (n = 82; Thiemann et al. 2008a) and analyzed adipose tissue samples from polar bears harvested during the annual subsistence hunts from 2010-2018 (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 x 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. (2001) and sulfuric acid was used as a catalyst to derive FA methyl esters (FAME) from the extracted lipid (Budge et al. 2006). FAME samples were analyzed using gas-liquid

chromatography and flame-ionization detection at the Canadian Institute for Fisheries Technology at Dalhousie University, Halifax, NS. 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 1998-2018 were downloaded in 25 km x 25 km grid cells from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data (Cavalieri et al. 1996) available from the National Snow and Ice Data Center in Boulder (NSIDC), Boulder, Colorado 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 (Cavalieri et al. 1996). 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 (2016). 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 Stern and Laidre 2016). Cherry et al. (2013) 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% (Cherry et al. 2013, Lunn et al. 2016).

Diet estimation

Quantitative FA signature analysis (QFASA) was used to estimate diet composition of polar bears (Iverson et al. 2004). 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 (Bromaghin et al. 2015b). 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 (Thiemann 2006, Thiemann et al. 2008a, Bromaghin et al. 2017a). In this study, we used the Aitchison distance measure to compare modelled and observed predator FA signatures (Bromaghin et al. 2015b, 2016) and a set of 30 dietary FAs (Galicia et al. 2015). Diet estimates were produced using the qfasar package (version 1.2.1, Bromaghin 2017) in R (version 3.5.1; R Development Core Team 2018).

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 (Bromaghin et al. 2017b). Thus, the analysis of prey library performance is an important step to accurately estimate diet. We used two diagnostic functions built into the qfasar package (version 1.2.1, Bromaghin 2017) 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 approximates 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; Bromaghin et al. 2017b). 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 (Bromaghin et al. 2017b). 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 Supplemental Material for details and results, Table S4.1).

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 2000-2012 (Thiemann et al. 2008b, Galicia et al. 2016, Sciullo et al. 2017) to estimate predator diet. We also analyzed additional blubber samples from bearded seal (n = 5), harp seals (n = 10), and ringed seals (n = 24) from 2013 and 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 (Douma and Weedon 2019). 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 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. (2015) and Galicia et al. (2016), although Cape Dorset was removed from analysis due to small sample size; Figure S4.1) and/or season (defined as per Sahanatien et al. 2015). 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 AIC_c to select the model that best explained variation in prey selection from a set of ecologically relevant candidate models defined a priori (Burnham and Anderson 2002). We calculated log-likelihood (LL), AIC_c values, ΔAIC_c, and AIC_c weights (w_i – relative likelihood of the model) using MuMIn package in R (version 1.43.17, Bartoń 2018). 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 > 0.6 and/or VIF > 5.0 (Zuur et al. 2009) were used in separate models. To assess uninformative parameters in top models, we investigated the relative importance of individual variables (i.e., cumulative weights) in top models $\Delta AIC_c < 2.00$, by calculating the sum of Akaike model weights across all models that included the variable (Arnold 2010).

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; Zuur et al. 2009). 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'; Krebs 2009) to calculate niche breadth (i.e., dietary diversity) of polar bears in Foxe Basin:

$$H' = -\sum_{s}^{j} p_j \ln p_j$$

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., 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

(generalized linear models). All statistical analyses were conducted using R (version 3.5.1; R Development Core Team 2018).

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 ± 2.68% in 1999-2003 and 36 ± 1.40% 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 (Figure 4.1).

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 (Table 4.1). 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: 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%; Figure 4.2a). 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 4 models had an $\Delta AIC_c < 2.00$ (Table S4.2). 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%; Figure 4.2b). Walrus consumption was also influenced by bear age class and sex, in addition to region (Table 4.1), and the top ranked model was 4.8 times more likely than the second ranked model which only included sex (Table S4.2). 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%; Figure 4.2c) with 46% of adult males having over 33% 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 $\Delta AIC_c > 2.00$ (Table S4.2), the overall model weight was only 0.29 leading to some model uncertainty (Table 4.1). Age class had the highest cumulative weight of 0.38 compared to 50% breakup (0.15) or sex (0.16). Adults had higher levels of bowhead whale in diets (1.7 ± 0.25%) compared to subadults (0.6 ± 0.13%; Figure 4.2d). 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 4.1) and was 4.5 times more likely than the second ranked model which included region and season (Table S4.2). 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%; Figure 4.3a, b). The top ranked model for beluga whale contribution also included region and period with a model weight of 0.77 (Table 4.1). Beluga whale consumption was higher in 1999-2003 (23 ± 0.89%) compared to 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 ± 1.17%; Figure 4.3a, 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 $\Delta AIC_c < 2.00$ (Table S4.2). Of the variables found in the top models, region had a higher cumulative weight of 0.99 compared to period (0.22) and year (0.21). The highest contribution of harp seal to diets occurred in Hudson Strait bears (20 ± 1.92%) compared to northern Foxe Basin (11 ± 1.26%) and southern Foxe Basin (9 ± 0.81%; Figure 4.3c).

Shannon-Wiener Index (H') values were significantly different between age class and sex ($F_{1,475} = 4.201$, $p = 0.041$), 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 to 1.65, difference of 1.20; and male subadults: 0.37 to 1.62, difference of 1.25).

The frequency of occurrence of prey types in diet varied over time (Figure 4.4a-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 1999-2018.

Harbour seal and walrus frequency remained consistent (Table 4.2). In 1999-2003, bearded seal appeared in the diets on an annual average of 51% of bears (ranging from 0-75%) and increased to 90% of bears (ranging from 84-95%) in 2010-2018 (Figure 4.4a). Harp seal was found in 60% of bears (ranging from 33-83%) in 1999-2003 and 84% of bears (ranging from 73-95%) in 2010-2018 (Figure 4.4c). Frequency of ringed seal in diets declined from 97% of bears (ranging from 88-100%) in 1999-2003 to 79% of bears (ranging from 54-95%) in 2010-2018 (Figure 4.4d). Beluga whale had the largest decrease in frequency of occurrence in diets, decreasing from 86% of bears (ranging from 80-100%) in 1999-2003 to 52% of bears (ranging from 21-82%) in 2010-2018 (Figure 4.4f). Bowhead whale frequency in diet had the second largest increase over the years with bowhead found in 10% of bears (ranging from 0-17%) in 1999-2003 and 42% of bears (30-54%) in 2010-2018 (Figure 4.4g).

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 (Table S4.3). 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 (Figure S4.2). Sea ice metrics were not included in any top ranked models for variation in prey contribution to polar bear diet (Table S4.2) 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 analyzed 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 (Figure 4.5a). 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 $R^2 = 0.231$, $p = 0.046$; Figure 4.5b). 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 4.3), where the frequency of occurrence decreased with a later breakup date (Figure 4.6a, c, g). Beluga whale and harbour seal frequency significantly increased with a later 50% breakup date (Figure 4.6b, f) and 30% breakup date (Table 4.3). Ringed seal and walrus frequency in diet showed no significant relationship to 50% or 30% breakup date (Table 4.3, Figure 4.6d, 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 $\beta = 0.028 \pm 0.012$, $z = 2.228$, $p = 0.026$, respectively). 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 (Post and Forchhammer 2008, Daase et al. 2013) 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 (Laidre et al. 2008), 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 suggests 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 (Stirling and Archibald 1977, Stirling and Øritsland 1995, Thiemann et al. 2008). We found polar bear diet composition in Foxe Basin was largely consistent with previous studies (e.g., Galicia et al. 2016) 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 1999-2003 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 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 (Ferguson et al. 2005).

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 (Sahanatien and Derocher 2012, Stapleton et al. 2016) 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 (Galicia et al. 2020). Adult males have a broader dietary niche compared to adult females and subadults likely because of their ability to capture larger-bodied prey including bearded seal and walrus (Thiemann et al. 2008a, 2011). The narrow dietary niche breadth of subadults and especially adult females, likely due to their smaller size (Derocher et al. 2005), may suggest their dependence and potential specialization on fewer prey species, primarily ringed seals (Thiemann et al. 2011). 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 (Ferguson et al. 2005, Chambellant et al. 2012a). 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 (Laidre et al. 2018). Our estimates of bowhead whale consumption (1999-2003: 0 ± 0% and 2010-2018: 2 ± 0%) were similar to previous studies in Foxe Basin (Galicia et al. 2016). However, bowhead dietary levels were lower than in the Southern Beaufort Sea where bears may derive 15% of their diet from bowhead whale (Bourque et al. 2020); a level of dietary intake facilitated by a high number of whales (~18) harvested annually and reocurring locations of unused tissue (known as "bone piles") for bears to scavenge (Schliebe et al. 2008, Lillie et al. 2019). 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; Higdon and Ferguson 2010), 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 (DFO 2015, Frasier et al. 2020), 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 (Matthews et al.

2020). Killer whales primarily target the mouthparts of bowheads, potentially leaving a largely intact carcass for polar bears and other terrestrial scavengers. In October and November of 2020, nine bowhead whales were found beached in central Nunavut (George 2020), 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 (Iverson et al. 2006, Thiemann et al. 2008). 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 (DFO 2002, COSEWIC 2006). 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 (Kingsley et al. 1985, Stirling 1997). The high levels of walrus found in diets of some bears in northern Foxe Basin (e.g., 80% in one adult male) suggests 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 (Sciullo et al. 2017, Johnson et al. 2019). In western Hudson Bay, an increase in harbour seal abundance has

been linked to longer periods of open water (Florko et al. 2018). 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 (Bajzak et al. 2013). 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 (Smith and Sjare 1990, Heide-Jørgensen et al. 2003, COSEWIC 2004, Paulic et al. 2014). Polar bears have been observed hunting beluga whales in open water and in river channels (Laidre et al. 2018), although this is likely less common. Killer whale predation on beluga whales (Higdon and Ferguson 2009, Westdal et al. 2016) and the possibility of struck and lost beluga from the subsistence harvest (although estimates are lacking) may provide beluga carrion available to scavenge (DFO 2018). 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 2012). 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 Laidre (2016). 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 prefer unconsolidated pack ice during breeding and to haul-out (Kingsley et al. 1985, Chambellant et al. 2012b). Harp seals are primarily pelagic and thought to be largely inaccessible to polar bears except for the on-ice whelping patch in Davis Strait (Iverson et al. 2006, Thiemann et al. 2008). 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 (Smith and Stirling 2019), 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-October; COSEWIC 2004, Turgeon et al. 2012, Smith et al. 2017). 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 (Richard et al. 1998). Harbour seal consumption also increased with a later breakup, consistent with the findings of Sciullo et al. (2017) 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 (Bajzak et al. 2013). 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 (Higdon and Ferguson 2009). 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, 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 (Post et al. 2013). 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. Thiemann et al. 2011). 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 benefiting 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.

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Table 4.1 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. All prey species were modelled separately, and only the top ranked models are shown. Included in the table are number of estimated parameters (K), log-likelihood (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.

Prey species	**Model**	**k**	**LL**	**AICc**	**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

Table 4.2 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 β coefficient, standard error, z and p values for the predictor variable. An asterisk beside p values indicate statistical significance for prey species.

Prey	***β* 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*

Table 4.3 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 50% breakup date models and 30% breakup date, showing the β coefficient, standard error, z and p values for the predictor variable. An asterisk beside p values indicate statistical significance for prey species.

	50% breakup date				**30% breakup date**			
Prey	***β* coefficient**	**SE**	**z**	***p***	***β* 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*

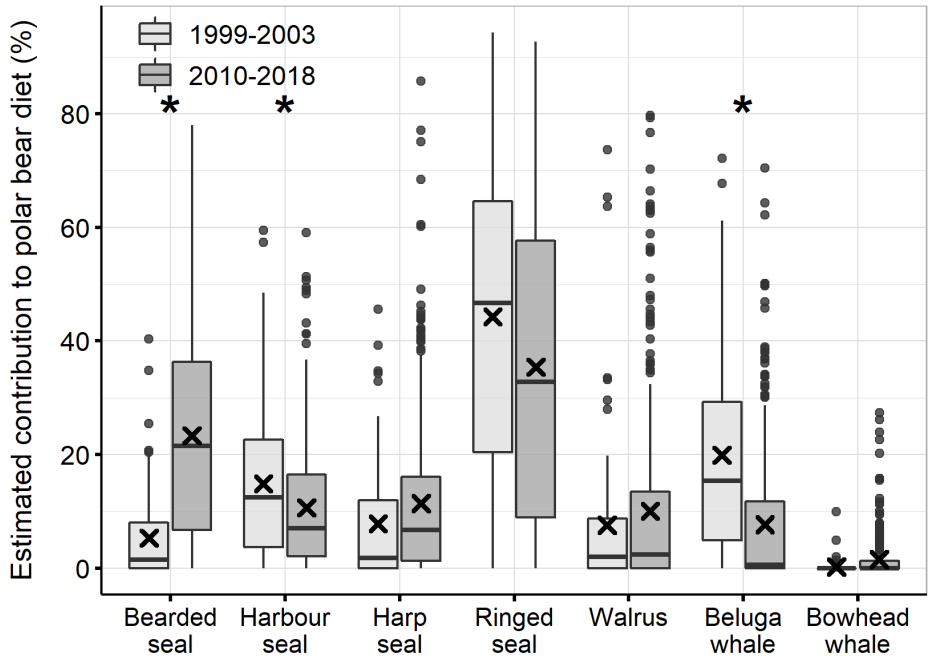

Figure 4.1 Diet composition of polar bears across the Foxe Basin subpopulation separated by time period 1999-2003 and 2010-2018 as estimated from QFASA. Data represent each prey species' biomass contribution to diet estimates shown as boxplots showing the 25th quartile, median, 75th quartile, and outliers shown as solid circles. Mean contribution for each is represented by "x". Prey dietary proportions that differed between time periods determined by Akaike's information criterion (corrected for small sample sizes) model selection have been identified with an * above the boxplot.

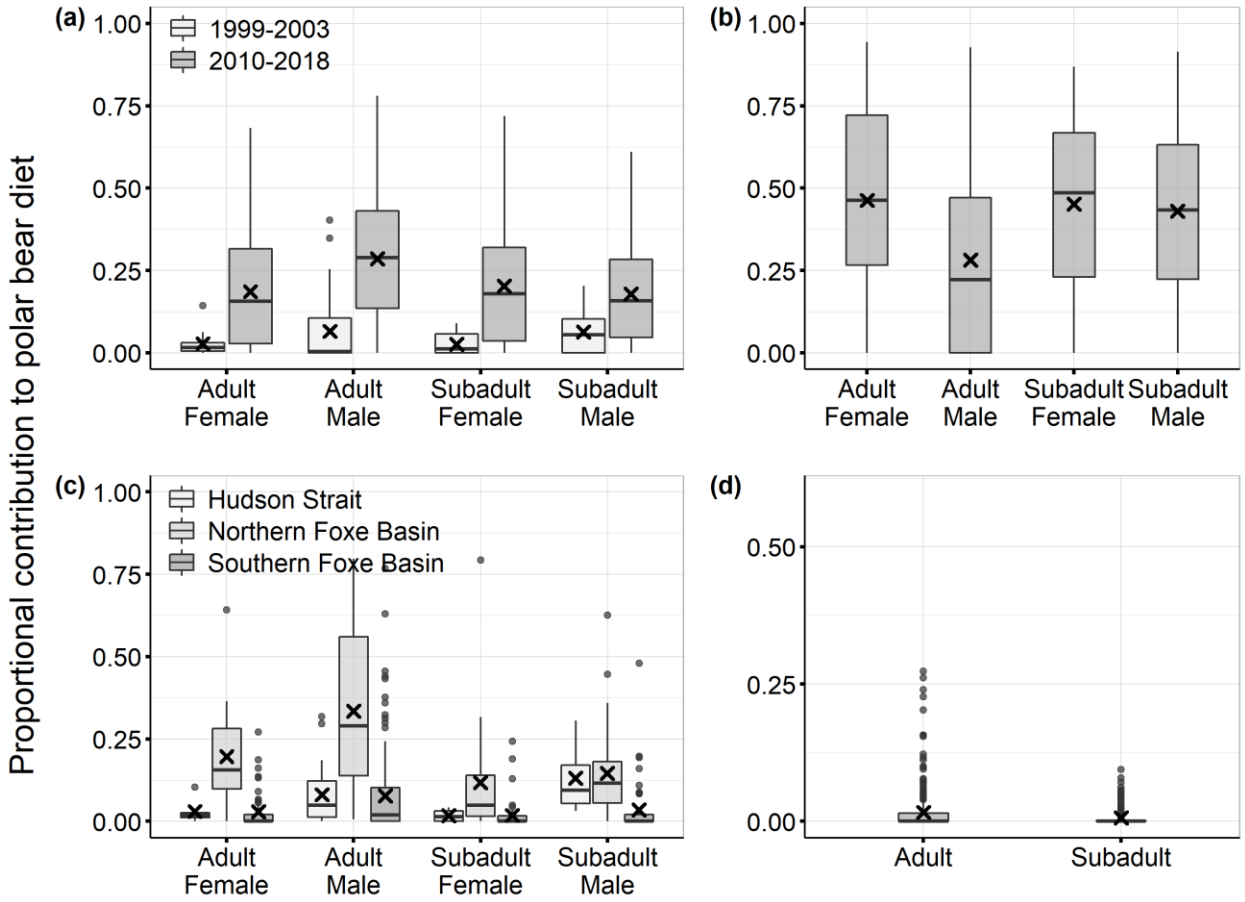

Figure 4.2 Prey contribution to polar bear diets across the Foxe Basin subpopulation in 1999-2003 and 2010-2018 from (a) bearded seal, (b) ringed seal, (c) walrus, and (d) bowhead whale as estimated from QFASA. Data represent each prey species' proportional biomass contribution to diet estimates shown 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.

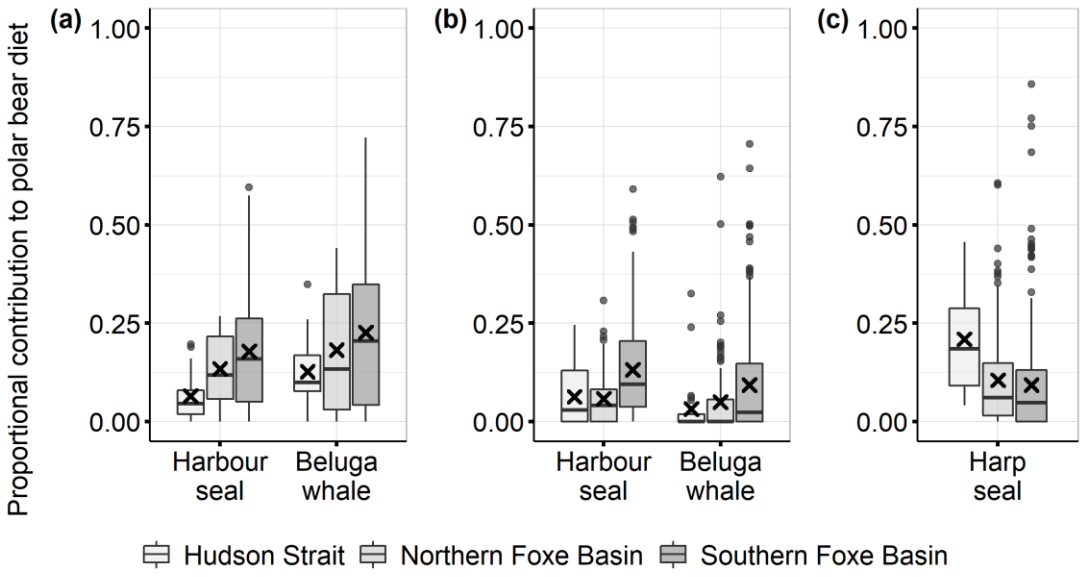

Figure 4.3 Prey contribution to polar bear diets across the Foxe Basin subpopulation of harbour seal and beluga whale in (a) 1999-2003 and (b) 2010-2018, and (c) harp seal in 1999-2003 and 2010-2018 as estimated from QFASA and separated by region (Hudson Strait, northern Foxe Basin, and southern Foxe Basin). 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.

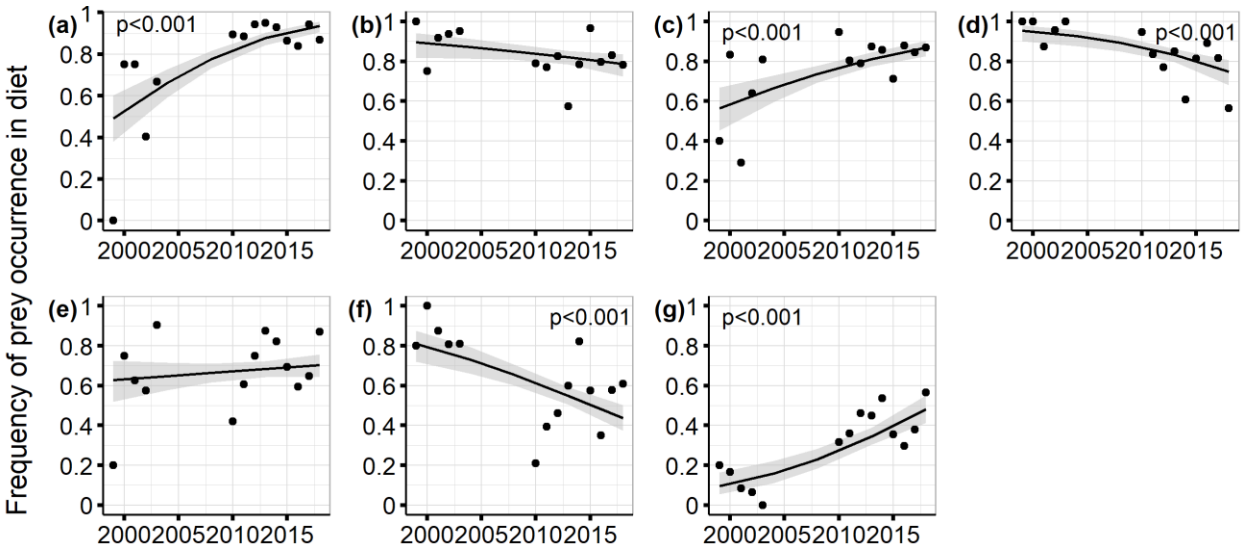

Figure 4.4 Annual frequency of occurrence of prey in diets of polar bears harvested in Foxe Basin, in 1999-2003 and 2010-2018, (a) bearded seal, (b) harbour seal, (c) harp seal, (d) ringed seal, (e) walrus, (f) beluga whale, and (g) bowhead whale as estimated from QFASA. Observed values (black dots) are shown in proportions (number of bears with prey present/number of bears sampled each year), predicted values as a solid line, and 95% confidence interval shaded in grey. Significant relationships are indicated with p values for each prey species.

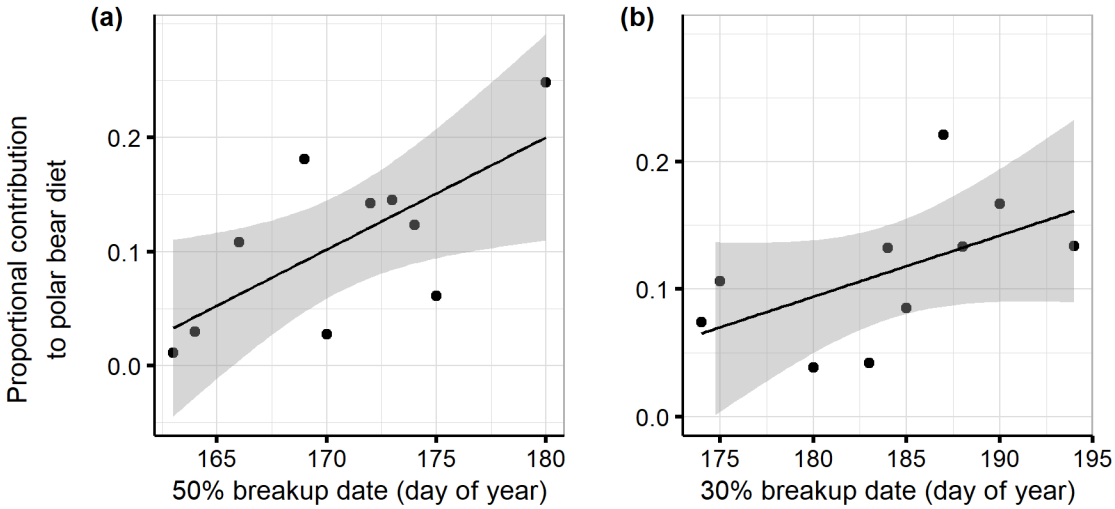

Figure 4.5 Relationship between prey contribution to diets of polar bears harvested in Foxe Basin, in 1999-2003 and 2010-2018 as estimated from QFASA and spring sea ice metrics, (a) beluga whale and 50% breakup date and (b) harbour seal and 30% breakup date. Observed values are shown as black dots, predicted values as solid line, and 95% confidence interval shaded in grey.

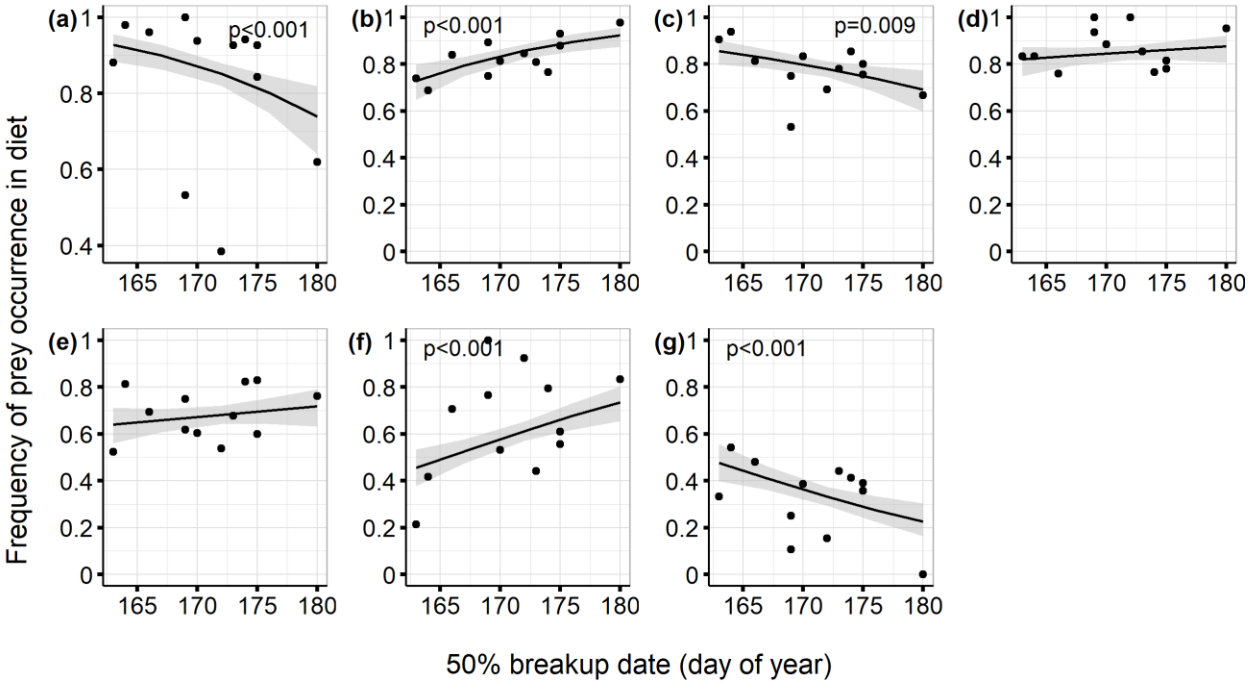

Figure 4.6 Relationship between frequency of occurrence of prey in diets of polar bears harvested in Foxe Basin in 1999-2003 and 2010-2018 as estimated from QFASA and 50% breakup date, (a) bearded seal, (b) harbour seal, (c) harp seal, (d) ringed seal, (e) walrus, (f) beluga whale, and (g) bowhead whale. 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.

Supplemental Material

Simulating predator diets

Simulations were used to evaluate the performance of the QFASA model based on estimators (e.g., prey library). Simulating predator diets is a function built into the qfasar package (version 1.2.1, Bromaghin 2017) in R (version 3.5.1; R Core Development Team 2018). Predator signatures were simulated based on a defined "true diet", the resulting simulated diet can then be compared to the true diet to evaluate the performance of the QFASA model (Iverson et al. 2004, Bromaghin et al. 2016). In this study, 1000 predators were simulated conditioned on a *realistic* mean diet from a set of 30 polar bears as the true diet (Bromaghin 2017). Simulation of predator signatures was performed using both the original prey library and partitioned prey library established using the divisive magnetic clustering function (Bromaghin 2017, Bromaghin et al. 2017). For comparison to the original prey library, estimates from the partitioned library were pooled back to the original prey types. The mean and standard error of the estimates for each simulated diet were computed by prey type and the mean was compared to the estimated diet to calculate bias. Summary measures across all prey types were computed as the sum of absolute values of bias (difference between estimated and simulated diet) and the square root of the sum of variances. The sum of absolute bias across all prey species increased by 122% and the square root of the sum of the variances decreased 16% with the partitioned prey library (Table S4.1). Thus, the original prey library was used to estimates the diets of bears in this study due to the lack of improvement in QFASA performance with the partitioned prey library.

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Iverson, S. J., C. Field, D. W. Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs 74:211–235.

R Development Core Team 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.r-project.org/.

Table S4.1 Bias and standard errors (SE) of diet estimates obtained from 1000 simulated signatures conditioned on the realistic diets from a set of 30 polar bears with the original which is the unpartitioned and the partitioned prey libraries.

		Bias		SE	
Prey	Diet	Original	Partitioned	Original	Partitioned
Bearded	0.143	0.011	-0.029	0.004	0.003
Beluga	0.041	0.021	0.045	0.003	0.002
Bowhead	0.008	0.010	0.014	0.001	0.001
Harbour	0.071	-0.008	-0.002	0.002	0.002
Harp	0.199	-0.041	-0.078	0.004	0.002
Ringed	0.442	0.001	0.046	0.006	0.004
Walrus	0.096	0.005	0.003	0.002	0.001
Over all prey	1.00	0.097	0.217	0.145	0.122

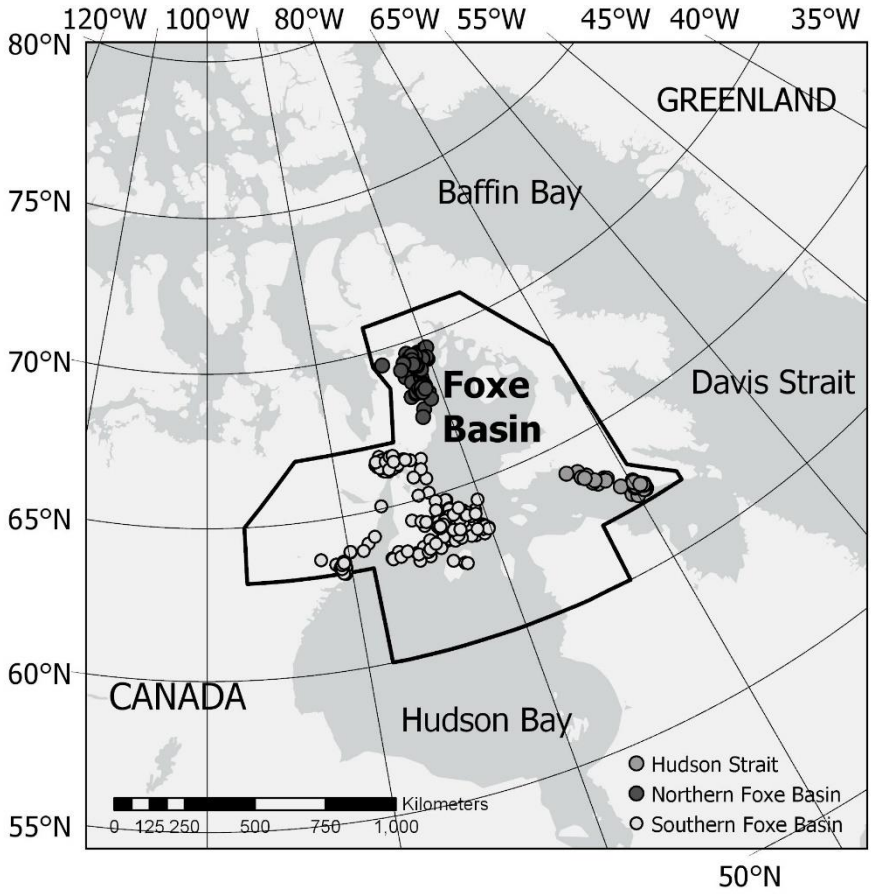

Figure S4.1 Location of polar bears (n = 426) harvested by Inuit hunters in 1999-2003 and 2010-2018 in Foxe Basin (black outline represents the subpopulation boundaries), separated by region (Hudson Strait, Northern Foxe Basin, and Southern Foxe Basin). Note: Cape Dorset bears were left out of the model selection for prey contribution to diets.

Table S4.2 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. All prey species were modelled separately, and top-five ranked models are shown with the top ranked model in bold. Included in the table are number of estimated parameters (K), log-likelihood (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.

Prey	Model	K	LL	AICc	ΔAICc	w_i
Bearded seal	**age class*sex + time period**	**7**	**16.16**	**-18.04**	**0.00**	**0.92**
	age class*sex + year	7	13.60	-12.93	5.11	0.07
	time period	4	7.03	-5.96	12.08	0.00
	time period + region	5	7.29	-4.43	13.61	0.00
	time period + season	5	7.22	-4.29	13.75	0.00
Harbour seal	**time period + region**	**5**	**190.67**	**-371.19**	**0.00**	**0.76**
	season + region	5	189.18	-368.21	2.98	0.17
	region	4	187.20	-366.3	4.89	0.07
	region + age class*sex	7	187.79	-361.31	9.88	0.01
	time period + season	5	182.47	-354.8	16.40	0.00
Harp seal	**region**	**4**	**82.93**	**-157.77**	**0.00**	**0.51**
	time period + region	5	83.10	-156.05	1.72	0.22
	year + region	5	83.05	-155.96	1.81	0.21
	region + age class*sex	7	83.94	-153.61	4.16	0.06
	season	4	76.84	-145.59	12.18	0.00
Ringed seal	**age class*sex**	**6**	**-154.95**	**322.1**	**0.00**	**0.33**
	age class*sex + year	7	-154.5	323.27	1.17	0.19
	age class*sex + time period	7	-154.71	323.69	1.59	0.15
	50% breakup + 50% freeze-up + age class*sex	8	-153.81	323.69	1.86	0.13
	30% breakup + 10% freeze-up + age class*sex	8	-158.72	324.74	2.64	0.09
Walrus	**age class*sex + region**	**7**	**-8.5**	**31.27**	**0**	**0.53**
	sex	4	-13.17	34.44	3.17	0.11
	age class*sex	6	-11.82	35.84	4.58	0.05
	region	4	-13.89	35.88	4.61	0.05
	age class*sex + time period	7	-10.81	35.89	4.63	0.05
Beluga whale	**time period + region**	**5**	**-83.78**	**177.71**	**0**	**0.77**
	time period	4	-87.09	182.27	4.56	0.08
	time period + season	5	-86.1	182.35	4.63	0.08
	year	4	-87.45	183	5.29	0.05
	time period + age class*sex	7	-86.24	186.75	9.04	0.01
Bowhead whale	**age class**	**4**	**50.03**	**-91.96**	**0**	**0.29**
	50% breakup	4	48.52	-88.95	3.01	0.06
	sex	4	48.48	-88.87	3.09	0.06
	harvest date	4	48.28	-88.47	3.49	0.05
	region	4	48.23	-88.36	3.6	0.05

Table S4.3 Linear regression models examining the relationship sea ice metrics and year in Foxe Basin from 1998-2018.

	Linear regression			β coefficient
	F	p	R^2	Day of year
Breakup 50%	0.047	0.831	0.002	0.005
Breakup 30%	0.032	0.861	0.002	-0.041
Freeze-up 50%	0.258	0.618	0.013	-0.086
Freeze-up 10%	1.258	0.276	0.062	-0.178

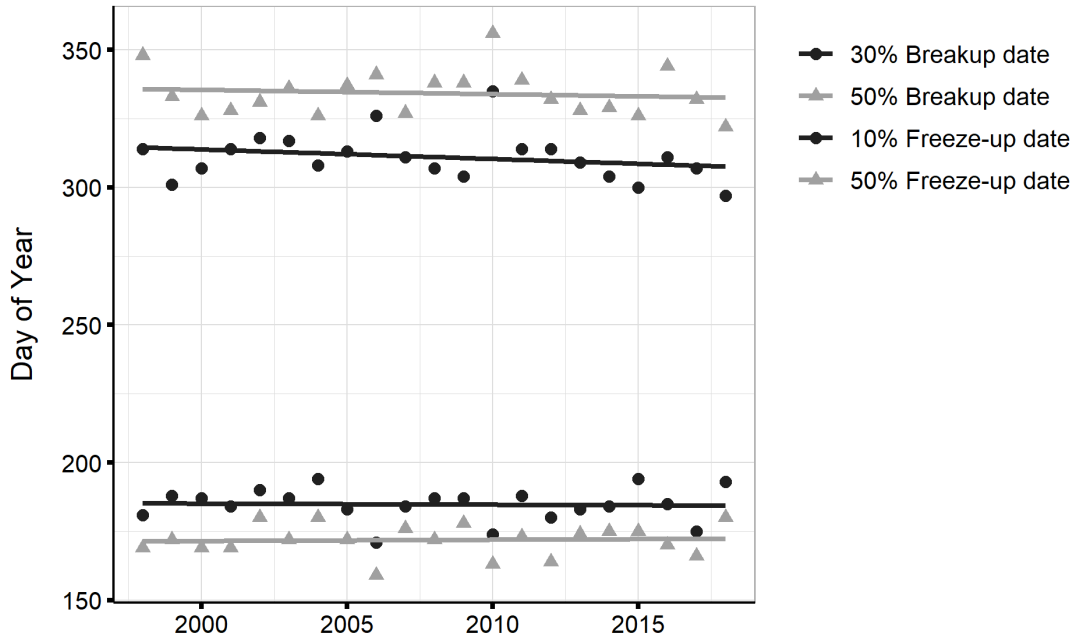

Figure S4.2 Temporal trends in sea ice metrics (breakup date at 50% and 30% threshold, and freeze-up date at 50% and 10% threshold) in Foxe Basin from 1998-2018.

Chapter 5: Polar bear diet composition reveals spatiotemporal distribution of Arctic marine mammals across Nunavut, Canada

Melissa P. Galicia*, Gregory W. Thiemann, Markus G. Dyck, and Steven H. Ferguson

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Abstract

Climate warming and associated physical and biological changes will likely force widespread species redistribution, particularly in polar environments. However, tracking such distributional shifts is difficult. The dietary habits of apex predators, like polar bears (*Ursus maritimus*), may provide early signals of distributional change in prey populations. We used harvest-based sampling to investigate the spatial feeding patterns of polar bears across Nunavut from 2010-2018 (n = 1570) and identify spatiotemporal clusters of different prey based on predator diet estimates. Quantitative fatty acid signature analysis and the Getis-Ord Gi* statistic identified spatial clusters of high or low dietary proportions (i.e., "hot spots" and "cold spots") reflecting seasonal and spatial availability of prey. Ringed seal (*Pusa hispida*) was the primary prey of bears throughout Nunavut followed by bearded seal (*Erignathus barbatus*), although proportional consumption varied spatially. A consistent ringed seal consumption hot spot was found in Gulf of Boothia indicating the importance of year-round availability of ringed seals. Spatial clusters of bearded seal and Atlantic walrus (*Odobenus rosmarus rosmarus*) throughout Foxe Basin suggested overlapping seasonal distributions and high regional abundance. Bears had consistently high dietary levels of harbour seal (*Phoca vitulina*) around Southampton Island and along the western coast of Hudson Bay suggesting a possible year-round concentration of this prey. Hot spots of harp seal (*Pagophilus groenlandicus*) consumption were evident throughout Davis Strait and a spring-summer hot spot around Jones Sound was consistent with harp seal migratory patterns. Year-round beluga whale (*Delphinapterus leucas*) hot spots were found along eastern Baffin Island and southern Viscount Melville Sound providing new knowledge of local conditions that promote polar bear predation or scavenging. Narwhal (*Monodon monoceros*) were less susceptible to predation with only one spatial cluster of high consumption appearing during spring-summer in Barrow Strait. Bowhead whale (*Balaena mysticetus*) hot

spots occurred around south-western Foxe Basin and seasonally in southern Viscount Melville Sound suggesting carcasses are locally accessible to bears and may act as a supplemental food source in particular areas and seasons. The congruence of polar bear feeding habits and known prey distribution suggests polar bears serve as ecological indicators and ongoing monitoring of their diets may reveal regional and broad-scale changes in prey population distributions and Arctic ecosystem functioning.

Introduction

Distributional shifts are associated with changing environmental conditions that can influence the structure and functioning of ecosystems (Dawson et al. 2011, Pecl et al. 2017). Marine organisms may respond to warming temperatures through behavioural responses (e.g., altered movement and migration) in an attempt to remain within their preferred habitat conditions resulting in geographic range shifts and declines in local abundance (Learmonth et al. 2006, Bates et al. 2014). Changing climatic conditions can be detrimental for migratory species relying on areas for seasonal life history processes, as well as restricting for species with limited ecological plasticity or low dispersal ability (Learmonth et al. 2006, Berg et al. 2010, Bates et al. 2014). Additionally, the detection and prediction of range shifts may be limited by the lack of broad-scale monitoring tools (Bates et al. 2014).

The Arctic ecosystem is experiencing climate warming up to 3 times faster than any other region (Voosen 2020, AMAP 2021). Observed and projected sea ice loss is expected to have profound impacts on species and their habitat (Laidre et al. 2008, Post et al. 2013). Endemic Arctic species have adapted to seasonal fluctuations in resource availability and habitat conditions (Kovacs and Lydersen 2008, Ernakovich et al. 2014) and are challenged by phenological changes linked to the rapid pace of climate change (Post et al. 2013). The severity

and timing of responses to climate change will be species- and region-specific (Laidre et al. 2008, Walsh 2008). However, distributional shifts and local reductions in abundance are expected with continued sea ice loss and warming temperatures (Kovacs et al. 2011). Arctic marine mammals with strict biological and physiological tolerances may alter migration patterns or experience range contraction if species' ecological needs are no longer met by local habitat conditions (Laidre et al. 2008). For example, sea ice conditions have been shown to affect beluga whale (*Delphinapterus leucas*) populations, expanding their distribution in offshore areas and northward in years with reduced ice cover (Heide-Jørgensen et al. 2010, Bailleul et al. 2012). Arctic cetaceans with a strict thermal tolerance such as narwhal (*Monodon monoceros*) and bowhead whale (*Balaena mysticetus*) are predicted to experience altered movement and compressed distribution due to warming surface temperatures (Chambault et al. 2018, 2020). Changes in prey availability may also indirectly affect Arctic species in combination with habitat loss. For example, declines in sea ice and shifts in preferred prey availability will likely lead to a northward range retraction for ice-dependent ringed seals (*Pusa hispida*; Laidre et al. 2008, Ferguson et al. 2020).

Climate warming will also lead to a greater prevalence of seasonally migrant species expanding their range northward and staying for longer periods, creating the potential for competition with year-round inhabitants (Moore and Huntington 2008). Heide-Jørgensen et al. (2013) suggested possible inter-specific competition with increased observations of temperate marine mammals such as common minke whales (*Balaenoptera acutorostrata*) and humpback whales (*Megaptera novaengliae*) using the biologically productive waters around the North Water Polynya. Competition is of particular concern if temperate and Arctic species have overlapping diet and spatiotemporal distribution that may displace Arctic species with cascading

effects on trophic structure. Northern expansion of temperate fish such as sand lance (*Ammodytes spp.*) and capelin (*Mallotus villosus*) due to changes in ice cover duration has resulted in a lower abundance of Arctic cod (*Boreogadus saida*), consequently leading to dietary shifts from the preferred Arctic cod to temperate species in seabirds (Gaston et al. 2012, Provencher et al. 2012), beluga whales (Watt et al. 2016), and ringed seals (Chambellant et al. 2013). Seasonally migrant species such as killer whales (*Orcinus orca*) are increasing in frequency and spending more time in Arctic waters due to a lengthening ice-free season (Higdon and Ferguson 2009), resulting in an increased risk of predation for Arctic marine mammals that previously used the sea ice to avoid predators (Higdon et al. 2012, Breed et al. 2017, Lefort et al. 2020, Matthews et al. 2020). Spatial and temporal shifts in distribution and relative abundance of marine mammals will influence ecosystem functioning through changes in the timing of key biological processes, prey availability, and species interactions. How species respond to climate-induced regime shifts remains unclear as warming continues, coupled with the logistical challenge to observe and track range shifts over broad geographic scales.

Ecosystem sentinel species reflect changes in underlying ecological processes in a timely and measurable way (Zacharias and Roff 2001, Hazen et al. 2019). Dietary patterns of marine predators can be used to monitor changes in prey populations at varying spatial and temporal scales (Hazen et al. 2019). A specialist predator may directly reflect climate-induced changes in a prey population. For example, migratory patterns of blue whales (*Balaenoptera musculus*) reflected changes in the abundance of preferred prey (adult euphausiids) linked to primary productivity (Croll et al. 2005). In contrast, a generalist predator diet may signal broad-scale changes in prey assemblages. For example, the diet of a generalist seabird, the elegant tern (*Thalasseus elegans*) reflected temporal changes in the abundance of multiple prey species (Horn

and Whitcombe 2015). Habitat conditions may also influence a prey's susceptibility to predation. Adélie penguin (*Pygoscelis adeliae*) diet composition varied depending on their access to foraging grounds (e.g., neritic versus pelagic waters), and consequently available prey species (Ainley et al. 2003). Thus, predator dietary patterns may reflect a change in relative abundance and distribution of prey populations, as well as provide insight into changes in prey accessibility linked to environmental conditions.

Polar bears (*Ursus maritimus*) are an apex predator with a circumpolar distribution. Although often characterized as specialist predators of ringed seals, polar bears are capable of a flexible foraging strategy when multiple prey species are spatially and temporally available (Thiemann et al. 2008a, Galicia et al. 2021). Bears are reliant on the sea ice platform to hunt marine mammals (Amstrup 2003) and have shown signs of reduced foraging efficiency linked to ice habitat loss (e.g., Cherry et al. 2009, Rode et al. 2014, 2018). In some regions, dietary flexibility of polar bears (i.e., the ability to shift between available prey) may not only help mitigate climatic-driven impacts of sea ice loss but may also provide early signals of bottom-up changes in lower trophic levels (i.e., resources used by prey). Polar bears have been previously suggested as a useful indicator of ecosystem change (i.e., ecosystem sentinels) given their widespread distribution, sensitivity to sea ice loss, and role as an apex predator (Laidre et al. 2008, Moore and Huntington 2008, Moore and Reeves 2018, Hazen et al. 2019). Iverson et al. (2006) suggested polar bear diets could reliably reflect regional changes in prey populations, although that study had limited spatial extent. Polar bear diets could be an especially useful ecological indicator given the limited information on marine mammal distribution across the Arctic (Laidre et al. 2015), and the lack of information on how Arctic marine mammals will respond to changes in habitat conditions.

Our objective was to examine the spatial structure of polar bear diet composition across Nunavut, the largest territory in Canada, spanning ~2.1 million km^2 with a wide longitudinal (60°W to 110°W) and latitudinal range (55°N to 80°N). We used fatty acid (FA) profiles of polar bears and their prey to identify local and seasonal clusters of diet composition. We hypothesized that polar bear diets would reflect the seasonal distribution of prey within and among polar bear subpopulations. Dietary patterns of polar bears could be used to monitor range shifts of Arctic marine mammals providing an index that would otherwise be expensive, time-consuming, and logistically challenging to obtain using conventional surveying methods. Given the wide geographic range of polar bears and year-round harvest-based sampling, ongoing monitoring of their diets may provide rapid, temporal and scale-dependent information on Arctic ecosystem functioning and resilience.

Materials and Methods

Sample collection and laboratory analysis

We analyzed adipose tissue samples from polar bears harvested during Inuit subsistence hunts from 2010-2018 (n = 1570) across 10 Canadian polar bear subpopulations: Baffin Bay (n = 158), Davis Strait (n = 208), Foxe Basin (n = 406), Gulf of Boothia (n = 250), Lancaster Sound (n = 371), M'Clintock Channel (n = 30), Norwegian Bay (n = 7), Southern Hudson Bay (n = 52), Viscount Melville Sound (n = 21), and Western Hudson Bay (n = 67; Figure 5.1). Samples were collected year-round from male and female adult (5+ years old), subadult (3-4 years old), and independent 2-year-old polar bears. Subcutaneous adipose tissue samples (ca. 6 cm x 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. Subsamples (~0.5 g) were taken from the core of the adipose tissue sample to avoid any desiccation or oxidization from external surfaces. We quantitatively extracted lipid from tissue subsamples according to Iverson et al. (2001) and FA methyl esters

(FAME) were derived from extracted lipid using a sulfuric acid catalyst (Budge et al. 2006). FAME samples were analyzed using gas-liquid chromatography and flame-ionization detection at the Canadian Institute for Fisheries Technology at Dalhousie University, Halifax, NS. 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 and expressed as mass percent of total FA ± 1 standard error.

Diet estimation

We used quantitative FA signature analysis (QFASA) to estimate diet composition of polar bears (Iverson et al. 2004). 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. 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 (Thiemann 2006, Thiemann et al. 2008a, Bromaghin et al. 2017a). We used the Aitchison distance measure to compare modelled and observed predator FA signatures (Bromaghin et al. 2015, 2016) and a set of 30 dietary FAs (Galicia et al. 2015). Diet estimates were produced using the qfasar package (version 1.2.1, Bromaghin 2017) in R (version 3.5.1; R Development Core Team 2018).

To estimate predator diet, we used an established library of FA data from marine mammals (n = 597) including bearded seals (*Erignathus barbatus*), beluga whales, bowhead whales, harbour seals (*Phoca vitulina*), harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), narwhal, ringed seals, and Atlantic walrus (*Odobenus rosmarus rosmarus*) sampled across Nunavut from 1994-2017 for each respective subpopulation (from Thiemann et al. 2008b, Galicia et al. 2015, 2016, 2021, Sciullo et al. 2017). We also analyzed additional

blubber samples from beluga whales (n = 20), and ringed seals (n = 220) from 2012 to 2017 for the prey library. Diets were modelled using prey species that were known to occur in a given region, and where possible modelled with prey samples collected from the same or adjacent regions. In all cases, FA variability among prey species was greater than within-species variability, which allowed us to pool prey from adjacent regions and over time (Thiemann et al. 2008b).

QFASA diet estimates will be more accurate when prey FA profiles are distinct from each other than when prey FA profiles are similar (Bromaghin et al. 2017b). We used two diagnostic functions in the qfasar package (version 1.2.1, Bromaghin 2017) to analyze the performance of the prey library: leave-one-prey-out (LOPO) and divisive magnetic clustering (DIMAC). The LOPO function temporarily removes an individual prey FA signature from the library and determines the mixture of remaining prey signatures that best estimates the removed prey (i.e., the prey signature is treated as if it were a predator). The process is repeated for each prey sample in the library. The output provides the proportion of prey samples correctly (distinctiveness) and incorrectly (confounding) identified for each prey species (Bromaghin et al. 2017b). LOPO outputs indicated that prey species were readily distinguishable within prey libraries specific to each subpopulation (Supplemental Material, Table S5.1). Although polar bears in Foxe Basin may have seasonal access to narwhal, there was confounding between narwhal and beluga FA signatures in the prey library. Given the low dietary levels of narwhal in past Foxe Basin studies (Thiemann et al. 2008a, Galicia et al. 2016) and to our knowledge no reports of ice entrapment events in the region, narwhal was left out of the prey library for Foxe Basin diet estimates. DIMAC is a clustering technique that identifies substructure within the library. The function partitions prey into clusters that are more similar than the original species-

based groups. We simulated predator diet using both the original and DIMAC-partitioned prey library to examine performance of the QFASA model using both libraries (Bromaghin et al. 2017b). We found no substructure within the prey library that would have led to a better performance by the QFASA model (Supplemental Material, Table S5.2).

Statistical analysis

We used the optimized hot spot analysis tool in ArcGIS Pro (version 2.3; Environmental Systems Research Institute) to examine spatial patterns of polar bear diets across Nunavut (Figure 5.1). The tool assessed whether high or low values (dietary proportions of different prey types) spatially cluster using the Getis-Ord Gi* statistic (Getis and Ord 1992). Proportional dietary values for each prey type were used to identify statistically significant spatial clusters of high and low prey consumption, and areas with no significant spatial structure (i.e., a lack of a significant spatial clustering) across our study area. The tool looked at each polar bear within the context of neighboring bears. To be statistically significant, a bear's diet estimate would need to have a high or low dietary value and be surrounded by other bears with high or low values, respectively. The local value for a bear and its neighbours is compared to the value of all bears (study area) and if the local value is different from the expected local value and too large to be the result of random chance it is deemed significantly different. Each bear will have a z-score and p-value and placed into a confidence level bin; features in the +/-3 bins are statistically significant at the 99% confidence level, +/-2 bins are statistically significant at the 95% confidence level, +/-1 bins are statistically significant at the 90% confidence level, and features with 0 are not statistically significant (ESRI 2020). A positive bin would signify a high dietary value and a negative bin would signify a low dietary value. The optimized hot spot analysis tool automatically corrects the bin field for multiple testing and spatial dependence using the false

discovery rate correction method. To ensure each bear has a neighbour within a specified distance we used the recommended fixed distance band (ESRI 2020). To create a continuous map surface, we used a kernel density estimation using confidence level bins created from the optimized hot spot analysis tool in the population field.

Bear diets were separated into spring-summer (including break-up and ice-free period: April-October) and fall-winter (beginning with freeze-up: November-March) to identify seasonal spatial patterns of prey consumption. Some subpopulations had a relatively equal monthly distribution of samples throughout the year (e.g., Foxe Basin), however most bears were harvested from November-May and thus sample sizes precluded further seasonal separation. Bears were sampled in both seasons with the exception of Southern Hudson Bay bears were only sampled during fall-winter and Norwegian Bay bears were only sampled during spring-summer. QFASA diet estimates reflect integrated diet composition over the preceding weeks to months (Iverson et al. 2004), and thus are well-suited to identify seasonal patterns. We tested for seasonal differences in diet composition within each subpopulation using permutation MANOVA for overall diet and permutation t-tests for each species' contribution to diet.

Previous studies have identified sex-specific differences in polar bear diets, with adult males typically having a more diverse diet given their ability to hunt larger-bodied prey (e.g., bearded seal) relative to adult females and subadults (Thiemann et al. 2011, Johnson et al. 2019, Galicia et al. 2021). Adult males may also be selectively harvested in Nunavut, where management has historically targeted 2 males:1 female sex ratio for harvested bears. We used Fisher's exact tests on proportions of adult male versus adult females and subadults (combined) by subpopulation per season to test for potential bias in samples. Proportions of adult males versus adult females and subadults did not differ within subpopulations ($p > 0.05$ in all cases).

Thus, we did not further divide bears into sex or age classes for spatial analysis; however, we did identify where hot spots of bearded seal or walrus consumption may have been influenced by foraging habits of adult male bears.

Results

Overall diet composition

Ringed seal was the primary prey species across all subpopulations, except for Davis Strait where harp seal (38 ± 1.5%; mean ± SEM) was the primary prey followed by ringed seal (23 ± 1.5%; Figure 5.2). The highest consumption of ringed seal occurred in Southern Hudson Bay (73 ± 2.9%). Although ringed seal consumption was high across our study area, the overall diet composition of polar bears varied regionally. Bearded seal was present in all subpopulations and was the secondary prey in 7 of 10 subpopulations (including Foxe Basin, Gulf of Boothia, Lancaster Sound, M'Clintock Channel, Norwegian Bay, Southern Hudson Bay, and Western Hudson Bay). Bearded seal consumption was highest in M'Clintock Channel (46 ± 5.3%), whereas harbour seal was highest in Western Hudson Bay (17 ± 1.7%). The highest levels of walrus were found in Foxe Basin bears (10 ± 0.8%) with lower proportions (< 4%) in all other subpopulations. Beluga whale varied spatially but was the second highest prey in Baffin Bay and Viscount Melville Sound bears (28 ± 1.7% and 32 ± 4.0%, respectively). Bowhead whale and narwhal were minor dietary components (< 6%) except for Norwegian Bay, where a relatively high proportion of narwhal (18 ± 6.6%) was largely driven by one individual with 56% in diet. Season had a significant effect on polar bear diet composition in Baffin Bay (permutation MANOVA, $p = 0.018$) with higher harp seal consumption in fall-winter (permutation t-test, $p = 0.004$) and Lancaster Sound (permutation MANOVA, $p = 0.002$) with higher narwhal consumption in spring-summer (permutation t-test, $p = 0.002$). There was no seasonal influence in any other subpopulation ($p > 0.050$; Figure 5.2).

Spatial analysis

Hot spot analysis identified seasonal spatial clusters of prey consumption across Nunavut. During spring-summer (Figure 5.3), polar bears had high dietary levels of bearded seal around Southampton Island (31 ± 2.4%) driven by adult males (38 ± 3.4%) and southern M'Clintock Channel (53 ± 8.9%). Bears around Southampton Island and along the western coast of Hudson Bay had high dietary levels of harbour seal (15 ± 1.4% and 16 ± 3.1%, respectively). Harp seal consumption was high in the eastern Canadian Arctic, throughout Davis Strait (Cumberland Sound: 33 ± 3.9% and Frobisher Bay: 30 ± 3.1%) and extended into Hudson Strait (Kimmirut; 27 ± 5.0%), with another hot spot around Jones Sound (Grise Fiord; 30 ± 4.0%). Ringed seal hot spots occurred in Gulf of Boothia (54 ± 1.7%) and Barrow Strait (Resolute; 49 ± 2.6%) and cold spots in Davis Strait (Cumberland Sound: 24 ± 3.8% and Frobisher Bay: 24 ± 3.3%). Walrus consumption was high in northern Foxe Basin (20 ± 3.7%). Beluga whale consumption was high throughout western Baffin Bay (31 ± 2.3%) and south Viscount Melville Sound (Hadley Bay; 33 ± 4.9%). Higher levels of bowhead whale were found in bears around Naujaat (6 ± 1.9%). Narwhal proportions were higher around Barrow Strait (11 ± 2.0%; Figure 5.3).

During fall-winter (Figure 5.4), bearded seal consumption was high among polar bears in Foxe Basin (including northern Foxe Basin: 24 ± 2.8% driven by adult males: 32 ± 4.5%; around Southampton Island: 21 ± 3.4% driven by adult males: 31 ± 5.8%; and around Kimmirut: 26 ± 4.9%), Western Hudson Bay (28 ± 3.3%) with another hot spot in M'Clintock Channel (42 ± 7.1%, driven by adult males: 49 ± 7.2%). Bears had high dietary levels of harbour seal around Southampton Island that extended along the western coast of Hudson Bay to Arviat (19 ± 1.4%). Harp seal consumption was high in Davis Strait (Cumberland Sound: 44 ± 3.1% and Frobisher Bay: 40 ± 2.4%), which matched with ringed seal cold spots (Cumberland Sound: 24 ± 3.0% and

Frobisher Bay: 21 ± 2.3%). Ringed seal hot spots occurred in south-eastern Hudson Bay (73 ± 2.9%), around western Gulf of Boothia (62 ± 1.9%), Arctic Bay (55 ± 2.6%), and Barrow Strait (56 ± 2.1%). Spatial clusters of high walrus proportions extended from northern Foxe Basin (23 ± 3.0%) to Southampton Island (Kinngait: 21 ± 3.6%, Naujaat: 11 ± 2.4%, and Coral Harbour: 20 ± 7.4% driven by adult males: 28 ± 10.4%). Walrus hot spots were matched with ringed seal cold spots in northern Foxe Basin (29 ± 4.6%), Naujaat (28 ± 7.1%), and Kinngait (29 ± 4.9%). Beluga whale consumption was high throughout Baffin Bay (23 ± 2.4%), east of Southampton Island (17 ± 3.4%), and south Viscount Melville Sound (Hadley Bay; 30 ± 6.7%). Polar bears had higher dietary levels of bowhead whale around Naujaat (4 ± 1.4%) and south Viscount Melville Sound (Hadley Bay; 6 ± 4.6%) and no spatial clusters were identified for narwhal consumption (Figure 5.4). Hooded seal was only included in Davis Strait dietary models and no spatial clusters (low or high consumption) were found across the subpopulation throughout the year (spring-summer: 16 ± 1.3% and fall-winter: 16 ± 1.1%).

Discussion

Climate-mediated shifts in preferred environmental conditions will result in species redistribution across ecosystems (Pecl et al. 2017). Arctic species are likely to retract northward, whereas temperate species are expected to become more prevalent in the Arctic and subarctic, and in some regions distributional shifts have already been observed (Laidre et al. 2008, Kovacs et al. 2011). However, shifts in distribution are challenging to track over large spatial and temporal scales, particularly with migratory species. The diet composition of polar bears may help identify local- and broad-scale changes in prey populations. We found that polar bear consumption of prey species varied across and within subpopulations. Polar bear diets were consistent with known patterns of seasonal and spatial prey availability across Nunavut. Our

results suggest that spatial structure in polar bear diet composition can be used to make inferences about the distribution, and availability of prey.

Spatial clusters of polar bear diet composition were generally similar to the seasonal cetacean and pinniped abundance hot spots identified using telemetry tracking (Yurkowski et al. 2019), suggesting polar bear diet estimates may be useful for monitoring marine mammal distribution where other data are limited. Within the Foxe Basin-Hudson Bay complex, Yurkowski et al. (2019) identified marine mammal hot spots in south-western and south-eastern Hudson Bay, north-west and southern Foxe Basin. These areas align with hot spots of polar bear feeding on harbour seal, ringed seal, and a combination of prey (bearded seal, bowhead whale, and walrus), respectively in this study. In the eastern Canadian Arctic, telemetry hot spots in Cumberland Sound and along eastern Baffin Island (Yurkowski et al. 2019) matched harp seal and beluga whale hot spots, respectively in this study. In the High Arctic, marine mammal hot spots in Jones Sound, Lancaster Sound, and Viscount Melville Sound (Yurkowski et al. 2019) were associated with polar bears feeding on harp seal, ringed seal and seasonal narwhal, and beluga whale and seasonal bowhead whale hot spots, respectively. We found additional hot spots including south Gulf of Boothia (ringed seal hot spot), Barrow Strait (ringed seal and narwhal hot spot), and north-western Hudson Bay (harbour and bearded seal hot spot) that lacked year-round marine mammal tracking data.

Some regions would be expected to support a highly productive food web linked to greater primary production (Eddy et al. 2021). Polynyas, for example are ecologically important areas of recurring open water within the Arctic ecosystem (Stirling 1980, 1997). A large polynya such as the North Water Polynya in northern Baffin Bay can support a high abundance of marine mammals year-round (Heide-Jørgensen et al. 2013, 2016) and influence biological productivity

in adjacent waters (Stirling 1997). Smaller polynyas and shore leads throughout the Arctic also provide local areas of high biological productivity and thus greater prey biomass for polar bears (Stirling 1997). Prey consumption hot spots identified in our study aligned with known polynyas and adjacent waters (Stirling and Cleator 1981, Stirling 1997). For example, Roes Welcome Sound polynya (extending from Naujaat south to Chesterfield Inlet) supports a high diversity of marine mammals (Stirling 1997) and matched the year-round bowhead whale and harbour seal hot spots, and fall-winter walrus hotpot in this study. High densities of ringed seals have been previously recorded near Bellot Strait polynya during the summer and potentially year-round (Stirling and Cleator 1981). We found a consistent ringed seal hot spot in Gulf of Boothia (south of Bellot Strait polynya) suggesting their year-round availability may be influenced by highly productive waters of these local polynyas.

Ringed seals and bearded seals are widely distributed across the circumpolar range of polar bears. In our study, ringed seal represented the dominant prey species based on proportional levels in diet, with bearded seal as the secondary prey across Nunavut. There were no overlapping hot spots in consumption perhaps due to differences in seal habitat preference; ringed seals prefer fast ice or consolidated pack ice whereas bearded seals prefer dynamic pack ice in winter (Stirling and Derocher 1993, Kovacs and Lydersen 2008, Chambellant et al. 2012). The relative importance of both prey species also varied spatially and seasonally. Areas with high dietary proportions of ringed seal, such as Gulf of Boothia and south-eastern Hudson Bay, had relatively low levels of other prey (defined as either cold spots or non-significant areas), suggesting that alternate prey are largely unavailable. In contrast, areas with low ringed seal consumption corresponded with high consumption of other prey species (e.g., bearded seal, harp seal, and walrus) suggesting polar bears will target alternate prey (i.e., species other than ringed

seals) based on availability. We did not test weather hot spots and cold spots were significantly different between seasons, but dietary proportions of ringed seal were higher in fall-winter than spring-summer for both Gulf of Boothia and Lancaster Sound. A similar trend was observed in Thiemann et al. (2008a) and attributed to an increase in migrant species becoming more accessible to bears. For example, in our study the lower consumption of ringed seals in spring-summer around Barrow Strait was matched with an increase in the consumption of narwhal, which seasonally migrate to the area (Heide-Jørgensen et al. 2003).

We identified harbour seal consumption hot spots throughout the year around Southampton Island and along western Hudson Bay, suggesting potential year-round availability. Harbour seal have been found to concentrate along the western Hudson Bay coast south of Naujaat, around Southampton Island and Chesterfield Inlet (Mansfield 1967) and show a preference for shallower waters (Bajzak et al. 2013). High consumption of harbour seal has been previously detected in the Western Hudson Bay subpopulation (Sciullo et al. 2017, Johnson et al. 2019), as well as southern Foxe Basin (Galicia et al. 2021) and our findings further emphasize their availability throughout the year in this region.

Spatial clusters of high harp seal consumption were found along the eastern Canadian Arctic with year-round hot spots occurring in Frobisher Bay and Cumberland Sound. Cold spots of low harp seal consumption were consistently found in the central Arctic, e.g., around Southampton Island and Gulf of Boothia. Our findings suggest harp seals are important prey for bears in Davis Strait likely as a function of their high regional abundance (Hammill et al. 2021), but their relative importance in other areas depends on seasonal movement. Higher proportions in Jones Sound during spring-summer reflected the movement of harp seals as sea ice retreats along the Canadian continental shelf towards High Arctic feeding areas. Because our diet

estimates are proportional, the ringed seal cold spot in Davis Strait may be explained by high proportional consumption of harp seal. However, Cumberland Sound and Frobisher Bay polynyas have been found to support relatively high numbers of harp seals (Stirling and Cleator 1981, Diemer et al. 2011) and a relatively low to moderate number of ringed seals (Stirling and Cleator 1981). Our results are consistent with previous broad-scale analyses showing high harp seal consumption by bears in Davis Strait (Iverson et al. 2006, Thiemann et al. 2008a).

We found a consistent hot spot of walrus consumption in northern Foxe Basin and seasonal hot spots around Naujaat, Coral Harbour, and Kinngait. The year-round hot spot found in northern Foxe Basin is consistent with the high regional concentration and the restricted seasonal movement of the Foxe Basin walrus population (COSEWIC 2006). Walrus overwinter in polynyas across Foxe Basin, but there is a predictable presence of walrus in the northwestern Foxe Basin polynya throughout winter (Stirling 1980, Stirling and Cleator 1981, COSEWIC 2006). The seasonal movement of the Northern Hudson Bay-Davis Strait walrus population is unknown; some individuals have been found to remain in areas year-round, whereas others undertake seasonal migrations (COSEWIC 2006). The spatial cluster in fall-winter in southern Foxe Basin and western Hudson Strait may indicate a seasonal availability of walrus in these regions. Ringed seal consumption was lower across Foxe Basin suggesting these two prey species have minimal spatial overlap, particularly during fall-winter when walrus hot spots were matched with ringed seal cold spots (i.e., low consumption). There is some evidence that ringed seals may avoid areas with large concentrations of walrus due to risk of predation (Kingsley et al. 1985, Stirling 1997). Spatial clusters of high bearded seal and walrus consumption during fall-winter were similar across Foxe Basin suggesting similarities in preferred habitat (e.g.,

overwintering in polynyas) and limited risk of bearded seals being killed by walrus (Nelson et al. 1985, Stirling 1997, Kovacs et al. 2011).

Beluga whale hot spots were identified in Baffin Bay and south Viscount Melville Sound likely due to dynamic sea ice conditions that expose belugas to predation by polar bears through ice entrapment or limited use of cracks and leads (Smith and Sjare 1990). Belugas are also susceptible to predation during the summer in swallow water estuaries (Smith and Sjare 1990) and when clumped together along the shore to avoid killer whales (Westdal et al. 2016). Possible scavenging may also occur on remains from subsistence harvested beluga whales (DFO 2018). High proportions of beluga whale in diet estimates of Baffin Bay polar bears have been similarly found in other studies (Thiemann et al. 2008a, Galicia et al. 2015). In winter, beluga whales use the cracks and leads throughout the North Water Polynya and adjacent waters (Richard et al. 1998, Heide-Jørgensen et al. 2016) which likely contribute to the high dietary levels in Baffin Bay diets. During the summer, beluga whales occur in fjords and polar bears congregate along coastlines of Baffin Island (Ferguson et al. 1997, Laidre et al. 2008). Although less common, polar bears have been observed hunting belugas in open water (Laidre et al. 2018) and this overlapping distribution may create opportunities for summer predation. Using harvest-based sampling in the Inuvialuit Settlement Region, Florko et al. (2021) found similar levels of beluga consumption (~37% across Viscount Melville Sound compared to 32% found in Hadley Bay in this study), suggesting beluga whales are an important polar bear prey item in this area. Although Viscount Melville Sound is historically characterized by extensive multi-year ice, declining sea ice may be facilitating the use of this region by greater numbers of beluga and early beluga migration into Viscount Melville Sound may increase their vulnerability to polar bear predation. Other beluga hot spots only appeared in fall-winter around Southampton Island suggesting

increased predation linked to heavier sea ice conditions possibly associated with entrapment events.

The narwhal consumption hot spot likely reflected the seasonal migration between summering and wintering areas. Although narwhal are adapted to heavy pack ice habitats, there is still risk of ice entrapment that may lead to natural mortality and/or exposure to polar bear predation (Laidre and Heide-Jørgensen 2005, Laidre et al. 2012, Watt et al. 2015). The Somerset Island narwhal population overwinters farther north than other narwhal populations and arrives in Lancaster Sound in mid-May (Dietz et al. 2008). Our results indicate a narwhal consumption hot spot around Somerset Island in April and May which is earlier than anticipated. Heide-Jørgensen et al. (2003) reported narwhal arriving in eastern Lancaster Sound as early as April, however waiting to enter Lancaster Sound until the sea ice retreats. If some individuals are entering Lancaster Sound earlier in April and May, heavier sea ice conditions may concentrate narwhal along narrow openings in the sea ice and expose them to polar bear predation leading to an increase in dietary levels. Some individual bears had high levels of narwhal in diets, however there were no other spatial clusters of high or low consumption (i.e., all non-significant areas) suggesting narwhal are likely hunted opportunistically or scavenged in most areas. Narwhal and beluga have similar distributions across Nunavut (Innes et al. 2002), however, the lack of spatial clusters for high consumption of narwhal compared to beluga found in our study suggests beluga are more susceptible to polar bear predation than narwhal. Although there has been evidence of polar bear predation on narwhal, proportions of narwhal in bear diet estimates have been minor in most studies (Thiemann et al. 2008a, Galicia et al. 2015).

Bowhead whale was a minor dietary component across the study area, however we found one consistent bowhead hot spot around Naujaat and another seasonal hot spot in Viscount

Melville Sound (fall-winter, Figure 5.4). The Bering-Chukchi-Beaufort and Eastern Canada-West Greenland populations are increasing which could potentially lead to an increase in bowhead whale strandings. Bowhead seasonally migrate into the eastern Beaufort Sea and Foxe Basin-Hudson Bay, during the late summer-early fall (Givens et al. 2013, Doniol-Valcroze et al. 2020, Ferguson et al. 2021). There is recent evidence that bowhead whales overwinter in the Beaufort Sea and Amundsen Gulf (their known summer foraging areas) driven by potential factors such as killer whale avoidance and warmer temperatures in the Bering and Chukchi Seas, or in an attempt to reduce energetic expenditure (Insley et al. 2021). Their increased presence during fall and winter could potentially result in more carcasses that become accessible to bears in Viscount Melville Sound leading to a dietary hot spot. In Foxe Basin, bowhead whale carcasses are becoming more common in polar bear diets due to increased subsistence harvest, natural mortality, and killer whale predation (Galicia et al. 2021). We identified a consistent hot spot for bowhead consumption within the Foxe Basin subpopulation, and more specifically Naujaat which reflects an increase in carcass availability to polar bears. Cold winter temperatures likely increase the longevity of a carcass to act as a supplemental food source resulting in higher dietary levels year-round. Killer whales may be attracted to the greater productivity due to the Roes Welcome Sound polynya (Stirling 1997) and the diversity of marine mammal prey including bowhead whales (Cosens and Innes 2000). This overlap in distribution may result in increased killer whale predation on bowhead and consequently an increased frequency of accessible carcasses to bears.

The spatial distribution of harvest-based sampling could have affected our interpretation of the spatial structure of polar bear diets. The spatial clusters (i.e., hot spots and cold spots) we identified were generally associated with Inuit communities. Polar bears have large home ranges

(Ferguson et al. 1999, Amstrup et al. 2000, Mauritzen et al. 2001, McCall et al. 2015) and the relationship between where a bear was harvested and where it foraged is to some extent uncertain. However, polar bears are often philopatric and differential space use strategies have led to genetic differentiation within subpopulations (Crompton et al. 2008, 2014, Viengkone et al. 2016, Maduna et al. 2021). Thus, the harvest-based samples collected in this study by hunters across Nunavut (Figure 5.1) likely reflect broad spatial patterns of prey availability. In some cases, hot spots and cold spots may not necessarily reflect relative abundance of prey species, but rather their vulnerability to predation.

Sea ice loss and warming temperatures will have profound impacts across the Arctic with cascading ecological consequences (Post et al. 2013). There remain considerable uncertainties surrounding the timing and specific responses of species to changing environmental conditions. Monitoring spatial patterns of diets can reveal localized areas of available prey that may otherwise be overlooked at larger subpopulation level investigations. Additionally, the year-round harvest of polar bears has provided insight into the seasonal diets of bears and seasonal distribution of their marine mammal prey. There is limited information on marine mammal abundance and distribution across the Arctic and studies can be logistically intensive and expensive. Although the spatial distribution of harvest samples may be biased towards human settlements, our study indicates that polar bear diets reflect known spatial and seasonal timing of prey availability and may serve as an index of distribution and short-term or localized changes in prey abundance. To identify potential range shifts in Arctic marine mammals (e.g., temperate species moving into Arctic waters), future studies of polar bear diets should include prey species that have not been historically known in the region. Identifying areas of polar bear and prey overlap may provide further understanding of regional predator-prey dynamics and help predict

the severity and influence of climate-induced change. Thus, polar bears can serve as indicators of regional and broad-scale changes in marine mammal prey populations and the functioning of the Arctic ecosystem.

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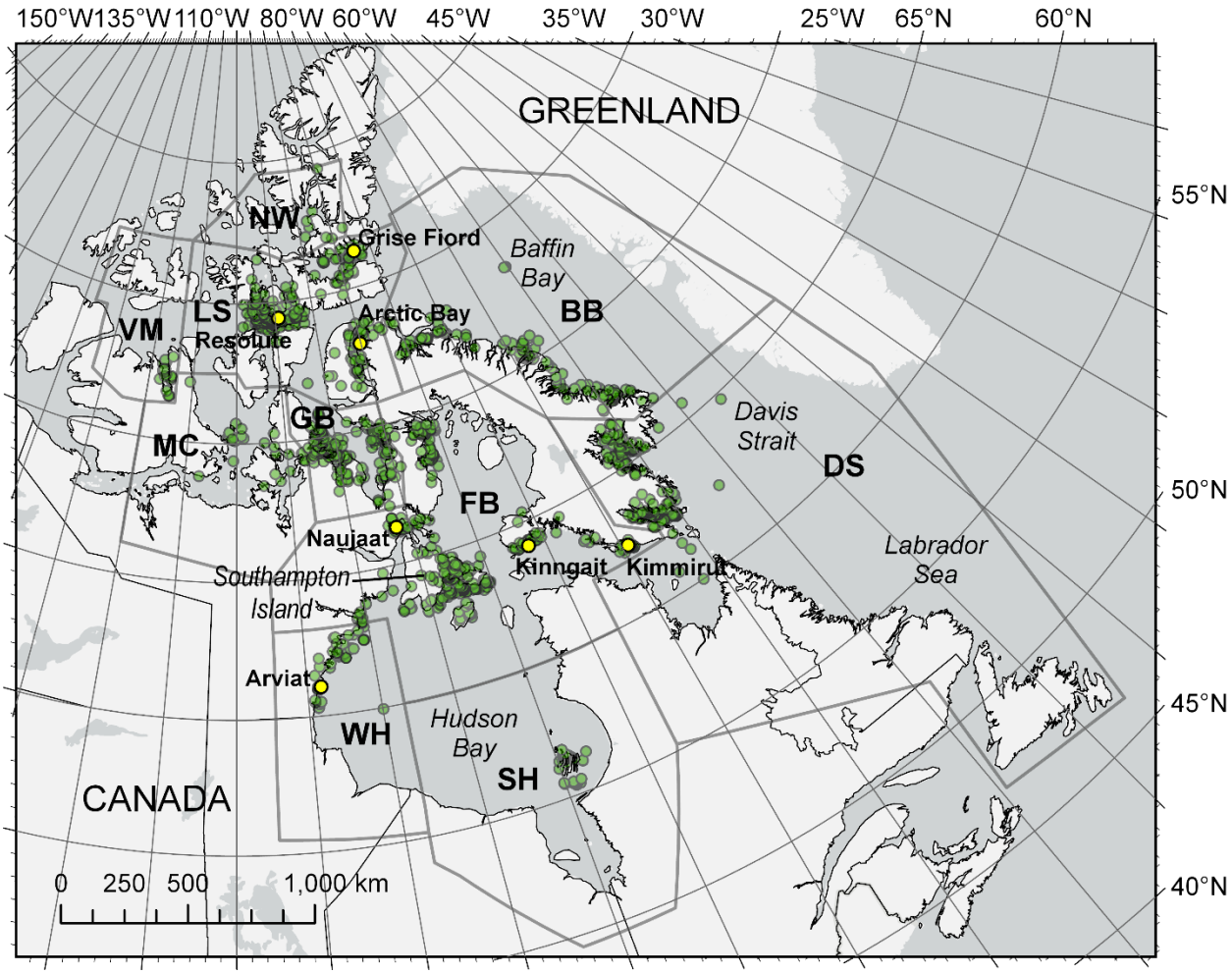

Figure 5.1 Map of Nunavut, Canada where polar bears were harvested by local Inuit hunters from 2010-2018 (n = 1570) in 10 Canadian subpopulations: Baffin Bay (BB, n = 158), Davis Strait (DS, n = 208), Foxe Basin (FB, n = 406), Gulf of Boothia (GB, n = 250), Lancaster Sound (LS, n = 371), M'Clintock Channel (MC, n = 30), Norwegian Bay (NW, n = 7), Southern Hudson Bay (SH, n = 52), Viscount Melville Sound (VM, n = 21), and Western Hudson Bay (WH, n = 67). Green dots represent locations of harvested bears and yellow dots represent select communities referred to in results section. The grey outline represents the subpopulation boundaries.

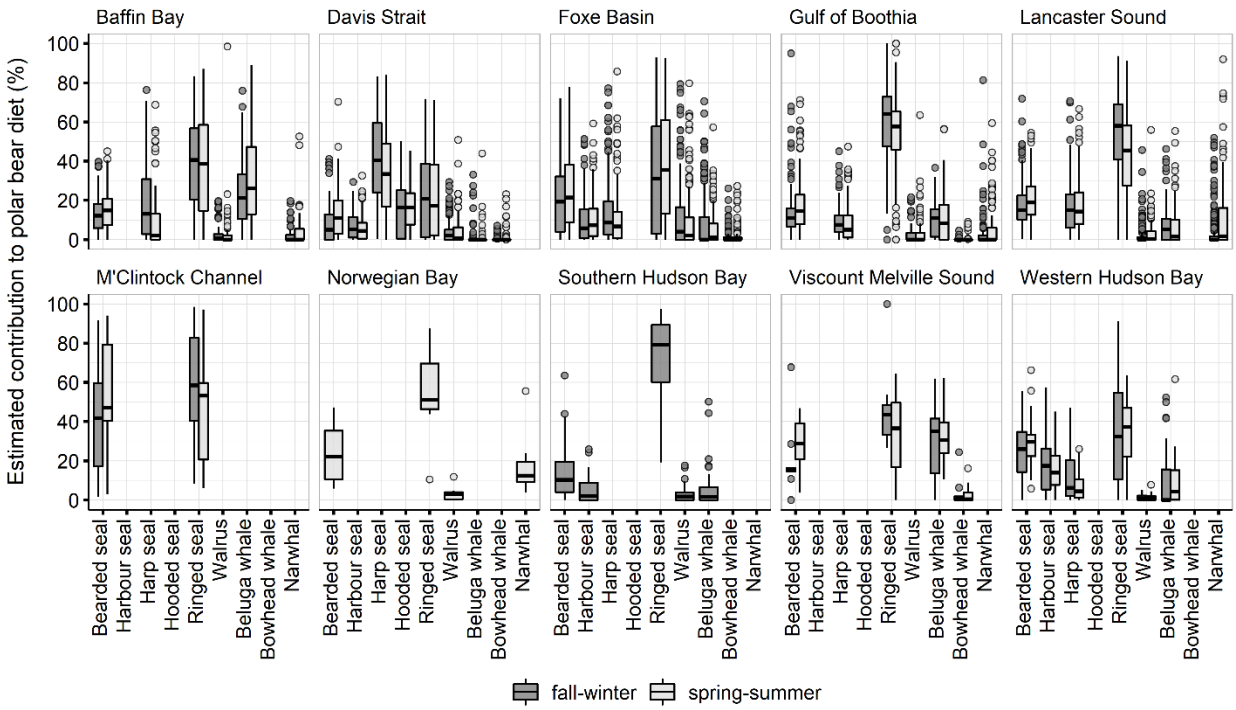

Figure 5.2 Diet composition of polar bears (n = 1570) across Nunavut from 2010-2018 as estimated from quantitative fatty acid signature analysis separated by season (spring-summer and fall-winter). Data represent each prey species' biomass contribution to diet estimates shown as boxplots showing the 25th quartile, median, 75th quartile, and outliers shown as solid circles.

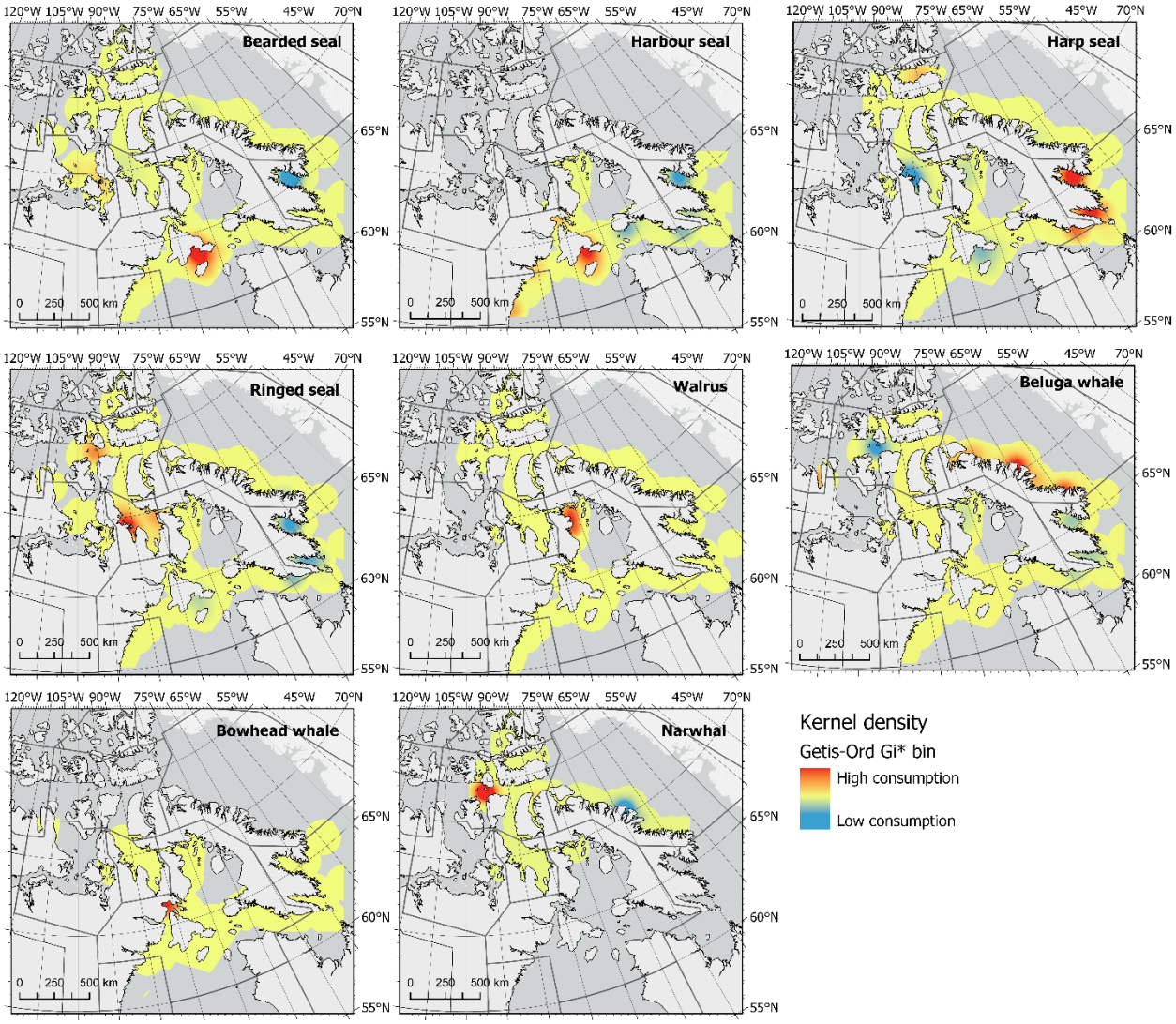

Figure 5.3 Kernel density surface of Getis-Ord Gi* bins of weighted prey contribution to polar bear diets across Nunavut in spring-summer from 2010-2018 as estimated from quantitative fatty acid signature analysis. Grey outlines represent the border of Nunavut polar bear subpopulations.

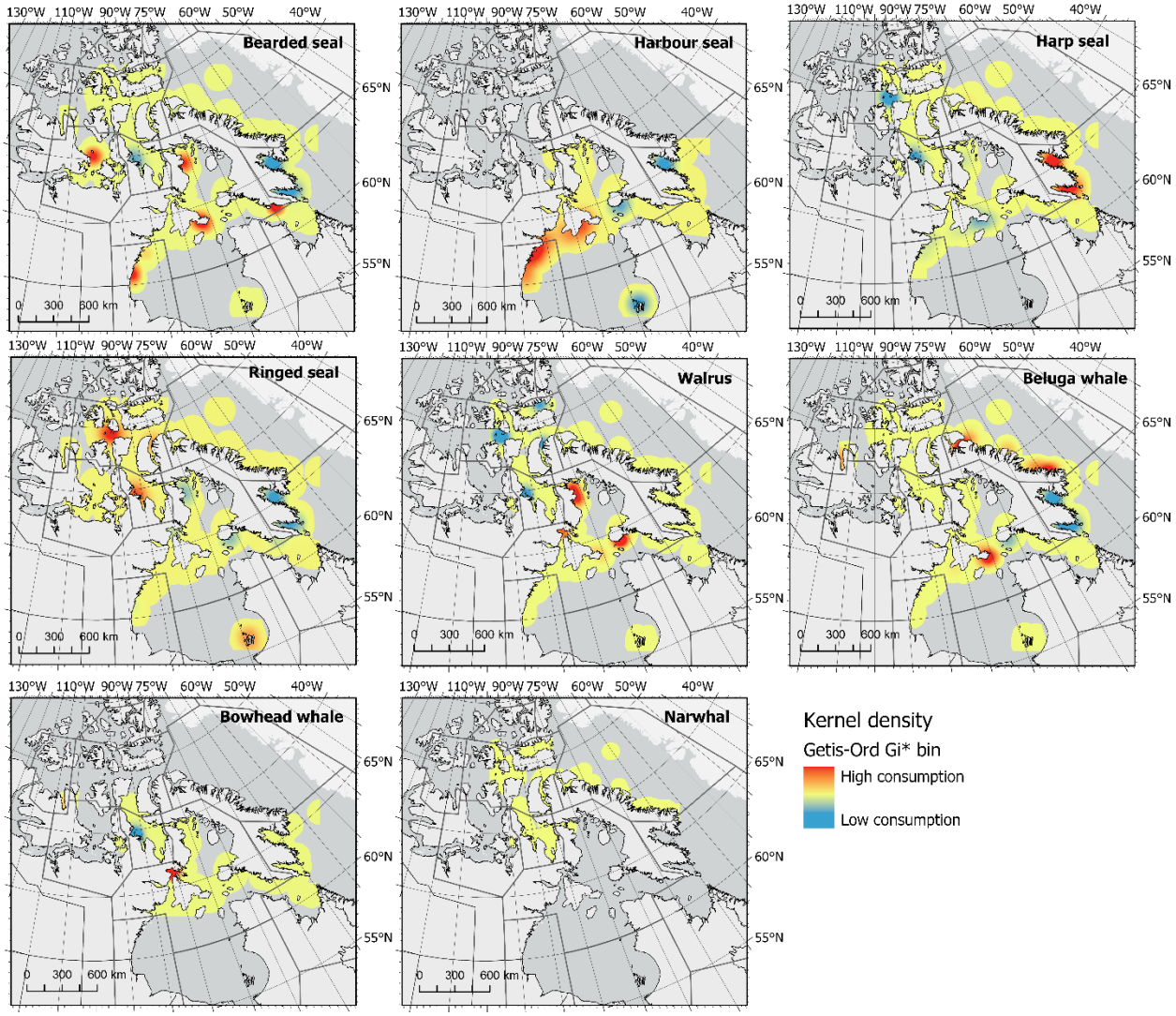

Figure 5.4 Kernel density surface of Getis-Ord Gi* bins of weighted prey contribution to polar bear diets across Nunavut in fall-winter from 2010-2018 as estimated from quantitative fatty acid signature analysis. Grey outlines represent the border of Nunavut polar bear subpopulations.

Supplemental Material

Results from diagnostic functions to assess prey libraries

Table S5.1 Proportion of leave-one-prey-out estimates attributed to the correct prey type within the prey library for each polar bear subpopulation.

Baffin Bay

	Bearded	Beluga	Harp	Narwhal	Ringed	Walrus
Bearded	0.76	0.03	0.02	0.00	0.04	0.15
Beluga	0.02	0.72	0.04	0.16	0.04	0.01
Harp	0.03	0.06	0.72	0.02	0.15	0.03
Narwhal	0.03	0.07	0.00	0.86	0.01	0.02
Ringed	0.03	0.03	0.09	0.03	0.78	0.04
Walrus	0.01	0.00	0.00	0.00	0.03	0.96

Davis Strait

	Bearded	Beluga	Bowhead	Harbour	Harp	Hooded	Ringed	Walrus
Bearded	0.76	0.03	0.00	0.08	0.01	0.01	0.03	0.07
Beluga	0.01	0.83	0.05	0.01	0.04	0.03	0.03	0.00
Bowhead	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Harbour	0.02	0.01	0.00	0.95	0.01	0.00	0.00	0.01
Harp	0.00	0.03	0.03	0.02	0.70	0.03	0.17	0.02
Hooded	0.00	0.06	0.05	0.04	0.06	0.78	0.00	0.00
Ringed	0.01	0.00	0.00	0.01	0.09	0.01	0.84	0.03
Walrus	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.98

Foxe Basin

	Bearded	Beluga	Bowhead	Harbour	Harp	Narwhal	Ringed	Walrus
Bearded	0.74	0.01	0.00	0.10	0.00	0.00	0.05	0.09
Beluga	0.01	0.79	0.03	0.01	0.02	0.10	0.04	0.00
Bowhead	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Harbour	0.01	0.00	0.00	0.95	0.01	0.01	0.01	0.01
Harp	0.01	0.03	0.04	0.02	0.76	0.02	0.11	0.02
Narwhal	0.01	0.06	0.04	0.00	0.00	0.89	0.00	0.01
Ringed	0.04	0.02	0.00	0.07	0.08	0.01	0.74	0.04
Walrus	0.01	0.00	0.00	0.01	0.00	0.00	0.04	0.94

Gulf of Boothia

	Bearded	Beluga	Bowhead	Harp	Narwhal	Ringed	Walrus
Bearded	0.76	0.03	0.01	0.01	0.01	0.07	0.11
Beluga	0.03	0.70	0.03	0.02	0.19	0.04	0.00
Bowhead	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Harp	0.01	0.02	0.03	0.76	0.02	0.14	0.02
Narwhal	0.05	0.09	0.05	0.00	0.79	0.01	0.02
Ringed	0.04	0.01	0.01	0.07	0.01	0.84	0.03
Walrus	0.05	0.00	0.00	0.00	0.00	0.02	0.94

Table S5.1. Continued.

Lancaster Sound

	Bearded	Beluga	Harp	Narwhal	Ringed	Walrus
Bearded	0.72	0.02	0.04	0.02	0.05	0.14
Beluga	0.03	0.72	0.01	0.19	0.05	0.00
Harp	0.01	0.03	0.86	0.00	0.06	0.04
Narwhal	0.05	0.12	0.01	0.80	0.00	0.01
Ringed	0.03	0.04	0.11	0.03	0.75	0.04
Walrus	0.05	0.00	0.00	0.00	0.01	0.94

M'Clintock Channel

	Bearded	Ringed
Bearded	0.84	0.16
Ringed	0.09	0.91

Norwegian Bay

	Bearded	Narwhal	Ringed	Walrus
Bearded	0.71	0.05	0.11	0.13
Narwhal	0.01	0.95	0.03	0.01
Ringed	0.05	0.06	0.86	0.03
Walrus	0.02	0.00	0.03	0.96

Southern Hudson Bay

	Bearded	Beluga	Harbour	Ringed	Walrus
Bearded	0.75	0.02	0.10	0.03	0.09
Beluga	0.01	0.93	0.00	0.02	0.03
Harbour	0.01	0.01	0.93	0.04	0.01
Ringed	0.03	0.10	0.14	0.73	0.00
Walrus	0.02	0.01	0.02	0.02	0.94

Viscount Melville Sound

	Bearded	Beluga	Bowhead	Ringed
Bearded	0.74	0.07	0.01	0.18
Beluga	0.02	0.80	0.05	0.14
Bowhead	0.01	0.01	0.96	0.02
Ringed	0.14	0.06	0.03	0.78

Western Hudson Bay

	Bearded	Beluga	Harbour	Harp	Ringed	Walrus
Bearded	0.76	0.01	0.10	0.01	0.03	0.09
Beluga	0.01	0.84	0.00	0.10	0.01	0.03
Harbour	0.01	0.01	0.93	0.00	0.03	0.01
Harp	0.01	0.03	0.05	0.77	0.11	0.03
Ringed	0.03	0.03	0.14	0.09	0.70	0.00
Walrus	0.03	0.00	0.02	0.00	0.01	0.94

Predator signature simulations were performed using both the original and partitioned prey library established using the divisive magnetic clustering function (DIMAC; Bromaghin 2017, Bromaghin et al. 2017). To compare partitioned to the original prey library, estimates from the partitioned library were pooled back to the original prey types. The mean and standard error of the estimates for each simulated diet were computed by prey type and the mean was compared to the estimated diet to calculate bias. Summary measures across all prey types were computed as the sum of absolute values of bias (difference between estimated and simulated diet) and the square root of the sum of variances. The sum of absolute bias across all prey species in Baffin Bay, Foxe Basin, Lancaster Sound, and Western Hudson Bay increased by 110%, 122%, 28%, and 204%, respectively. The square root of the sum of the variances decreased 4% and 16% in Baffin Bay and Foxe Basin, respectively, and increased by 2% and 8% in Lancaster Sound and Western Hudson Bay, respectively with the partitioned prey library (Table S5.2). The original prey library was used to estimate the diets of bears in this study due to the lack of improvement in QFASA performance with the partitioned prey library.

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Table S5.2 Results of predator simulations with the original (unpartitioned) and DIMAC-partitioned prey libraries. Bias and standard errors (SE) of diet estimates obtained from 1000 simulated signatures conditioned on the realistic diets from polar bears in Baffin Bay, Foxe Basin, Lancaster Sound, and Western Hudson Bay (as examples).

			Bias		SE	
Subpopulation	**Prey**	**Diet**	**Orig.**	**Part.**	**Orig.**	**Part.**
Baffin Bay	Bearded	0.068	0.000	0.028	0.002	0.002
	Beluga	0.243	0.042	0.026	0.005	0.004
	Harp	0.186	-0.006	0.071	0.005	0.004
	Narwhal	0.012	-0.056	-0.068	0.004	0.003
	Ringed	0.424	0.024	-0.070	0.004	0.004
	Walrus	0.067	-0.004	0.013	0.001	0.003
	Over all prey	1.000	0.131	0.276	0.147	0.141
Foxe Basin	Bearded	0.143	0.011	-0.029	0.004	0.003
	Beluga	0.041	0.021	0.045	0.003	0.002
	Bowhead	0.008	0.010	0.014	0.001	0.001
	Harbour	0.071	-0.008	-0.002	0.002	0.002
	Harp	0.199	-0.041	-0.078	0.004	0.002
	Ringed	0.442	0.001	0.046	0.006	0.004
	Walrus	0.096	0.005	0.003	0.002	0.001
	Over all prey	1.000	0.098	0.218	0.145	0.122
Lancaster Sound	Bearded	0.155	0.036	0.041	0.003	0.003
	Beluga	0.036	-0.023	-0.015	0.003	0.002
	Harp	0.231	0.021	-0.018	0.004	0.004
	Narwhal	0.021	-0.026	-0.048	0.003	0.003
	Ringed	0.548	0.010	0.045	0.006	0.005
	Walrus	0.009	-0.018	-0.006	0.001	0.003
	Over all prey	1.000	0.134	0.172	0.139	0.142
Western Hudson Bay	Bearded	0.232	0.009	-0.077	0.005	0.006
	Beluga	0.046	-0.020	-0.049	0.002	0.003
	Harbour	0.046	-0.039	-0.071	0.004	0.006
	Harp	0.169	0.002	0.123	0.004	0.003
	Ringed	0.472	0.059	0.090	0.006	0.005
	Walrus	0.035	-0.010	-0.015	0.001	0.003
	Over all prey	1.000	0.140	0.426	0.151	0.163

Chapter 6: Conclusion

Summary

Continued climate warming will likely alter the structure and functioning of Arctic ecosystems with negative consequences on endemic species. Polar bears (*Ursus maritimus*) are dependent on the sea ice as a platform to hunt, travel, and mate (Amstrup 2003). Changing ice conditions may lead to reduced foraging opportunities, shifts in prey availability, or increased energetic demand that influence body condition and diet, and subsequently survival and reproduction of polar bears. In this dissertation, I examined the foraging ecology of polar bears in Nunavut, Canada by analyzing seasonal body condition and quantifying diet. Overall, the findings of this dissertation provide new knowledge on the foraging ecology of polar bears that reflect the seasonal and spatial availability of prey across Nunavut. A primary outcome was the increased understanding of ecological mechanisms that may help drive the resilience of polar bears to environmental shifts. This dissertation also further highlights the ability of harvest-based and remote biopsy-based adipose tissue samples to provide valuable ecological information over a broad spatiotemporal scale.

The magnitude of climatic-driven effects on polar bears will be influenced by the precise timing of feeding in relation to sea ice conditions (e.g., ice break-up). In chapter 2, I used adipose tissue lipid content to examine seasonality in body condition of polar bears harvested in Nunavut, Canada. I found evidence that bears continued to accumulate fat stores into early summer suggesting any advance in spring sea ice break-up will directly influence foraging opportunities for bears. The same general patterns were found in all subpopulations examined (i.e., Baffin Bay, Davis Strait, Foxe Basin, Gulf of Boothia, and Lancaster Sound) where polar bears reached their lowest body condition in March-April in time for when seal pups are most vulnerable and accessible, then continued to accumulate fat into early summer beyond break-up,

reaching their highest body condition in the fall. The link between sea ice loss and declining body condition is well-established (Stirling et al. 1999, Regehr et al. 2007, Lunn et al. 2016), however the response of polar bears to future environmental change remains poorly understood. This study provides new insights into the seasonal patterns of body condition in relation to sea ice conditions and demonstrates the usefulness of harvest-based samples to monitor polar bear body condition.

Understanding the relationship between wildlife populations and their habitat may at times require the capture and handling of free-ranging animals. However, the live capture of large mammals such as polar bears may be logistically challenging, expensive, and does not always align with the research priorities and values of northern Indigenous people (Henri et al. 2010, Wong et al. 2017). In chapter 3, I examined the utility of adipose tissue obtained from remote biopsies used in genetic mark-recapture studies of polar bears. I compared adipose lipid content, fatty acid data, and diet composition estimates from remote biopsies and harvest-based samples from two subpopulations (Davis Strait and Gulf of Boothia). I found that adipose lipid content from remote biopsies did not provide comparable estimates to harvest samples, likely because of the superficially removed tissue (i.e., outer layer) compared to the entire depth taken from harvested samples. In contrast, fatty acids have been found to be uniform across the entire depth of the tissue (Thiemann et al. 2006). In this study, I found the distribution of individual fatty acids and diet estimates between remote biopsy and harvest samples were similar and any small difference likely reflected regional, intraspecific, or temporal variation as opposed to the sample type. This study validates the utility of remote biopsies to reliably estimate fatty acid and diet composition of polar bears.

The Foxe Basin subpopulation has remained stable (Stapleton et al. 2016) despite sea ice loss, increased fragmentation and shifts in the timing of break-up and freeze-up (Sahanatien and Derocher 2012). In chapter 4, I used quantitative fatty acid signature analysis (QFASA) to measure changes in polar bear diet composition over an 18-year period. My results suggest polar bears in Foxe Basin are exploiting a wide diversity of prey and may switch between prey types based on availability, subsequently contributing to the subpopulation's demographic stability. Ringed seal remained the primary prey across the subpopulation, however overall diet composition varied spatially, temporally, and by intrinsic factors (i.e., sex and age class) and the frequency of prey in diets varied over time likely reflecting variation in availability. The large body size of adult male bears presumably allowed them to capture and perhaps target large-bodied prey leading to a broader dietary niche and lower vulnerability to declines in the sea ice compared to smaller bears (i.e., adult females and subadults) with more constrained dietary habits. My results also suggest a potential synergistic interaction where polar bears are benefiting from killer whales, an emerging top predator in the Arctic that are depredated on bowhead whales leading to an increase in available carcasses that can serve as a supplemental food source for bears. These findings suggest flexible foraging strategies of polar bears may provide alternatives during years when preferred prey are less abundant and help buffer the negative consequences of sea ice loss, at least in the near term.

Climate-mediated environmental change will result in Arctic species retracting northward and temperate species becoming more prevalent in the Arctic and subarctic (Laidre et al. 2008, Kovacs et al. 2011). There is limited information on marine mammal distribution throughout the Arctic, and since most large-bodied species at high latitudes tend to migrate, attempts to track distributional shifts are logistically challenging. In chapter 5, I quantified spatial structure in the

feeding patterns of polar bears and assessed the feasibility of using predator diet as a monitoring tool to identify range shifts of prey. I used QFASA to estimate diet and a new method (hot spot analysis tool in ArcGIS) to identify areas with high and low consumption of different prey. Polar bear diet varied within and across Canadian subpopulations and generally matched known patterns of seasonal and spatial prey availability. Ringed seal (*Pusa hispida*) were the primary prey followed by bearded seal with no overlapping spatial clusters, likely as a result of differences in habitat preference. Year-round spatial clusters of walrus (*Odobenus rosmarus*), harbour seal (*Phoca vitulina*), and harp seal (*Pagophilus groenlandicus*) consumption were linked to known areas with high regional abundance. Chapter 5 also provided new knowledge of local conditions that promote polar bear predation on beluga whale (*Delphinapterus leucas*), as well as locally accessible bowhead whale (*Balaena mysticetus*) carcasses that serve as a supplemental food source. I found similarities between polar bear feeding patterns and known prey distribution that suggests continued monitoring of diet will reveal future local- and broad-scale changes in prey populations.

This dissertation provides evidence of the breadth of knowledge that can be obtained from adipose tissue of polar bears either harvested or remote biopsied during genetic mark-recapture studies. Overall, this research focused on polar bear subpopulations with limited knowledge on body condition (chapter 2) and diet (chapter 4 and 5). Additionally, chapter 3 suggested the possibility of using a less invasive sampling approach that would reliability provide dietary information for polar bears in Nunavut. Continued monitoring of polar bear feeding patterns will be important to assess population-level shifts linked to ongoing environmental change. This research provides a more comprehensive understanding of polar bear

vulnerability and resilience to climate change and may help wildlife managers and policy makers make informed decisions about management regulations and conservation status.

Conservation Implications and Future Directions

Polar bears are listed as "vulnerable" on the IUCN Red List (Wiig et al. 2015) and "Special Concern" under the Canadian Species at Risk Act (COSEWIC 2018). Subpopulation trends range from likely decreased to very likely increased with 8 subpopulations classified as data deficient (IUCN/SSC Polar Bear Specialist Group 2019). The foraging strategies of polar bears, as well as prey distribution and sea ice conditions, differ across the subpopulations, and consequently the timing and degree of climate-induced change also differs (Stirling and Derocher 2012). This dissertation highlights the need for broad spatial and temporal scale studies to capture regional differences in polar bear foraging in relation to local and seasonal ecological conditions in areas of the Arctic where short- and long-term data are limited. The results of this dissertation provide novel insights into polar bear ecology by analyzing samples obtained during subsistence hunts, further emphasizing the importance of community-based programs. A better understanding of the relationship between species and their habitat will be essential to maintain viable populations and manage species affected by environmental change.

This dissertation provides insights into polar bear foraging ecology in relation to ongoing environmental change across Nunavut. Although harvest-based samples have provided insight into the temporal, spatial, and demographic factors affecting the body condition and diet of polar bears, there are limitations when it comes to investigating polar bears across different reproductive classes (e.g., females with dependent cubs versus adult males). However, remote biopsy samples (chapter 3) offer the opportunity to examine foraging behaviour via fatty acid analyses of females with dependent cubs that are prohibited to hunt under harvest regulations.

Additionally, remote biopsy samples provide the ability to sample the same individual providing a better understanding of individual dietary specialization and possible consequences of changing prey populations.

In chapter 2 and 4, I demonstrated the effects of sea ice conditions, in particular how shifts in break-up and freeze-up can affect body condition and prey selection of polar bears. However, the sea ice habitat is more complex than potentially one metric can describe with the possibility of interacting variables and thus there is a need for further investigation into how sea ice conditions (e.g., leads or ice fragmentation) can influence the foraging behaviour and success of polar bears. Specific ice metrics that may enhance the capture of a given prey species could be examined. For example, increased climate variability that results in opening and re-freezing of leads and cracks may consequently increase the frequency of beluga and narwhal entrapment events, in turn increasing their vulnerability to bear predation.

Episodic changes in large-scale atmospheric circulation patterns may result in abrupt and unpredictable ecological regime shifts (Ferguson et al. 2017). Climatic oscillation patterns have been linked to variability in sea ice conditions with negative consequences on prey abundance and polar bear population dynamics (Pilfold et al. 2015, Rode et al. 2018, 2021). For example, Rode et al. (2021) found that polar bear recruitment was inversely correlated with winter Arctic Oscillation (AO) index and Pilfold et al. (2015) suggested the winter AO influenced polar bear predation rate. There is also evidence of the North Atlantic Oscillation (NAO), AO, and El Nino-Southern Oscillation significantly influencing sea ice and snow conditions leading to higher stress levels, low ovulation and pregnancy rates, reduced body condition, and overall variation in density of ringed seals, the primary prey of polar bears (e.g., Ferguson et al. 2005, 2017). Climatic oscillation indices (e.g., NAO and AO) may provide a broad-scale metric with the

ability to incorporate weather and climate patterns that influence sea ice conditions not reflected in sea ice satellite data and important for foraging success (Pilfold et al. 2015, Rode et al. 2021). Thus, future studies on polar bear foraging behaviour could include broad atmospheric circulation patterns, in addition to local environmental conditions. This dissertation provided the longest studied timeframe of polar bear foraging ecology in Nunavut to date (8 years in examined subpopulations and 18-year span in Foxe Basin specifically). However, continued monitoring of polar bear foraging behaviour using harvest-based samples will provide an opportunity to examine not only gradual and regional changes, but also the consequences of extreme climatic events or decadal-scale patterns that may influence population dynamics and the structure and functioning of the Arctic ecosystem.

Harvest-based sampling provides an opportunity to compile ecological information over a broad spatial and temporal scale. This dissertation provides evidence of the dietary flexibility of polar bears (chapter 4 and 5), however monitoring of harvested polar bear diets could be expanded through analysis of stable isotopes to identify long-term changes in ecosystem structure. Stable isotope analysis in ringed seal muscle tissue, de la Vega et al. (2021) identified a shortened food chain length in the Canadian Archipelago (high latitude area) with similar values to Baffin Bay (mid-latitude area), where ringed seals in the Canadian Archipelago have decreased in trophic position likely as a function of a changing zooplankton community and environmental conditions. My dissertation quantified lipid-rich marine mammal prey in diets of polar bears, however, low-fat terrestrial foods were excluded from the QFASA model. Evidence to date suggests that terrestrial foods make only a minor contribution to the energy budgets of polar bears in North America and only a small proportion of polar bears have been observed feeding on terrestrial foods (Hobson et al. 2009, Rode et al. 2015a, Dey et al. 2017, Jagielski et

al. 2021). However, increased land use is expected with continued sea ice loss (Rode et al. 2015b) and stable isotope analysis may better quantify low-fat food sources in diets than fatty acid analysis and the overall importance of terrestrial foods for polar bears. Thus, a more comprehensive study of polar bear foraging ecology including fatty acid-based and stable isotope analysis may provide new insight into ecosystem level changes associated with a rapidly changing Arctic environment occurring across trophic levels.

In this dissertation, attempts were made to investigate if body condition of polar bears was related to specific prey types found in their diet, however, I was unable to determine a direct relationship. Rode et al. (2021) recently found evidence of a direct relationship between body condition of polar bears and the body condition of both ringed seal and bearded seal. Polar bears will experience a shortened foraging period with any advance in break-up (chapter 2); however, the caloric return of prey may also be affected with changing sea ice conditions, in turn affecting the body condition of bears. Thus, continued research focused on polar bear foraging coupled with shifts in habitat conditions, and prey body condition will provide a more comprehensive understanding to assess the current and future status of polar bears.

This dissertation has demonstrated the wide breadth of knowledge on polar bear foraging ecology and trophic relationships that can be obtained from dietary analysis. It has provided new insights into the ecological mechanisms influencing polar bear body condition and diet composition and revealed the utility of polar bears as an ecological indicator. The results of this dissertation can be used as a basis for the long-term monitoring of polar bears across Nunavut linked to current and projected changes in population and ecological dynamics.

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Galicia, M. P., G. W. Thiemann, and M. G. Dyck*. 2020. Correlates of seasonal change in the body condition of an Arctic top predator. Global Change Biology 26:840–850.

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Gregory W. Thiemann (he/him)
Associate Professor
Faculty of Environmental & Urban Change
YORK UNIVERSITY
271 HNES Building • 4700 Keele Street
Toronto ON • Canada M3J 1P3
T [redacted]
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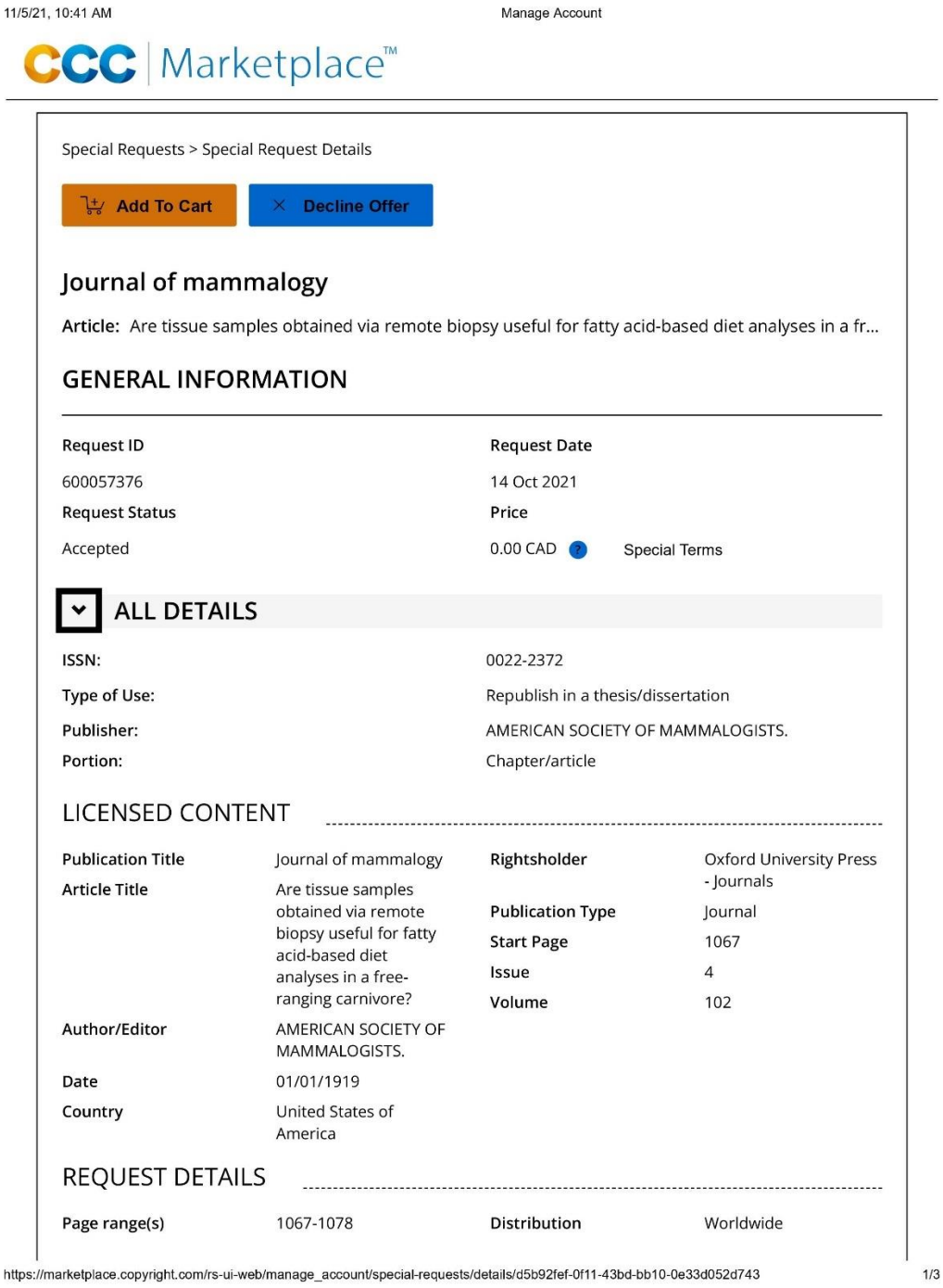

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Faculty of Environmental & Urban Change
YORK UNIVERSITY
271 HNES Building • 4700 Keele Street
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Thank you,

Dr. Steven H. Ferguson
Fisheries and Oceans Canada,
Program Lead, Marine Mammal Program
Arctic Aquatic Research Division, Fisheries and Oceans Canada
501 University Crescent, Winnipeg, MB, R3T 2N6, Canada
phone [redacted]
fax [redacted]
email [redacted]

Chapter 4

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Gregory W. Thiemann (he/him)
Associate Professor
Faculty of Environmental & Urban Change
YORK UNIVERSITY
271 HNES Building • 4700 Keele Street
Toronto ON • Canada M3J 1P3
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Fisheries and Oceans Canada,
Program Lead, Marine Mammal Program
Arctic Aquatic Research Division, Fisheries and Oceans Canada
501 University Crescent, Winnipeg, MB, R3T 2N6, Canada
phone [redacted]
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Yours sincerely,
Ian Stirling

Adjunct Professor
Department of Biological Sciences
University of Alberta
Edmonton, AB T6G 2E9

and: Research Scientist Emeritus
Wildlife Research Division
Environment and Climate Change Canada

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Co-author permission

PhD dissertation - permission to reprint articles

Gregory W Thiemann <[redacted]>
Mon 2021-10-18 12:04 PM
To: Melissa Galicia <[redacted]>

To whom it may concern,

I grant permission for Melissa Galicia to use our co-authored published material for her PhD dissertation. Melissa Galicia contributed to the conceptualization and was responsible for data curation, formal analysis, visualization and writing the original drafts of each of the following publications:

Galicia, M. P., G. W. Thiemann, and M. G. Dyck. 2020. Correlates of seasonal change in the body condition of an Arctic top predator. Global Change Biology 26:840–850.
Galicia, M. P., G. W. Thiemann, M. G. Dyck, and S. H. Ferguson. 2021. Are tissue samples obtained via remote biopsy useful for fatty acid-based diet analyses in a free-ranging carnivore? Journal of Mammalogy 102:1067–1078.
Galicia, M. P., G. W. Thiemann, M. G. Dyck, S. H. Ferguson, and I. Stirling. 2021. Prey selection of polar bears in Foxe Basin, NU, Canada: evidence of dietary flexibility in a specialized predator. Oxford Open Climate Change 1:1–14.
Galicia, M. P., G. W. Thiemann, M. G. Dyck, and S. H. Ferguson. 2021. Polar bear diet composition reveals spatiotemporal distribution of Arctic marine mammals across Nunavut, Canada. Ecological Indicators 132:108245.

Gregory W. Thiemann (he/him)
Associate Professor
Faculty of Environmental & Urban Change
YORK UNIVERSITY
271 HNES Building • 4700 Keele Street
Toronto ON • Canada M3J 1P3
T [redacted]
[redacted] • www.EUC.yorku.ca

Fisheries and Oceans Canada | Pêches et Océans Canada

Freshwater Institute

501 University Crescent
Winnipeg, Manitoba
R3T 2N6

Institut des eaux douces

501 University Crescent
Winnipeg, (Manitoba)
R3T 2N6

Monday, October 18, 2021

SUBJECT: Melissa Galicia PhD dissertation - permission to reprint articles

This letter acknowledges my co-author permission to use the journal articles as chapters in Melissa Galicia's PhD thesis. Melissa was the primary contributor to each of the papers accounting for approximately 90% of work:

Galicia, M. P., G. W. Thiemann, M. G. Dyck, and S. H. Ferguson. 2021. Are tissue samples obtained via remote biopsy useful for fatty acid-based diet analyses in a free-ranging carnivore? Journal of Mammalogy 102:1067–1078.

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Galicia, M. P., G. W. Thiemann, M. G. Dyck, and S. H. Ferguson. 2021. Polar bear diet composition reveals spatiotemporal distribution of Arctic marine mammals across Nunavut, Canada. Ecological Indicators 132:108245.

Thank you,

Dr. Steven H. Ferguson
Fisheries and Oceans Canada,
Program Lead, Marine Mammal Program
Arctic Aquatic Research Division, Fisheries and Oceans Canada
501 University Crescent, Winnipeg, MB, R3T 2N6, Canada
phone [redacted]
fax [redacted]
email [redacted]