VARIABILITY IN THE FORAGING PATTERNS OF POLAR BEARS (*URSUS MARITIMUS*)

IN THE CANADIAN HIGH ARCTIC AND FOXE BASIN

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Abstract

Ongoing climate warming is projected to cause further declines in sea ice across the Arctic; as a result the foraging ecology of marine species will change. This thesis aimed to investigate the ecological patterns associated with polar bear diet selection. I characterized polar bear diet in the High Arctic, an area that supports a high density of bears and Foxe Basin, a subpopulation that has remained stable despite shifts in sea ice habitat. I used adipose tissue samples and quantitative fatty acid signature analysis to quantify diet composition. Lipid content was used as an indicator of body condition and decreased from fall to spring in bears when prey are less available. Diet estimates revealed spatial differences in polar bear foraging and identified the importance of locally and seasonally abundant prey. The ability of some individuals to alternate between prey species may help mitigate the effects of a declining sea ice habitat.

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Chapter 1: Introduction

Background

Food web dynamics involve the understanding of feeding roles and relationships within an ecosystem. Foraging patterns of top predators can provide important insights into predator-prey interactions, diet, and habitat use which are essential components influencing the structure and functioning of a community. Top predators are found at the highest trophic level of a food chain and a shift in diet or foraging behaviour can exert strong top-down effects (Krebs 2009, Baum and Worm 2009). Food web dynamics can therefore be influenced by a predator's preference for a specific prey species and ultimately foraging behaviour (Post et al. 2000). Consequently, top predators can play an important role as indicator species, reflecting broad scale change in the functioning of an ecosystem (Bowen 1997, Sergio et al. 2008). A better understanding of the foraging behaviour and diets of apex predators in combination with prey availability and environmental drivers can ultimately aid in assessing population dynamics and improving conservation and management strategies.

Foraging behaviour and diet choice are based on the principle that a predator will attempt to maximize their energetic return in relation to handling time (MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977, Pyke 1984). A predator's foraging preference can be explained by optimal foraging theory, which is a cost-benefit function of encounter rate, probability of attack, success of capture, and consumption of a given prey item (Schoener 1971, Krebs 2009, Sih 2011). Diet choice is formed on the basis of energetic profitability – highest energetic return per unit of time (Stephens and Krebs 1986), and therefore a predator will show preference for the most profitable prey species when in high abundance (Schluter 1981, Pyke 1984, Sih 1993, 2011, Post et al. 2000). In contrast, a high frequency of encounters with a less profitable prey species will have no influence on a predator's consumption of that given prey item (Schluter 1981, Sih

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1993, Fryxell and Lundberg 1994). For instance, Hayward and Kerley (2005) reviewed 32

studies which examined the diets of lions (*Panthera leo*) and the preferred prey species based on

body mass (equal or larger in size to lions). Lions were found to show preference towards a

given prey item within their preferred weight range, whereas a prey species outside the preferred

weight range was unlikely to be depredated despite high encounter rates and abundance

(Hayward and Kerley 2005).

When a more profitable prey species becomes less available (i.e., decreased abundance or

scarcity in the habitat), a given predator may switch and/or broaden their diet (Schluter 1981).

Thus, the inclusion of alternate prey species in a predator's diet will only occur when the

preferred or most profitable prey species is in low abundance. Common voles (*Microtus arvalis*)

and European water voles (*Arvicola terrestris*), for example, are the main prey species for barn

owls (*Tyto alba*). The frequency of the two vole species in the diet of the barn owls is a reflection

of their densities in their respective habitats. Although less-preferred prey such as the Eurasian

shrew (*Sorex araneus*) and Millet's shrew (*Sorex coronatus*), had a high density in the habitat,

they were still not reflected in the barn owl diet. Barn owls foraged on the two shrew species

only when voles were low in abundance, suggesting that prey selection was driven by the density

and availability of the most profitable prey species (Bernard et al. 2010). Shifts to less profitable

prey species when preferred prey are unavailable has been previously documented in a number

of taxa including fish (Galarowicz et al. 2006), birds (Steenhof and Kochert 1988, Rutz and

Bijlsma 2006), and mammals (Roth 2003, Prugh 2005).

Polar bear foraging ecology

Polar bears (*Ursus maritimus*) are apex predators in the Arctic marine food web with a

circumpolar distribution which extends throughout five nations: Canada, Greenland, Norway,

Russia, and the United States (Prestrud and Stirling 1994). Currently, polar bears are classified into 19 discrete subpopulations, in which the name refers to a given subpopulation and not directly to the body of water for which they are named (Obbard et al. 2010). Improved understanding of polar bear foraging and the underlying ecological factors supporting polar bear subpopulations will ultimately aid in understanding how polar bears will respond to projected shifts in Arctic sea ice habitat.

Polar bears are ice-associated mammals dependent on sea ice as a platform for travelling, mating, and foraging (Amstrup 2003). Annual ice over the continental shelf is the preferred foraging habitat for polar bears due to the high biological productivity in comparison to deeper waters of the polar basin (Stirling 1997, Derocher et al. 2004). Polar bears have a high fat diet feeding almost exclusively on the blubber of marine mammals, consuming the subcutaneous fat layer and often leaving much of the muscle (Stirling and McEwan 1975, Stirling and Oritsland 1995). Ringed seals (*Pusa hispida*) are the primary prey of polar bears due to their small body size and high abundance throughout their range, resulting in a close predator-prey relationship (Stirling and McEwan 1975, Stirling and Archibald 1977, Smith 1980, Hammill and Smith 1991, Stirling and Oritsland 1995, Stirling 2002, Iverson et al. 2006, Thiemann et al. 2008a). Moreover, bearded seals (*Erignaathus barbatus*) are an important alternate prey species throughout their range (Stirling and Archibald 1977, Smith 1980, Stirling and Oritsland 1995). Polar bears also exploit locally abundant prey such as harp seals (*Pagophilus groenlandicus;* Derocher et al. 2002, McKinney et al. 2013), beluga whales (*Delphinapterus leucas;*Lowry et al. 1987, Thiemann et al. 2008a), narwhals (*Monodon monoceros;*Smith and Sjare 1990) and walrus (*Odobenus rosmarus*; Kiliaan and Stirling 1978, Calvert and Stirling 1990, Thiemann et al. 2007a).

Past methods used in diet studies

A variety of methods have been used to study predator diets, including scat analysis commonly used for terrestrial carnivores (e.g., Ferreras and Macdonald 1999, Lanszki et al. 2006, Munro et al. 2006, Martins et al. 2011), kill remains (Gende et al. 2001, Sand et al. 2005, Knopff et al. 2010), and stomach contents (Holst et al. 2001, Lowry et al. 2004). Both direct and indirect (i.e. kill remains and scat analysis) observations have been used to study polar bear feeding behaviour on marine mammals (e.g., Stirling and Archibald 1977, Lowry et al. 1980, 1987, Smith 1980, Calvert and Stirling 1990, Smith and Sjare 1990). These techniques are largely opportunistic and rare prey species tend to be underrepresented or misidentified in scat analysis (Dellinger and Trillmich 1988, Spaulding et al. 2014). In addition, certain prey species may be entirely consumed before identification, thus precluding the use of kill remains (Thiemann 2008, Webb et al. 2008). Although the above methods have provided insight into predator-prey dynamics, only a snapshot of the most recent meal is identified and the long-term diet composition of mammals, in particular polar bears, remains poorly understood in areas throughout the Arctic.

Fatty acid analysis

Fatty acids are the primary components of most lipids. Fatty acids typically have a methylene interrupted structure, with a terminal methyl group (CH_3), terminal carboxyl group (COOH), and a methylene group (CH_2) separating each double bond (Iverson et al. 2004, Budge et al. 2006, Thiemann 2008, Iverson 2009). The standard notation to represent fatty acids is A:Bn – X, where A represents the number of carbon atoms (length of the carbon chain), B represents the number of double bonds, and X indicates the position of the first double bond relative to the terminal methyl group. Saturated fatty acids (SFA) have zero double bonds; monounsaturated

fatty acids (MUFA) have one double bond; and polyunsaturated bonds have two or more double bonds (Budge et al. 2006, Iverson 2009). Fatty acids are rarely present in free form and are generally esterified to a glycerol backbone (Budge et al. 2006). Triaglycerols (TAG) are the common form of storage lipid deposited in the adipose tissue and blubber of vertebrates with three fatty acids esterified to a glycerol backbone (Budge et al. 2006).

Fatty acids can predictably reflect a given predator's diet, since fatty acids with a chain length of 14 or more carbons are directly deposited into the adipose tissue with little or no modification, unlike protein or carbohydrates that get degraded during digestion (Iverson et al. 2004, Budge et al. 2006, Thiemann 2008, Iverson 2009). Each individual predator, as well as prey will have a unique fatty acid signature (also known as profile or composition) that indicates the combination and proportion of each fatty acid in the adipose tissue or blubber. The Arctic marine ecosystem has low species diversity and thus a more simplistic food chain, although a large diversity of fatty acids can be found within the marine ecosystem (Iverson et al. 2004).

Fatty acid analysis has been used on a number of marine species including invertebrates and fish (Budge et al. 2002, Iverson et al. 2002), seabirds (Iverson et al. 2007), and marine mammals (e.g., Beck et al. 2005, Iverson et al. 2006, Thiemann et al. 2007b, 2008, Budge et al. 2008). Qualitative fatty acid analysis compares fatty acid profiles to infer variation among or within species such as differences between sexes or age classes, however it cannot be used to identify the specific proportion in which each prey item is found in the predator's diet or in most cases the actual prey species consumed by the predator (Budge et al. 2006, Thiemann 2008).

Biomarkers are unique fatty acids which can be linked to a specific prey species and when that particular fatty acid is found in unusual amounts in the predator's diet it can indicate

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the relative importance of the given prey species (Budge et al. 2006, Thiemann 2008, Iverson 2009). Non-methylene interrupted fatty acids have been used as biomarkers to indicate polar bear foraging on bearded seals and Atlantic walrus (Thiemann et al. 2007a). Although this approach can be a useful tool to indicate patterns in diet, variability in resources, and other ecological fluctuations, it cannot determine the amount each prey item contributed to a predator's diet (Budge et al. 2006, Iverson 2009).

Quantitative fatty acid signature analysis

Fatty acid analysis has become an important and effective ecological tool for the determination of the diet composition of free-ranging predators with the ability to indicate both population- and individual-level dietary shifts at multiple temporal and spatial scales (Iverson et al. 2004, Budge et al. 2006, Thiemann 2008). Quantitative fatty acid signature analysis (QFASA), as developed by Iverson et al. (2004), estimates the diet composition of individual predators. The model is based on the principle that fatty acids are deposited in a predictable way and compares the fatty acid profile of a predator's adipose tissue to that of its potential prey to assess the diet of individuals. QFASA provides a better indication of diet over a longer period of time than methods based on direct observations, kill remains or scat analysis (Iverson et al. 2004, Thiemann 2008). The model identifies fatty acids that have been integrated into the adipose tissue over the preceding days, weeks, and months, as opposed to a snapshot of a recent meal as seen in previous methods (Iverson et al. 2004, Iverson 2009).

QFASA first applies calibration coefficients to individual predator data to account for patterns of fatty acid deposition and metabolism, since particular fatty acids can be biosynthesized in addition to coming from dietary sources. Thus, the predator's fatty acid signature will never exactly match that of its component prey (Iverson et al. 2004). The QFASA

model then compares the individual predator fatty acid signature to the average fatty acid signature of each prey species, then identifies the combination of prey signatures that most closely matches a given predator's fatty acid signature (Iverson et al. 2004, Budge et al. 2006). To accurately estimate the diet composition of a predator, it is essential for each potential prey type to be represented, since the model can only determine the consumption of a prey item with a known fatty acid signature (Iverson et al. 2004).

The QFASA method will provide a better understanding of the foraging patterns of polar bears, predator-prey dynamics, and ultimately the functioning of Arctic marine food webs. Polar bear diets can reflect annual or seasonal fluctuations in prey availability in response to environmental change occurring in the marine ecosystem (Iverson et al. 2006). This approach has been used to quantify diets of a variety of species such as, grey seals (Beck et al. 2007), seabirds (Iverson et al. 2007), beluga whales (Loseto et al. 2009), harp and hooded seals (Tucker et al. 2009), along with polar bears (Iverson et al. 2006, Thiemann et al. 2008a, 2011, Rode et al. 2014).

Body condition

Body condition is an indicator of physiological/nutritional stress, reproductive potential and overall health of an individual in relation to food availability and foraging success (Atkinson and Ramsay 1995, Jakob et al. 1996, Peig and Green 2009). Typically, body condition (i.e., overall fatness) is a measure of energy reserves in terms of percent body fat of an individual and can be extrapolated to the population level (Cattet et al. 2002, Stevenson and Woods 2006). A change in body condition at the population level can reflect fluctuations in food resources and environmental conditions, a relationship that has been seen in a variety of vertebrates including birds (Kitaysky et al. 1999, Lovvorn et al. 2003), lemurs (Lewis and Kappeler 2005), and marine

mammals (Haug et al. 2002, Chambellant et al. 2012). The overall fatness of a species which undergoes periods of limited resources and decreased foraging (e.g., seasonal fasts associated with hibernation or reproduction) will fluctuate as a result of food availability. For instance, when prey resources are abundant, polar bears can shift to a state of hyperphagia. Conversely, when prey availability is limited, polar bears will slow down metabolism, though bears will continue to lose fat as the fasting period progresses (Stirling and McEwan 1975, Messier et al. 1992, Stirling and Oritsland 1995).

The adipose tissue found in the subcutaneous layer of polar bears acts as the main energy storage site, which becomes essential during the ice-free period in some parts of their range when bears are forced to migrate onshore and rely on fat stores for energy (Pond et al. 1992). Individual fat cells known as adipocytes will swell or shrink depending on the deposition of lipid (fattening) or the mobilization of lipid (fasting) of a vertebrate (Schemmel 1976). Body condition has been previously assessed in captured polar bears using body mass and morphometric measurements such as body length, axillary girth, and skull width (Rode et al. 2010, 2012, McKinney et al. 2014), as well as morphometric-based body condition indices (e.g., Cattet et al. 2002) and body composition models (Molnár et al. 2009). Additionally, a subjective fatness index has been used to assess the body condition of individuals; the index rates an individual polar bear from 1 to 5, with 1 categorized as an emaciated bear and 5 categorized as an obese bear (Stirling et al. 2008). The lipid content of adipose tissue, relative to water and other cellular components, provides an accurate indication of overall fatness in polar bears (Thiemann et al. 2006, Stirling et al. 2008, McKinney et al. 2014). Body condition assessments based on adipose lipid content have been documented only in the Southern Beaufort Sea (Stirling et al. 2008,

McKinney et al. 2014) and Western Hudson Bay (Thiemann et al. 2006, Stirling et al. 2008) and have not yet used harvest-based samples in other regions of the Arctic.

Effects of climate change

Satellite imagery has shown that sea ice extent has declined at a faster rate than initially modeled from 1950 to 2000 (Stroeve et al. 2007). Furthermore, projections indicate a continued accelerated decline until 2100 (Holland et al. 2006, Stroeve et al. 2007). The effects of climate change in the Arctic are not well understood, and low species diversity makes these ecosystems vulnerable to changing sea ice conditions (Derocher et al. 2004). Loss in sea ice habitat will have a significant effect on ice-associated species such as polar bears and their marine mammal prey (Stirling et al. 1999, Derocher et al. 2004, Laidre et al. 2008, Kovacs et al. 2011).

Increased sea ice fragmentation has been observed in the southern portion of the polar bear's range (Hudson Bay, Foxe Basin, and Hudson Strait) and has resulted in an overall decrease in optimal foraging habitat (Sahanatien and Derocher 2012). Sea ice conditions and response to environmental shifts vary across regions of the Arctic. For instance, southern areas have experienced longer ice free seasons than in previous years (Stirling et al. 1999, Stirling and Parkinson 2006, Stirling and Derocher 2012). In contrast, areas in the High Arctic have experienced relatively little change thus far and shifts in sea ice conditions may initially benefit polar bears as transitions from multi-year ice to thinner annual ice may be associated with near-term increases in biological productivity (Derocher et al. 2004, Stirling and Derocher 2012). Although regions across the Arctic will experience climate change at varying degrees and rates, the same general trend of sea ice habitat loss will ultimately apply across regions. The Arctic is expected to have an ice-free summer as early as the first half of this century and will continue for the foreseeable future (Overland and Wang 2013).

Research objectives

The overall goal of this thesis was to investigate the ecological patterns and processes associated with the diet selection of polar bears. A better understanding of the link between predator and prey is essential to better assess current and future effects of climate change in the Arctic and the potential response of polar bears. Body condition in terms of the percent lipid content found in adipose tissue of polar bears was examined to provide insight on seasonal trends in the fluctuations of polar bear body condition. To my knowledge, this is the first study to track lipid content through the fall and winter in relation to variation in prey availability and foraging conditions in the Canadian High Arctic and Foxe Basin. Quantitative fatty acid signature analysis was used to determine the diet composition of polar bears in four Canadian subpopulations. The resulting diet estimates for individuals were linked to key environmental (e.g., location, habitat) and life history characteristics (e.g., age and sex). My findings can be applied to future conservation efforts and sustainable management strategies for polar bear subpopulations.

In Chapter 2, *Characterization of polar bear (Ursus maritimus) diets in the High Arctic subpopulations: Baffin Bay, Gulf of Boothia, and Lancaster Sound,* I investigated the foraging ecology of polar bears in the Canadian High Arctic. These three subpopulations support some of the highest densities of polar bears in the world (Vongraven and Peacock 2011); however, the ecological factors supporting these polar bears are poorly understood. The objective of this chapter was to investigate the similarities in diet between all three regions and identify ecological factors supporting the high density of polar bears in these regions. I examined the relationship of polar bear diets to seasonal shifts in prey distribution and availability in relation to sea ice conditions. This is the first study to reliably estimate the diets of polar bears in the Canadian

High Arctic. I hypothesized that polar bears in the High Arctic exhibit diverse and seasonally variable diets related to marine mammal migration routes and sea ice conditions.

In Chapter 3, *Spatial variation in the diet of polar bears (Ursus maritimus) in Foxe Basin, Nunavut*, I quantified the diet composition of polar bears in Foxe Basin. The Foxe Basin subpopulation spans a large geographic area; however studies have not examined the spatial variation in polar bear diets within the subpopulation. The objective of this chapter was to characterize the diets of polar bears at multiple spatial scales to better understand the foraging patterns of polar bears at both local and regional levels. The ecological factors supporting this subpopulation are poorly understood and the response of polar bears to future sea ice decline in this region remains unclear. Consequently, this study sought to identify potential reasons for why the Foxe Basin subpopulation has remained stable despite shifts in sea ice habitat. To date, this is the first study to quantify polar bears scavenging on bowhead whales in Foxe Basin. I hypothesized that polar bear diet composition within Foxe Basin would vary spatially as a result of variable ecological conditions. I also hypothesized that bowhead whale carcasses may be providing an additional food source for polar bears during the ice-free season as a result of natural mortality, killer whale predation, and perhaps Inuit harvest.

In Chapter 4, *Conclusions,* I provided an overall summary of my main findings and conclusions. In addition, implications on conservation and suggestions for future directions are included in the chapter.

Chapter 2: Characterization of polar bear (*Ursus maritimus*) diets in the

High Arctic: Baffin Bay, Gulf of Boothia, and Lancaster Sound

Climate-driven changes in the quality and availability of sea ice habitat are expected to affect Arctic species primarily through altered foraging opportunities. However, trophic interactions in Arctic marine systems are generally poorly understood. I used adipose tissue samples to examine the diets of 198 polar bears (*Ursus maritimus*) harvested in 2010/2011 and 2011/2012 harvest seasons in Baffin Bay, Gulf of Boothia, and Lancaster Sound. The objective was to investigate the similarities in diet between all three regions and identify ecological factors supporting the high density of polar bears in these regions. In addition, I used adipose tissue lipid content as an indicator of overall body condition (i.e., fatness). Across all three regions, adipose lipid content in polar bears decreased through the fall and winter when prey species are typically less accessible. Diet composition of polar bears was comprised primarily of ringed seals (*Pusa hispida*), whereas bearded seals (*Erignathus barbatus*) and beluga whales (*Delphinapterus leucas*) were important alternate prey. Harp seals (*Pagophilus groenlandicus*) were a key food source in Baffin Bay. Dietary diversity was greatest in Baffin Bay perhaps because marine mammals were attracted to the nutrient-rich waters of the North Water polynya. In Baffin Bay, adult females had high levels of bearded seal in diet, whereas adult males and younger individuals consumed high levels of harp seal. There were no sex or age differences in Gulf of Boothia and Lancaster Sound, most likely due to scavenging on larger prey carcasses. Seasonal variation in polar bear foraging was correlated with known migration patterns of marine mammals and similarities in diet composition are attributed to shared resources among adjacent subpopulations. To my knowledge, this is the first study to track polar bear body condition through the fall and winter and the first to reliably estimate the diets of polar bears in the Canadian High Arctic.

Introduction

Apex predators can reveal broad scale changes in the structure and functioning of ecosystems (Bowen 1997). The Arctic region is experiencing rapid change with temperatures warming faster than any other area of the world (Stroeve et al. 2007). Satellite images have shown that sea ice cover is declining faster than forecasted, and future declines in sea ice extent are expected to accelerate (Stroeve et al. 2007, Overland and Wang 2007, Comiso et al. 2008). The effects of climate change in the Arctic are not well understood, and low species diversity makes these ecosystems vulnerable to changing sea ice conditions (Derocher et al. 2004).

As apex predators, polar bears (*Ursus maritimus*) may be sensitive indicators of environmental change (Stirling and Derocher 1993, Peacock et al. 2011). Sea ice is the primary habitat for polar bears, which use it as a platform for hunting, travelling, and mating (Stirling and Derocher 1993, Amstrup 2003). Evidence to date suggests that polar bears across their circumpolar range feed primarily on ringed seals (*Pusa hispida*) and perhaps opportunistically on a variety of other species, including bearded seals (*Erignathus barbatus;* Stirling and Archibald 1977, Smith 1980, Stirling and Oritsland 1995, Iverson et al. 2006, Thiemann et al. 2008a), harp seals (*Phagophilus groenlandicus;* Derocher et al. 2002, Iverson et al. 2006, McKinney et al. 2013), beluga whales (*Delphinapterus leucas;* Lowry et al. 1987, Smith and Sjare 1990, Thiemann et al. 2008a), narwhals (*Monodon monoceros;* Smith and Sjare 1990), and walrus (*Odobenus rosmarus;* Kiliaan and Stirling 1978, Calvert and Stirling 1990, Thiemann et al. 2007a).

Projected changes to sea ice conditions will likely alter the accessibility of ice-associated prey species and in turn the feeding ecology of polar bears. Thus, understanding current patterns of polar bear foraging and the link between prey distribution and sea ice conditions will be an

important aspect to better assess how the ecosystem will be affected. High Arctic research is increasingly important because the impacts of rapid ice cover reduction in this area are largely unknown (Stirling and Derocher 2012). Studies have predicted an initial increase in primary productivity as first-year ice replaces thicker multi-year ice, but longer term reductions in sea ice ultimately mean the loss of polar bear foraging habitat (Derocher et al. 2004).

In southern parts of their range, polar bears are forced on land when the sea ice melts in summer. During the ice-free period, polar bears rely on stored fat for energy. Although polar bears have been known to feed on a wide variety of terrestrial foods (both natural – plant and animal food items and anthropogenic; Russell 1975, Derocher et al. 1993, Gormezano and Rockwell 2013). A population-level shift from a marine-base diet to a terrestrial diet is unlikely, as studies have found no evidence of significant energetic contribution from terrestrial food during the fasting period (Ramsay and Hobson 1991, Hobson et al. 2009). Although there is reason to believe consumption of terrestrial food may increase as the fasting period gets longer and bears get hungrier (Iverson et al. 2014), polar bears will still depend on sea ice habitat to acquire most of their energy. Terrestrial feeding would also be less of an issue in the High Arctic, where the open water period is brief or non-existent.

Fatty acid analysis has become an important and effective tool for detecting population- and individual-level dietary shifts in a variety of taxa, including sea birds (Iverson et al. 2007), marine mammals (Iverson et al. 1997, Beck et al. 2007, Loseto et al. 2009), and polar bears (Iverson et al. 2006, Thiemann et al. 2008a). The largest contribution of fatty acids (FA) in monogastric predators such as polar bears comes from the direct deposition of dietary FA which are not degraded during digestion as are carbohydrates and proteins (Iverson et al. 2004, Budge et al. 2006, Thiemann 2008). FA with a chain length of 14 or more carbons are incorporated into

the adipose tissue with little or no modification, predictably reflecting the diet of a predator over days, weeks, and months (Iverson et al. 2004). Quantitative fatty acid signature analysis (QFASA) as developed by Iverson et al. (2004), uses a statistical model to compare the fatty acid profiles of predator and potential prey and generates diet estimates for individual animals.

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 Oritsland 1995). Adipose tissue is primarily used as an energy storage site in polar bears (Pond et al. 1992). When lipid is deposited or mobilized, individual fat cells will swell or shrink, respectively. Thus, as the individual accumulates and stores energy, the proportion of lipid, relative to non-lipid components of the adipose tissue would increase. Lipid content is consistent across the large subcutaneous fat depots of a polar bear (Thiemann et al. 2006). Recent evidence indicates that adipose lipid content provides a reliable indicator of body condition in polar bears (Thiemann et al. 2006, Stirling et al. 2008, McKinney et al. 2014).

Body condition has been previously assessed using a combination of morphometric measurements including body mass, length, skull size, and girth (Rode et al. 2010, 2012, McKinney et al. 2014) along with calculated body condition index (Cattet et al. 2002) and storage energy (Molnár et al. 2009). Biologists have used a qualitative fatness index to assess the condition of live-captured bears, assigning individuals a rating from 1 (most lean) to 5 (obese) (Stirling et al. 2008). There are no published records of hunters using the fatness index during annual subsistence harvests. However, a qualitative assessment of body condition by hunters may be a rapid and efficient way to increase long-term monitoring of polar bear populations in less studied areas.

There are few quantitative studies examining the trophic relationships between polar bears and their prey in the Canadian High Arctic. Previous work by Thiemann et al. (2008a) found that polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound had similar fatty acid profiles that were distinct from bears anywhere else in the Canadian Arctic. However, dietary estimates based on QFASA were ambiguous because the QFASA model could not reliably distinguish harp seals from other potential prey (Thiemann et al. 2008a).

The objective of this study was to characterize polar bear diet composition and body condition in three High Arctic subpopulations, Baffin Bay, Gulf of Boothia, and Lancaster Sound, which contain some of the highest densities of polar bears in their circumpolar range. I sought to correlate polar bear diet and body condition to potential shifts in seasonal prey distribution and sea ice conditions. Polar bears in the High Arctic have not yet experienced a major decline in sea ice condition in comparison to southern regions. Moreover, predictable areas of open water in northern Baffin Bay and the Arctic Archipelago may serve as important habitat for migratory and resident marine mammals. I hypothesized that polar bears in the High Arctic will exhibit diverse and seasonally variable diets related to marine mammal migration routes and sea ice conditions. The ability to exploit diverse marine mammal prey has been identified as a factor mitigating the effects of sea ice loss (Rode et al. 2014). Thus, a better understanding of predator-prey dynamics within these regions is essential to better assess current and future effects of climate change in the Arctic.

Methods

Sample collection

Polar bears

I analyzed adipose tissue samples from 198 individual polar bears (Table 1-1) in 3

subpopulations: Baffin Bay, Gulf of Boothia, and Lancaster Sound (Figure 1-1). The samples

were collected by local Inuit hunters during the 2010/2011 and 2011/2012 subsistence harvest

seasons (Figure 1-1). Harvest seasons extend from July 1 to June 30 of the following year. The

collection of samples included male and female adults (5+ years), subadults (3-4 years), and

independent 2-year-olds (Table 1-1). Annual hunting occurs on a 2:1 male:female ratio, and it is

illegal to hunt females with dependent cubs (Table 1-1). Body condition (i.e., the amount of

subcutaneous fat on the body) was qualitatively assessed by hunters using a scale 1 to 5 (1 being

the leanest and 5 being the most obese; Stirling et al. 2008). Adipose tissue samples (ca. 6 cm x 3

cm) were taken through the full depth of the subcutaneous adipose layer over the rump. Samples

were individually wrapped in aluminum foil, sealed in a Whirl-Pak, and stored at -20°C until

analysis.

Table 1-1. Number of polar bear harvest samples used in the examination of diet composition

across 3 subpopulations in the Canadian Arctic.

Subpopulation	Total (*n*)	Adult			Subadult		Independent, 2 years old	
		Female	Male	Unknown	Female	Male	Female	Male
Baffin Bay	56	10	26	0	3	10	3	4
Gulf of Boothia	62	12	32	0	6	12	0	0
Lancaster Sound	80	9	44	1	5	15	3	3
Total	198	31	102	1	14	37	6	7
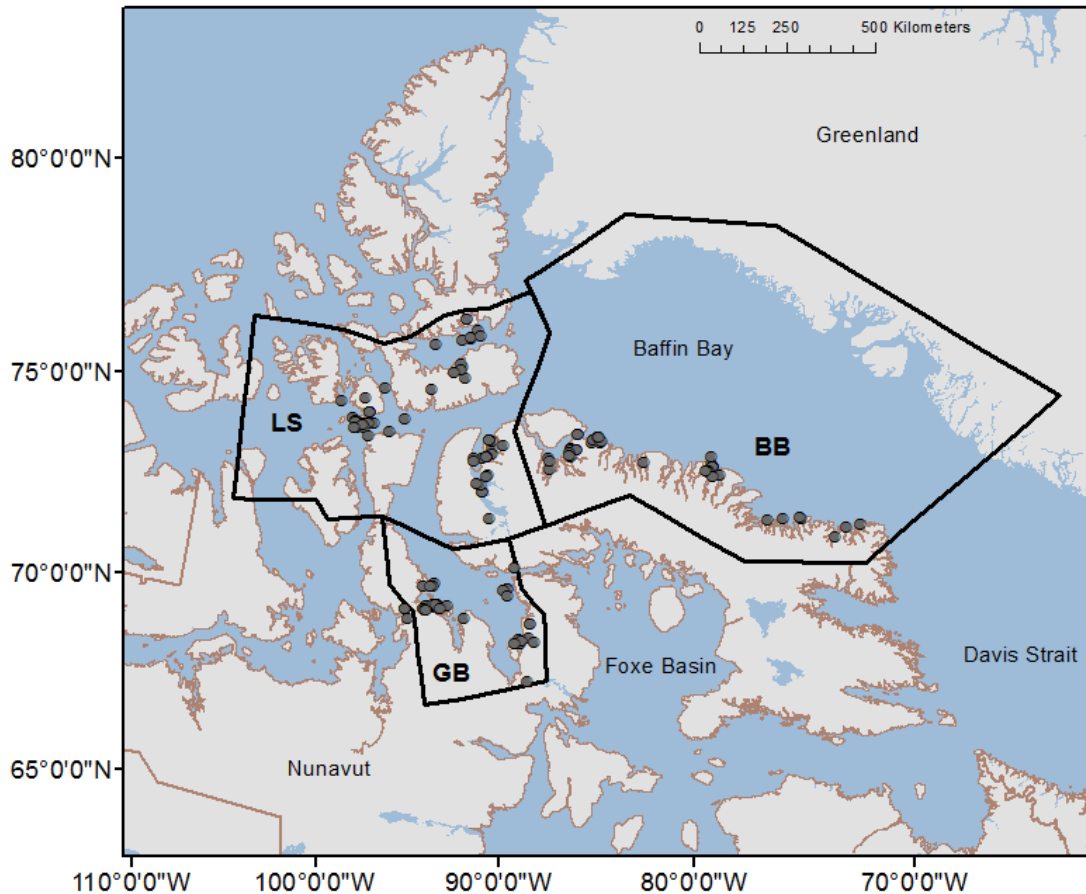
Figure 1-1. Location of polar bears (n = 198) harvested by local Inuit hunters in 2010/11 to 2011/12 in 3 Canadian subpopulations: Baffin Bay (BB), Gulf of Boothia (GB), and Lancaster Sound (LS).

Polar bear prey

A total of 332 blubber samples were collected from potential polar bear prey, including ringed seals, bearded seals, harp seals, harbour seals, beluga whales, narwhals, and walrus (Table 1-2). Blubber samples were collected during Inuit subsistence hunts across the Canadian Arctic (Figure 1-2) from 2004 to 2012. The collection of seal and whale samples included all sex and age classes. Adipose tissue was sampled through the full depth of the blubber, since studies have found significant vertical stratification in blubber of cetaceans and pinnipeds (Koopman et al. 1996, Best et al. 2003). Samples were wrapped in aluminum foil, sealed in labeled Whirl-Pak

bags and stored at -20°C until analysis. Data from Thiemann et al. (2008b) for 314 marine

mammals (bearded seals (n = 31), beluga whales (n = 105), harp seals (n = 110), and narwhals (n

= 10) were also included, for a total prey library of 646 samples.

Table 1-2. Distribution of marine mammals sampled across the Canadian Arctic collected by

local hunters from 2004 to 2012 and includes prey species from Thiemann et al. 2008.

Species	Total (*n*)	Location	Sample (*n*)
Bearded seal	74	Arviat	33
		Cape Dorset	1
		Davis Strait - Unknown	31
		Hall Beach	1
		Kugaaruk	4
		Repulse Bay	4
Beluga whale	162	Coral Harbour	13
		Frobisher Bay	1
		Grise Fiord	5
		Igloolik	21
		Iqaluit	9
		Northern Beaufort Sea	9
		Pangnirtung	4
		Repulse Bay	9
		Resolute	11
		Southern Beaufort Sea	52
		Southern Hudson Bay	16
		Whale Cove	12
Harbor seal	17	Arviat	17
Harp seal	119	Newfoundland and Labrador	101
		Pangnirtung	9
Narwhal	47	Arctic Bay	14
		Clyde River	6
		Grise Fiord	10
		Pond Inlet	8
		Taloyoak	3
		Repulse Bay	6
Ringed seal	206	Allen Bay	11
		Cape Dorset	5
		Hall Beach	4
		Kugaaruk	15
		Repulse Bay	39
		Resolute	132
Walrus	21	Grise Fiord	3
		Hall Beach	11
		Igloolik	7
Total	646		646

Figure 1-2. Locations of all marine mammal harvest samples (n =332) collected for this study from 2004 to 2012 in Nunavut, Canada.

Laboratory analysis

Sample analysis

Lipid was quantitatively extracted from each adipose tissue sample according to Iverson et al. (2001). Lipid content was expressed as % total sample wet weight ± 1 standard error. A subsample of approximately 0.5 g was taken from the center of larger tissue pieces. Fatty acid methyl esters (FAME) were derived from isolated lipid extracts using sulfuric acid as a catalyst (Budge et al. 2006).

Individual fatty acids (FA) were identified and quantified using temperature-programmed gas chromatography according to Budge et al. (2006). FA data were reported as the mass % of total FA ± 1 SEM and expressed by the shorthand nomenclature of A:Bn – X, where A represents the length of the carbon chain, B represents the number of double bonds, and X indicates the position of the first double bond relative to the terminal methyl group. GC peaks were identified as corresponding FA and integrated using Varian Star 6.41 Chromatography Workstation software. Each chromatogram was inspected and peak identities corrected if retention times had shifted. There were typically >70 FAs identified in each adipose tissue sample.

QFASA modelling

I used quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004) to estimate the diet composition of individual polar bears. The QFASA model estimates diet by comparing the predator FA profile, or "signature", to the average FA signatures of its potential prey. The model identifies the weighted combination of prey FA signatures that most closely matches a given predator's FA signature, after accounting for predator lipid metabolism via the use of calibration coefficients (Thiemann et al. 2008a). The combination of prey FA profiles that minimizes the statistical distance between the prey and the calibrated predator represents the relative contribution of each prey type to the predator's diet, on a lipid biomass basis.

Polar bear diets were estimated using 30 dietary FA similar to Thiemann et al. (2008a). Dietary FAs are those derived solely or primarily from the diet (Iverson et al. 2004). The only difference between my modeling FA set and that of Thiemann et al. (2008a) was the exclusion of 20:1n-11, which appeared to contribute to the overlap among prey species during PCA. When

20:1n-11 was removed from diet simulations (see below), beluga whales and harp seals were better resolved.

Certain FAs, in addition to coming from the diet, may be synthesized *de novo* from non-lipid precursors. Ingested FAs may also be modified or utilized before deposition in tissue. Therefore, calibration coefficients are used to account for predator lipid metabolism. Calibration coefficients used to model polar bears in this study were developed by Thiemann et al. (2008a) from captive feeding studies on mink (*Neovison vison*); a terrestrial carnivore fed a marine-based diet.

In combination with multivariate statistical comparisons, diet simulation studies were used to determine the ability of the QFASA model to accurately distinguished and quantify prey types. Diet simulations were based on the methods of Iverson et al. (2004). Briefly, the first step was to create a hypothetical diet composition for a polar bear (for example, 60% ringed seal, 30% bearded seal, and 10% beluga whale). Prey samples were split into a simulation set (used to create a "pseudo bear" with the specified diet proportions) and a modeling set used to estimate the diet of the pseudo bear. The simulation repeats the creation and modeling of the pseudo bear 1000 times (Iverson et al. 2004). When available, prey species from the specific subpopulation were used to model predator diet composition of that same region. However, when necessary, samples collected from another region were used to increase the sample size (Table 1-2). All diet simulations and QFASA estimates were performed in R (R Version 2.1.0, The R Foundation for Statistical Computing, 2005).

Table 1-3. List of prey species and sampling regions used in the QFASA model for each polar

bear subpopulation.

Subpopulation	Prey species	Sampling region	Number of samples
Baffin Bay	Bearded seal	DS, FB, GB, WH	74
	Beluga whale	DS, FB, LS, WH	119
	Harbour seal	WH	17
	Harp seal	DS	36
	Narwhal	BB, LS	29
	Ringed seal	LS	123
	Walrus	FB, LS	20
Gulf of Boothia	Bearded seal	DS, FB, GB, WH	74
	Beluga whale	DS, LS, NB, SB, SH, WH	119
	Harp seal	DS	36
	Narwhal	BB, FB, GB, LS	38
	Ringed seal	GB, LS	138
	Walrus	FB, LS	20
Lancaster Sound	Bearded seal	DS, FB, GB, WH	74
	Beluga whale	DS, LS, NB, SB, SH, WH	119
	Harp seal	DS	36
	Narwhal	LS	23
	Ringed seal	LS	123
	Walrus	FB, LS	20

Note: Baffin Bay (BB), Davis Strait (DS), Foxe Basin (FB), Gulf of Boothia (GB), Lancaster

Sound (LS), Northern Beaufort Sea (NB), Southern Beaufort Sea (SB), Southern Hudson Bay

(SH), Western Hudson Bay (WH).

Statistical analyses

Spearman's correlation analysis was used to test for a relationship between fatness index

rated by the hunters and the lipid content of each individual polar bear. I performed a simple

linear regression to investigate the influence of harvest date on the lipid content in the adipose

tissue of polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound.

Inter- and intra-specifc variation in FA profiles was tested using principal component

analysis (PCA) and multivariate analysis of variance (MANOVA). PCA was used in an

exploratory manner to determine relationships among FA, examine clusters of polar bears by

region or prey species, and reduce a large number of variables to a few components (Goedkoop et al. 2000, Budge et al. 2006, 2008). Instead of using a MANOVA on a subset of FA (typically 17 of the most variable and/or abundant), I used a PCA to analyze a larger set of 38 FA (32 dietary FA and 6 extended dietary FA) on polar bear samples and polar bear prey. This FA set was based on the dietary and extended dietary set from Iverson et al. (2004), where dietary FA are obtained only or primarily from diet and extended dietary FA are obtained both from biosynthesis and diet. Thus, the FA set included all the FA used in the model in addition to FA that were the most abundant and/or variable. PCA was performed on log-transformed FA data according to the following equation: $x_{trans} = \ln(x_i/c_r)$, where x_{trans} is the transformed FA, x_i is the abundance of FA i expressed as percent of total FAs, and c_r is the reference FA, which was 18:0 (Budge et al. 2002, 2006). I also restricted the sample:variable ratio to 5:1 as suggested by Budge et al. (2008). For instance, a maximum of 39 FA could be used in the analysis of 198 polar bear samples. An ANOVA or MANOVA was then used to compare regional, intra-population (including sex and age class), and seasonal groups using the new PCA components.

Permutational MANOVA was used to test for geographic, sex, age class, and seasonal differences in polar bear diet composition (Anderson 2001a, 2001b). Diet composition data were not normally distributed due to variation among individuals (i.e. some individuals may have 100% biomass or zero biomass of a given prey item in diet, and other individuals have a combination of prey items), thus MANOVAs with 10000 permutations were carried out. To test sex and age class differences within each region, a two-way MANOVA was performed. A two-way MANOVA was also used to test spatial and seasonal variation while accounting for sex effects on polar bears diet composition. Seasons were defined as fall (September to November),

winter (December to February), and spring (March to May). Summer (June to August) was excluded from all the seasonal analyses, due to a small sample size.

Shannon-Wiener Index (H') was used to calculate diversity in diet composition (Beck et al. 2007, Thiemann et al. 2008a):

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

where, p_j is the proportion of prey species j found in the diet and s is the total number of prey species. An ANOVA was performed to test spatial, sex, age class, and seasonal differences in dietary diversity. All statistical analyses were performed in R (R Version 2.15.3, The R Foundation for Statistical Computing, 2013).

Results

Lipid content

There was a significant, positive relationship between % lipid content and fatness index rating in polar bears in the High Arctic ($r_s = 0.400$, $p < 0.001$; Figure 1-3). Furthermore, polar bears had decreasing adipose tissue lipid from October to March-April in the High Arctic (Baffin Bay: $R^2 = 0.098$, $p = 0.022$; Gulf of Boothia: $R^2 = 0.124$, $p = 0.005$; Lancaster Sound: $R^2 = 0.080$, $p = 0.012$; Figure 1-4). Polar bears killed as problem bears were removed from the analysis because they did not appear to be representative of the overall population. For instance, of the 3 polar bears indicated as problem bears in Baffin Bay, 2 were independent 2-year-olds with less than 60% adipose lipid content. These bears may have been abandoned cubs. Baffin Bay showed monthly fluctuations in adipose lipid, whereas Gulf of Boothia and Lancaster Sound

showed a more consistent decreasing trend from fall to spring. Monthly average lipid content in all 3 regions never fell below 70%.
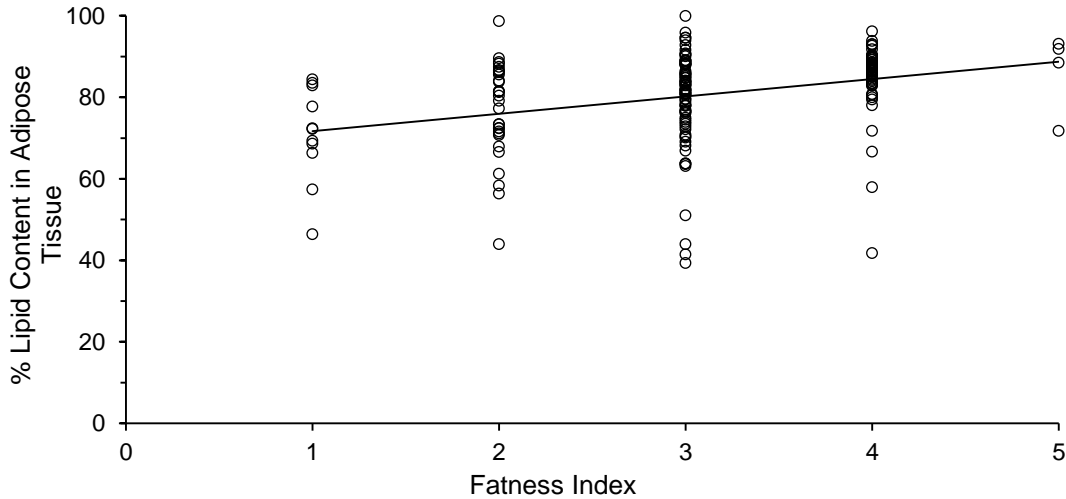
Figure 1-3. Correlation between fatness index (rating out of 5) and lipid content in the adipose tissue (% total wet weight) of polar bears sampled in the High Arctic (n = 180) from 2010/11 to 2011/12. Lipid content was calculated for all 198 polar bear adipose tissue samples, however only bears assigned a fatness index rating were included in the analysis. There was a significant positive relationship between fatness index assessed by hunters and % lipid content (r_s = 0.400, p < 0.001).
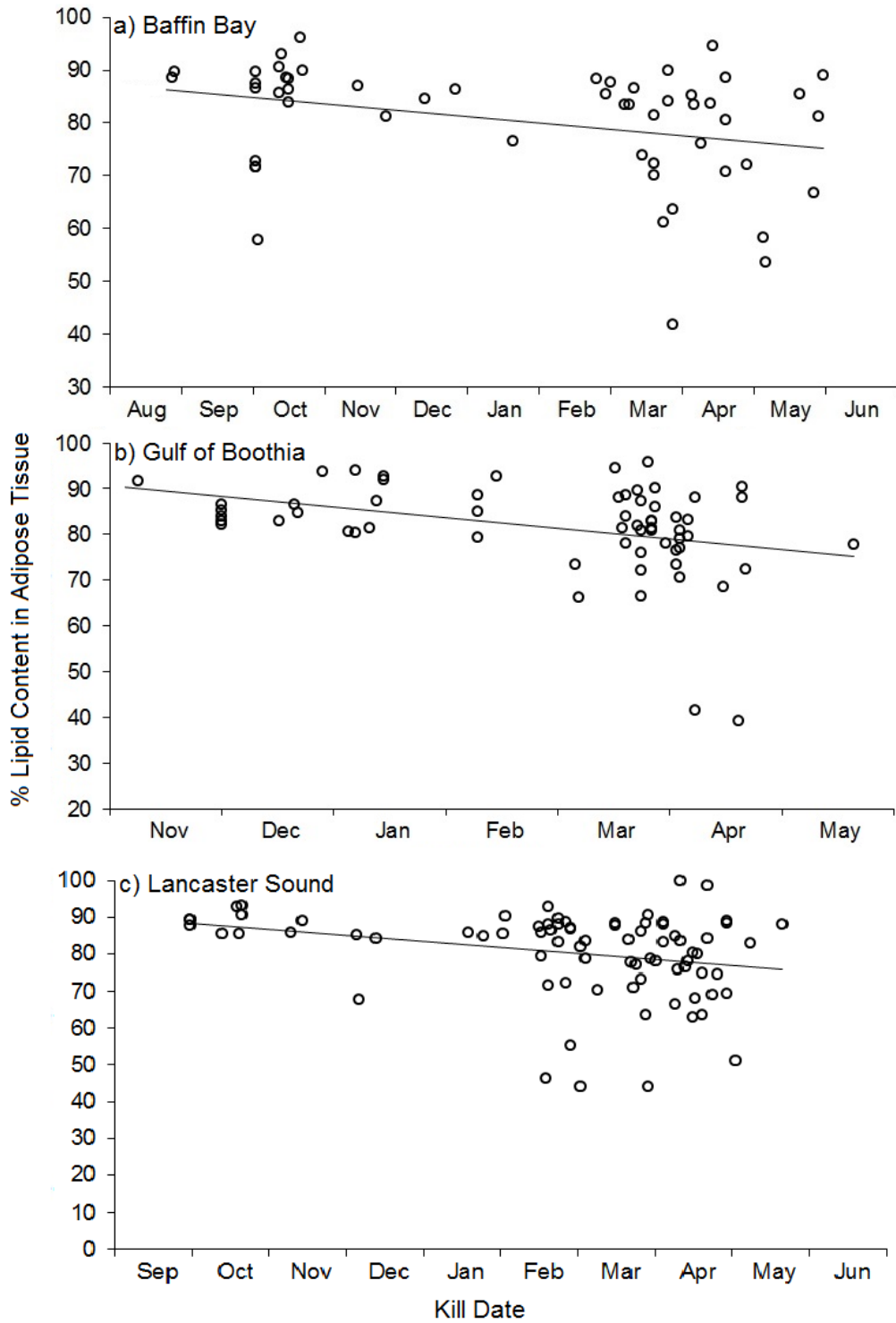
Figure 1-4. Relationship between ordinal kill date and adipose lipid content (% total wet weight) of polar bears sampled during the 2010/11 and 2011/12 harvest seasons in a) Baffin Bay (n = 53), b) Gulf of Boothia (n = 61), and c) Lancaster Sound (n = 78).

Variation in polar bear FA signature

PCA was performed on 38 FA (Table 1-3) which generated 3 principal components (PC) explaining 78% of the total variance. There was no clear regional separation among polar bears (Figure 1-5). The FA with the highest loadings on PC1 were 16:3n-4, 16:4n-3, 16:4n-1, 18:4n-3, 18:4n-1, 20:5n-3, on PC2 were 20:1n-9, 22:1n-11, 22:1n-9, 22:1n-7, 22:4n-3, and on PC3 was 18:3n-6. A MANOVA carried out on PC scores showed a significant regional difference between the 3 polar bear subpopulations (MANOVA, Wilks' $\lambda = 0.73$, $p < 0.001$). Only PC3 had a significant effect on the regional variation. Another PCA was performed on each subpopulation separately and MANOVA carried out on PC scores for effects of sex, age class, year, and season. Sex and age class had no significant effect on polar bear FA in any region (MANOVA, $p > 0.06$). There was no significant seasonal effect on polar bear FA signatures in Gulf of Boothia (MANOVA, Wilks' $\lambda = 0.97$, $p = 0.579$). However, season did have a significant effect on Baffin Bay (MANOVA, Wilks' $\lambda = 0.71$, $p < 0.001$) and Lancaster Sound polar bear FA signature (MANOVA, Wilks' $\lambda = 0.80$, $p = 0.011$).

Table 1-4. Fatty acid composition (by major lipid class; % mass of total FA ± SEM) of polar bears sampled.

Fatty Acid	Baffin Bay (n = 56)			Gulf of Boothia (n = 62)			Lancaster Sound (n = 80)		
Saturated fat									
14:0[*]	2.83	±	0.06	2.90	±	0.07	2.95	±	0.05
Iso15	0.22	±	0.01	0.15	±	0.01	0.22	±	0.02
15:0	0.20	±	0.01	0.18	±	0.01	0.19	±	0.01
16:0[*]	5.35	±	0.15	5.40	±	0.13	5.56	±	0.13
7Me16:0	0.20	±	0.01	0.21	±	0.01	0.21	±	0.01
17:0[*]	0.13	±	0.01	0.11	±	0.00	0.12	±	0.00
18:0	1.77	±	0.05	1.73	±	0.04	1.84	±	0.09
Monounsaturated fat									
14:1n-5	0.62	±	0.02	0.70	±	0.02	0.69	±	0.02
16:1n-11	0.29	±	0.02	0.23	±	0.01	0.29	±	0.02
16:1n-9	0.55	±	0.01	0.53	±	0.01	0.57	±	0.02
16:1n-7[*]	10.61	±	0.40	14.30	±	0.57	13.17	±	0.44
17:1	0.22	±	0.01	0.18	±	0.00	0.18	±	0.00
18:1n-11	7.02	±	0.22	4.92	±	0.25	6.10	±	0.17
18:1n-9[*]	19.68	±	0.31	20.06	±	0.40	18.93	±	0.31
18:1n-7[*]	4.13	±	0.09	4.77	±	0.07	4.47	±	0.06
18:1n-5	0.47	±	0.01	0.51	±	0.01	0.49	±	0.01
20:1n-11[*]	4.45	±	0.19	3.16	±	0.15	3.98	±	0.16
20:1n-9[*]	13.35	±	0.34	12.69	±	0.40	11.58	±	0.32
20:1n-7[*]	1.13	±	0.04	1.14	±	0.03	1.07	±	0.03
22:1n-11[*]	2.88	±	0.14	2.05	±	0.10	2.64	±	0.15
22:1n-9[*]	0.98	±	0.03	0.85	±	0.03	0.95	±	0.04
22:1n-7[*]	0.12	±	0.00	0.11	±	0.00	0.13	±	0.01
Polyunsaturated fat									
16:2n-6[*]	0.03	±	0.00	0.04	±	0.00	0.04	±	0.00
16:2n-4[*]	0.13	±	0.00	0.10	±	0.00	0.11	±	0.00
16:3n-6[*]	0.34	±	0.01	0.44	±	0.01	0.41	±	0.01
16:3n-4[*]	0.05	±	0.00	0.07	±	0.01	0.07	±	0.00
16:4n-3[*]	0.02	±	0.00	0.02	±	0.00	0.03	±	0.00
16:4n-1[*]	0.05	±	0.00	0.07	±	0.01	0.06	±	0.01
18:2n-6[*]	1.22	±	0.02	1.57	±	0.03	1.31	±	0.11
18:2n-4[*]	0.09	±	0.00	0.10	±	0.00	0.10	±	0.00
18:3n-6[*]	0.09	±	0.00	0.14	±	0.01	0.13	±	0.00
18:3n-4[*]	0.17	±	0.00	0.18	±	0.00	0.17	±	0.00
18:3n-3[*]	0.33	±	0.01	0.31	±	0.01	0.28	±	0.01
18:3n-1[*]	0.05	±	0.00	0.05	±	0.00	0.04	±	0.00
18:4n-3[*]	0.33	±	0.02	0.33	±	0.02	0.32	±	0.02
18:4n-1[*]	0.09	±	0.01	0.10	±	0.01	0.11	±	0.01
20:2n-6[*]	0.27	±	0.01	0.29	±	0.01	0.25	±	0.00
20:3n-6[*]	0.13	±	0.00	0.17	±	0.00	0.14	±	0.00
20:4n-6[*]	0.24	±	0.02	0.25	±	0.01	0.28	±	0.01
20:3n-3[*]	0.05	±	0.00	0.03	±	0.00	0.03	±	0.00
20:4n-3[*]	0.32	±	0.01	0.28	±	0.01	0.27	±	0.01
20:5n-3[*]	2.24	±	0.19	2.45	±	0.19	2.75	±	0.18
21:5n-3[*]	0.28	±	0.01	0.32	±	0.01	0.29	±	0.01
22:4n-6[*]	0.12	±	0.01	0.15	±	0.01	0.13	±	0.00
22:5n-6[*]	0.12	±	0.00	0.10	±	0.00	0.11	±	0.00
22:4n-3[*]	0.07	±	0.00	0.06	±	0.00	0.05	±	0.00
22:5n-3[*]	6.73	±	0.15	6.91	±	0.13	7.13	±	0.16
22:6n-3[*]	7.97	±	0.20	7.36	±	0.17	7.84	±	0.19

Note: Only FA representing >0.2% of total FA and FA used in the PCA and QFASA model.

(*) represents dietary and extended dietary FA used for fatty acid comparisons and accounts for approximately 98% of the total FA across all polar bear subpopulations. **Bold** represents the 30 dietary FA used to generate polar bear diet estimates (QFASA model).
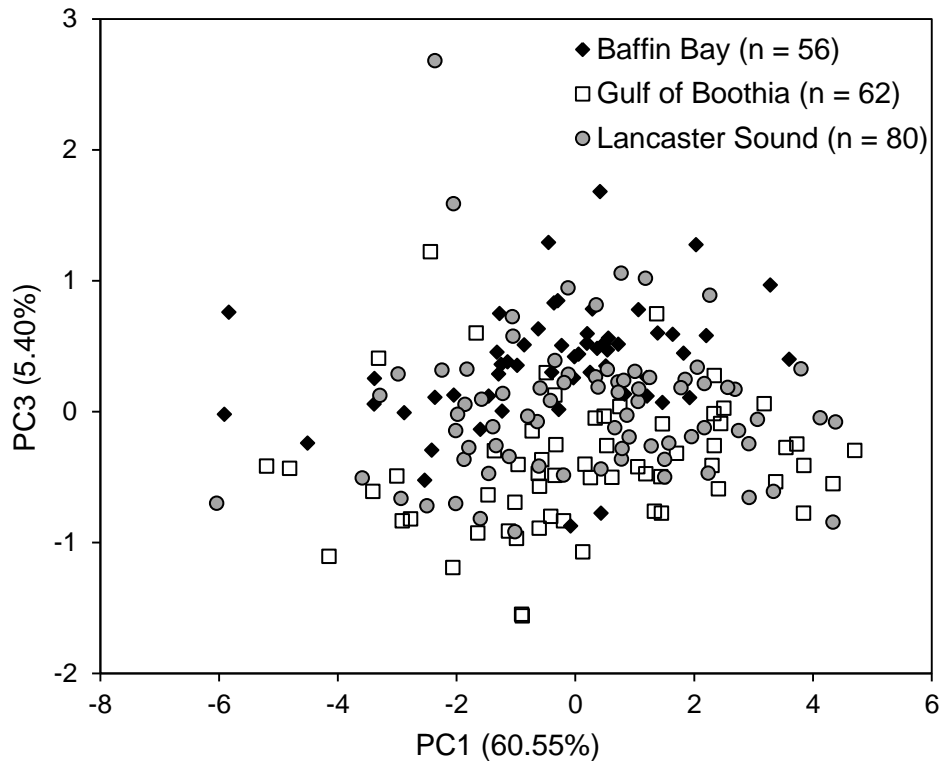
Figure 1-5. Principal component analysis of the 38 dietary and extended dietary FA on polar bears according to subpopulation. PCA score plot on PC1 and PC3 which explained 65.9% of total variance. I included PC1 because it explained the most variation and PC3 instead of PC2 because PC3 had a significant influence on the variability in polar bear FA signature.

Variation in polar bear prey FA signature

Differences among species

A PCA was conducted on 38 FA on polar bear prey FA profiles (Table 1-4) which generated 5 principal components that explained 88% of total variance (Figure 1-6). The FA with the highest loading on PC1 were 16:3n-6, 16:3n-4, 16:4n-1, whereas 22:1n-11, 22:1n-9, 22:1n-7 had the highest loading on PC2 and 16:4n-3 had the highest loading on PC3. Marine mammals were separated into 3 main clusters: the first included cetaceans (beluga whales and narwhals),

the second included bearded seals, harbour seals, and walruses, and the third included harp seals

and ringed seals (Figure 1-6). A MANOVA on all 5 principal components; there was a

significant difference among all prey species (MANOVA, Wilks' $\lambda = 0.009$, $p < 0.001$ and *post*

hoc Tukey's test, $p < 0.01$ in all cases). All 5 principal components had a significant influence on

the variability between prey species.
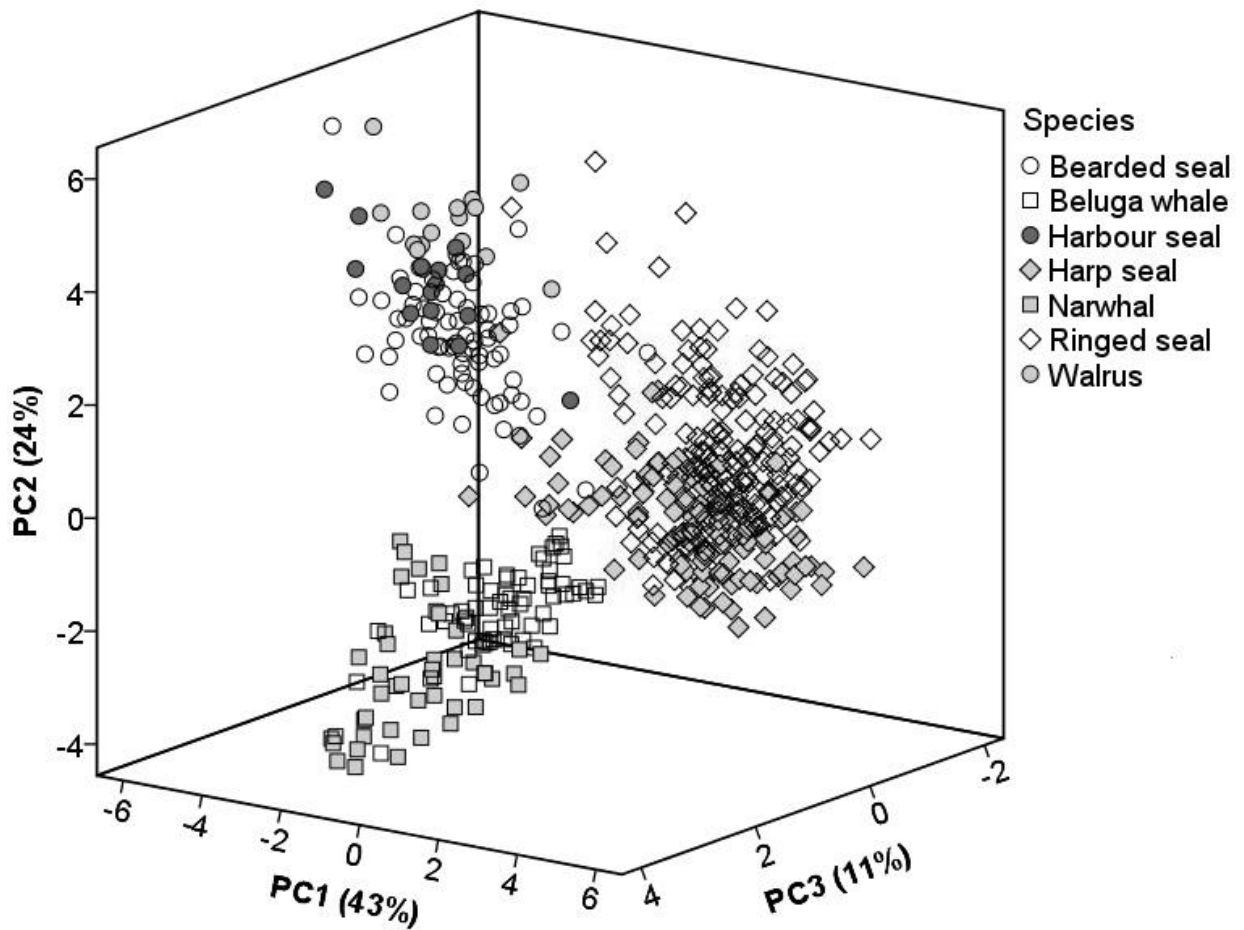
Figure 1-6. Principal component analysis of 38 dietary and extended dietary FA on polar bear

prey (marine mammal) samples separated by species. PCA score plot on PC1, PC2, and PC3

which accounts for 77.8% of the total explained variance.

Table 1-5. Fatty acid composition, by major lipid class (% mass of total FA ± SEM), of marine mammals sampled across the Canadian Arctic from 2000 to 2012 (n = 594).

Fatty acid	Bearded seal (n = 74)			Beluga whale (n = 87)			Harbour seal (n = 17)			Harp seal (n = 119)			Narwhal (n = 48)			Ringed seal (n = 206)			Walrus (n = 21)		
Saturated fat																					
12:0	0.14	±	0.00	0.89	±	0.05	0.14	±	0.00	0.08	±	0.00	0.86	±	0.08	0.11	±	0.01	0.11	±	0.02
14:0[*]	3.15	±	0.07	5.36	±	0.09	3.16	±	0.09	5.29	±	0.09	5.53	±	0.23	3.96	±	0.07	3.22	±	0.10
Iso15	0.15	±	0.01	0.89	±	0.07	0.27	±	0.02	0.18	±	0.00	1.94	±	0.38	0.12	±	0.00	0.08	±	0.00
Anti15	0.15	±	0.01	0.11	±	0.01	0.11	±	0.01	0.07	±	0.00	0.17	±	0.02	0.06	±	0.00	0.58	±	0.09
15:0	0.34	±	0.01	0.28	±	0.01	0.30	±	0.01	0.26	±	0.00	0.30	±	0.01	0.18	±	0.00	0.37	±	0.02
Iso16	0.15	±	0.01	0.26	±	0.04	0.14	±	0.01	0.07	±	0.00	0.20	±	0.03	0.04	±	0.00	0.12	±	0.02
16:0[*]	10.02	±	0.21	6.26	±	0.13	10.12	±	0.22	8.33	±	0.16	6.05	±	0.17	5.89	±	0.13	9.85	±	0.33
7Me16:0	0.31	±	0.00	0.29	±	0.00	0.30	±	0.01	0.25	±	0.00	0.24	±	0.01	0.30	±	0.00	0.27	±	0.01
Iso17	0.31	±	0.01	0.13	±	0.01	0.29	±	0.02	0.12	±	0.00	0.14	±	0.01	0.06	±	0.00	0.49	±	0.04
17:0[*]	0.27	±	0.01	0.08	±	0.00	0.19	±	0.01	0.12	±	0.00	0.07	±	0.00	0.06	±	0.00	0.26	±	0.02
18:0	1.83	±	0.06	0.87	±	0.04	1.22	±	0.06	1.20	±	0.03	0.82	±	0.04	0.71	±	0.02	2.22	±	0.16
Monounsaturated fat																					
14:1n-9	0.09	±	0.01	0.85	±	0.06	0.07	±	0.01	0.19	±	0.01	0.71	±	0.08	0.18	±	0.00	0.14	±	0.01
14:1n-7	0.07	±	0.00	0.70	±	0.06	0.12	±	0.01	0.04	±	0.00	0.70	±	0.08	0.08	±	0.00	0.09	±	0.00
14:1n-5	0.52	±	0.03	1.86	±	0.10	1.00	±	0.12	0.53	±	0.03	2.32	±	0.38	1.08	±	0.00	0.55	±	0.12
16:1n-11	0.38	±	0.01	1.46	±	0.06	0.38	±	0.02	0.34	±	0.01	1.76	±	0.12	0.55	±	0.02	0.29	±	0.01
16:1n-9	0.39	±	0.01	1.59	±	0.08	0.56	±	0.03	0.24	±	0.01	1.65	±	0.13	0.47	±	0.01	0.40	±	0.02
16:1n-7	22.11	±	0.42	24.17	±	0.59	18.46	±	1.20	12.67	±	0.31	25.54	±	0.74	20.76	±	0.23	18.52	±	1.25
17:1	0.41	±	0.16	0.22	±	0.01	0.55	±	0.03	0.19	±	0.01	0.23	±	0.01	0.19	±	0.01	0.28	±	0.02
18:1n-13	0.27	±	0.01	0.05	±	0.00	0.18	±	0.01	0.08	±	0.00	0.06	±	0.00	0.06	±	0.00	0.42	±	0.05
18:1n-11	0.84	±	0.07	4.01	±	0.09	0.48	±	0.08	2.30	±	0.08	5.08	±	0.25	3.74	±	0.13	0.19	±	0.09
18:1n-9	14.89	±	0.26	15.72	±	0.22	18.06	±	0.39	11.39	±	0.28	16.77	±	0.62	12.69	±	0.21	13.95	±	0.47
18:1n-7	7.91	±	0.20	3.76	±	0.08	5.35	±	0.13	3.37	±	0.10	3.15	±	0.10	4.43	±	0.06	10.67	±	0.35
18:1n-5	0.62	±	0.01	0.47	±	0.01	0.61	±	0.02	0.53	±	0.01	0.40	±	0.01	0.60	±	0.01	0.40	±	0.01
20:1n-11[*]	0.97	±	0.05	2.38	±	0.07	0.43	±	0.04	1.53	±	0.05	3.74	±	0.19	1.51	±	0.05	1.18	±	0.09
20:1n-9[*]	3.34	±	0.21	8.04	±	0.28	2.01	±	0.20	12.29	±	0.35	7.12	±	0.36	7.90	±	0.26	1.97	±	0.15
20:1n-7[*]	1.30	±	0.04	0.60	±	0.02	0.49	±	0.02	0.78	±	0.03	0.57	±	0.03	0.75	±	0.02	4.61	±	0.37
22:1n-11[*]	0.83	±	0.11	3.60	±	0.20	0.26	±	0.08	7.14	±	0.30	3.53	±	0.27	1.98	±	0.12	0.10	±	0.02
22:1n-9[*]	0.31	±	0.03	0.70	±	0.04	0.18	±	0.02	1.12	±	0.05	0.62	±	0.05	0.67	±	0.03	0.15	±	0.02
22:1n-7[*]	0.09	±	0.01	0.11	±	0.01	0.04	±	0.01	0.16	±	0.01	0.10	±	0.01	0.10	±	0.01	0.12	±	0.01
24:1n-9	0.12	±	0.01	0.13	±	0.01	0.08	±	0.01	0.24	±	0.01	0.10	±	0.01	0.08	±	0.00	0.07	±	0.01

Table 1-5. Continued

Fatty acid	Bearded seal (n = 74)			Beluga whale (n = 87)			Harbour seal (n = 17)			Harp seal (n = 119)			Narwhal (n = 48)			Ringed seal (n = 206)			Walrus (n = 21)		
Polyunsaturated																					
16:2n-6[*]	0.05	±	0.00	0.06	±	0.00	0.07	±	0.01	0.06	±	0.00	0.06	±	0.00	0.07	±	0.00	0.07	±	0.00
16:2n-4[*]	0.28	±	0.02	0.25	±	0.01	0.54	±	0.03	0.22	±	0.01	0.22	±	0.01	0.12	±	0.01	0.08	±	0.01
16:3n-6[*]	0.31	±	0.01	0.51	±	0.01	0.19	±	0.01	0.52	±	0.01	0.42	±	0.01	0.73	±	0.01	0.36	±	0.02
16:3n-4[*]	0.12	±	0.00	0.10	±	0.00	0.08	±	0.01	0.32	±	0.01	0.06	±	0.00	0.28	±	0.01	0.09	±	0.01
16:4n-3[*]	0.09	±	0.01	0.19	±	0.02	0.17	±	0.01	0.10	±	0.00	0.13	±	0.01	0.07	±	0.00	0.02	±	0.00
16:4n-1[*]	0.16	±	0.01	0.10	±	0.00	0.06	±	0.01	0.55	±	0.02	0.07	±	0.01	0.41	±	0.02	0.21	±	0.02
18:2n-7[*]	0.07	±	0.00	0.05	±	0.00	0.11	±	0.01	0.04	±	0.00	0.07	±	0.01	0.08	±	0.00	0.11	±	0.01
18:2n-6[*]	1.91	±	0.06	1.39	±	0.04	1.94	±	0.13	1.28	±	0.03	0.79	±	0.04	1.14	±	0.03	0.75	±	0.03
18:2n-4[*]	0.18	±	0.00	0.09	±	0.00	0.10	±	0.00	0.10	±	0.00	0.07	±	0.00	0.14	±	0.00	0.36	±	0.02
18:3n-6[*]	0.17	±	0.00	0.08	±	0.00	0.17	±	0.01	0.12	±	0.00	0.05	±	0.00	0.20	±	0.00	0.13	±	0.01
18:3n-4[*]	0.14	±	0.00	0.10	±	0.00	0.10	±	0.01	0.11	±	0.00	0.10	±	0.00	0.13	±	0.00	0.32	±	0.02
18:3n-3[*]	0.43	±	0.02	0.22	±	0.01	0.93	±	0.08	0.53	±	0.03	0.22	±	0.01	0.35	±	0.01	0.23	±	0.01
18:3n-1[*]	0.11	±	0.01	0.08	±	0.00	0.17	±	0.01	0.06	±	0.00	0.09	±	0.02	0.05	±	0.00	0.06	±	0.00
18:4n-3[*]	0.82	±	0.05	0.33	±	0.01	1.58	±	0.12	1.57	±	0.06	0.18	±	0.01	0.85	±	0.03	0.72	±	0.04
18:4n-1[*]	0.13	±	0.01	0.12	±	0.00	0.04	±	0.00	0.18	±	0.01	0.09	±	0.01	0.16	±	0.00	0.32	±	0.02
20:2n-6[*]	0.49	±	0.02	0.17	±	0.01	0.38	±	0.01	0.22	±	0.00	0.17	±	0.01	0.21	±	0.00	0.72	±	0.03
20:3n-6[*]	0.12	±	0.00	0.06	±	0.00	0.09	±	0.01	0.06	±	0.00	0.05	±	0.00	0.11	±	0.00	0.26	±	0.01
20:4n-6[*]	1.02	±	0.03	0.23	±	0.01	0.93	±	0.07	0.29	±	0.01	0.21	±	0.01	0.35	±	0.01	0.59	±	0.05
20:3n-3[*]	0.08	±	0.00	0.03	±	0.00	0.12	±	0.01	0.06	±	0.00	0.03	±	0.00	0.04	±	0.00	0.08	±	0.01
20:4n-3[*]	0.55	±	0.02	0.33	±	0.01	0.73	±	0.05	0.54	±	0.02	0.19	±	0.01	0.35	±	0.00	0.73	±	0.03
20:5n-3[*]	8.63	±	0.22	3.24	±	0.14	6.39	±	0.43	6.89	±	0.17	1.92	±	0.13	9.13	±	0.14	6.96	±	0.46
21:5n-3[*]	0.44	±	0.01	0.13	±	0.01	0.30	±	0.01	0.41	±	0.01	0.07	±	0.00	0.40	±	0.01	0.75	±	0.04
22:4n-6[*]	0.26	±	0.01	0.08	±	0.02	0.28	±	0.03	0.06	±	0.00	0.04	±	0.00	0.07	±	0.00	0.61	±	0.16
22:5n-6[*]	0.22	±	0.01	0.06	±	0.01	0.24	±	0.01	0.09	±	0.00	0.04	±	0.00	0.07	±	0.00	0.13	±	0.03
22:4n-3[*]	0.08	±	0.00	0.03	±	0.00	0.12	±	0.01	0.09	±	0.00	0.02	±	0.00	0.05	±	0.00	0.09	±	0.01
22:5n-3[*]	4.36	±	0.09	1.76	±	0.10	4.75	±	0.21	4.52	±	0.09	1.04	±	0.10	5.89	±	0.07	6.63	±	0.50
22:6n-3[*]	9.67	±	0.37	3.78	±	0.20	12.90	±	0.58	9.45	±	0.25	2.03	±	0.01	8.82	±	0.11	4.46	±	0.23

Note: Only FA representing > 0.1% of total FA are shown in the table.

(*) represents the 38 FA used for fatty acid signature comparisons and accounts for approximately 99% of the total FA across all marine mammals.

Bold represents the FA used in the QFASA model to determine diet estimates of polar bears.

Geographic differences in FA signature

To capture geographic variability within marine mammal species, a PCA was conducted on each prey species separately. The generated PC scores were used to carry out a MANOVA on blubber samples from species captured in multiple geographic regions. Marine mammal blubber samples were pooled into the respective polar bear subpopulation from which they were harvested, further known as broad geographic regions. There were not enough samples to test regional differences in walrus and harbour seals. PCA on bearded seals generated 3 principal components which accounted for 74.8% of the explained variance, bearded seals from Davis Strait, Gulf of Boothia, and Foxe Basin clustered together and Western Hudson Bay bearded seals made up a separate cluster. Bearded seals differed significantly across polar bear subpopulations (MANOVA, Wilks' λ = 0.305, p < 0.001), except in the case of Gulf of Boothia and Foxe Basin, where bearded seals did not significantly differ (*post hoc* Tukey's test, Wilks' λ = 0.448, p = 0.157). PCA on beluga whales generated 3 principal components which explained 79.2% of total variance. Beluga whale FA significantly varied between Davis Strait, Foxe Basin, Lancaster Sound, and Western Hudson Bay (*post hoc* Tukey's test, p < 0.001 in all cases), however did not significantly differ between Davis Strait and Western Hudson Bay (*post hoc* Tukey's test, Wilks' λ = 0.813, p = 0.199). However within Foxe Basin, beluga whales were collected from 3 locations: Igloolik, Repulse Bay, and Coral Harbour and there was no significant difference found in beluga whale FA within the subpopulation (MANOVA, Wilks' λ = 0.861, p = 0.495). PCA on narwhals generated 3 principal components which accounted for 73.9% of total variance. Narwhals from Gulf of Boothia were excluded from the analysis due to the small sample size, however there was a significant difference between Baffin Bay and Foxe Basin (MANOVA, Wilks' λ = 0.471, p = 0.018), as well as Baffin Bay and Lancaster Sound (MANOVA, Wilks' λ = 0.471, p < 0.001) and no significant difference between Foxe Basin and

Lancaster Sound (MANOVA, Wilks' $\lambda = 0.752$, $p = 0.145$). A PCA on ringed seals generated 3

principal components accounting for 84.4% of total variance; Gulf of Boothia and Lancaster

Sound ringed seals clustered together separate from Foxe Basin samples. Geographic regions had

a significant effect on ringed seal FA signature (MANOVA, Wilks' $\lambda = 0.361$, $p < 0.001$).

Diet simulations

Diet simulations were performed using the prey species typically found in each

subpopulation. In all 3 subpopulations, polar bear prey could be accurately identified in the

simulated diets (Figure 1-7). Bearded seal tended to be underestimated and harp seal was

overestimated in the diet simulation. I tried multiple combinations of potential prey species from

varying regions and the simulation had the best resolution by using more numerous samples, also

more distant samples (pooling samples across geographic regions). As well, prey species

appeared to have greater variability among species than within species (see above).
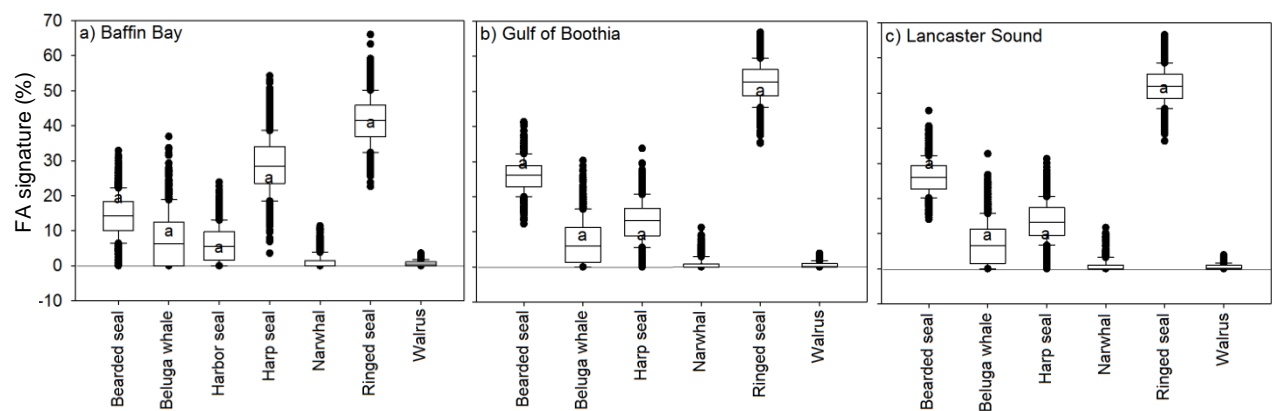
Figure 1-7. Results of simulation studies for Baffin Bay, Gulf of Boothia, and Lancaster Sound

prey data sets. The results are presented as boxplots, showing the 25th, median, and 75th

percentiles of the 1000 diet estimates and solid circles represent outliers. The specified diet

composition is represented as 'a' in plots.

Polar bear diet composition

Geographic differences in polar bear diet

There was a significant regional difference in polar bear diet composition between the

three subpopulations: Baffin Bay, Gulf of Boothia, and Lancaster Sound (permutation two-way

MANOVA, p < 0.001; Figure 1-8). Shannon-Wiener Index values indicated that Baffin Bay diet

composition was the most diverse (H' =0.996), followed by Lancaster Sound (H' =0.833), and

Gulf of Boothia (H' =0.809; ANOVA, F (1, 196) = 14.34, p < 0.001), although similar prey

species were consumed in all three High Arctic regions. Ringed seal contributed the highest

biomass in all three subpopulations: Baffin Bay: 41 ± 3%, Gulf of Boothia: 56 ± 3% and

Lancaster Sound 49 ± 2%. Gulf of Boothia polar bears consumed the highest biomass of ringed

seal compared to Baffin Bay and Lancaster Sound (permutation ANOVA, p = 0.020). Although,

ringed seal consumption was more frequent than any other prey species since ringed seal biomass

was present in the diet of the majority of bears across all 3 regions (Baffin Bay: 95% of bears,

Gulf of Boothia: 100% of bears, and Lancaster Sound: 93% of bears). Bearded seal was most

abundant in the diets of bears in Gulf of Boothia and Lancaster Sound (permutation ANOVA, p <

0.001) and most bears consumed bearded seal (89% and 90% of bears, respectively). Whereas,

harp seal was most abundant (21 ± 2%) and found most frequently (84% of bears) in diets of

polar bears in Baffin Bay, but present as a minor component in Gulf of Boothia (6 ± 1%) and

Lancaster Sound (10 ± 1%; permutation ANOVA, p < 0.001). Beluga whales had the third

highest biomass contribution in all three subpopulations, however there was no significant

difference in biomass consumed between the three regions (Baffin Bay 19 ± 4%, Gulf of Boothia

15 ± 3%, and Lancaster Sound 15 ± 3%; permutation ANOVA, p = 0.235). Beluga whale

consumption was less frequent (Baffin Bay: 55% of bears, Gulf of Boothia: 48% of bears, and

Lancaster Sound: 43% of bears), though present in high levels in some individuals with the majority of their diet consisting of beluga whale biomass.
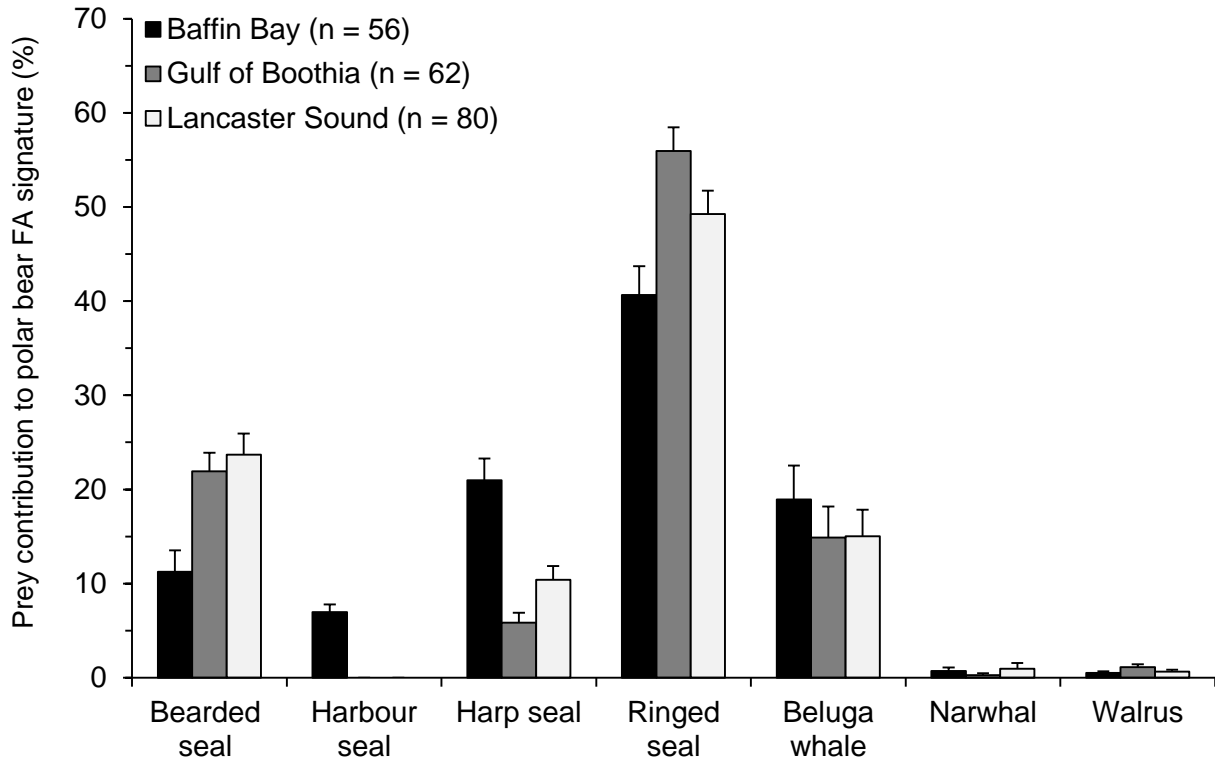
Figure 1-8. Diet composition of polar bears (n = 198) in each of the three subpopulations (Baffin Bay, Gulf of Boothia, and Lancaster Sound). Prey contribution is represented as each species' biomass to polar bear diet. Data are shown as means ± SE. Diet composition of Gulf of Boothia and Lancaster Sound polar bears were not modelled using harbour seals because the species is not available in these two regions.

Sex and age class differences in diet

In Baffin Bay, there was a significant interaction between sex and age class in overall diet composition (permutation two-way MANOVA, p = 0.006; Figure 1-9a). In contrast, sex and age class had no effect on polar bear diet composition in Gulf of Boothia (permutation two-way

MANOVA, p = 0.833; Figure 1-9b) or Lancaster Sound (permutation two-way MANOVA, p = 0.231; Figure 1-9c). In Baffin Bay, bearded seal consumption was significantly higher in adult females than adult males and younger age classes (permutation ANOVA, p < 0.001). Most adult females consumed bearded seal (90% of bears), although the overall high levels present in diet seem to be driven by 3 individuals with over 50% bearded seal biomass in diet. There was a significant interaction between sex and age class for harp seal consumption, as adult females had significantly less harp seal in diet composition than adult males and subadults (permutation ANOVA, p = 0.028). Harp seal was found most frequent in the diet of adult males (96% of bears) and subadult females (100% of bears). Sex and age class did not significantly affect the consumption of ringed seal (permutation ANOVA, p = 0.217) or beluga (permutation ANOVA, p = 0.163) in Baffin Bay. However, beluga whales were found more often in the diet of adult males (77% of bears) and subadult females (83% of bears), than in adult females (10% of bears) or subadult males (33% of bears).
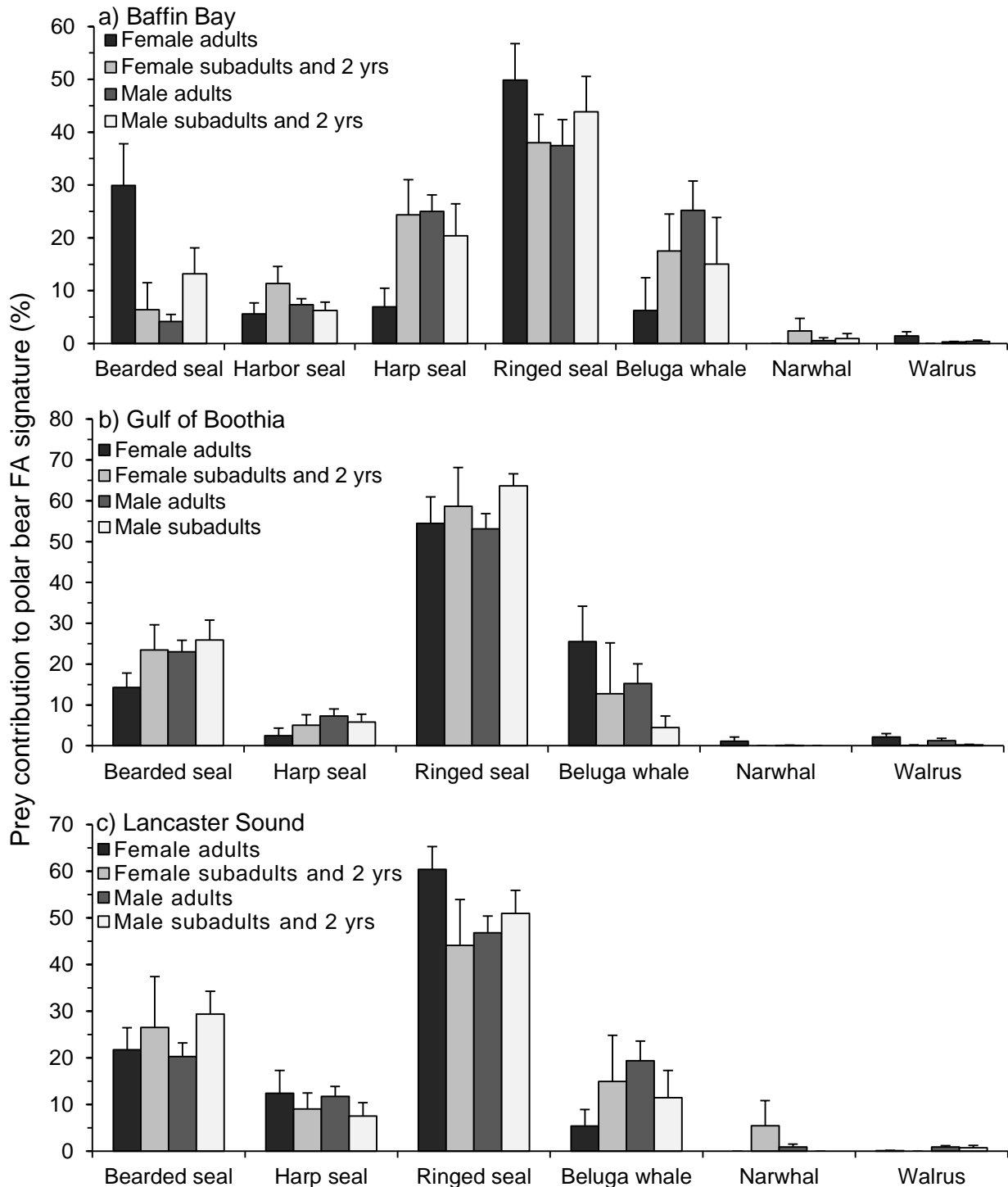
Figure 1-9. Sex and age class variation in polar bear diet composition sampled in the High Arctic subpopulations in 2010/11 and 2011/12. Diet estimates are represented as mean ± SE. (a) Baffin Bay, (b) Gulf of Boothia, and (c) Lancaster Sound.

Seasonal differences in polar bear diet composition

Season had no significant effect on overall diet composition in Baffin Bay (permutation two-way MANOVA, p = 0.669) or Lancaster Sound (two-way permutation MANOVA, p = 0.056; Figure 1-10a, c). In Gulf of Boothia, there were too few samples to compare fall diets, but winter and spring diets differed (two-way permutation MANOVA, p = 0.023), although the diversity remained consistent between the two seasons (winter, $H' = 0.812$; spring, $H' = 0.816$, Figure 1-10b). Ringed seals were consistently the primary prey in all three High Arctic regions throughout the year, whereas other prey species showed seasonal fluctuations in dietary biomass. In Gulf of Boothia, bearded seal consumption was higher in the winter than the spring (ANOVA, p = 0.017) and 100% of bears consumed bearded seal in the winter in comparison to 83% of bears in spring. Beluga whale became the most abundant prey next to ringed seal in the spring but declined in the winter (permutation ANOVA, p = 0.022). Beluga whale was found more often in the diet of polar bears in the spring (61% of bears) compared to winter (25% of bears). Walrus was a minor component in Gulf of Boothia diets during the spring (permutation t-test, p = 0.006). Given that the most fluctuation occurred in ringed seal, bearded seal, and beluga whale consumption in all 3 subpopulations, biomass for these three prey species was shown on a monthly scale (Figure 1-11). The opportunistic sampling protocol precluded statistical analysis.
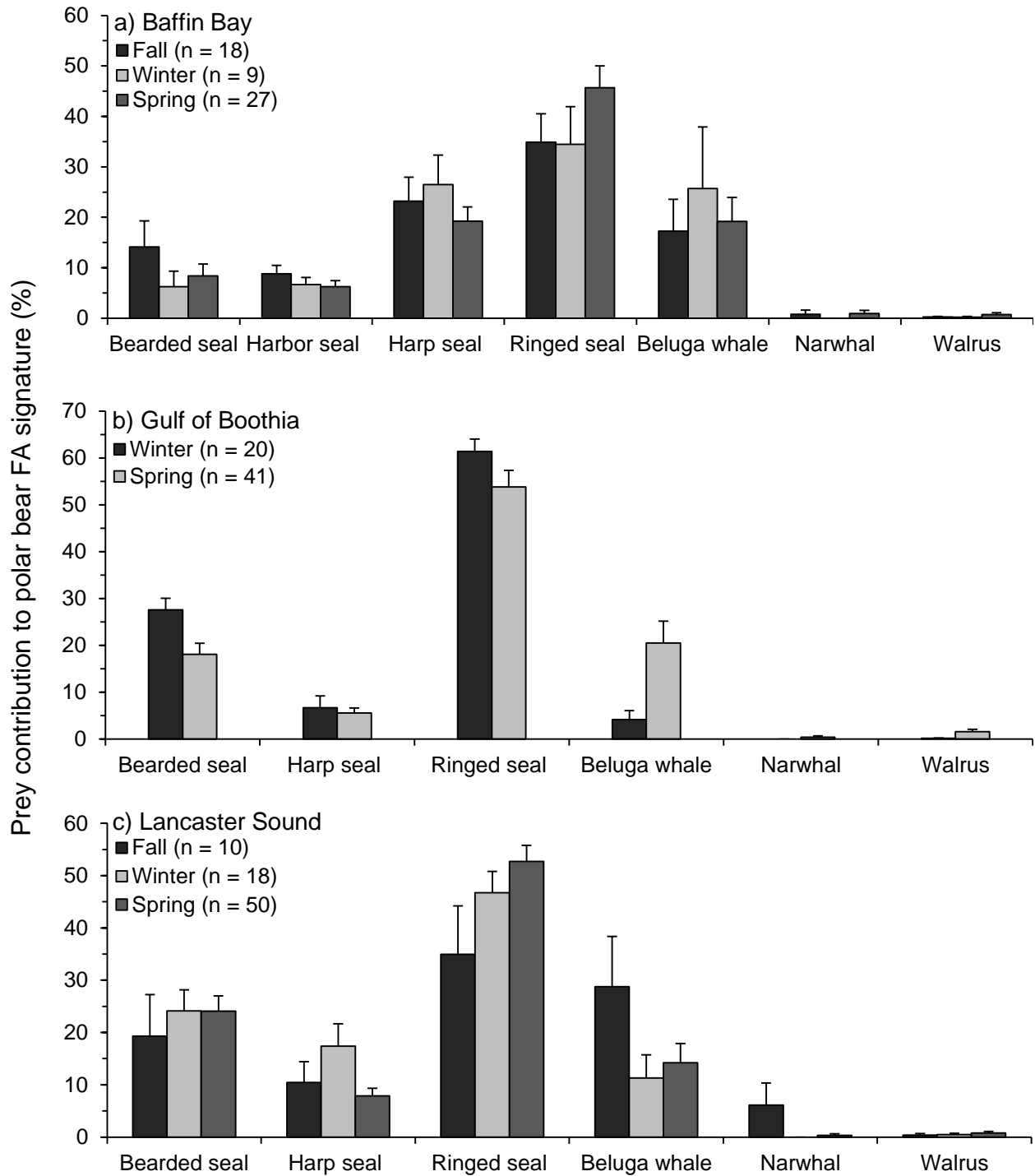
Figure 1-10. Seasonal diet composition of polar bears sampled in 2010/11 and 2011/12 in a) Baffin Bay, b) Gulf of Boothia, and c) Lancaster Sound. Diet estimates are repesented as mean ± SE.
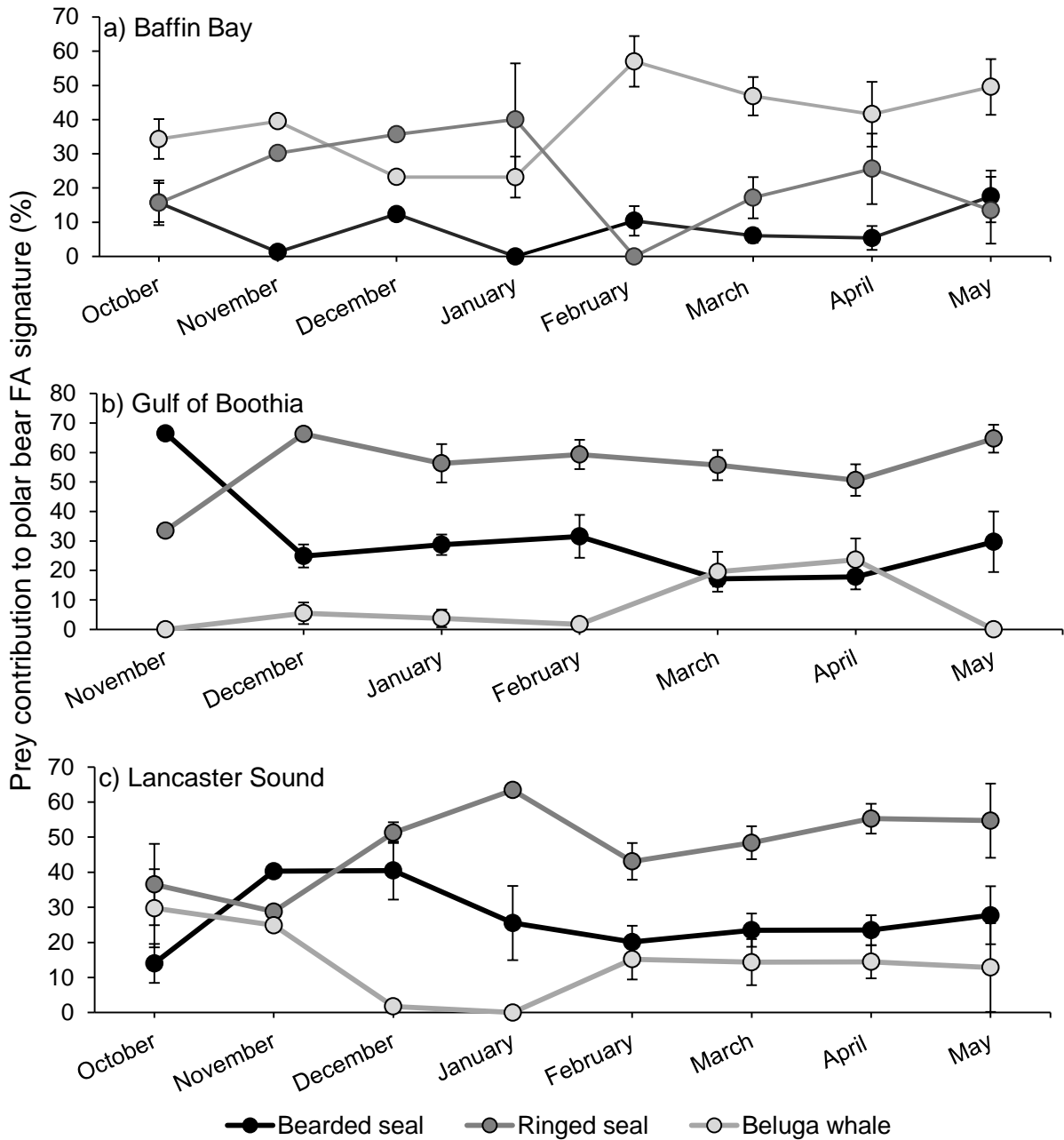
Figure 1-11. Monthly diet composition of polar bears sampled in 2010/11 and 2011/12 in a) Baffin Bay, b) Gulf of Boothia, and c) Lancaster Sound. Diet estimates are repesented as mean ± SE. Polar bear adipose tissue samples are collected opportunistically, therefore sample sizes across months are uneven and particular months have a small sample size. In Baffin Bay, the sample size ranged from 2 in November to 16 in October; in Gulf of Boothia, 1 in November to 20 in March; in Lancaster Sound, 2 in November to 25 in April.

Discussion

Diet composition of polar bears within Baffin Bay, Gulf of Boothia, and Lancaster Sound was comprised of a diversity of prey species which migrate between all 3 regions. To the best of my knowledge, this study is the first to reliably estimate the diet composition of polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound. My results help explain the ecological similarities previously observed among bears in these 3 regions and potentially reveal the factors supporting the high density of polar bears inhabiting these regions, where sea ice conditions may not yet be strongly affected by climate change. Seasonal variation in diet suggests a link between sea ice conditions and the migration routes of polar bear prey. Although few quantitative data are currently available, long-term reductions in sea ice will likely alter trophic relationships in these regions.

Lipid content

The fatness index rating has been used by biologists to qualitatively assess the overall body condition of individual polar bears (Stirling et al. 2008). The fatness index rating of polar bears in this study was correlated with adipose tissue lipid content, which suggests that adipose lipid content was a reliable indicator of body condition. This relationship is consistent with previous studies (Stirling et al. 2008, McKinney et al. 2014). Moreover, my results reveal, for the first time, that fatness index ratings provided by hunters also reliably reflect the body condition of harvested polar bears. Continued monitoring of polar bear body condition via harvest-based fat samples and hunter assessments may reveal emergent relationships between environmental conditions and polar bear foraging success.

Adipose lipid content as an indicator of overall body condition has only been used in Western Hudson Bay and the Beaufort Sea (Thiemann et al. 2006, Stirling et al. 2008, McKinney

et al. 2014). This is the first study to date which has recorded lipid content in polar bears within the High Arctic regions. Previous studies have documented seasonal differences in adipose lipid content, which tends to be higher in polar bears in fall than in the spring (Thiemann et al. 2006, McKinney et al. 2014). However, this is the first study to track body condition patterns through the fall and winter. The seasonal pattern in lipid content I observed (Figure 1-3) suggests that polar bear body condition changes in association with seasonal shifts in sea ice conditions and seal abundance in the High Arctic. Specifically, polar bears appear to lose body fat throughout the winter months, when snow and heavy ice conditions limit prey availability and thus polar bear feeding opportunities (Stirling and Oritsland 1995). Polar bears likely reach their lowest body weights in early spring, just prior to the time when lipid-rich, newly weaned ringed seals are available and mature seals haul out on the ice to moult (Stirling and Oritsland 1995, Stirling 2002). During the summer, the amount of open-water increases and seals become less available. Thus, late April to July is the critical feeding period for polar bears to accumulate the fat stores they rely on for much of the rest of the year.

Polar bear prey fatty acid signatures

Polar bear prey species were distinguished by species according to their fatty acid profile. Although prey species were well separated, there was clustering consistent with previous studies, most likely due to similar foraging patterns (Figure 1-6; Iverson et al. 2006, Thiemann et al. 2008a). For instance, both bearded seal and walrus feed on benthic invertebrates (Thiemann et al. 2007a, Budge et al. 2007) which are also identified as an occasional food source for harbour seals (Thiemann et al. 2007a). Similarly, the clustering of ringed seals and harp seals is consistent with the primarily pelagic feeding habits of these species (Wathne et al. 2000, Holst et al. 2001, Tucker et al. 2009). The similarity in beluga and narwhal FA profiles was probably affected by

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both similarities in diet (Laidre et al. 2008) and genetic factors. Spatial variation in fatty acid signature within a species reflects variation in diet and foraging across locations (Thiemann et al. 2007b, 2008b). The results of this study also indicate regional differences within species, though differences were relatively small in comparison to among species differences. Therefore, pooling prey species from various locations likely had little effect on the reliability of polar bear diet estimates using the QFASA model.

Polar bear fatty acid signatures

This study identified similar polar bear fatty acid signatures among these 3 adjacent subpopulations which is consistent with previous studies (Thiemann et al. 2008a). The fatty acid profiles of these subpopulations are most likely similar as a result of common prey species available to polar bears inhabiting these regions or the result of polar bears moving towards a common abundant resource. In addition, these polar bears primarily prey on ringed seals, followed by bearded seals which is common in most subpopulations (Iverson et al. 2006, Thiemann et al. 2008a). Although the FA profiles of polar bears in the three subpopulations studied here were similar, they are collectively distinct from polar bears in other parts of the Canadian Arctic (Thiemann et al. 2008a). The relative distinctiveness of these High Arctic polar bears may be a consequence of the relatively high level of beluga whale and harp seal in their diet.

Regional variation in polar bear diet

Polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound had a variety of prey species present in their diet composition with Baffin Bay having the highest, likely because of access to harbour seals migrating northward from Davis Strait. Polar bears in adjacent subpopulations had similar diets suggesting shared prey which migrate throughout all three

regions. However, the timing of migration may alter the accessibility of certain prey within a region. As a result, polar bears may be exploiting locally abundant prey as they become available. Ringed seals are the primary prey species of polar bears throughout their circumpolar range because of their relatively small size and high abundance (Stirling and Archibald 1977, Kingsley et al. 1985, Stirling and Oritsland 1995). Typically, predation on species other than ringed seals is considered opportunistic; however some individual bears may specialize in capturing larger prey species more frequently (Thiemann et al. 2011).

Bearded seals were an important alternate prey species in the three High Arctic regions I studied, making up a significant portion of the diet especially in Gulf of Boothia and Lancaster Sound. Although predation on bearded seals has been well-documented (Smith 1980, Derocher et al. 2002, Iverson et al. 2006, Thiemann et al. 2008a), little is known about the distribution, abundance, and movement patterns of bearded seals within the High Arctic. Stirling and Archibald (1977) suggested a higher abundance of bearded seals in the western Arctic compared to the Canadian Archipelago because of the greater amount of drifting pack ice. As a result the study suggested a greater importance of bearded seals in the diet of polar bears inhabiting the western Arctic, which contrasts the results of this study.

Beluga whales also made up a large portion of polar bear diet in the studied subpopulations. Belugas may be most accessible to polar bears during months with possible sea ice entrapment and leads (Heide-Jørgensen et al. 2003). Polar bears have been observed feeding on beluga whales in the Canadian High Arctic, however previous studies have suggested the high abundance of beluga whales in the Archipelago was underutilized as a food resource (Smith and Sjare 1990). The substantial proportion of beluga whale in the diet (16%) suggests that polar bears within these regions are taking advantage of the large number of beluga whales annually

migrating to their summer aggregation within the Arctic Archipelago. Thiemann et al. (2008a) also quantified polar bears feeding more heavily on beluga whales in higher latitudes than other southern regions of the Arctic.

Narwhals and walrus were present as minor components in the diet composition. A large walrus may be too difficult for most polar bears to successfully capture (Calvert and Stirling 1990). Narwhals may be abundant in various summering grounds within the Canadian Archipelago and over-winter in Baffin Bay; however narwhals may be less accessible than belugas because of their preference for deeper offshore waters (Smith and Sjare 1990).

Harp seals migrate from their wintering range (area off southern Labrador and northern Newfoundland) northward as the sea ice retreats reaching northwest Baffin Bay in early July and reaching feeding grounds within Lancaster Sound during the summer months when the region becomes ice free (Finley et al. 1990, DFO 2011). As the sea ice begins to reform in late September, harp seals migrate back to southern areas (Finley et al. 1990). Polar bears have been observed foraging on harp seals during the summer in Svalbard when available (Derocher et al. 2002). In addition McKinney et al. (2013) recorded an increase in harp seals and hooded seals in the diet composition of polar bears suggesting a shift from Arctic species such as ringed seal to subarctic species in East Greenland. Harp seals have increased in numbers over the past four decades (DFO 2011) and may be an important alternate prey species. The highest level of harp seal consumption was found in Baffin Bay, where polar bears would have access during the spring and fall migration. It is also possible that some polar bears in Baffin Bay migrate south to prey on harp seals in the whelping patches off Newfoundland and Labrador (DFO 2011). Harp seals were less abundant in the diets of bears in Lancaster Sound and Gulf of Boothia. Harp seals are generally found in these two regions during the ice free period and thus would be less

accessible to polar bears. To date, this is the first study to reliably quantify harp seals in the diet of polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound. In previous studies the QFASA model was unable to distinguish harp seals from other species such as ringed seals and bearded seals and thus was modelled without harp seals (Thiemann et al. 2008a).

In this study, the set of FA used to estimate the diets of polar bears excluded 20:1n-11. This fatty acid seemed to contribute too much to the overlap among prey fatty acid signatures and thus potentially led to an overestimation of harp seals in the diet composition of polar bears. Diet simulations showed that the removal of 20:1n-11 produced more accurate diet estimates. This improved set of fatty acids, and increased prey sample sizes relative to previous studies in the region, increase the reliability of the current results. Nevertheless, increased sampling of harp seals in the High Arctic may also provide better resolution of food sources in polar bear diets. Harp seals may become more abundant at high latitudes as climate warming progresses and future studies will need to account for temporal and spatial variation in harp seal fatty acid profiles (Finley et al. 1990, Tucker et al. 2009).

Each of the 3 subpopulations studied here supports a high density of polar bears (Obbard et al. 2010). Even though these regions are adjacent, there is variation in sea ice conditions. Baffin Bay belongs to the seasonal ice ecoregion, characterized by annual sea ice break-up in the spring, an ice-free summer, and ice freeze-up in the fall (Amstrup et al. 2008). In winter, the Arctic Archipelago (which includes Gulf of Boothia and Lancaster Sound) is completely covered by densely packed sea ice and in July, ice cover begins to retreat reaching the lowest sea ice extent in September (Sou and Flato 2009). Sea ice cover and thickness within the Arctic Archipelago has remained relatively stable, however the extent of summer sea ice is predicted to decrease in the future (Sou and Flato 2009). The North Water Polynya is the largest recurring

polynya in the Canadian Arctic extending from northern Baffin Bay to eastern Lancaster Sound (Stirling 1997, Born et al. 2004, Heide-Jørgensen et al. 2013). A variety of marine mammals are attracted to the highly productive waters, including ringed seals, bearded seals, beluga whales, narwhals, and walrus (Stirling 1980, Laidre et al. 2008, Heide-Jørgensen et al. 2013). The similarity of polar bear fatty acid profiles and diets in the High Arctic may be a consequence of bears targeting common feeding areas, perhaps in the North Water and adjacent areas.

The productivity and diversity of polynya systems may also contribute to the wide diversity of prey used by High Arctic bears relative to those in other regions. Lancaster Sound has shallow water over the continental shelf along with several small polynyas that leads to highly productive waters (Stirling 1980, 1997, Welch et al. 1992). Bears from the adjacent waters of the Gulf of Boothia may be benefitting from the nutrient-rich waters in Lancaster Sound, leading to a higher diversity of prey species and ultimately higher densities of polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound. Predator-prey dynamics are likely to shift as open-water persists for longer periods of time. The wide diversity of prey species available to polar bears within these regions may help mitigate the effects of declining habitat quality, as individuals have the ability to alter foraging to locally abundant prey and not rely on foraging for a single species. A similar pattern was identified in the Chukchi Sea, where shallow water over the broad continental shelf results in high prey density and diversity and bears have shown no obvious negative effects despite extensive sea ice loss to date (Rode et al. 2014).

Sex and age variation in polar bear diet

Sex and age class had a significant influence on the variation among polar bears in Baffin Bay, although ringed seal consumption was consistently high in all sex and age classes. In past studies, adult male polar bears have often been found to have a higher level of bearded seal in

their diet (Iverson et al. 2006, Thiemann et al. 2008a). The larger body size of adult males (Atkinson et al. 1996, Derocher et al. 2005, 2010) provides a greater ability to capture larger prey items, like bearded seals. My results showed a reverse trend among polar bears in Baffin Bay where adult females fed more on bearded seal than adult males. Perhaps female bears are targeting younger, smaller bearded seals, or adult males are targeting harp seal and beluga whale. The presence of large prey items in the diets of subadults is most likely due to scavenging on kill remains left by larger adult males.

In Gulf of Boothia and Lancaster Sound, there was no difference in diets between sexes or age classes of polar bears, which is consistent with Thiemann et al. (2008a). Diet composition was similar with a high proportion of ringed seal followed by larger prey species such as bearded seal, harp seal, and beluga whale. Again, the high level of large prey items in the diets of adult males is consistent with previous studies (Iverson et al. 2006, Thiemann et al. 2007a, 2008a), although larger prey species are also frequently present in the diet of adult females and subadults. Subordinate individuals may be scavenging on the remains of kills made by larger adult male bears. Previous studies have suggested scavenging by polar bears to be an important opportunistic food source for less experienced individuals (Stirling and McEwan 1975, Derocher et al. 2002) and scavenging was particularly high within the Canadian Archipelago (Smith and Sjare 1990). Observations of polar bear foraging has indicated that during times when numerous belugas are killed, a large number of bears will be attracted to the area and share the carcasses in a non-aggressive manner (Lowry et al . 1987, Derocher et al. 2002). Thus, a lack of sex and age difference in Gulf of Boothia and Lancaster Sound is consistent with the exploitation of very large-bodied prey such as beluga whale.

Seasonal variation in polar bear diet

Ringed seals were consistently dominant in the diet of polar bears throughout the year. However, ringed seal consumption increased during the spring as hunting conditions become more favourable (Figure 1-10). The high level of bearded seal and beluga whale in diets suggest that polar bears in these regions have the ability to seasonally switch to alternate prey species when abundant. From July to October with sea ice breakup, bearded seals are found within the Canadian Archipelago in the preferred habitat of drifting pack ice (Finley and Evans 1983). Thus, bearded seals may be more accessible to polar bears during the summer and fall in the Gulf of Boothia and may explain the higher biomass of bearded seals found in the diets of bears sampled in winter rather than spring.

Beluga whales in the Eastern-High Arctic move from Northern Baffin Bay into Lancaster Sound at the beginning of June as the ice retreats, and then migrate south to the summer feeding grounds around Somerset Island (Smith and Martin 1994, Richard et al. 2001). During the fall, belugas migrate north-eastward through Lancaster Sound to winter in the North Water Polynya and use shore leads in adjacent areas (Richard et al. 2001, Heide-Jørgensen et al. 2003). Among Baffin Bay and Lancaster Sound polar bears, beluga whale biomass was highest during winter and fall respectively, suggesting polar bear foraging is associated with migration patterns. Although difficult to quantify, it is not uncommon for beluga whales to become entrapped in ice within regions of the Archipelago and local community members have recorded beluga whale and narwhal entrapment events during the fall in Lancaster Sound, particularly in Arctic Bay and Grise Fiord (Stewart 2001). The fall timing and location of ice entrapment records coincide with an increase in beluga whale consumption among polar bears in Lancaster Sound.

In the Gulf of Boothia, beluga whales appeared in the diet of polar bears in early spring; however migration into the Canadian Archipelago does not typically occur until early June during the initial ice breakup (Smith and Martin 1994, Richard et al. 2001). Thus, beluga whales are likely most abundant in the Gulf of Boothia during mid-July to the end of August. It is possible that polar bears in Gulf of Boothia with a large proportion of beluga whale in their diet may be moving north towards southern Lancaster Sound to exploit beluga whales in shore leads, where there is an increased chance for ice entrapment. Reports from local community members have documented beluga whale ice entrapment from late November to April (Stewart 2001). Substantial interchange of polar bears between Gulf of Boothia and Lancaster Sound, driven by shared food resources, would explain the strong similarity of FA profiles of these two groups (see Figure 1-5, also Thiemann et al. 2008a) and perhaps explain the very high density of polar bears in the Gulf of Boothia.

Satellite telemetry of polar bears may help identify important foraging grounds of polar bears throughout the study area, especially around the rich-nutrient waters of Lancaster Sound. Moreover, continued and future studies of polar bear habitat use and foraging will provide a better understanding of the link between ecological conditions and seasonal patterns of prey selection and how they may be shaped by ongoing environmental change.

Implications for conservation

The diets of polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound are dominated by ringed seals; however a large portion of the remaining diet is comprised of alternate prey species including bearded seals and beluga whales. Other regions within the Canadian Arctic rely more heavily on ringed seals, followed by bearded seals (Iverson et al. 2006, Thiemann et al. 2008a), suggesting the foraging dynamics within these three High Arctic

regions fundamentally differ from other regions of the Arctic. My results provide further support for designatable units first suggested by (Thiemann et al. 2008c). Currently, polar bears are considered as a single unit in terms of conservation status but are divided into 19 subpopulations for management purposes (COSEWIC 2008). Ecological factors such as primary productivity, prey distribution, and sea ice conditions vary spatially and temporally across the Canadian Arctic; as well, the rate at which subpopulations will be affected by climate change varies (Stirling and Derocher 2012). Thiemann et al. (2008c) recommended five distinct designatable units: Beaufort Sea, Central Arctic, High Arctic, Hudson Bay/Foxe Basin and Davis Strait. Baffin Bay, Gulf of Boothia, and Lancaster Sound would comprise part of the Central Arctic Unit. The similarity of polar bear diets, as well as the likely interchange of prey and possibly polar bears, further supports the idea that bears in these three subpopulations share a common conservation status driven by broader ecological dynamics, including sea ice conditions and biological productivity.

In summary, this study identifies the high diversity of prey species present in the diet of polar bears in Baffin Bay, Gulf of Boothia, and Lancaster Sound. The North Water polynya and highly productive waters of Lancaster Sound may attract various marine mammals and support the high density of polar bears within these high latitude areas. Annual migrations of marine mammals are consistent with observed shifts in the diets of polar bears exploiting seasonally abundant prey. This study confirmed polar bear foraging on harp seals in all three regions, but particularly in Baffin Bay. The results of the QFASA model have helped better understand the predator-prey dynamics within these regions and will help identify long-term dietary shifts in relation to future sea ice conditions.

Chapter 3: Spatial variation in the diet of polar bears (*Ursus maritimus*) in

Foxe Basin, Nunavut

Polar bear (*Ursus maritimus*) subpopulations with a seasonal sea ice regime have shown signs of reduced body condition and reproductive rates as a result of declining sea ice habitat. This study aimed to identify potential reasons for why the Foxe Basin subpopulation has remained stable despite shifts in sea ice habitat. I used fatty acid analysis to examine polar bear feeding patterns and adipose tissue lipid content as an indicator of body condition. Adipose tissue samples were collected from 102 polar bears harvested by Inuit hunters within the Foxe Basin subpopulation during the 2010/2011 and 2011/2012 harvest seasons. In addition, I specifically tested the hypothesis that polar bears may be exploiting the growing bowhead whale (*Balaena mysticetus*) population. Polar bear diet composition varied spatially among northern Foxe Basin, southern Foxe Basin, and Hudson Strait. Ringed seal (*Pusa hispida*) was the primary prey in northern and southern Foxe Basin, whereas polar bears in Hudson Strait consumed an equal proportion of ringed seal and harp seal (*Pagophilus groenlandicus*) biomass. Walrus (*Odobenus rosmarus*) consumption was highest in northern Foxe Basin, followed by Hudson Strait, a trend driven by the ability of adult male polar bears to capture large prey. Bowhead whale biomass contributed to polar bear diets in all 3 areas, as well as within all age classes and sexes, with bowhead carcasses potentially providing an important food source during the ice free period. My results indicate the importance of locally abundant prey throughout Foxe Basin. Bowhead whale consumption may be an indirect result of killer whale predation, which should be studied further as the potential increase in killer whales could alter the dynamics of this Arctic marine food web.

Introduction

Ecological flexibility can play an important role in a species' ability to cope with environmental change; on the other hand, highly specialized species can be sensitive to climate change and habitat loss (Colles et al. 2009, Kovacs et al. 2011, Gilg et al. 2012). Polar bears (*Ursus maritimus*), are top predators within their Arctic circumpolar range and may be sensitive to environmental change because of their reliance on the sea ice habitat for travelling, mating and foraging (Stirling and Derocher 1993, Laidre et al. 2008). As sea ice extent and habitat quality decline because of climate warming, prey species may become less accessible resulting in nutritional stress and ultimately reduced body condition, reproductive rates, and survival (Stirling et al. 1999, Stirling and Parkinson 2006, Stirling and Derocher 2012). The effects of environmental shifts on polar bears vary throughout their range and the response to change is poorly understood in certain geographic areas, since most studies have focused on Western Hudson Bay and the Beaufort Sea (e.g., Regehr et al. 2007, Rode et al. 2010, Schliebe et al. 2008).

Across the Arctic, the primary prey of polar bears are ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus;* Stirling and Archibald 1977, Smith 1980, Stirling and Oritsland 1995). Locally abundant marine mammals may also provide an important food source for polar bears throughout the Arctic. Harp seals (*Pagophilus groenlandicus*) are often the primary prey of polar bears in Davis Strait (Iverson et al. 2006) and in Svalbard (Derocher et al. 2002). In addition, polar bears have been found to opportunistically feed on larger prey species such as beluga whales (*Delphinapterus leucas*; Richard et al. 2001, Thiemann et al. 2008a), narwhals (*Monodon Monoceros*; Smith and Sjare 1990), and walrus (*Odobenus rosmarus*; Kiliaan and Stirling 1978, Calvert and Stirling 1990, Thiemann et al. 2007a). Furthermore, polar

bears have been observed scavenging on the carcasses of bowhead whales (*Balaena mysticetus*) left on shore during subsistence harvests (Bentzen et al. 2007, Herreman and Peacock 2013).

The long-term monitoring of polar bear foraging ecology can provide insight into shifts in prey availability or changes in sea ice conditions (Iverson et al. 2004, Budge et al. 2006, Thiemann 2008). Fatty acid analysis has been used to examine the foraging ecology of a number of species including seabirds (Iverson et al. 2007), marine mammals (Iverson et al. 1997, Beck et al. 2007, Budge et al. 2008, Loseto et al. 2009), and polar bears (Iverson et al. 2006, Thiemann et al. 2008a, 2011). Dietary fatty acids are incorporated into the adipose tissue of a predator with little or no modification and reflect diet over the preceding weeks and months (Iverson et al. 2004, Budge et al. 2006, Thiemann 2008). Diet composition in individual predators can be estimated using quantitative fatty acid signature analysis (QFASA) which uses a statistical model to estimate the proportional combination of available prey that most closely matches the observed predator (Iverson et al. 2004).

A previous study by Thiemann et al. (2008a) examined the diet composition and diversity of polar bears across the Canadian Arctic, including Foxe Basin. However, the authors only considered the mean diet of bears in Foxe Basin, despite the fact this region spans approximately 1.18 million km^2 from Hudson Strait north to Fury and Hecla Strait and south to the northwestern coast of Quebec (Figure 1-1; Vongraven and Peacock 2011). Thus, the large geographic area, and diverse ecological conditions may result in spatially variable foraging patterns, which have not yet been assessed.

Foxe Basin is seasonally ice-free and polar bears are forced to migrate on shore and rely on stored fat for energy when the sea ice melts each year. The sea ice season has declined from 9

to 7 months from 1979 to 2008 (Sahanatien and Derocher 2012). As a result, the fasting period

begins earlier and has increased in length, thus providing less foraging time to accumulate fat in

the spring and early summer (Stirling and Parkinson 2006, Sahanatien and Derocher 2012). In

addition, Foxe Basin and adjacent areas in Hudson Bay and Hudson Strait have all shown an

overall increase in sea ice fragmentation (Sahanatien and Derocher 2012). Loss of preferred ice

habitat can reduce on-ice foraging time for polar bears and accessibility to prey, along with

increased frequency and swimming distance between patches of ice (Stirling et al. 1999, Regehr

et al. 2007, Sahanatien and Derocher 2012, Rode et al. 2012). Studies have already identified

population level shifts such as reduced body condition, reproductive rates, and abundance in

Western Hudson Bay in relation to a longer open water season (Stirling et al. 1999, Regehr et al.

2007).

Polar bears in Foxe Basin have experienced similar declining sea ice trends as seen in

Western Hudson Bay, although population-level effects associated with environmental shifts

have not been recorded (Stapleton et al. 2012). The population size was estimated in 2009/2010

to be 2,580 (95% CI: 2,093 – 3,180) based on aerial surveys during the open-water season

(Stapleton et al. 2012) and previously estimated as 2,197 (95% CI: 1,677 – 2,717) in 1994 via

mark-recapture methods (Obbard et al. 2010). Polar bear body condition was assessed during the

aerial survey using a qualitative fatness index rating of 1 to 5. Bears appeared to be in good body

condition showing no negative effects of sea ice reduction (Stapleton et al. 2012). The ecological

factors supporting this stable subpopulation in the face of declining sea ice quality and duration

are unclear.

Ongoing environmental change has created the potential for a shift in food web dynamics

within this region as killer whales (*Orcinus orca*) have expanded their range into Hudson Bay

and Foxe Basin (Higdon and Ferguson 2009, Higdon et al. 2012). Historically limited by sea ice conditions in Hudson Strait, killer whales now feed on a variety of marine mammals in the region, including bowhead whales, ringed seals, beluga whales, and narwhals, thus potentially competing with polar bears for the same prey (Higdon and Ferguson 2009). Killer whales may target smaller individuals and since northern Foxe Basin acts as an important summer nursery for cow-calf pairs and feeding ground for juveniles, bowhead whales within this region have become increasingly vulnerable to predation (Cosens and Blouw 2003, Higdon and Ferguson 2010). Killer whales may target the head and mouthparts of a baleen whale (Jefferson et al. 1991, Ford et al. 2005) and thereby leave a large carcass that can drift on shore. Thus, killer whale predation on bowhead whales may be creating an additional food source for polar bears, in addition to natural strandings.

Bowhead whale carcasses are a known source of food for polar bears in Beaufort Sea and Chukchi Sea, where bowhead whale remains from subsistence harvests are aggregated into bone piles (consisting of trimmed blubber, remnant meat, and bones) along the Alaskan coast (Herreman and Peacock 2013). Previous studies have observed high concentrations of polar bears scavenging on carcasses throughout the fall and winter (Miller et al. 2006, Schliebe et al. 2008, Herreman and Peacock 2013). Schliebe et al. (2008) recorded upwards of 65 polar bears on a single bowhead whale carcass. Furthermore, bowhead whales were quantified as minor dietary components among polar bears in the Southern Beaufort Sea (Bentzen et al. 2007) and Chukchi Sea (Rode et al. 2014). On average, remains from 18 bowhead whales are deposited among the piles each year in Alaska (Herreman and Peacock 2013), whereas only 2 to 3 bowhead whales are landed each year across Nunavut (DFO 2008). Bowhead whale carcasses are, thus, frequently and predictably available to bears in the Beaufort Sea and Chukchi Sea. In contrast, the few bowhead

whales annually harvested in Nunavut provide a rare additional food source unlike in Alaska where subsistence harvest is the primary source of bowhead whale carcasses.

The objective of this study was to characterize the diets of polar bears in Foxe Basin over multiple spatial scales. I sought to better understand the foraging patterns of polar bears at both local and regional scales. I hypothesized that polar bear diet composition within Foxe Basin would vary spatially as a result of variable ecological conditions. I also hypothesized that bowhead whale carcasses may be providing an additional food source for polar bears during the ice-free season as a result of natural mortality, killer whale predation, and perhaps Inuit harvest.

Methods

Sample Collection

Polar bears

I examined adipose tissue samples from 102 individual polar bears (Table 2-1) harvested throughout the Foxe Basin subpopulation (Figure 2-1). The samples were collected by local Inuit hunters during the 2010/2011 and 2011/2012 harvest seasons, which extend from July 1 to June 30 of the following year. Adipose tissue samples were received from 7 communities in Nunavut: Cape Dorset, Chesterfield Inlet, Coral Harbour, Hall Beach, Igloolik, Kimmirut, and Repulse Bay. The collection of samples includes females and males, as well as different age classes: adults (5+ years old), subadults (3 – 4 years old), and independent 2-year-old individuals (Table 2-1). Harvest management targets a 2:1 male:female sex ratio and prohibits taking females with dependent cubs. A sample of subcutaneous adipose tissue samples (ca. 6 cm x 3 cm) were taken

from the rump of each bear and wrapped in aluminum foil, sealed in a labeled Whirl-Pak and stored at -20°C until analysis.

Table 2-1. Distribution of polar bear harvest adipose tissue samples collected during the 2010/11 and 2011/12 harvest seasons within the Foxe Basin subpopulation separated into Inuit communities.

Community	Total (*n*)	Adult		Subadult			Independent, 2 years old	
		F	M	F	M	Unk	F	M
Cape Dorset	5	1	2	0	2	0	0	0
Chesterfield Inlet	3	0	2	0	1	0	0	0
Coral Harbour	54	7	25	14	7	0	1	0
Hall Beach	14	1	4	5	3	1	0	0
Igloolik	13	2	7	1	3	0	0	0
Kimmirut	12	2	8	1	1	0	0	0
Repulse Bay	2	1	1	0	0	0	0	0
Total	103	14	49	21	17	1	1	0

Polar bear prey species

I analyzed 202 marine mammal blubber samples from bearded seals, beluga whales, harbour seals, harp seals, narwhals, ringed seals, and Atlantic walrus (Table 2-2) harvested during annual subsistence hunts in Foxe Basin and nearby regions (Table 2-2) from 2003 to 2012 (Figure 2-1). The collection of seal and whale samples included all sex and age classes. Studies have found significant vertical stratification in blubber of cetaceans and pinnipeds (Koopman et al. 1996, Best et al. 2003), consequently blubber samples (ca. 5 cm x 5 cm) were taken through the full depth of the layer. Samples were wrapped in aluminum foil and placed in a labeled Whirl-Pak bag and stored at -20°C. Bowhead whale fatty acid data (n = 41) were provided by Dr. Steve Ferguson (Freshwater Institute, Department of Fisheries and Oceans Canada (DFO), Winnipeg, Manitoba) for a total of 243 marine mammal samples.
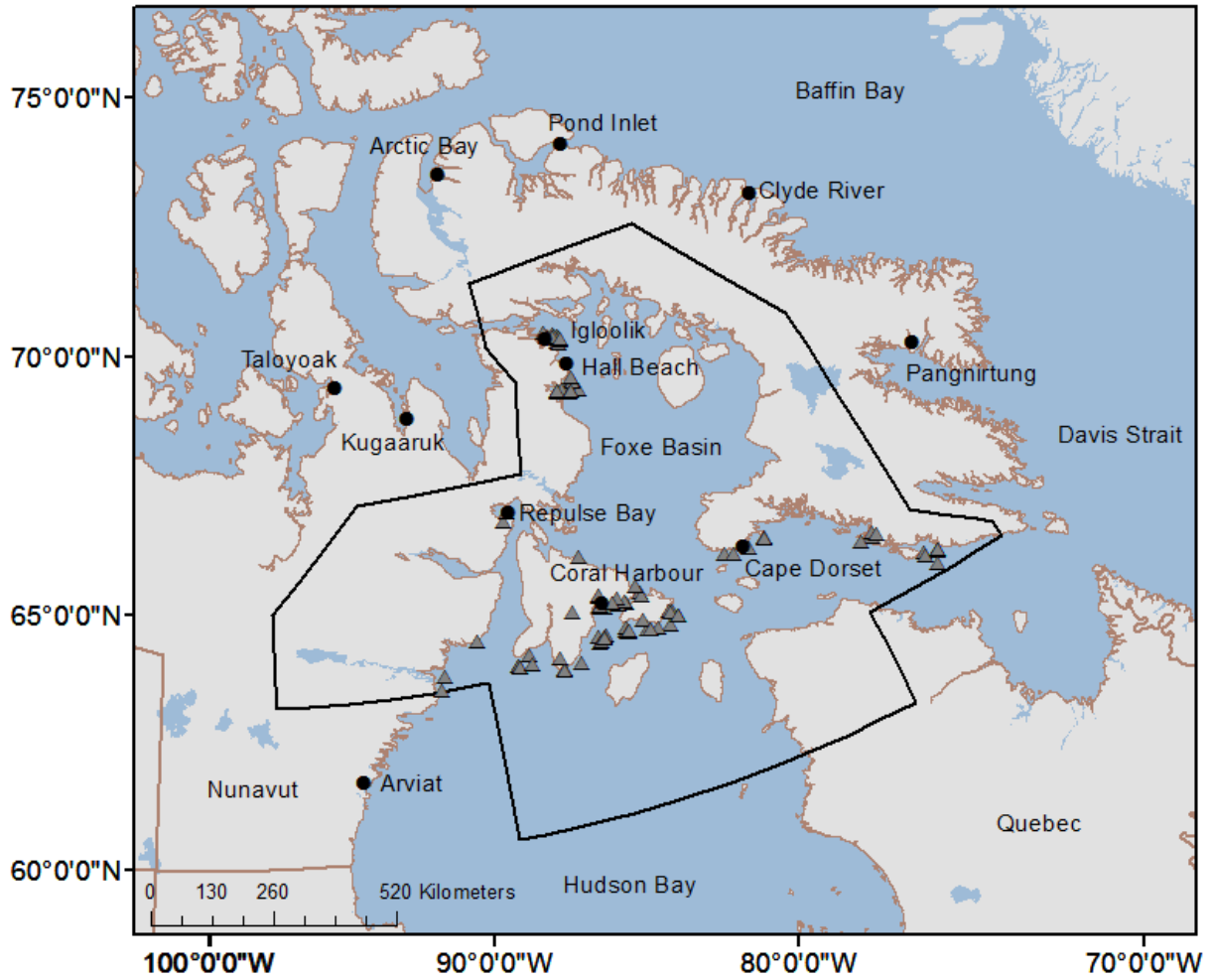
Figure 2-1. Location of polar bears (n = 102) harvested by local Inuit hunters from 2010/11 and 2011/12 across the Foxe Basin subpopulation. Harvest locations of polar bears are represented as (▲). Location of marine mammal samples (n = 202) collected for this study from 2003 to 2012 in Nunavut, Canada. Communities where marine mammals were collected are represented as (●).

Table 2-2. Distribution of prey blubber samples collected from various locations within the Canadian Arctic (2003 – 2012). Table includes bowhead whale samples (DFO). Prey species and sampling regions used in the QFASA model for Foxe Basin diet estimates (n = 243).

Species	Total (*n*)	Location	Sample (*n*)
Bearded seal	43	Arviat	33
		Cape Dorset	1
		Hall Beach	1
		Igloolik	21
		Kugaaruk	4
		Repulse Bay	4
Beluga whale	31	Coral Harbour	13
		Igloolik	9
		Repulse Bay	9
Bowhead whale	41	Arctic Bay	5
		Cape Dorset	1
		Hall Beach	1
		Northern Foxe Basin	38
		Not recorded	1
		Repulse Bay	1
Harbour seal	17	Arviat	17
Harp seal	9	Pangnirtung	9
Narwhal	37	Arctic Bay	14
		Clyde River	6
		Pond Inlet	8
		Repulse Bay	6
		Taloyoak	3
Ringed seal	48	Cape Dorset	5
		Hall Beach	4
		Repulse Bay	39
Atlantic walrus	17	Hall Beach	11
		Igloolik	6

Laboratory Analysis

Lipid Extraction and Transesterification

A subsample approximately 0.5 g was taken through the entire depth of the polar bear or prey sample to avoid any oxidized tissue. Lipid was quantitatively extracted according to Iverson et al. (2001). The lipid content of polar bear samples was expressed as percent total wet weight ±

1 SEM and was used as an indicator of overall body condition (Thiemann et al. 2006, McKinney et al. 2014). Lipid content reflects overall fatness because the adipocytes swell and shrink as fat is stored and mobilized, respectively. Sulfuric acid was used as a catalyst to derive fatty acid methyl esters (FAME) from the extracted lipid (Budge et al. 2006).

Gas Chromatography

Temperature-programmed gas chromatography was used to identify and quantify individual fatty acids (FA) according to Budge et al. (2006). Typically, over 70 FAs are identified in each adipose tissue and blubber sample and expressed as the mass percentage of the total FA $\pm$ 1 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. Each chromatogram peak corresponds to an individual FA and each chromatogram was manually corrected using Varian Star 6.41 Chromatography to ensure correct identification.

QFASA modelling

Quantitative fatty acid signature analysis (QFASA) was used to estimate the proportion of biomass each prey species contributed to the diet of polar bears (Iverson et al. 2004, 2006, Thiemann et al. 2008a). The QFASA model compares the average prey FA profile (or "signature") with each individual predator FA profile and determines the weighted combination of prey FA that minimizes the Kullback-Leibler distance to the predator's FA signature, after accounting for patterns of FA metabolism (Iverson et al. 2004, Budge et al. 2006). FA may be modified or utilized before deposition in the adipose tissue, thus calibration coefficients for each FA are incorporated into the model to account for lipid metabolism (Iverson et al. 2004). The calibration coefficients used to model polar bear diet composition in this study were based on

captive feeding studies of mink (*Neovison vison*), a terrestrial carnivore raised on a controlled

marine-based diet (Thiemann et al. 2008a).

Polar bear diets were estimated using 30 dietary FA similar to Thiemann et al. (2008a),

which are obtained solely or primarily from diet (Iverson et al. 2004). This FA set differed from

Thiemann et al. (2008a) with the exclusion of 20:1n-11 since it appeared to contribute to overlap

among prey species FA profiles. When 20:1n-11 was removed from diet simulations (see below),

the prey species were better resolved. I used a dataset including 8 ecologically relevant and

accessible prey species for polar bears in Foxe Basin. Diet simulations were used to determine

the ability of the QFASA model to accurately distinguish among prey types based on their FA

signature. The diet simulations were conducted according to Iverson et al. (2004), where a subset

of prey data were used to create a "pseudo bear" with a hypothetical diet (for instance, 70%

ringed seal and 30% bearded seal). The remaining prey data were used as a modelling set to

estimate the diet of the pseudo bear. Simulations were repeated 1000 times (Iverson et al. 2004).

All diet simulations and QFASA estimates were performed in R (R Version 2.1.0, The R

Foundation for Statistical Computing, 2005).

Statistical analyses

Seasonal variation in body condition (i.e., overall fatness) of polar bears was examined

using a simple linear regression of kill date vs. lipid content in adipose tissue. Variation in FA

profiles among prey species was tested using principal component analysis (PCA) and

multivariate analysis of variance (MANOVA). PCA was conducted on 38 FA (32 dietary FA and

6 extended dietary FA) in polar bear prey, where dietary FA are obtained solely or primarily from

the diet and extended dietary FA are obtained from both biosynthesis and diet (Iverson et al.

2004). PCA was used in an explanatory manner to reduce the number of FA to fewer components

representing the most variation among species as opposed to selecting a set of FA *a priori* (Budge et al. 2006, 2008). PCA was performed on log-transformed data according to the following equation: $x_{trans} = \ln(x_i/c_r)$, where x_{trans} is the transformed FA, x_i is the abundance of FA i expressed as percent of total FAs, and c_r is the reference FA, 18:0 (Budge et al. 2002, 2006). A MANOVA was then carried out on the new principal components (PC).

Hierarchical cluster analysis was performed on the average diet composition of polar bears grouped by region to identify patterns of spatial variation. Intrapopulation differences in polar bear diet composition were analyzed using permutational MANOVA because diet data were not normally distributed (Anderson 2001a, 2001b). I used a permutational two-way MANOVA to identify potential spatial differences within the subpopulation while controlling for sex effects. A permutational two-way MANOVA was conducted to test sex and age class differences within each geographic area. Additionally, I performed a permutational MANOVA to test seasonal variation in the diet composition of polar bears in each geographic area separately. I did not control for sex variation because there were too few samples collected from each sex in every season. Seasons were defined as fall (September to November), winter (December to February), spring (March to May), and summer (June to August). Dietary diversity was measured using the Shannon-Wiener Index (H') (Beck et al. 2007, Thiemann et al. 2008a):

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

where, p_j is the relative contribution of prey species j to the diet and s is the total number of prey species. An ANOVA was used to test variation in dietary diversity in polar bears. All statistical tests were performed in R (R Version 2.15.3, The R Foundation for Statistical Computing, 2013).

Results

Lipid Content

There was a significant negative relationship between % adipose lipid content and ordinal date ($R^2 = 0.189$, $p < 0.001$; Figure 2-2).
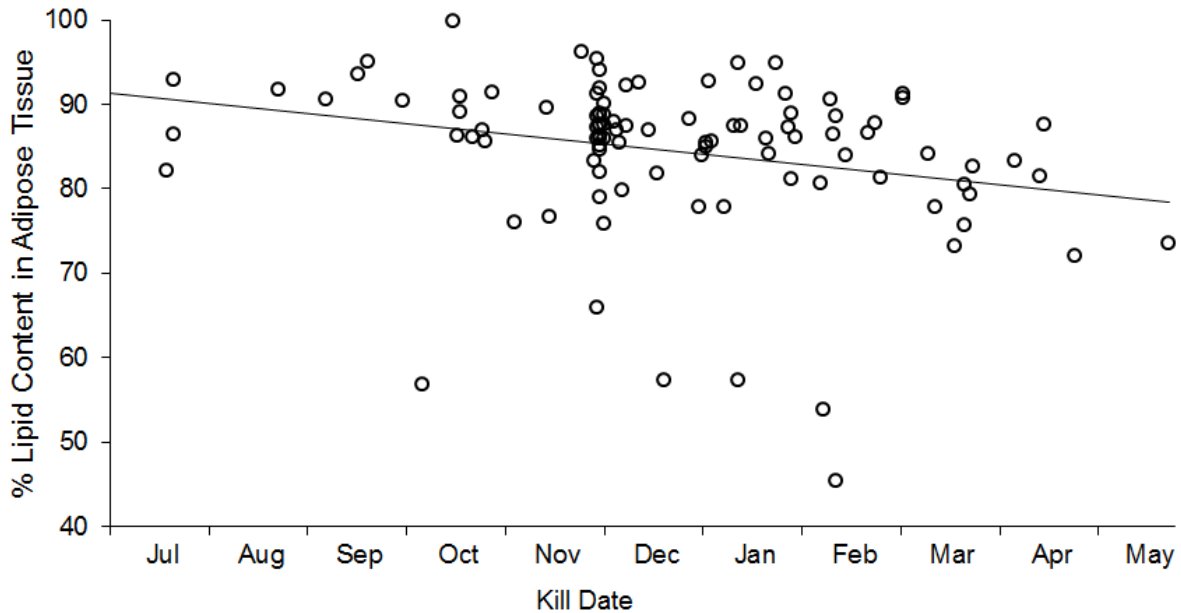
Figure 2-2. Relationship between ordinal kill date and adipose lipid content (% total wet weight ± SE) of adipose tissue samples collected in Foxe Basin during the 2010/11 and 2011/12 harvest seasons (n = 102).

Variation in polar bear prey FA signature

To assess differences among polar bear prey FA signatures, PCA was conducted on 38 FA (Table 2-3) which generated 3 principal components (PC) explaining 77% of total variance (Figure 2-3). The FA with the highest loadings on PC1 were 22:1n-11, 22:1n-9, 20:1n-9, and 22:4n-6; 16:3n-6 and 16:4n-3 on PC2; 16:4n-1 and 18:4n-3 on PC3. The PC scores were used to carry out a MANOVA to test differences among species. All 3 principal components contributed to a

significant difference among prey species (MANOVA, Wilks' $\lambda = 0.002$, p < 0.001 and *post hoc* Tukey's test, p < 0.001). Marine mammals were separated into clusters: 2 cetacean clusters (first included beluga whales and narwhals, and the second bowhead whales), another cluster of bearded seals, harbour seals, and walruses, and finally ringed seals and harp seals.
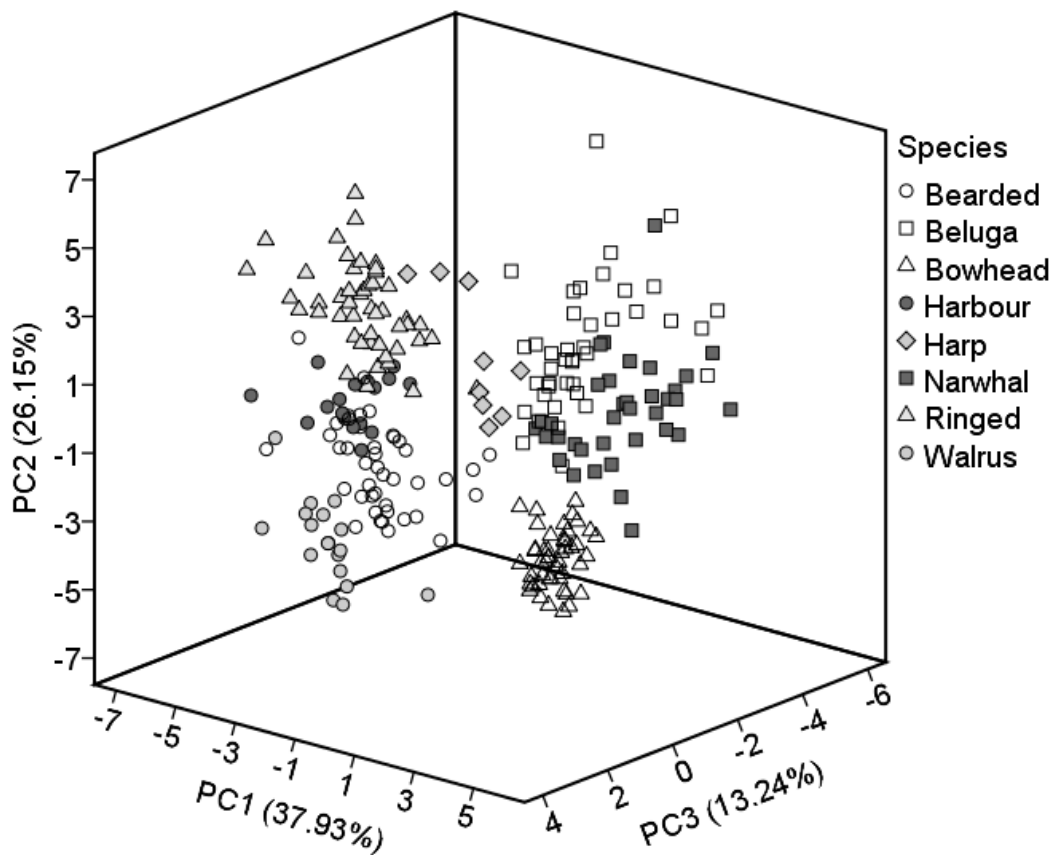
Figure 2-3. Principal component analysis of 38 dietary and extended dietary FA on polar bear prey samples separated by species. PCA scores were plotted for PC1, PC2, and PC3 which accounted for 77% of total explained variance. Bowhead whale FA signature (△) was distinct from all other marine mammals.

Diet Simulation

Diet simulations were performed using all potential prey species geographically available to polar bears in Foxe Basin. Studies have found within species variation (Thiemann et al. 2007b,

2008b), although when ringed seals were separated by sex and age class diet simulations were poorly resolved and were not accurately distinguished by sex or age class according to FA signature. Similarly when harp seals were divided by sex and age class the diet simulations were again poorly resolved. Polar bear prey types were most accurately distinguished and better resolved separated by species (Figure 2-4). Ringed seals and bearded seals were slightly underestimated, whereas harp seal was slightly overestimated. I tried multiple combinations of potential prey species from different regions and the prey dataset given in Table 2-2 provided the best resolution.
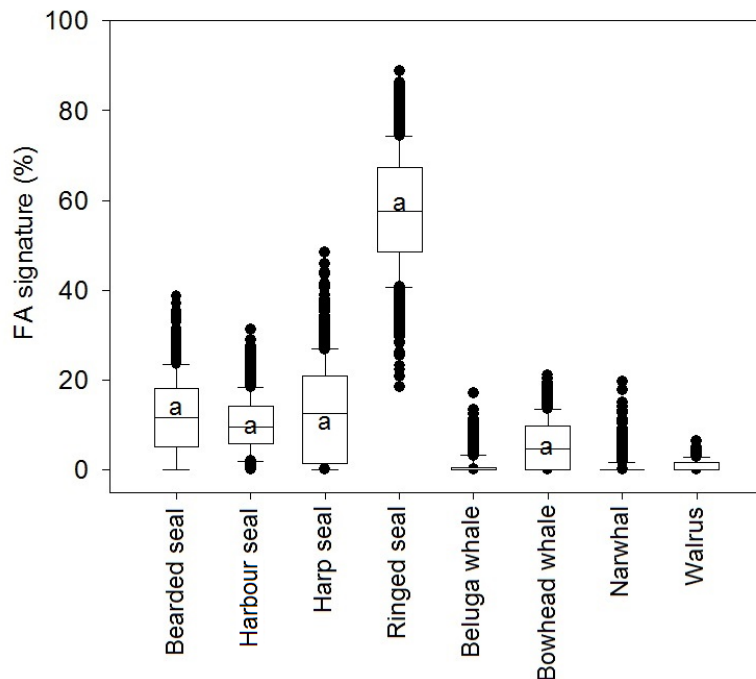
Figure 2-4. Diet simulation results for the Foxe Basin subpopulation prey dataset which are presented as boxplots showing the 25th, median and 75th percentiles of the 1000 diet estimates and solid circles represent outliers. The specified diet composition is represented as 'a' in plots and designated as followed: 15% bearded seal, 0% beluga whale, 5% bowhead whale, 10% harbour seal, 10% harp seal, 0% narwhal, 60% ringed seal, and 0% walrus.

Table 2-3. Fatty acid composition divided into major lipid class (% mass of total FA ± SEM) of all harvest blubber samples of all marine

mammals across the Canadian Arctic collected from 2000 to 2012 (n = 243).

Fatty acid	Bearded seal (*n* = 43)			Beluga whale (*n* = 31)			Bowhead whale (*n* =41)			Harbour seal (*n* = 17)			Harp seal (*n* = 9)			Narwhal (*n* = 37)			Ringed seal (*n* = 48)			Walrus (*n* = 17)		
Saturated fat																								
12:0	0.14	±	0.01	0.96	±	0.08	0.08	±	0.00	0.14	±	0.00	0.06	±	0.00	0.84	±	0.10	0.17	±	0.02	0.10	±	0.02
14:0*	3.10	±	0.12	5.48	±	0.16	3.17	±	0.05	3.16	±	0.09	4.28	±	0.28	5.71	±	0.29	4.68	±	0.15	3.19	±	0.11
Iso15	0.17	±	0.01	0.17	±	0.01	0.03	±	0.00	0.27	±	0.02	0.14	±	0.01	2.25	±	0.48	0.15	±	0.01	0.08	±	0.01
Anti15	0.12	±	0.01	0.12	±	0.01	0.02	±	0.00	0.11	±	0.01	0.06	±	0.00	0.17	±	0.03	0.10	±	0.01	0.63	±	0.10
15:0	0.34	±	0.01	0.28	±	0.01	0.17	±	0.00	0.30	±	0.01	0.20	±	0.01	0.32	±	0.02	0.22	±	0.01	0.39	±	0.02
Iso16	0.15	±	0.01	0.14	±	0.03	0.07	±	0.00	0.14	±	0.01	0.05	±	0.00	0.15	±	0.03	0.07	±	0.01	0.14	±	0.03
16:0*	10.00	±	0.34	6.02	±	0.22	5.00	±	0.09	10.12	±	0.22	5.74	±	0.59	6.28	±	0.20	7.12	±	0.27	9.95	±	0.37
7Me16:0	0.29	±	0.00	0.31	±	0.01	0.02	±	0.00	0.30	±	0.01	0.24	±	0.01	0.24	±	0.01	0.32	±	0.01	0.28	±	0.01
Iso17	0.31	±	0.01	0.10	±	0.00	0.09	±	0.02	0.29	±	0.02	0.07	±	0.00	0.13	±	0.01	0.09	±	0.00	0.53	±	0.04
17:0*	0.27	±	0.01	0.07	±	0.00	0.07	±	0.00	0.07	±	0.00	0.09	±	0.01	0.07	±	0.00	0.07	±	0.00	0.27	±	0.02
18:0	1.83	±	0.09	0.79	±	0.06	1.09	±	0.04	1.09	±	0.04	0.80	±	0.10	0.85	±	0.05	0.70	±	0.03	2.35	±	0.16
Monounsaturated fat																								
14:1n-9	0.09	±	0.01	0.98	±	0.11	0.06	±	0.00	0.07	±	0.01	0.17	±	0.01	0.66	±	0.09	0.11	±	0.01	0.14	±	0.01
14:1n-7	0.06	±	0.00	0.85	±	0.11	0.04	±	0.00	0.12	±	0.01	0.04	±	0.00	0.67	±	0.09	0.09	±	0.00	0.08	±	0.01
14:1n-5	0.56	±	0.04	2.02	±	0.20	0.64	±	0.02	1.00	±	0.12	0.95	±	0.20	2.43	±	0.26	1.35	±	0.06	0.50	±	0.12
16:1n-11	0.34	±	0.01	1.55	±	0.11	0.41	±	0.01	0.38	±	0.02	0.38	±	0.04	1.64	±	0.14	0.40	±	0.02	0.30	±	0.01
16:1n-9	0.34	±	0.01	1.87	±	0.16	0.29	±	0.01	0.56	±	0.03	0.31	±	0.05	1.58	±	0.16	0.43	±	0.02	0.40	±	0.02
16:1n-7	17.23	±	0.62	26.19	±	1.05	19.91	±	0.32	18.46	±	1.20	13.33	±	0.95	26.04	±	0.95	22.01	±	0.47	18.11	±	1.26
17:1	0.47	±	0.02	0.23	±	0.01	0.03	±	0.01	0.55	±	0.03	0.20	±	0.02	0.23	±	0.01	0.23	±	0.01	0.29	±	0.02
18:1n-13	0.28	±	0.02	0.04	±	0.00	0.04	±	0.00	0.18	±	0.01	0.05	±	0.00	0.06	±	0.00	0.08	±	0.00	0.47	±	0.06
18:1n-11	0.59	±	0.08	3.81	±	0.10	4.46	±	0.11	0.48	±	0.08	3.40	±	0.41	4.95	±	0.31	1.54	±	0.17	0.07	±	0.01
18:1n-9	15.31	±	0.38	16.06	±	0.34	10.55	±	0.23	18.06	±	0.39	12.83	±	1.46	16.35	±	0.75	14.51	±	0.32	14.18	±	0.56
18:1n-7	7.78	±	0.32	3.81	±	0.16	3.20	±	0.07	5.35	±	0.13	3.16	±	0.24	3.15	±	0.12	5.27	±	0.13	11.33	±	0.29
18:1n-5	0.65	±	0.02	0.48	±	0.02	0.60	±	0.01	0.61	±	0.02	0.52	±	0.02	0.41	±	0.02	0.60	±	0.02	0.41	±	0.01
20:1n-11*	0.83	±	0.07	2.19	±	0.09	3.67	±	0.09	0.43	±	0.04	2.40	±	0.17	3.63	±	0.23	0.69	±	0.06	1.19	±	0.10
20:1n-9*	2.92	±	0.32	6.81	±	0.40	16.20	±	0.32	2.01	±	0.20	14.40	±	1.06	7.02	±	0.43	3.90	±	0.35	1.94	±	0.13
20:1n-7*	1.31	±	0.07	0.52	±	0.04	1.95	±	0.04	0.49	±	0.02	0.94	±	0.09	0.57	±	0.04	0.43	±	0.02	4.86	±	0.38
22:1n-11*	0.79	±	0.17	2.87	±	0.27	9.24	±	0.39	0.26	±	0.08	7.84	±	1.26	3.56	±	0.33	0.66	±	0.10	0.07	±	0.01
22:1n-9*	0.31	±	0.04	0.56	±	0.06	2.03	±	0.08	0.18	±	0.02	1.42	±	0.21	0.61	±	0.06	0.25	±	0.02	0.15	±	0.02
22:1n-7*	0.11	±	0.01	0.09	±	0.01	0.37	±	0.02	0.04	±	0.01	0.20	±	0.04	0.10	±	0.01	0.05	±	0.00	0.13	±	0.01
24:1n-9	0.14	±	0.02	0.13	±	0.01	0.10	±	0.00	0.08	±	0.01	0.31	±	0.05	0.10	±	0.01	0.06	±	0.01	0.07	±	0.01

Table 2-3. Continued

Fatty acid	Bearded seal (n = 43)			Beluga whale (n = 31)			Bowhead whale (n = 41)			Harbour seal (n = 17)			Harp seal (n = 9)			Narwhal (n = 37)			Ringed seal (n = 48)			Walrus (n = 17)		
Polyunsaturated fat																								
16:2n-6[*]	0.05	±	0.00	0.07	±	0.00	0.05	±	0.00	0.07	±	0.01	0.05	±	0.00	0.06	±	0.00	0.07	±	0.00	0.07	±	0.00
16:2n-4[*]	0.37	±	0.03	0.29	±	0.01	0.57	±	0.01	0.54	±	0.03	0.22	±	0.02	0.22	±	0.01	0.15	±	0.01	0.09	±	0.01
16:3n-6[*]	0.30	±	0.01	0.52	±	0.02	0.00	±	0.00	0.19	±	0.01	0.56	±	0.03	0.40	±	0.01	0.59	±	0.02	0.35	±	0.02
16:3n-4[*]	0.11	±	0.01	0.09	±	0.00	0.18	±	0.00	0.08	±	0.01	0.28	±	0.03	0.05	±	0.00	0.28	±	0.02	0.09	±	0.01
16:4n-3[*]	0.07	±	0.01	0.30	±	0.03	0.11	±	0.00	0.17	±	0.01	0.03	±	0.00	0.15	±	0.01	0.09	±	0.00	0.02	±	0.00
16:4n-1[*]	0.15	±	0.01	0.09	±	0.00	0.31	±	0.01	0.06	±	0.01	0.52	±	0.07	0.05	±	0.00	0.53	±	0.06	0.21	±	0.02
18:2n-7[*]	0.07	±	0.00	0.05	±	0.00	0.00	±	0.00	0.11	±	0.01	0.04	±	0.00	0.08	±	0.01	0.08	±	0.00	0.11	±	0.01
18:2n-6[*]	1.73	±	0.06	1.65	±	0.04	0.85	±	0.02	1.94	±	0.13	1.13	±	0.11	0.80	±	0.05	1.80	±	0.09	0.74	±	0.03
18:2n-4[*]	0.15	±	0.01	0.09	±	0.01	0.12	±	0.00	0.10	±	0.00	0.10	±	0.01	0.08	±	0.00	0.13	±	0.00	0.39	±	0.02
18:3n-6[*]	0.17	±	0.01	0.07	±	0.00	0.13	±	0.00	0.17	±	0.01	0.09	±	0.00	0.05	±	0.00	0.21	±	0.01	0.12	±	0.01
18:3n-4[*]	0.15	±	0.00	0.11	±	0.00	0.16	±	0.01	0.10	±	0.01	0.12	±	0.01	0.10	±	0.00	0.12	±	0.00	0.33	±	0.02
18:3n-3[*]	0.51	±	0.03	0.21	±	0.01	0.32	±	0.01	0.93	±	0.08	0.37	±	0.04	0.21	±	0.01	0.50	±	0.02	0.24	±	0.01
18:3n-1[*]	0.14	±	0.01	0.11	±	0.01	0.03	±	0.00	0.17	±	0.01	0.06	±	0.01	0.11	±	0.03	0.07	±	0.00	0.06	±	0.00
18:4n-3[*]	0.92	±	0.08	0.31	±	0.02	0.73	±	0.02	1.58	±	0.12	0.96	±	0.06	0.18	±	0.01	1.38	±	0.09	0.73	±	0.04
18:4n-1[*]	0.13	±	0.01	0.12	±	0.01	0.43	±	0.02	0.04	±	0.00	0.18	±	0.01	0.09	±	0.01	0.15	±	0.01	0.34	±	0.02
20:2n-6[*]	0.42	±	0.01	0.17	±	0.01	0.16	±	0.00	0.38	±	0.01	0.18	±	0.01	0.18	±	0.01	0.25	±	0.00	0.75	±	0.03
20:3n-6[*]	0.12	±	0.01	0.06	±	0.01	0.12	±	0.00	0.09	±	0.01	0.07	±	0.00	0.06	±	0.00	0.08	±	0.01	0.27	±	0.01
20:4n-6[*]	1.04	±	0.05	0.23	±	0.02	0.29	±	0.01	0.93	±	0.07	0.25	±	0.02	0.23	±	0.02	0.41	±	0.03	0.57	±	0.05
20:3n-3[*]	0.09	±	0.00	0.02	±	0.00	0.04	±	0.00	0.12	±	0.01	0.04	±	0.00	0.03	±	0.00	0.06	±	0.00	0.08	±	0.01
20:4n-3[*]	0.62	±	0.03	0.31	±	0.02	0.41	±	0.02	0.73	±	0.05	0.38	±	0.01	0.19	±	0.01	0.39	±	0.01	0.76	±	0.04
20:5n-3[*]	9.03	±	0.34	3.02	±	0.23	5.56	±	0.19	6.39	±	0.43	5.89	±	0.30	1.95	±	0.15	10.13	±	0.29	7.05	±	0.49
21:5n-3[*]	0.42	±	0.02	0.12	±	0.01	0.04	±	0.00	0.30	±	0.01	0.40	±	0.02	0.07	±	0.01	0.45	±	0.01	0.79	±	0.03
22:4n-6[*]	0.28	±	0.02	0.14	±	0.06	0.01	±	0.00	0.28	±	0.03	0.07	±	0.01	0.04	±	0.00	0.07	±	0.01	0.68	±	0.19
22:5n-6[*]	0.26	±	0.01	0.07	±	0.02	0.02	±	0.00	0.24	±	0.01	0.08	±	0.01	0.04	±	0.01	0.09	±	0.01	0.13	±	0.03
22:4n-3[*]	0.09	±	0.01	0.03	±	0.00	0.06	±	0.00	0.12	±	0.01	0.09	±	0.00	0.02	±	0.00	0.05	±	0.00	0.10	±	0.01
22:5n-3[*]	4.45	±	0.12	1.62	±	0.19	1.92	±	0.07	4.75	±	0.21	4.52	±	0.37	1.10	±	0.13	5.57	±	0.15	7.29	±	0.41
22:6n-3[*]	10.88	±	0.54	3.64	±	0.41	3.05	±	0.09	12.90	±	0.58	8.52	±	0.53	2.11	±	0.21	9.71	±	0.27	4.42	±	0.25

Note: Only FA representing > 0.1% of total FA are shown in the table.

(*) represents the 38 FA used for fatty acid signature comparisons and accounts for approximately 99% of the total FA across all marine mammals.

Bold represents the FA used in the QFASA model to determine diet estimates of polar bears.

Polar bear diet composition

Spatial variation in polar bear diet

The QFASA model was conducted using 30 dietary FA (Table 2-4). Ringed seal was the dominant prey species in Foxe Basin polar bear diets (56 ± 2.7%), followed by bearded seal (20 ± 1.6%) and harp seal (11 ± 1.7%; Figure 2-5). Harbour seal, bowhead whale and walrus were minor dietary components comprising 6 ± 1.1%, 4 ± 0.7%, and 4 ± 0.9%, respectively across the entire subpopulation. Three main clusters of samples were used to examine regional differences: northern (Hall Beach and Igloolik), southern (Coral Harbour, Chesterfield Inlet, and Repulse Bay), and Hudson Strait (Kimmirut). Cape Dorset (eastern Foxe Basin) had too few samples (n = 5) to run statistical analysis by itself, although it was unclear where polar bears harvested around Cape Dorset would show the most similarity. Therefore, a cluster analysis was conducted on the diet estimates of the 4 groupings. Hierarchical cluster analysis indicated diet composition of Cape Dorset was more similar to polar bears harvested in northern Foxe Basin than southern Foxe Basin and Hudson Strait (Figure 2-6).

Table 2-4. Fatty acid composition divided into major lipid class (% mass of total FA ± SEM) of

polar bear adipose tissue sampled during the 2010/11 and 2011/12 harvest seasons.

Fatty Acid	Foxe Basin (n = 103)		
Saturated fat			
14:0	3.15	±	0.06
Iso15	0.20	±	0.01
15:0	0.26	±	0.01
16:0	7.20	±	0.14
7Me16:0	0.24	±	0.01
17:0	0.18	±	0.01
18:0	2.25	±	0.06
Monounsaturated fat			
14:1n-5	0.77	±	0.02
16:1n-11	0.24	±	0.01
16:1n-9	0.49	±	0.01
16:1n-7	14.23	±	0.30
17:1	0.24	±	0.00
18:1n-11	2.17	±	0.11
18:1n-9	21.27	±	0.24
18:1n-7	5.84	±	0.11
18:1n-5	0.57	±	0.01
20:1n-11	2.29	±	0.09
20:1n-9	7.54	±	0.25
20:1n-7	1.30	±	0.08
22:1n-11	1.45	±	0.09
22:1n-9	0.50	±	0.02
22:1n-7	0.09	±	0.00
Polyunsaturated fat			
16:2n-6	0.04	±	0.00
16:2n-4	0.14	±	0.00
16:3n-6	0.35	±	0.01
16:3n-4	0.05	±	0.00
16:4n-3	0.05	±	0.00
16:4n-1	0.04	±	0.00
18:2n-6	2.25	±	0.05
18:2n-4	0.13	±	0.00
18:3n-6	0.11	±	0.00
18:3n-4	0.21	±	0.00
18:3n-3	0.42	±	0.01
18:3n-1	0.06	±	0.00
18:4n-3	0.42	±	0.02
18:4n-1	0.14	±	0.01
20:2n-6	0.38	±	0.01
20:3n-6	0.13	±	0.00
20:4n-6	0.33	±	0.01
20:3n-3	0.06	±	0.00
20:4n-3	0.42	±	0.01
20:5n-3	3.04	±	0.13
21:5n-3	0.40	±	0.01
22:4n-6	0.21	±	0.01
22:5n-6	0.17	±	0.00
22:4n-3	0.08	±	0.00
22:5n-3	7.11	±	0.11
22:6n-3	9.04	±	0.17

Note: Only FA representing >0.2% of total FA and FA used in the QFASA model.

Bold represents the 30 dietary FA used to generate polar bear diet estimates (QFASA model).
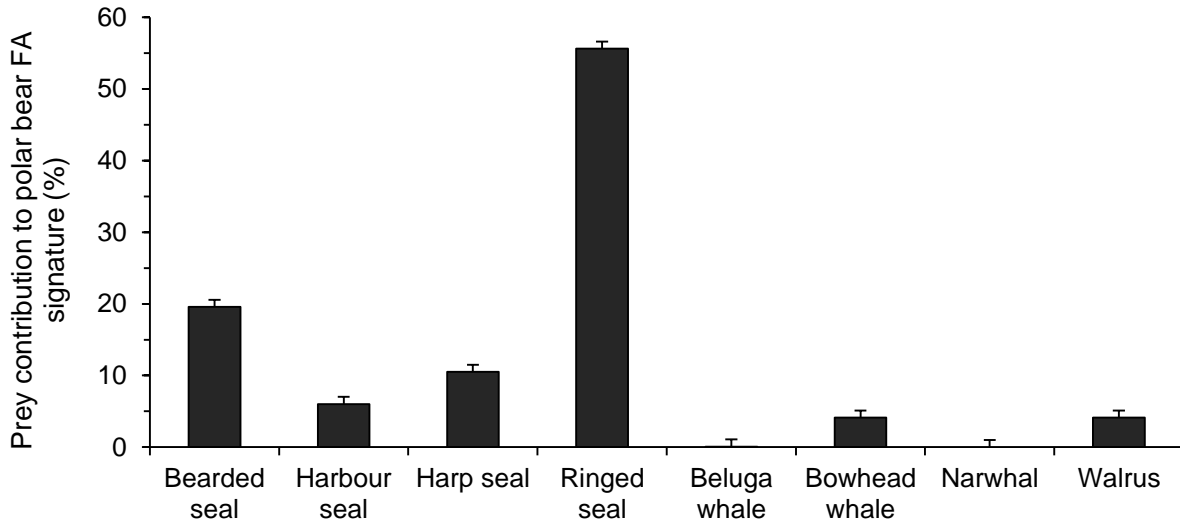
Figure 2-5. Diet composition of polar bears (n = 102) in the Foxe Basin subpopulation. Prey

contribution is represented as each prey species' biomass to polar bear diet estimates and data is

expressed as mean ± SE.
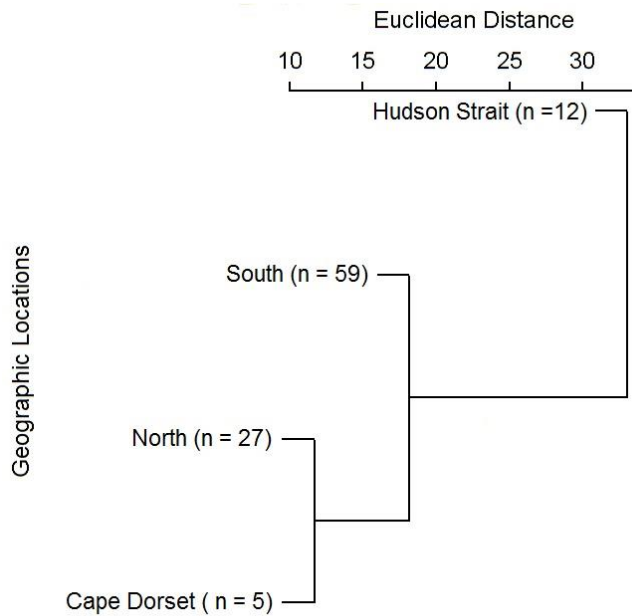
Figure 2-6. Hierarchical cluster analysis of average diet estimates of polar bears in Foxe Basin

during the 2010/11 and 2011/12 harvest seasons. Clusters were formed based on Euclidean

distance and between-groups linkage method.

Southern Foxe Basin, northern Foxe Basin, and Hudson Strait were all significantly different from each other (permutation two-way MANOVA, p < 0.03 in all cases; Figure 2-7). Although the hierarchical cluster analysis indicated bears around Cape Dorset were most similar to northern Foxe Basin bears, they were not significantly different from any of the other harvest areas within Foxe Basin (permutation two-way MANOVA, p > 0.170 in all cases). Therefore, Cape Dorset could not be pooled with any of the 3 other geographic clusters (southern Foxe Basin, northern Foxe Basin, and Hudson Strait) and Cape Dorset samples were excluded from further analysis.

Dietary diversity differed across geographic areas in Foxe Basin (ANOVA, $F (3, 99) =$ 2.92, p = 0.038), although only Southern Foxe Basin and Hudson Strait were significantly different from each other (*post hoc* Tukey's HSD, p = 0.048). The highest dietary diversity was seen in bears in Hudson Strait ($H' = 1.04$), followed by Cape Dorset ($H' = 0.94$), and northern Foxe Basin ($H' = 0.91$). Southern Foxe Basin polar bears were found to have the least diverse diet ($H' = 0.78$) with ringed seal and bearded seal comprising 83% of the overall diet.

Bearded seal and harbour seal consumption did not differ across parts of the subpopulation (permutation ANOVA, p = 0.395 and p = 0.663, respectively). Bearded seal was the second most consumed prey species in southern Foxe Basin (20 ± 2.0%) and northern Foxe Basin (19 ± 3.5%). Ringed seal consumption was highest in southern Foxe Basin (63 ± 3.1%) and northern Foxe Basin (49 ± 5.4%) compared to Hudson Strait (permutation ANOVA, p < 0.001). In contrast, bears in Hudson Strait consumed roughly equal proportions of ringed seal and harp seal (35 ± 7.6% and 33 ± 6.9%, respectively). Harp seal was more abundant in Hudson Strait diets than southern Foxe Basin and northern Foxe Basin (permutation ANOVA, p < 0.001). In southern and northern Foxe Basin, ringed seal was present in the diet of the majority

of bears (98% and 89% of bears, respectively), whereas harp seal was less frequent in the diets (46% of bears in southern Foxe Basin and 44% of bears in northern Foxe Basin). In contrast, ringed seal and harp seal were found at equal frequencies in Hudson Strait bears (both prey species present in 75% of bears).

There was no significant spatial difference in bowhead whale consumption (permutation ANOVA, p = 0.262), although bowhead was consumed most frequently by northern Foxe Basin bears (56% of bears), followed by Hudson Strait (50% of bears) and southern Foxe Basin (37% of bears). There was no detectable narwhal consumption by any individual and beluga whale biomass was rare in diets, found in low levels in 3% of southern Foxe Basin bears and 17% of Hudson Strait bears. Walrus consumption was significantly higher in northern Foxe Basin and Hudson Strait than southern Foxe Basin (permutation ANOVA, p < 0.001). Walrus consumption was also more frequent in northern Foxe Basin and Hudson Strait (63% of bears and 67% of bears, respectively), and relatively rare in southern Foxe Basin (14% of bears).
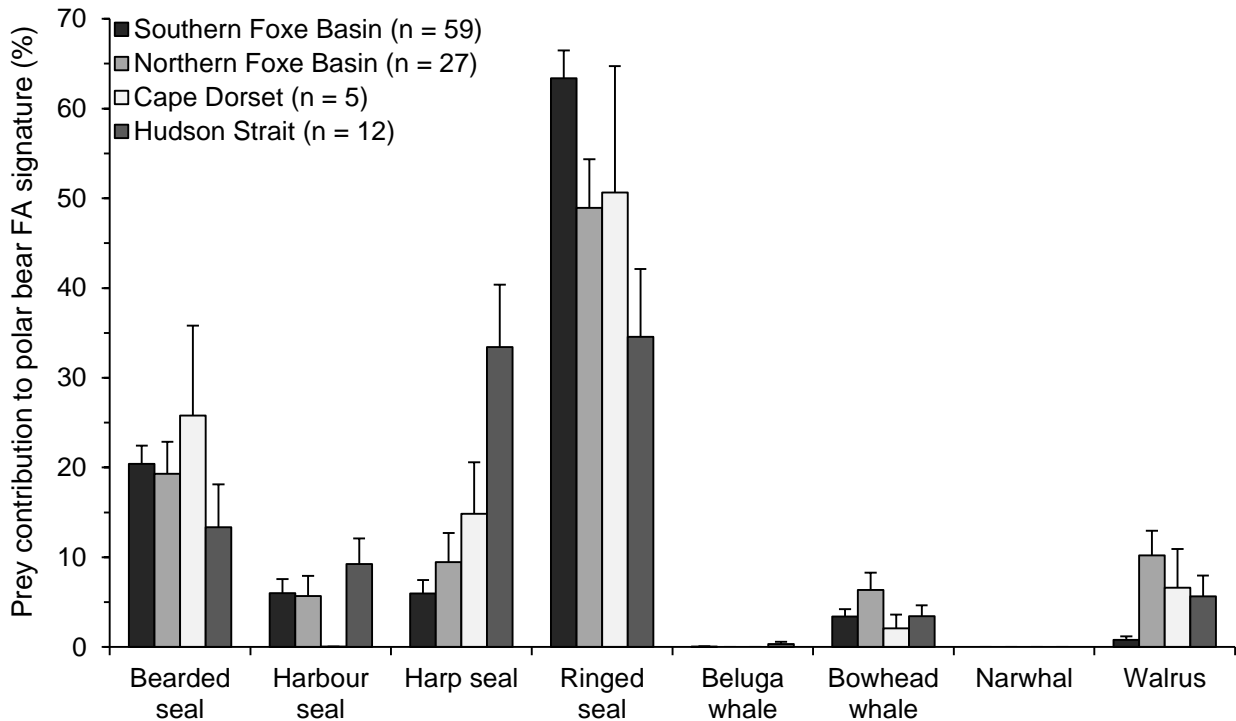
Figure 2-7. Spatial variation in diet composition in Foxe Basin polar bears during the 2010/11 and 2011/12 harvest seasons and separated according to geographic location (southern Foxe Basin: Chesterfield Inlet, Coral Harbour, and Repulse Bay; northern Foxe Basin: Hall Beach and Igloolik; Hudson Strait: Kimmirut). Diet estimates are expressed as mean ± SE.

Age- and sex-specific variation in polar bear diet

In southern Foxe Basin, there was a significant sex-specific difference in diet composition (permutation two-way MANOVA, p = 0.040) and no significant difference in age class (permutation two-way MANOVA, p = 0.1391, Figure 2-8a). However, consumption of particular prey species did not significantly differ between female and male bears (permutation t-test, p > 0.091 in all cases). Ringed seal contributed the most to biomass in all age classes and sexes (Figure 2-8a), ringed seal was found in the majority of bears (96% of female bears and all male bears). Bearded seal was present in the majority of bears (91% of female bears and 97% of

male bears). Dietary diversity did not differ between male ($H' = 0.83$) and female bears ($H' = 0.71$; t-test, t(56) = 1.59, p = 0.118).

Diets of bears in northern Foxe Basin were significantly influenced by age class and not sex (permutation two-way MANOVA, p = 0.027 and p = 0.133, respectively, Figure 2-8b). In northern Foxe Basin, diversity of prey species present in diet did not significantly adult and subadult bears ($H' = 1.01$ and $H' = 0.80$, respectively; t-test, t(21) = 1.74, p = 0.096). Ringed seal consumption was higher in subadult bears ($61 \pm 8.0\%$) than adults ($36 \pm 6.0\%$; permutation t-test, p = 0.022), whereas adult bears consumed more bearded seal than did subadults ($27 \pm 5.4\%$ and $12 \pm 3.5\%$, respectively, permutation t-test, p = 0.031). The higher level of bearded seal and lower level of ringed seal in adult bears was primarily driven by adult males. Bowhead whale consumption was significantly influenced by age class (permutation t-test, p = 0.022). Subadults had significantly higher levels of bowhead whale in diets than adults ($11 \pm 3.6\%$ and $2 \pm 1.4\%$, respectively), in addition bowhead whale was more frequently present in subadults (77% of bears) compared to adults (36% of bears). Walrus consumption was the highest in adult bears (permutation t-test, p = 0.045), which was driven by adult males with the highest contribution to the diets in northern Foxe Basin ($18 \pm 5.6\%$ in adult males).

There were too few samples collected in Hudson Strait for statistical analysis on the effects of age class and sex (Figure 2-8c). However, adults had diets dominated by ringed seal and harp seal (Figure 2-8c). Harp seal ($43 \pm 7.7\%$) was the primary prey species in the diets of adult males followed by ringed seal ($23 \pm 6.9\%$). Walrus only contributed to the diets of males (8 out of 9 bears).
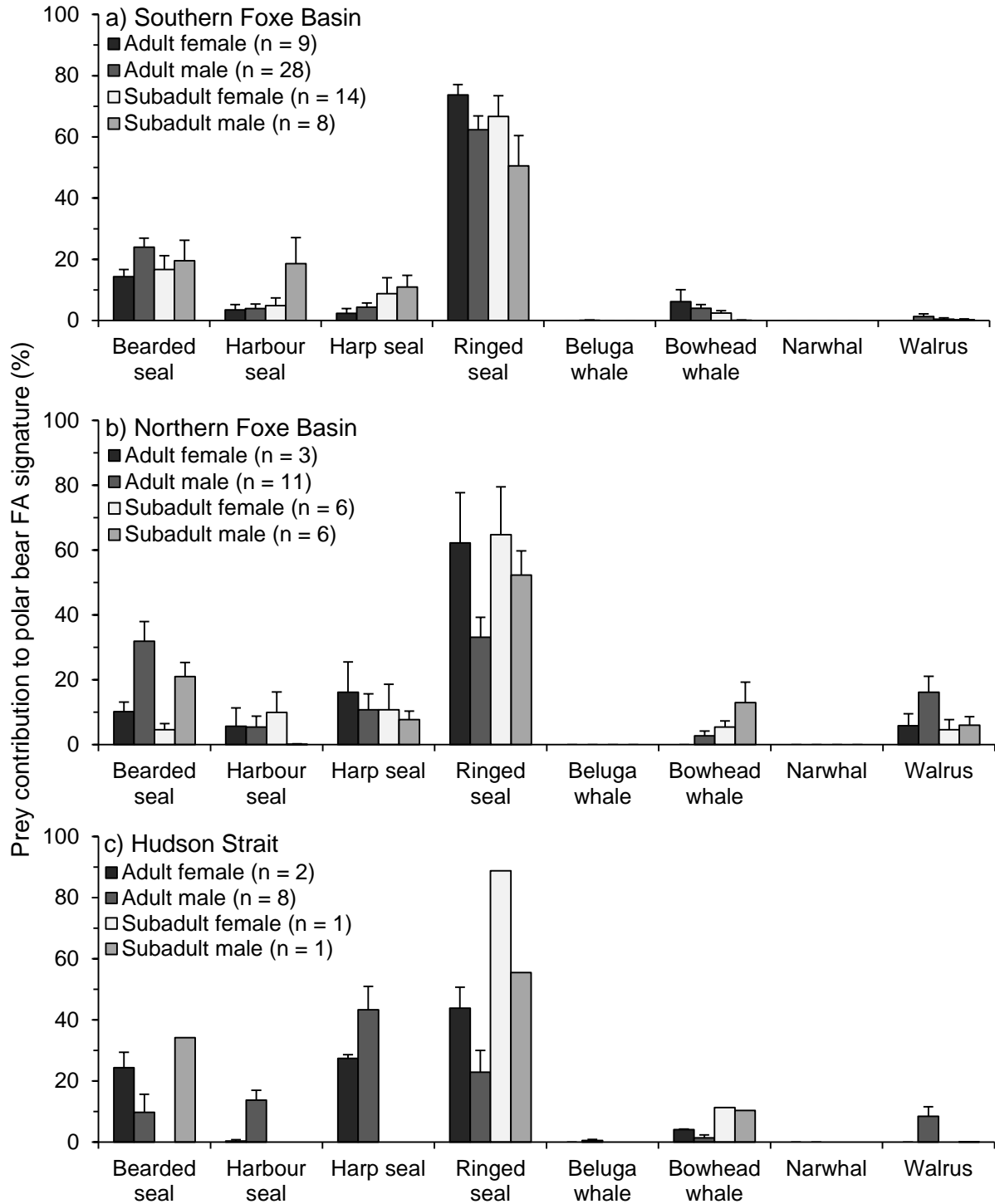
Figure 2-8. Sex and age class variation in diets of polar bears sampled in a) southern Foxe

Basin, b) northern Foxe Basin, and c) Hudson Strait during the 2010/11 and 2011/12 harvest

seasons. Diet estimates are represented as mean ± SE.

Seasonal variation in polar bear diet

There was a seasonal effect on polar bear diets in northern Foxe Basin (permutation MANOVA, p = 0.030; Figure 2-9a) and Hudson Strait (permutation MANOVA, p = 0.044; Figure 2-9b). In southern Foxe Basin, season had no significant effect on diet composition (permutation MANOVA, p = 0.192; Figure 2-9c). In northern Foxe Basin, summer was excluded from the analysis since there was only one sample collected in August. Ringed seal consumption was highest in bears sampled in the fall compared to bears sampled in winter and spring (permutation ANOVA, p = 0.015). Walrus biomass was highest among bears sampled in the spring (33 ± 9.8%; permutation ANOVA, p = 0.006).

In Hudson Strait, bearded seal contribution was significantly higher during the winter than spring (permutation t-test, p = 0.030; Figure 2-9b). Bearded seal was also more often found in diets of bears in winter (80% of bears) than spring (33% of bears). Harbour seal biomass was higher during the spring compared to winter (permutation t-test, p = 0.035) and more frequent in spring (83% of bears) than winter (60% of bears). Although not statistically significant (permutation t-test, p = 0.160), harp seal biomass was higher in the spring (46 ± 14%) than winter (25 ± 6.7%). Walrus consumption was not statistically different seasonally (permutation t-test, p = 0.069).
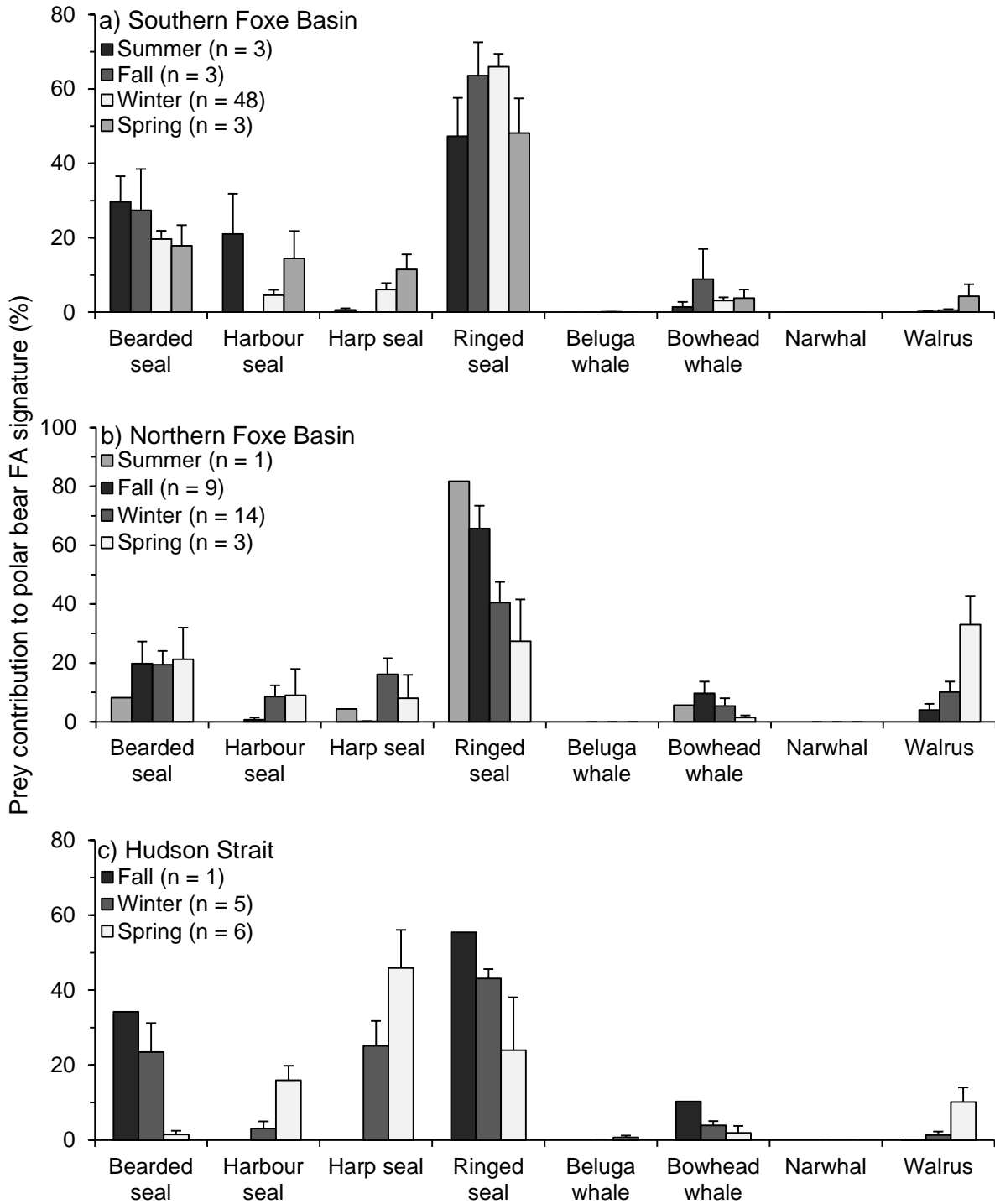
Figure 2-3. Seasonal diet composition of polar bears sampled in a) southern Foxe Basin, b) northern Foxe Basin, and c) Hudson Strait during the 2010/11 and 2011/12 harvest seasons. Diet estimates are represented as mean ± SE.

Discussion

This is the first study to identify spatial differences in polar bear diet composition within the Foxe Basin subpopulation. This study is also the first to quantify the contribution of bowhead whale to the diets of polar bears in the eastern Arctic. My results indicate that polar bears within this region are exploiting locally abundant prey sources and some individuals may be switching between alternate prey species. Consistent with earlier evidence from the western Arctic (Rode et al. 2014), the relatively high diversity of prey in the region may buffer Foxe Basin polar bears from the effects of sea ice loss, at least in the early stages. My results provide a better understanding of polar bear feeding ecology in a region currently undergoing changes in sea ice habitat conditions.

Lipid Content

The percent lipid content in the adipose tissue of an individual polar bear can be used as an indicator of overall body condition (Stirling et al. 2008, McKinney et al. 2014). There was a decreasing trend in body condition (Figure 2-2) from the open-water season (July and August), when polar bears are forced on shore, until the following spring (March-May). The higher lipid content of adipose tissue during July and August reflects the end of an extensive feeding period when bears accumulate fat (Stirling and Oritsland 1995, Stirling et al. 1999). The continuous declining trend in lipid content throughout winter suggests that polar bears have less access to prey due to heavier sea ice conditions (Messier et al. 1992, Derocher et al. 2004). Although previous studies have identified differences in body condition between fall and spring (Thiemann et al. 2006, McKinney et al. 2014), this is the first study to document a continuous linear decline in body condition through the winter. These trends suggest a seasonal association between body condition of polar bears and seasonal prey availability and indicate that polar bears in Foxe Basin

rely on a relatively brief window of feeding in the spring to sustain them through much of the year. Continued monitoring of this subpopulation, using harvest-based sampling, could reveal more precisely the timing of spring hyperphagia, a key consideration in predicting the effects of future climate change. The closer to breakup peak feeding occurs, the more vulnerable the population will be to changes in seasonal sea ice regimes (Molnár et al. 2011).

Polar bear prey fatty acid signatures

Polar bear prey types were well distinguished by species according to their fatty acid profile (Figure 2-3), although there was some clustering among marine mammals. The main clusters were similar to previous studies and grouped in relation to ecological and phylogenetic patterns (Iverson et al. 2006, Thiemann et al. 2008b). For instance, bearded seals and walruses primarily feed on benthic invertebrates (Thiemann et al. 2007a, Budge et al. 2007), which is an occasional food source for harbour seals (Thiemann et al. 2007a). Ringed seals and harp seals have overlapping pelagic feeding grounds which contribute to the similarities in fatty acid signatures between the two species (Wathne et al. 2000, Holst et al. 2001, Tucker et al. 2009). The toothed whales clustered together and the baleen whale was relatively distinct.

Various combinations of prey samples were tested using diet simulations to determine the set of samples that would provide the best resolution among species and most accurate estimation of polar bear diets. Intra-specific differences have been identified in previous studies (Iverson et al. 2006, Thiemann et al. 2007b, 2008b), however prey (such as ringed seal) was poorly distinguished when subdivided by sex and/or age. Thus, the diet simulations indicated that the fatty acid signature of a specific sex or age class was not distinct enough for a clear separation and within species variation was relatively small compared to among species

variation. Therefore, the variation among prey species provides further confidence that polar bear diets can be reliably estimated using prey species FA profile in the QFASA model.

Spatial variation in polar bear diet

Polar bears in Foxe Basin have access to a wide variety of potential prey species, which is reflected in their diet composition (Figure 2-5). The primary prey of polar bears in Foxe Basin was ringed seal which are preferred because of their small size and ubiquitous distribution. The dominance of ringed seal in polar bear diets was consistent with previous coarse-scale analyses of the Foxe Basin food web (Thiemann et al. 2008a). To date, this is the first study to attempt to quantify the consumption of bowhead whale by polar bears in the eastern Arctic. Bowhead whale biomass was low in the overall diet of the subpopulation. The study also found differences across areas within Foxe Basin, suggesting the importance of locally abundant prey contributing to the diet of polar bears within a specific area.

Polar bears in southern Foxe Basin had the least diverse diet with the majority of the diet comprised of ringed seal and few alternate prey species (Figure 2-7). Polar bear diets in this southern area of Foxe Basin are similar to the diet composition of bears in Western Hudson Bay (Iverson et al. 2006, Thiemann et al. 2008a) suggesting a shared food source between adjacent subpopulations. Polar bears in Hudson Strait polar bears had the highest dietary diversity of all areas and consumed roughly equal proportions of ringed seal and harp seal (Figure 2-7). These patterns are more similar to the diets of polar bears in the adjacent Davis Strait subpopulation rather than other geographic areas in Foxe Basin. A high consumption of harp seal was previously identified in Davis Strait polar bears (Iverson et al. 2006, Thiemann et al. 2008a). The results of this study suggest that polar bears in Hudson Strait may be moving eastward towards Davis Strait to exploit locally abundant prey species such as harp seal which have increased in

numbers over the past four decades (DFO 2011). Polar bears in the eastern portion of the subpopulation are not limited by physical barriers and may overlap into adjacent subpopulations (i.e., Davis Strait). Individuals have been observed moving into Hudson Strait and Foxe Basin from Davis Strait, although this movement pattern was typically rare (Taylor et al. 2001, Peacock et al. 2013). As well, Sahanatien and Derocher (2010) found polar bears moving from Foxe Basin into the adjacent subpopulations of Western Hudson Bay and Davis Strait. In addition to the movement of bears, dietary similarities in adjacent subpopulations may be a function of shared, migratory prey. Harp seals commonly migrate from the Labrador Sea into Hudson Strait as the sea ice recedes in summer (Sergeant 1976). Future research should investigate seasonal variation in diet in relation to polar bear movement and prey patterns.

In northern Foxe Basin, polar bears had a high dietary diversity with a high abundance of ringed seals, along with a variety of alternate prey species such as bearded seal, harbour seal, harp seal, bowhead whale, and walrus (Figure 2-7). The diet composition of polar bears harvested in Cape Dorset was more similar to the diet composition of polar bears in northern Foxe Basin than the two other geographic areas (southern Foxe Basin and Hudson Strait; Figure 2-6). The similarity can be attributed to the high levels of walrus and low levels of harp seal in polar bear diets; however polar bears harvested in Cape Dorset were not significantly different from any of the other regions in Foxe Basin. Polar bears in Cape Dorset may be benefiting from prey migrating through eastern Foxe Basin to northern Foxe Basin or perhaps bears are moving towards northern Foxe Basin for increased feeding opportunities instead of eastward to Davis Strait. The spatial patterns within the Foxe Basin subpopulation may become clearer with increased sampling in the region, since currently there were fewer polar bears sampled around Cape Dorset.

Walrus consumption was high in northern Foxe Basin and Hudson Strait, whereas in southern Foxe Basin walrus were relatively rare in diets (Figure 2-6). There are two populations of walrus that overlap with polar bears in Foxe Basin, that are separated by a large distance which limits movement between the two areas and results in two distinct populations: Northern-Hudson Bay-Davis Strait and Foxe Basin (DFO 2002, COSEWIC 2006). The Northern-Hudson Bay-Davis Strait population spans over a large area of approximately 385,000 km^2 from the north-west coast of Hudson Bay through Hudson Strait and northward along the eastern coast of Baffin Island (COSEWIC 2006). Whereas, walruses from the Foxe Basin population are distributed over a smaller area of approximately 50,000 km^2 in the northern areas of Foxe Basin (COSEWIC 2006). Little is known about the seasonal movements of walrus, however walrus have been found in high concentrations year-round in northern Foxe Basin, north-western Hudson Bay, and Hudson Strait (DFO 2002, COSEWIC 2006). Although walrus overlap with polar bears in all 3 regions of Foxe Basin, only northern Foxe Basin and Hudson Strait polar bears are exploiting this locally abundant prey source. My results suggest that although present throughout the entire year, walrus are a rare opportunistic food source for bears in southern Foxe Basin, however an important and frequent alternate prey species in northern Foxe Basin and Hudson Strait.

Bowhead whale biomass was present in polar bear diets in all 3 regions throughout Foxe Basin; however consumption was highest in northern Foxe Basin followed by Hudson Strait (Figure 2-6). Bowhead whale carcasses become available for polar bears to scavenge from natural stranding/mortality, remains from subsistence hunts and predation by killer whales. Carcasses represent an opportunistic food source that can provide a high caloric intake for some individuals

(Miller et al. 2006, Higdon and Ferguson 2010, Herreman and Peacock 2013, Rode et al. 2014). The Hudson Bay-Foxe Basin bowhead whale stock aggregates in two different summer feeding areas: the first in northwestern Hudson Bay around Repulse Bay and the second in northern Foxe Basin around Igloolik Island (Cosens and Innes 2000, Cosens and Blouw 2003). Hudson Strait is a wintering ground for bowhead whales which remain in the dense pack ice (Koski et al. 2006). Northern Foxe Basin acts as a summer feeding ground for bowhead whale cow-calf pairs and juveniles (Cosens and Blouw 2003, Ferguson et al. 2010).

Historically, killer whales were present in Baffin Bay and Davis Strait and absent in Hudson Bay and Foxe Basin due to heavy pack ice in Hudson Strait which previously limited their movement (Higdon et al. 2012). However, the range of killer whales expanded into Hudson Bay and Foxe Basin in the 1950s and currently killer whales presence in the region occurs on an annual basis (Higdon and Ferguson 2009, Higdon et al. 2012). The expansion was correlated to a reduction in sea ice cover in Hudson Strait (Higdon and Ferguson 2009). As the abundance of killer whales increases in Hudson Bay and Foxe Basin, the food-web dynamics are likely to change, since killer whales are also a top predator and depredate the same species as polar bears. Typically, killer whales target smaller individuals such as calves and juveniles and as a result bowhead whale predation occurs more frequently in northern Foxe Basin (Higdon et al. 2012). Thus, polar bears in northern Foxe Basin are likely to have a greater opportunity for scavenging on bowhead whale carcasses as a result of increased killer whale predation. This trend was reflected in the results of this study with bowhead whales found more frequently in the diet of polar bears inhabiting northern Foxe Basin.

Given that carcasses will be most accessible when they wash up on shore, bowhead whales are potentially providing a substantial resource to polar bears during the open water

season when other marine mammal prey are generally less available. A comparison of current and future polar bear harvest samples with archived fatty acid data may help link a temporal increase in bowhead whale scavenging with an increase killer whale predation. There is a limited bowhead whale subsistence hunt throughout Nunavut which resumed in 1996 (DFO 2008). Two bowhead whales were harvested in late summer/early fall in southern Foxe Basin (Repulse Bay in 2010 and Coral Harbour in 2011); therefore polar bears were most likely scavenging on the bowhead whale kill remains from the subsistence hunt. However, the main source of bowhead whale in the diets of polar bears in northern Foxe Basin can be attributed to natural stranding or killer whale attacks, since the most recent harvest in this area occurred in 2008.

Age and sex variation in polar bear diet

Female bears generally had a lower dietary diversity than males and there was a sex-specific effect on diet composition in southern Foxe Basin (Figure 2-8a). In northern Foxe Basin, polar bear diet composition was significantly influenced by age; subadult diets were generally less diverse than adults (Figure 2-8b). My results suggest that some individuals have a greater ability to switch between prey types when preferred foods are less accessible. Typically, larger adult males have the ability to exploit a larger variety of prey, as well as successfully capture larger prey than adult females and younger individuals due to their larger body size (Derocher et al. 2005, 2010). In northern Foxe Basin, there was no significant interaction between sex and age class and on average adults had higher levels of larger prey species such as bearded seal and walrus and lower levels of ringed seal. The larger prey items are still present in the diets of female bears and younger individuals, which is most likely attributed to scavenging on the kill remains made by larger adult males (Stirling and McEwan 1975, Derocher et al. 2002). My findings suggest scavenging may be an important additional food source for subordinate bears.

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Bowhead whale scavenging decreased with age in northern Foxe Basin, and the frequency of bowhead whale present in diets of subadults suggests an important food source for less experienced individuals. However, in all 3 regions of Foxe Basin bowhead whale was still present in the diets of all age classes and sexes which was consistent with observations from the Beaufort Sea (Herreman and Peacock 2013, Rode et al. 2014). A large whale carcass will attract a large number of bears which subsequently share the resource and behave non-aggressively (Schliebe et al. 2008, Herreman and Peacock 2013). Bowhead whale carcasses may therefore be an important additional food source for all nearby polar bears regardless of age, sex, or size.

Earlier studies have identified harp seal as the primary prey of Davis Strait polar bears (Iverson et al. 2006). I found that adult male polar bears in Hudson Strait fed primarily on harp seal (43%) as opposed to ringed seal (23%). These results suggest that adult male bears are more likely to move eastward into the adjacent subpopulation to exploit the food source than younger individuals. As well, walrus was only quantified in diets of male bears, which reinforces the ability of larger individuals to successfully capture larger prey species, along with the ability to forage on multiple prey species. Increased harvest-based samples around Hudson Strait will help better distinguish sex- and age-specific variation in the diet composition of polar bears within this region.

Seasonal variation in polar bear diet

Polar bear diets shifted seasonally in Foxe Basin, which reflects the change in prey availability throughout the year associated with seasonal sea ice conditions. There is a time lag of weeks to months between the consumption of the prey and its reflection in the bear's fat. Polar bears showed a seasonal increase of walrus in diets of all 3 regions during early spring. Although walrus are available year-round within the 3 areas, the species may become particularly

vulnerable to predation during late winter and early spring if heavy ice conditions limit access to open water, leaving walruses potentially stranded on the ice (Calvert and Stirling 1990, DFO 2002). The high level of walrus (33%; Figure 2-9b) in Foxe Basin may reflect this increased vulnerability. In Hudson Strait, harp seal comprise a large portion of polar bear diets during the spring (46%) compared to winter (25%), which may reflect the increased vulnerability of harp seals during the whelping period (March) off Newfoundland and Labrador (Stirling and Parkinson 2006, DFO 2011). It is possible that some individual bears, especially wide-ranging adult males, may migrate to the Labrador Sea to take advantage of the seasonal pulse of harp seal productivity.

Implications of Climate Change

The effects of climate change on polar bears has been most extensively studied in the Western Hudson Bay subpopulation, with evidence of individual- and population-level effects including reduced body condition, reproduction, survival and abundance associated with the increased ice free period (Stirling et al. 1999, Regehr et al. 2007, Hochheim et al. 2010). Baffin Bay and Davis Strait, which are also seasonal ice ecoregions (Amstrup et al. 2008), have shown signs of reduced body condition in relation to sea ice declines (Rode et al. 2012). Foxe Basin has a seasonal ice regime and polar bears have experienced an earlier sea ice breakup and later freeze-up, similar to trends seen in Western Hudson Bay (Regehr et al. 2007), Baffin Bay, and Davis Strait (Stirling and Parkinson 2006), although aerial surveys have identified a stable population within the region (Stapleton et al. 2012). To examine temporal changes in body condition, long-term monitoring should continue within this region to better understand the relationship between changes in lipid content and shifts in habitat. The wide variety of prey species available to polar bears in Foxe Basin and the ability of some individuals to shift between

locally or seasonally abundant prey may aid polar bears in maintaining a relatively stable body condition in a reduced sea ice habitat. Although the abundance of most Arctic marine mammals is poorly understood, relatively high prey diversity may help buffer against habitat loss within Foxe Basin (Rode et al. 2014).

In summary, the spatial variation in diet composition across the Foxe Basin subpopulation gives a good indication of the locally available prey resources. Polar bears in Hudson Strait appear to be seasonally exploiting harp seals in adjacent areas. This study confirmed polar bear scavenging on bowhead whale carcasses throughout Foxe Basin which may provide a substantial food resource during the ice-free period. Walrus were also identified as seasonally important prey species with one individual walrus providing a large caloric gain. Future studies should focus on quantifying long-term trends in bowhead whale contribution on polar bear diet with the killer whale range expansion into northwestern Hudson Bay and Foxe Basin as a potential factor for increased availability. Although diet estimates from the QFASA model have provided significant insight into polar bear foraging and the diversity of potential prey available within this region, continued long-term monitoring will help better assess shifts in polar bear diet in relation to changing sea ice conditions.

Chapter 4: Conclusion

Summary

Ongoing shifts in the Arctic ecosystem pose a threat to the survival of polar bears and will likely alter food web dynamics as well as the structure and function of the ecosystem. The overall goal of this thesis was to investigate the ecological patterns and prey availability associated with the diet selection of polar bears. I quantified the diet composition of polar bears in the High Arctic (Baffin Bay, Gulf of Boothia, and Lancaster Sound) and Foxe Basin using the quantitative fatty acid signature analysis (QFASA) model. The focus was to better understand the underlying ecological factors supporting the high density of polar bears in the High Arctic (Obbard et al. 2010) and the stable population in Foxe Basin (Stapleton et al. 2012). A better understanding of the relationship between predator and prey will help predict the response of polar bears to future effects of climate change.

A seasonal change in body condition, as inferred from adipose lipid content, was recorded in both chapters, with winter sea ice conditions limiting the accessibility to prey and thus resulting in declining condition from fall through spring. The polar bear harvest season is year-round and thus can reflect monthly trends in body condition, whereas capture-based research programs typically only examine differences between two seasons, often fall and spring (Thiemann et al. 2006, Stirling et al. 2008, McKinney et al. 2014). To my knowledge, this is the first study to examine patterns in body condition of polar bears during the winter months in the Canadian High Arctic and eastern Arctic. My results further confirm spring to be an important period for bears to accumulate enough fat stores to last for the remainder of the year, prior to the open water season (Stirling and McEwan 1975, Messier et al. 1992, Stirling and Oritsland 1995).

The importance of locally and seasonally abundant prey species in the diets of polar bears was common in both the High Arctic and Foxe Basin. The ability to alternate between prey

species during periods when preferred prey is less abundant may help individuals cope with the shifts in environmental conditions that will ultimately be seen throughout the Arctic. Polar bear diets reflected a seasonal change in prey availability related to seasonal sea ice conditions throughout the year. Seasonally varied diets were associated with known prey migration routes through these high latitude areas. Essentially, this thesis provides new and important information on the foraging ecology and predator-prey dynamics in four poorly studied polar bear subpopulations: Baffin Bay, Foxe Basin, Gulf of Boothia, and Lancaster Sound. Furthermore, my findings reveal the importance of harvest-based sampling for long-term monitoring of body condition in addition to diet.

The underlying ecological factors supporting the high density of polar bears within these adjacent subpopulations are poorly understood (Obbard et al. 2010). A primary goal for this study was to better understand these ecological factors which influence polar bear diet selection. Diet composition was similar between the 3 High Arctic regions studied (Baffin Bay, Gulf of Boothia, and Lancaster Sound), which is consistent with earlier preliminary studies (Thiemann et al. 2008a). Ringed seal was the primary prey across the 3 regions with bearded seal and beluga whale as important alternate prey. The similarity in polar bear diets in addition to the high density of polar bears in these regions is consistent with the use of a common resource; the high number of prey species attracted to the North Water polynya and the shallow productive waters of Lancaster Sound. Polar bears are not restricted by subpopulation boundaries (Ferguson et al. 1999, Stirling 2002, Sahanatien and Derocher 2010, Peacock et al. 2013) and it may be possible that polar bears are moving between adjacent subpopulations to exploit similar food sources.

In Gulf of Boothia and Lancaster Sound, there was evidence of adult females and less experienced bears scavenging on the remains of kills made by larger adult males. A lack of sex

and age differences in diet reflects the importance of scavenging on larger prey species such as bearded seal and beluga whale and may act as an important food source for subordinate bears. The results of this study provide significant insights into polar bear diet in the High Arctic and the ecological factors driving polar bear feeding ecology. This study is an important first step in better understanding the predator-prey dynamics within these less studied areas and will help assess long-term dietary shifts in relation to future sea ice conditions.

Recent aerial surveys conducted in 2009 and 2010 reported Foxe Basin as a healthy and stable population with no signs of reduced body condition despite declines in habitat quality (Stapleton et al. 2012, Sahanatien and Derocher 2012). The relative diversity of prey species accessible to polar bears in Foxe Basin may help bears maintain a stable body condition throughout the year in an already reduced sea ice habitat. Polar bear diets varied spatially within Foxe Basin, and my results reflect the importance of locally abundant prey species. In Hudson Strait the high levels of harp seal in the diets of polar bears reflects the likelihood of individuals moving into Davis Strait to exploit the abundant harp seal population off the coast of Newfoundland and Labrador (DFO 2011). Walrus are found in all 3 geographic areas analyzed; however high levels of walrus were only quantified in northern Foxe Basin and Hudson Strait and were relatively rare in southern Foxe Basin. Thus, polar bears in northern Foxe Basin and Hudson Strait likely have better success or perhaps optimal hunting conditions for capturing the larger prey species such as walrus within these 2 areas.

In southern and northern Foxe Basin, the large body size of adult males allowed these individuals to successfully capture larger prey items such as bearded seal and walrus, and this trend has been consistently seen in previous studies (Iverson et al. 2006, Thiemann et al. 2008a). The ability of larger individuals to exploit a variety of prey resources may help mitigate the

effects of changing sea ice conditions. My results also confirmed scavenging on bowhead whales by polar bears of all age and sex classes and thus may act as an important food resource during the ice free period. In southern Foxe Basin, subsistence harvest may be a key supplier of bowhead whale carcasses, whereas in northern Foxe Basin natural stranding or killer whale predation may be the main source of whale carcasses. As killer whales increase in numbers, the food web dynamics within this region are likely to change. Thus, this study was important for better understanding predator-prey dynamics within the Foxe Basin subpopulation which may be affected by shifts in top predators and habitat loss.

Implications for Conservation

To date, there are approximately 20,000-25,000 polar bears in the world with two thirds inhabiting the Canadian Arctic (Vongraven and Peacock 2011). Currently in Canada, all polar bears share the same conservation status of "special concern" according to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2008). The species' assessment status has not changed since 1991. Across geographic areas, polar bears have different life history characteristics and foraging strategies in relation to their environment and sea ice patterns (Stirling 2002). As well, the timing and response of climate change varies throughout the Canadian Arctic and thus the impact on polar bears varies spatially (Stirling et al. 1999, Stirling and Parkinson 2006, Stirling and Derocher 2012, Rode et al. 2014).

My findings provide further evidence for variation in polar bear diets which reflect differential prey availability and in turn ecological factors supporting polar bears across Arctic regions. Threats to polar bears (e.g., habitat quality, prey accessibility) and thus long-term population trends are not uniform throughout the 19 subpopulations (Stirling and Derocher 2012). This study confirmed the need to establish conservation status relevant to each

subpopulation. Designatable units for polar bears were first suggested by Thiemann et al. (2008c), to cluster polar bear subpopulations according to conservation status, with bears sharing similar life history characteristics, foraging ecology, and regional sea ice conditions combined into larger units. Within the Canadian Arctic there were 5 designatable units suggested: Beaufort Sea, High Arctic, Central Arctic, Davis Strait, and Hudson Bay (Thiemann et al. 2008c). Consequently, the 5 designated units would provide a more applicable conservation status for each subpopulation as opposed to managing all polar bears under the same conservation status (Thiemann et al. 2008c).

Overall, the key findings of this thesis can be used to better assess future conservation and management strategies in response to climate change. In addition, this study established baseline lipid content data which can be used to monitor future long-term trends in polar bears in the less studied subpopulations. Adipose lipid content of polar bears has been previously validated as an accurate indicator of overall body condition in polar bears (Stirling et al. 2008, McKinney et al. 2014). This study was the first to correlate percent lipid content in adipose tissue with fatness index rating assessed by hunters, and my results suggest that hunters can reliably use the fatness index as a qualitative method for community-based monitoring programs and future conservation decisions. The increased monitoring of overall body condition of bears through lipid content and fatness index will aid in assessing nutritional stress in relation to shifts in environmental conditions.

Future Directions

My thesis is the first step to identifying variations in diet in the less studied areas of the Canadian Arctic in relation to seasonal variation. However, this study was limited to two hunting seasons (2010/11 and 2011/12), and thus, was unable to investigate temporal shifts in diet.

Continued polar bear sampling within the High Arctic (Baffin Bay, Gulf of Boothia, and Lancaster Sound) and Foxe Basin will be important for assessing future population-level dietary shifts. Polar bear diets within these regions need to be investigated long-term to provide further insight into annual fluctuations and decadal trends in polar bear foraging patterns. Moreover, temporal trends in polar bear diet can help identify inter-annual variation in diet as a result of shifts in sea ice conditions and indirectly, changes to prey availability and distribution.

In addition to continued harvest-based polar bear sampling, it would also be interesting to investigate past polar bear fatty acid signatures and diet estimates in Baffin Bay, Foxe Basin, Gulf of Boothia, and Lancaster Sound to compare past diet composition with current diet composition. This study confirmed polar bear foraging on harp seal in all 3 High Arctic regions, but especially in Baffin Bay. Quantifying harp seals in the diet of past samples may help better indicate potential shifts in prey species from preferred ringed seal to an increase in alternate prey items. For instance, McKinney et al. (2013) recorded a shift in diets from Arctic species such as ringed seal to increased subarctic species such as harp seal and hooded seal in East Greenland in relation to warmer temperatures. Therefore, past diet estimates can reveal potential shifts which may have already occurred within these high latitude areas.

This was the first study to quantify bowhead whale contribution to the diets of polar bears in the eastern Arctic and thus, the importance of scavenging on bowhead whale is still relatively unknown. The Foxe Basin subpopulation has been identified as healthy, despite decreased habitat quality, thus quantifying bowhead whale levels in polar bear diet over time will help assess the current and future importance of bowhead whale carcasses. It will test the hypothesis that increased bowhead whale carcasses are linked to an increase in killer whale presence in Foxe Basin, specifically the northern areas of Foxe Basin. Furthermore, information on

subsistence hunting in Nunavut and killer whale attacks on bowhead whales may provide additional insight into the main source of bowhead whale carcasses. In summary, this continued research will help better understand predator-prey and food web dynamics within the Arctic marine ecosystem and ultimately provide information for applicable future conservation and management decisions.

In both chapters, polar bear diet composition reflected locally and seasonally abundant prey species. This study identified the potential for polar bears to move among adjacent subpopulations to exploit food resources. To further test this theory it is important to link movement patterns with diet composition of polar bears in all 4 Arctic regions. In the High Arctic, movement studies would help further assess the ecological and dietary similarities among the 3 subpopulations. In addition, understanding movement patterns would provide empirical evidence of resource use and determine if polar bears are attracted to common areas of high biological productivity. Spatial variation in diet in Foxe Basin was identified in this study; movement studies in Foxe Basin will help establish potential pockets of high prey abundance which result in the spatial separation within the subpopulation.

In summary, this thesis provided new insights into the foraging ecology of polar bears in the High Arctic and Foxe Basin. In addition, it was the first study to examine lipid content throughout the winter months. As well, the QFASA model included more potential prey species to quantify polar bear diets (i.e. harp seal in the High Arctic and bowhead whale in Foxe Basin) than in previous studies. This study confirmed varying diet composition in polar bears associated with different ecological factors and sea ice conditions across the Arctic. This study identified the importance of quantifying diet in less studied areas, and the use of harvest-based samples to examine body condition and foraging ecology of polar bears throughout Nunavut. Although

further research still needs to be conducted to examine key aspects of polar bear foraging, this thesis was a good first step and increased our knowledge in less studied areas of the Arctic.

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