Monitoring Ecosystem Dynamics in the Beaufort Sea using Stable Isotopes in Polar Bears (*Ursus maritimus*) and Ringed Seals (*Pusa hispida*)

by

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ABSTRACT

Extensive declines in sea ice extent and thickness are occurring within the Arctic and are projected to continue in the future due to amplified polar warming. As a result, community composition and structure are changing within Arctic ecosystems. Animal diets are influenced by accessibility and availability of prey, and therefore, the diets of predators may provide insights into ecological shifts. To study ecosystem dynamics in the Beaufort Sea, I used polar bear (*Ursus maritimus*) and ringed seal (*Pusa hispida*) stable isotopes. I assessed whether sectioning guard hairs and claws of polar bears captured in 2007 to 2011 could be used to identify seasonal dietary trends, and evaluated whether variation in stable isotopes of polar bears could predict their space use patterns (i.e. coastal or pelagic) following an examination of home range fidelity. Sectioning of claws, but not guard hairs, identified seasonal dietary trends. Polar bears showed fidelity to their home ranges between years. Coastal polar bears were depleted in $\delta^{15}N$ either due to feeding upon a $\delta^{15}N$ depleted food web, relying upon more bowhead whale (*Balaena mysticetus*) carcasses from subsistence hunts, and/or experiencing less nutritional stress. Next, I examined temporal variation of polar bear stable isotopes, diet proportions and niche widths from 2004 to 2012 within the northern and southern Beaufort Sea subpopulations, in relation to sea ice dynamics, climate indices and biological factors. Ringed seal made up the highest proportion of the diet of polar bears in all ages, sexes, and subpopulations. However, dietary proportions varied between years. Stable isotopes of polar bears were affected by ringed seal ovulation rate, Arctic oscillation, sea ice dynamics and temperature, which influence availability of prey. Polar bears altered their foraging in response to prey availability, with larger niche widths in years of reduced ringed seal ovulation rates. As such, polar bear diets can reflect a measure of seal population dynamics which are currently understudied in the Beaufort Sea. Following examination of polar bear stable isotopes, I investigated spatial and temporal variation in ringed seal stable isotopes from 1964 to 2011 in relation to age, sex, sea ice dynamics, climate indices, temperature, and spatial distribution of the killed ringed seal in the longest study on ringed seal diet to date. Age and sex were not related to stable isotope value. Cyclonic circulation regimes were related to enriched $\delta^{13}C$, possibly due to changes to primary productivity. Depletion of $\delta^{15}N$ occurred during warmer years, which may be due to ringed seals feeding at a lower trophic level. Both $\delta^{15}N$ and $\delta^{13}C$ were enriched in years with high seal population productivity.

Increasing ringed seal niche width from the 1960s indicated ringed seal diet diversification, which may be a result of range expansions of sub-Arctic prey species. Overall, I found evidence suggesting that polar bear and ringed seal diets can be used to assess ecosystem dynamics, as their diets reflect prey availability and diversity. I found that abiotic variables that affect sea ice dynamics, such as temperature, were related to the diet of both species, reflecting the biological significance of sea ice to polar bears and ringed seals. My research highlights the importance of understanding how biotic and abiotic factors, as well as spatial distribution of the animal, influence diet when monitoring ecological changes. The results from this research may be applied to predict ecosystem changes in the future within the Arctic ecosystem.

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CHAPTER 1 – INTRODUCTION

1.1 Monitoring Ecosystems

Globally, modifications to ecological systems caused by anthropogenic climate change are a growing concern (Parmesan 2006, Post et al. 2009, Walther 2010, Beaugrand and Kirby 2018). Mounting evidence indicates that climate change has large scale ecological impacts, including habitat loss and species extinctions (Chapin et al. 1995, Thomas et al. 2004, Deutsch et al. 2015, Jantz et al. 2015, Urban 2015, Pacifici et al. 2017). Understanding the effects of climate change requires comprehensive, long-term ecosystem monitoring and is vital when working towards management strategies, identifying environmental issues, determining the effects of environmental conditions, and assessing ecosystem health. However, the complexity and scale of ecosystems can make them difficult and expensive to monitor fully. These limitations necessitate a cost-effective proxy to quantify ecosystem condition, which may be accomplished by monitoring single or small groups of species whose biological trends capture ecosystem change.

Indicator species have biological parameters (e.g. population size, diet, health) that can serve as a proxy measure of environmental health, habitat quality, ecosystem structure and function, and population trends of other species (Landres et al. 1988). Effective indicators are easy and cost-effective to study, widely distributed, sensitive to ecological changes and capture variation within other species (Carignan and Villard 2002). However, ecosystem complexity is often not fully captured by a single species (Kremen 1992, Carignan and Villard 2002), and confounding factors are not always accounted for (Steele et al. 1984, Morrison 1986). Species responses may vary across a gradient of environmental conditions, and this variation is not always accounted for (Zettler et al. 2013). Therefore, forming a thorough understanding of the species ecology and how they are affected by environmental conditions is fundamental when using the species' parameters, such as diet, to monitor ecosystem changes.

Diet can synthesize information about ecosystems, such as prey abundance, distribution and availability (Baird 1990, Stirling et al. 2008, Andrade et al. 2016), ecosystem structure and function (Carroll et al. 2013), and ecosystem health (St Louis et al. 2011). Optimal foraging theory predicts that individuals will forage in a way that maximizes energy intake, while minimizing cost (Emlen 1966, MacArthur and Pianka 1966, Pyke et al. 1977). According to this theory, foraging strategy will be influenced by availability and accessibility of food (Fantino and Preston 1988, Abrams 1991). Therefore, diet can provide a measure of ecosystem change by capturing evidence on abundance and distribution of prey, particularly for high trophic level species (Baird 1990, Windberg and Mitchell 1990, Hansen and Beauchamp 2014). Diet can be determined through several methods, but many are time consuming (e.g. observations), invasive (e.g. stomach content analysis) or only provide a snap-shot of diet (e.g. fecal analysis). Analyses that integrate long term information on diet, such as stable isotope analysis, are ideal to monitor ecosystems.

The diet of a species can be described using stable isotope analysis, which quantifies the abundance of stable isotopes within a tissue (Peterson and Fry 1987, Hobson and Welch 1992, Ben-David and Flaherty 2012). Stable isotope analysis can capture a variety of information on diet, such as trophic level (Minagawa and Wada 1984), diet composition (Bentzen et al. 2007), food source (Smith et al. 1996), and nutritional stress (Polischuk et al. 2001). Typically, studies on diet analyze nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), although other elements may be used (e.g. oxygen, hydrogen, sulfur).

Nitrogen stable isotope values are indicators of trophic level, as well as nutritional stress and nutrient source (Hobson et al. 1993, Ben-David and Flaherty 2012). Due to increased ^{14}N excretion in nitrogenous wastes, $\delta^{15}N$ typically enriches about 3‰ per trophic level (DeNiro and Epstein 1981, Minagawa and Wada 1984). When an animal fasts, nutrient uptake decreases, metabolism of internal nitrogen resources increases, and elimination of nitrogenous waste continues, resulting in the individual's $\delta^{15}N$ increasing (Doi et al. 2017). The individual's $\delta^{15}N$ depends on whether its food is derived from a marine or terrestrial source, as marine plants are typically enriched in $\delta^{15}N$ compared to terrestrial (Wada et al. 1975, DeNiro and Epstein 1981). As many factors may affect nitrogen stable isotopes (DeNiro and Epstein 1981, Ben-David and Flaherty 2012), food or nutrient source is best determined when $\delta^{13}C$ is considered with $\delta^{15}N$.

Enrichment of $\delta^{13}C$ with increasing trophic level is relatively minor compared to $\delta^{15}N$, and therefore, patterns in carbon are more informative about foraging habitat or food source (DeNiro and Epstein 1978, Marshall et al. 2007). Carbon stable isotopes can distinguish between marine and terrestrial diets as $\delta^{13}C$ is depleted in terrestrial animals due to the difference in $\delta^{13}C$ of dissolved inorganic and atmospheric carbon (Boutton 1991). Food chains with a base of C_3 or C_4 plants can be differentiated with $\delta^{13}C$, due to C_3 plants favoring fixation of CO_2 carrying ^{12}C (Marshall et al. 2007). Geographic location influences $\delta^{13}C$ with $\delta^{13}C$ decreasing with latitude due to patterns in primary productivity (Goericke and Fry 1994, Kelly 2000). Numerous factors can affect $\delta^{13}C$, including temperature (Goericke and Fry 1994), salinity (Gillikin et al. 2006), and primary productivity rates (Goering et al. 1990). Overall, stable isotope values can be affected by many factors (DeNiro and Epstein 1978, 1981, Ben-David and Flaherty 2012), and identifying sources of variation is important if using stable isotopes to monitor ecosystems, such as the Arctic.

1.2 A Warming Arctic

Over the past century, climate change caused large-scale environmental modifications within the Arctic such as reduced sea ice (Johannessen et al. 2004, Parkinson 2014, Galley et al. 2016), warmer temperatures (Screen and Simmonds 2010, Judah et al. 2012), and altered circulation patterns (Deser et al. 2000, Wood et al. 2013). Sea ice extent has decreased, and young, thin sea ice makes up more of the ice cover than in previous years (Stroeve et al. 2012). In strongly affected regions, ice break-up is up to two months earlier (Stammerjohn et al. 2012). As a result, a feedback loop occurs where reduced ice results in increased temperatures, which in turn reduces ice formation (Screen and Simmonds 2010, Stroeve et al. 2012).

Loss of sea ice is expected to accelerate in the future (Stroeve et al. 2007, Wang and Overland 2009, Overland and Wang 2013), and monitoring Arctic ecosystem dynamics as environmental conditions change will be vital to management strategies. Arctic research is significantly more expensive than research at lower latitudes (Mallory et al. 2018), and therefore, methods to monitor Arctic ecosystems must be effective and comprehensive. Examining the diets of polar bears (*Ursus maritimus*) and ringed seals (*Pusa hispida*), both circumpolar and endemic to the Arctic (Reeves 1998, Amstrup 2003), may be an effective way to monitor Arctic ecosystems. Polar bears and ringed seals are pagophilic (i.e. dependent upon sea ice) making them both sensitive to climate change (McLaren 1958, Smith 1980, Laidre et al. 2008). Both species are ecologically linked, as ringed seals are an important food source to polar bears (Stirling and Øritsland 1995). Lastly, as polar bears and ringed seals feed at a high trophic level (Stirling and Archibald 1977, Lowry et al. 1978), changes in the food web may be detected within their diets.

1.3 Polar Bears and Climate Change

Due to their iconic status, polar bears may act as both an umbrella and flagship species for conservation. Polar bears are currently listed as ‘vulnerable’ by the IUCN Red List, with a population size of 15,972 to 31,212 split between 19 subpopulations (Hamilton and Derocher 2018). Polar bear survival is linked with sea ice which is used for foraging and reproduction (Amstrup 2003). Polar bear diets cycle between periods of hyperphagia in the spring and fasting through the open water season (Lunn and Stirling 1985). During the spring, polar bears use the sea ice to hunt ringed and bearded seal (*Erignathus barbatus*) pups and basking adults (Stirling and Archibald 1977, Smith 1980). Following sea ice break-up, bears are forced to migrate away from high quality foraging habitat to land or multiyear sea ice (Amstrup et al. 2000, Pongracz and Derocher 2017).

Polar bears are opportunistic foragers (Lunn and Stirling 1985, Smith and Sjare 1990, Derocher et al. 1993b, Thiemann et al. 2008, Galicia et al. 2015). Seals are the main prey of polar bears (Stirling and Archibald 1977, Smith 1980, Thiemann et al. 2008, Pilfold et al. 2012), but bears will feed opportunistically on whale carcasses, walruses (*Odobenus rosmarus*), birds and eggs, vegetation, and terrestrial mammals (Russell 1975, Derocher et al. 1993b, Smith and Hill 1996, Bentzen et al. 2007). These dietary components vary by region, sex, age, and size of the individual (Thiemann et al. 2008). Large bears can hunt difficult to handle prey, such as belugas (*Delphinapterus leucas*) (Lowry et al. 1987b, Smith and Sjare 1990). Scavenging upon carcasses is common (Herreman and Peacock 2013). Increased foraging of polar bears upon alternative prey may be a result of climate change, due to the reduced accessibility of seals or increased availability of alternative prey sources (Derocher et al. 2004).

Loss of sea ice threatens the survival of polar bears by causing nutritional and physiological stress (Derocher et al. 2004). When sea ice break-up is earlier, the duration that polar bears fast increases due to reduced access to seals (Derocher et al. 1993b, Derocher et al. 2004). In addition, loss of sea ice may reduce ringed seal reproductive rates, recruitment, and body condition (Ferguson et al. 2005, Harwood et al. 2012b, Ferguson et al. 2017). Fasting has increased in several polar bear subpopulations (Rode et al. 2018), and increased foraging on alternative food sources has been documented (Smith et al. 2010, Prop et al. 2015). However, to sustain their body weight at thermoneutral temperatures, polar bears need between 12,000 and 16,000 kcal/day, which is best met by a high calorie, lipid-rich diet (Best 1985, Pagano et al. 2018). Alternative foods, particularly terrestrial ones, likely do not provide enough calories to meet an individual's energy budget (Rode et al. 2015b). Subpopulations that exhibit increased foraging on terrestrial food sources such as in Hudson Bay continue to decline during periods of poor sea ice conditions, indicating that nutritional needs are not being fulfilled (Stirling et al. 1999, Regehr et al. 2010, Lunn et al, 2016). As well, the quantities of terrestrial foods required to maintain polar bear populations are unsustainable and may decimate the populations of other species, such as snow goose (*Chen caerulescens*) (Smith et al. 2010, Rode et al. 2015b).

Malnutrition is expected to have numerous effects upon polar bears (Derocher et al. 2004, Laidre et al. 2008, Stirling and Derocher 2012). Starvation is estimated to occur after 222 ± 12 days of fasting in adult male polar bears (Molnár et al. 2010, Molnár et al. 2014, Pilfold et al. 2016). Nutritional stress may increase chance of drowning (Durner et al. 2011), reduce hunting ability due to muscle atrophy (Whiteman et al. 2017), and increase susceptibility to pathogens (Burek et al. 2008). Reproductive and recruitment rates are expected to decrease with poorer nutrition, due to reduced investment into gestation and lactation (Derocher et al. 1993a, Stirling and Derocher 1993, Atkinson and Ramsay 1995). Poor maternal condition is expected to reduce reproductive success, litter sizes, and cub mass (Molnár et al. 2011). Females with larger fat stores produce heavier cubs, and cub body mass is a positive predicter of survival (Atkinson and Ramsay 1995, Derocher and Stirling 1996). Cannibalism of cubs may occur when food is scarce (Amstrup et al. 2006). Decreasing sea ice forces polar bears onto land, resulting in more polar bear-human interactions as bears seek out anthropogenic resources (Towns et al. 2009). These negative effects of malnutrition may result in climate change negatively affecting polar bear populations across the Arctic (Stirling et al. 1999, Derocher et al. 2004).

1.4 Ringed Seals and Climate Change

Ringed seals are a keystone species in the Arctic, as both a high trophic level predator and an important food source for polar bears (Stirling and Archibald 1977, Lowry et al. 1978, Lowry et al. 1980). Sea ice is vital to ringed seals, and is used for reproduction, moulting and resting (McLaren 1958, Smith and Stirling 1975). During spring (March-April), ringed seals give birth in snow-covered lairs over breathing holes in the ice which are maintained using their claws (Smith and Stirling 1975). Polar bears predate upon seals within these birth lairs, utilizing the seals as a high caloric food source (Smith 1980, Best 1985). Following this reproductive period, during the open water season, seals disperse over long distances to forage intensively for prey (Harwood and Stirling 1992, Kelly et al. 2010, Harwood et al. 2012a).

The diet of ringed seals is diverse, and includes over 70 species across their Arctic range, from fish (e.g. Gadidae spp.) to crustaceans (e.g. Amphipoda spp.) (McLaren 1958, Lowry et al. 1978, Lowry et al. 1980, Dehn et al. 2005). Ringed seal diet varies regionally, seasonally, and demographically (Lowry et al. 1980, Dehn et al. 2007, Young et al. 2010). Fish consumption is higher in females and older seals (Lowry et al. 1980, Dehn et al. 2007, Yurkowski et al. 2016b). The diet of ringed seals is likely to change in the future, as sea temperatures warm and allow invasions of new species (Rand and Logerwell 2011, Young and Ferguson 2014). Marine communities may shift to be dominated by pelagic species due to the reduced sea ice (Bluhm and Gradinger 2008), which may be reflected in seal diets (Carroll et al. 2013).

Ringed seals may be less sensitive to climate change than polar bears, but are still expected to experience negative effects (Laidre et al. 2008). Initially, earlier break-ups may even benefit seals, due to reduced predation risk and increased food availability (Ferguson et al. 2005). However, warm temperatures, decreased snow and increased rainfall will increase the chance of birth lair roofs collapsing, exposing seals to the elements and increased predation risk (Stirling and Smith 2004, Hezel et al. 2012). As a result, adults may have less energy to invest into pups or may separate before the lactation period is complete, leading to young seals in poor body condition or recruitment failure (Ferguson et al. 2005). Ringed seal body condition, which is correlated to ovulation rate, has declined likely due to changes in prey availability and distribution (Harwood et al. 2000, Harwood et al. 2012b). Climate change will alter community composition within the marine Arctic ecosystem, and it is unknown how this will affect the diet of ringed seals.

1.2 Study System: The Beaufort Sea

The effects of climate change are experienced throughout the Arctic; however, the Beaufort Sea may be more affected due to rapid sea ice loss (Comiso et al. 2017). The Beaufort Sea stretches between Banks Island, Northwest Territories to Barrow, Alaska, extending east into the Amundsen Gulf, and bordered by the Arctic Ocean and Chukchi Sea. Due to a cold climate, sea ice plays an important role in the Beaufort Sea ecosystem. The wind-driven, clockwise Beaufort Gyre regulates sea ice movement and acts as a freshwater reservoir (Proshutinsky et al. 2002), causing sea ice to be thicker and undergo more deformation than other regions (Bourke and Garrett 1987). Sea ice is present for most of the year with ice beginning to break-up in May and freeze-up in September (Galley et al. 2008, Galley et al. 2016). Ice break-up begins in the Cape Bathurst polynya which is located near the mouth of the Amundsen Gulf and is a site of high biological productivity within the region (Stirling 1980). During the open water season, productivity blooms occur, drawing in migratory species like bowhead whales (*Balaena mysticetus*) to feed from the nearby seas (Braham et al. 1980). Many species inhabit the Beaufort Sea, including seals and polar bears.

Two polar bear subpopulations have been identified within this region (Wiig et al. 2015). The southern Beaufort (SB) subpopulation ranges along the southwestern Beaufort Sea from Cape Lyon, Northwest Territories to Wainwright, Alaska, and is declining (Regehr et al. 2010, Bromaghin et al. 2015). The northern Beaufort (NB) subpopulation remains stable and uses the northeastern Beaufort Sea from the Amundsen Gulf north along the western Arctic Archipelago (Stirling et al. 2011). Ringed seals are the dominant prey of SB and NB bears (Bentzen et al. 2007, Thiemann et al. 2008). Predation on seals by polar bears varies with seal productivity and climate, which affect the availability and accessibility of seals, respectively (Stirling et al. 2008, Pilfold et al. 2015, McKinney et al. 2017, Rode et al. 2018). Ringed seals are abundant throughout the Beaufort Sea (Stirling et al. 1982). However, ringed seal population estimates (Stirling et al. 1977, Stirling et al. 1982) are outdated.

Reliance on alternative food sources, such as whale carcasses, is increasing in polar bears (Rogers et al. 2015, McKinney et al. 2017). Land use has increased in SB bears (Schliebe et al. 2008, Pongracz and Derocher 2017), which may result in a larger terrestrial diet component. The number of fasting bears in the Beaufort has increased from the 1980s to early 2000s (Cherry et al. 2009, Pilfold et al. 2015, Rode et al. 2018). Stable isotopes have been examined in SB bears (Bentzen et al. 2007, Cherry et al. 2011, Rogers et al. 2015), but these studies do not cover long periods or all demographics. Dietary studies on NB bears are limited (e.g. Thiemann et al. 2008) and stable isotopes have not been examined in this population.

Within the Beaufort Sea, ringed seals have experienced a decline in body condition from 1992 to 2011, which was tied to late ice break-up (Harwood et al. 2012b). During late ice break-up years, body condition and ovulation of seals is reduced (Harwood et al. 2000, Harwood et al. 2012b). Changes to prey assemblages and productivity may affect seal body condition (Harwood et al. 2012b). As well, invasions of species northward have been recorded in the Beaufort Sea (Rand and Logerwell 2011). Pelagic species may become more dominant within the Beaufort Sea (Bluhm and Gradinger 2008). Carroll et al. (2013) postulated that low nitrogen stable isotope values during years with low quantities of sea ice may indicate pelagic foraging. Cyclonic circulation regimes may also affect ringed seal foraging, by causing earlier breakups and affecting prey abundance (Nguyen et al. 2017). Studies on ringed seal stable isotopes in the Beaufort Sea are limited (Dehn et al. 2007, Carroll et al. 2013) and only cover short time periods.

1.5 Thesis Outline

In Chapter 2, I explore the relationship between stable isotopes and space use patterns of SB polar bears from 2007 to 2011. Using data from GPS-collared polar bears, I evaluate spatial fidelity between years, and contrast coastal (nearshore) or pelagic (offshore) space use patterns to diet. I assess the usefulness of sectioning polar bear guard hairs and claws for stable isotope analysis to aid in identifying seasonal diet trends. I expected that resource availability would vary between space use patterns, with coastal bears having access to terrestrial or anthropogenic resources (e.g. whale carcasses from subsistence hunts) that are limited for pelagic bears. I hypothesized that sectioned tissues would reveal seasonal diet trends which reflect changes in abundance and availability of prey, as well as nutritional stress. This chapter highlights the importance of understanding space use patterns of individuals when interpreting diet.

In Chapter 3, I examine temporal trends in NB and SB polar bear diets from 2004 to 2012 using stable isotopes in guard hairs and relate dietary trends to both biotic and abiotic factors. I assess shifts in niche width and discuss how trends in polar bear diets may reveal ringed seal population dynamics. I hypothesized that polar bear diets would reflect variation in seal populations, and that alternative prey species in the diet (e.g. bowhead whale) would increase in years with fewer ringed seals. In years with fewer seals, I predicted that niche widths of bears would increase. This chapter provides a cross-sectional study of NB and SB polar bear stable isotopes. The research emphasizes the need to understand how environmental and biological conditions impact stable isotopes when monitoring ecosystem dynamics.

In Chapter 4, I investigate trends in ringed seal diets in the Beaufort Sea from 1964 to 2011 using stable isotopes in claw growth bands in relation to population demographics, environmental conditions, and location where the seal was killed. I hypothesized that ringed seal stable isotopes would be related to geographic location due to spatial distribution of prey, and to body condition and productivity due to availability of resources. I expected that sea ice dynamics and temperature would influence seal stable isotopes due to the effect on prey productivity and distribution, respectively. This chapter consists of the longest examination of ringed seal stable isotopes, which act as an archive of ecological change within the Arctic.

Lastly, in Chapter 5, I review the overall implications of the results of my dissertation for polar bears and ringed seals, as well as ecosystem monitoring. I discuss the influence of geographic location and environmental variables upon both species and highlight the relationship of polar bears and ringed seals to sea ice dynamics. I predict future changes in space use patterns of polar bears and examine the implications of increasing coastal space use in polar bears in regard to inter- and intraspecific competition, as well as human-bear conflicts. I examine how ringed seals may be affected by climate change in the future due to changes in seal distribution and food webs. Following, I suggest future avenues of research in regard to ecosystem monitoring in the Arctic and stable isotope analysis of metabolically inactive tissues.

CHAPTER 2 – SPACE USE PATTERNS AFFECT STABLE ISOTOPES OF POLAR BEARS (*URSUS MARITIMUS*) IN THE BEAUFORT SEA

2.1 Introduction

Spatial and temporal variation in resources, as well as intraspecific variation in foraging patterns, can affect the diet of an animal (Thiemann et al. 2008, Edwards et al. 2011, Toscano et al. 2016). Within a landscape, the distribution, diversity, and availability of resources change through time and space. To cope with heterogenous resources, animals should select foraging habitats that maximize their energy gain, and thereby increase their fitness (Pyke et al. 1977). Space use and foraging behaviors can vary within a population, and selection of habitats will affect foraging opportunities (Mauritzen et al. 2001, Sullivan et al. 2006, Brown and Sherry 2008, Edwards et al. 2011, Zeppelin et al. 2015). Characterizing dietary variation can be difficult, particularly for species that are elusive or expensive to monitor, but is integral to understanding a species' ecology and for making informed conservation and management decisions.

Stable isotope analysis can be used to quantify diet, intraspecific diet variation, trophic level using nitrogen ($\delta^{15}N$), and food source using carbon ($\delta^{13}C$) (Minagawa and Wada 1984, Marshall et al. 2007). Stable isotopes are integrated into the animal based on the turnover rate of the tissue (Hobson and Clark 1992, Carleton et al. 2008, Bauchinger et al. 2010). Tissues that grow progressively and become metabolically inactive, such as hair and claws, retain isotopes incorporated during their growth; these tissues can be sectioned to allow for finer-scale stable isotope analysis (Rubenstein and Hobson 2004, Dalerum and Angerbjorn 2005). Sectioning tissues for stable isotope analysis has several assumptions including: 1) the stable isotope value of tissues remains unchanging after cessation of growth (Hobson and Clark 1992, Rubenstein and Hobson 2004), 2) tissue growth is continuous and constant (Cherel et al. 2009), and 3) changes in stable isotope values are primarily due to changes in diet (Hobson et al. 1996). Conditional on these assumptions being true, changes in stable isotope values within and between tissues are likely evidence of a change in diet, and therefore, the method is suitable for assessing diet, particularly in variable ecosystems such as the Arctic (Hobson et al. 1996, Dalerum and Angerbjorn 2005).

The Arctic marine ecosystem is dynamic with spatial and temporal variability in resources (Stirling et al. 1977, Stirling and Øritsland 1995, Bluhm and Gradinger 2008). The extent of sea ice cover varies seasonally and during the spring melt and ice-free season, the Arctic experiences a peak in biological productivity (Arrigo and van Dijken 2004, Ji et al. 2013). For sea ice-dependent species, such as polar bears (*Ursus maritimus*), resource availability can vary with distance to shore (Pilfold et al. 2014b), sea ice dynamics (Schliebe et al. 2008), and season (Smith 1980, Lunn and Stirling 1985), among other factors. However, climate change is modifying sea ice dynamics which alters the abundance and distribution of pagophilic species, and will likely result in changes to food webs and species interactions (Laidre et al. 2008, Wassmann et al. 2011). Animals with different space use patterns may respond to these changes uniquely, making it important to study spatial, temporal, and intraspecific variation in diet.

Polar bears are distributed throughout the circumpolar Arctic in 19 subpopulations in association with sea ice where they hunt ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), and other marine mammals (Stirling and Archibald 1977, Smith 1980, Thiemann et al. 2008). Hunting predominantly occurs from sea ice in late winter to break-up when seals are pupping, mating, and hauling out (Latour 1981, Lunn and Stirling 1985, Robbins et al. 2012). Space use patterns within each polar bear subpopulation depend upon regional patterns of sea ice break-up and freeze-up. For example, in Hudson Bay sea ice melts completely, forcing bears onto land (Derocher and Stirling 1990, Derocher et al. 1993b). In the Beaufort Sea, polar bears may move to either multi-year sea ice in the Arctic basin or land when the sea ice breaks up (Atwood et al. 2016, Pongracz and Derocher 2017).

Sea ice covers the majority of the Beaufort Sea in the winter (Galley et al. 2008). Breakup usually begins in May with ice retreating north, and following the sea ice minimum extent in September, freeze-up begins and nears completion in October-November (Galley et al. 2008, Galley et al. 2016). Within the Beaufort Sea, individual polar bears may show different space use patterns in response to sea ice dynamics, either remaining near-shore (coastal) or further out on the pack ice following the ice retreat (pelagic) (Rogers et al. 2015, Atwood et al. 2016, Pongracz and Derocher 2017, Whiteman et al. 2017, Whiteman et al. 2018). These patterns may have developed due to a trade-off between prey abundance and safety. Pelagic bears are exposed to a more dynamic environment due to the large-scale changes in the sea ice that occur offshore (Pongracz and Derocher 2017). Further, prey availability may differ between habitats. Seals may aggregate in areas of moderate sea ice concentration (Kingsley et al. 1985, Harwood and Stirling 1992, Frost et al. 2004, Freitas et al. 2008a), which may benefit pelagic polar bears as likelihood of hunting success increases with sea ice concentration (Pilfold et al. 2014a, Pilfold et al. 2015). During sea ice breakup, pelagic bears undergo energetically expensive migrations to follow sea ice retreat northward into the Arctic Basin; however, fewer seals may be available in these deeper waters (Harwood and Stirling 1992, Durner et al. 2017). In contrast, coastal bears may remain on more solid land-fast ice, which may reduce exposure of cubs to cold water and limit long-distance swimming events (Blix and Lentfer 1979, Stirling et al. 1993, Monnett and Gleason 2006, Pilfold et al. 2017). Polar bears using areas nearshore may have foraging opportunities that are unavailable on the sea ice, such as access to bowhead whale (*Balaena mysticetus*) carcasses from subsistence hunts (Rogers et al. 2015), nesting waterfowl and eggs (Smith and Hill 1996, Stempniewicz 2006), vegetation (Russell 1975, Derocher et al. 1993b), and garbage (Russell 1975). However, terrestrial foods are nutritionally limited compared to marine mammal resources that polar bears primarily feed upon (Rode et al. 2015a).

While the pelagic space use pattern has historically dominated within Beaufort Sea bears, the number of bears using coastal areas has increased (Durner et al. 2009, Atwood et al. 2016, Pongracz and Derocher 2017). Within the Beaufort Sea, there is a trend of later sea ice formation, earlier ice break-up and reduced ice concentration, which can increase the fasting period for bears (Stern and Laidre 2016). Increased fasting during the spring was observed over time in the Beaufort Sea polar bears, which may indicate declining food availability (Cherry et al. 2009, Rode et al. 2018). Use of coastal areas increases in Beaufort Sea polar bears in years with reduced sea ice (Schliebe et al. 2008, Atwood et al. 2016). Coastal bears can supplement their diet with bowhead whale carcasses, which may offset the fasting and muscle atrophy experienced by pelagic bears (Bentzen et al. 2007, Rogers et al. 2015, Whiteman et al. 2017, Laidre et al. 2018, Whiteman et al. 2018). Whale carcasses can support a large number of bears; however, they are an unreliable food source (Herreman and Peacock 2013, Laidre et al. 2018). Rogers et al. (2015) found that bowhead whales make up to 70% of the coastal bear autumn diet, but only 40% of the pelagic bear diet. While dietary studies comparing these space use patterns have been completed on the Alaskan side of the Beaufort Sea subpopulation, a comparison has not been completed on the Canadian side.

The objectives of this study were to: 1) to assess temporal patterns in stable isotopes using sectioned hair and claw tissues, 2) examine relationships between stable isotopes and space use, and 3) estimate prey proportions and temporal variation in Beaufort Sea polar bear diet. I compared the nitrogen and carbon stable isotopes in sectioned polar bear hair and claw samples to space use patterns (i.e., coastal or pelagic), that were determined using telemetry data collected from 2007 – 2011. Site fidelity was assessed to determine whether space use patterns were similar between years. Because the resources available to coastal and pelagic polar bears differ, I expected that stable isotope values would reflect these differences and be recorded in their hair and claws.

2.2 Methods

Sample collection

Sampling occurred in late April to early May in 2007–2011 in the Canadian side of the Beaufort Sea, primarily along the mainland coast (Fig. 2-1). Claw and hair samples were collected from polar bears live-captured from a helicopter using standard immobilization techniques (Stirling et al. 1989). Protocols approved by the University of Alberta Animal Care and Use Committee for Biosciences were followed for all capture and handling. Sampling was <150 km from shore due to range constraints of the helicopter. A section from the side of a claw approximately 2cm in length was collected using a vegetable peeler. The tip of the claw was collected using dog nail clippers. Claw samples were not taken from a certain digit or paw but were stored with the tip upwards, so orientation was known. Guard hairs were shaved from the rump beside the tail, covering an area of approximately 2.5cm in diameter. All samples were frozen at -20°C until analysis. Adult females and subadults of both sexes were collared with global positioning system (GPS) Argos satellite-linked collars (Telonics, Mesa, AZ) programmed to provided locations every four hours. Collars had pre-programmed release mechanisms and a corrodible link to aid release.

Stable isotopes in polar bear hair are thought to represent a period of about six months, with the molt starting in late spring (ca. May) and ending in autumn (ca. October-November) (Amstrup 2003, Cardona-Marek et al. 2009, Rogers et al. 2015). The hair tip is from late spring growth, while the base is grown in late summer. Polar bears may fast in late summer, and feed mainly on seals in spring (Derocher et al. 1993b). Therefore, the base of a polar bear hair may reflect a period of fasting, or reduced feeding, and the tip may reflect the hyperphagic period. However, in the Beaufort Sea, bowhead whales may provide subsistence for some bears through the open water season and may offset this fasting (Whiteman et al. 2017, Whiteman et al. 2018).

Unlike hair, claws may represent diet during the winter months; however, limited studies on claw growth rate in ursids are available. The suggested growth rate for polar bear claws is 4-6 mm/month, although measurements were based off a small sample size (*n* = 3) from spring to autumn (Holladay 1988). This growth rate is similar to other mammal species (Belant et al. 2006, Ethier et al. 2010, Hénaux et al. 2011). The visible portion of a claw is estimated to be 2-3 months of growth (Holladay 1988), so samples taken in May from the visible portion of the claw should represent diet in winter, before March. Belant et al. (2006) suggests that ursid claw growth is continuous, but that the growth rate varies seasonally with metabolic activity. Therefore, it is possible that 4-6mm/month does not represent polar bear claw growth rate over winter. Claw keratin homogenizes at the tip, and therefore, the temporal estimate for the tip of the claw is unknown (Ethier et al. 2010).

Tissue growth rates can vary between and within individuals, and may depend on factors such as the animal's age, nutritional state, hormone levels, and location on the body (Schwertl et al. 2003). Therefore, one caveat of my study is that the time period assigned to each tissue is an estimate and may vary between and within individuals. For hair, I attempted to account for variation in growth rate within the individual by pooling multiple guard hairs for analysis, and always collecting hair from the rump of the bear. However, the digit sampled for claws varied. No difference between claws of different digits has been found in ringed seals (Ferreira et al. 2011, Carroll et al. 2013); however, this has not been studied in polar bears.

Stable isotope analysis

The University of Alberta Biogeochemical Laboratory (Edmonton, AB) analyzed polar bear claws and hair for nitrogen and carbon stable isotopes. All samples were sectioned for finer-scale tissue analysis to assess possible seasonal variation in diet. I cut guard hairs and claws into thirds: tip, middle, and base. While guard hairs vary in length, only similar sized hairs were selected for analysis. The clipped tip for claws was also analyzed. I assumed that tissues were grown over the same period, and each section of hair would reflect approximately the same duration, irrespective of tissue length. All samples were washed in a 2:1 chloroform:ethanol solution, rinsed by deionized water, and air dried before analysis. I ground claw samples to a fine powder using liquid nitrogen and a mortar and pestle. Stable isotopes were expressed using the delta notation:

$$[1]\ \delta X\ (‰) = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

where the heavier form of nitrogen (^{15}N) or carbon (^{13}C) is X, and R is the ratio of heavy to light isotopes (^{15}N:^{14}N or ^{13}C:^{12}C) for the standard (Carbon = Pee Dee Belemnite, Nitrogen = atmospheric nitrogen) or sample (polar bear claw or hair). QA/QC checks during analyses were completed using National Institute of Standards and Technology 8416 whole egg power Standard Reference Material. Analytical error was ±0.1‰ for $\delta^{13}C$ and $\delta^{15}N$ based on standard deviation of replicates.

Spatial Fidelity and Space Use Patterns

To classify individual polar bears as coastal or pelagic, I produced annual (May 1 to April 30) home range estimates for each individual, assessed spatial fidelity as collar deployment was typically at the time of tissue sampling, and determined the proportion of home range ≤150 km from the coast. Only bears with ≥8 months of movement data were used in the analyses. I calculated annual 95% fixed kernel density home ranges using the package 'adehabitatHR' for R for each individual (Calenge 2006, R Development Core Team 2017). Tissue samples represent seasons before sampling and typically, telemetry data was available only after sampling. Therefore, I assessed spatial fidelity of polar bears to determine whether individuals utilize the same space use patterns between years. I determined home range fidelity using overlap analysis (0-100%) of year 1 and 2, calculated by the function 'kerneloverlaphr' in the package 'adehabitatHR' (Calenge 2006) in R (R Development Core Team 2017). If I determined a high (≥50%) mean home range fidelity, I assumed that the polar bears would retain a coastal or pelagic space use pattern between years. If low mean spatial fidelity was determined, only bears with concurrent telemetry and hair growth data were used. The proportion of annual home range ≤150km of the coast was determined for each bear. Polar bears were classified as either coastal (≥50% of 95% kernel home range ≤150 km of shore) or pelagic (<50% of 95% kernel home range ≤150 km of shore).

Section Analysis

Differences in mean $\delta^{13}C$ and $\delta^{15}N$ between tissue types were compared using a single factor ANOVA. I assessed hair and claw tissue sections for differences in $\delta^{15}N$ and $\delta^{13}C$ for all bears, as well as bears separated by space use pattern, using repeated-measures ANOVAs in SPSS 20 (SPSS Inc., Chicago Il, USA). The Shapiro-Wilk test (Shapiro and Wilk 1965) and Mauchly's test of sphericity (Mauchly 1940) were used to assess the assumption of normality and sphericity, respectively. Pairwise comparisons using the Bonferroni correction were used to further examine significance between sections. Differences were considered statistically significant at $p \leq 0.05$.

Space Use Model

I fitted a binomial generalized linear model (GLM) with a logit link function to the data to determine whether $\delta^{15}N$ and $\delta^{13}C$ isotopes could predict space use pattern (i.e. coastal or pelagic). Only nine polar bears had both hair samples and telemetry data so only claw isotopes were used in the GLM. I grouped bears by class: adult females, adult females with cubs of all ages, or subadults (both sexes). Cub presence during hair growth for bears captured without cubs was unknown. Therefore, the females without cubs category may include females that did not reproduce, lost cubs or separated from two-year old cubs. Class (adult females with cubs, adult females or subadults), home range size, year, and $\delta^{15}N$ and $\delta^{13}C$ stable isotopes were included in the models. Number of cubs was not included in the model, as females may have had more cubs in the previous summer. Candidate models were compared to the null model using Akaike's information criterion corrected for small sample size (AIC_c), with models with a ΔAIC_c of <2 having significant support. I selected the most parsimonious model in cases with multiple models of $AIC_c < 2.00$. The Hosmer-Lemeshow goodness of fit test was used to assess how well the models fit the data.

Mixing model diet estimation

I assessed diet proportions of the sampled polar bears using stable isotopes in claws and hair using the Bayesian mixing model MixSIAR version 3.1 (Stock and Semmens 2016). If tissue sections did not differ, I averaged stable isotope values for use in the mixing model. Prey muscle $\delta^{15}N$ and $\delta^{13}C$ means and standard deviations for the Beaufort Sea were taken from the literature (Table 2-1). I used the trophic enrichment factor (TEF) provided by Hilderbrand et al. (1996), which was calculated for American black bears (*U. americanus*), used for all tissues, and has been applied for polar bears (Bentzen et al. 2007, Rogers et al. 2015). All models were run with uninformed priors.

2.3 Results

Sample Collection

In total, I sampled 65 polar bears. Sample sizes do not match for hair (*n* = 26) and claws (*n* = 65) due to sampling issues. Of these bears, 53 were collared. However, only 49 bears (claws: *n* = 49, hair: *n* = 12) had sufficient data to determine their space use patterns.

Space use patterns

The mean ± SE home range size was 391,340 ± 39,847 km^2 (*n* = 49, range = 36,909 to 1,284,371 km^2). Only a subset of the collared polar bears (*n* = 16) had sufficient tracking data for sequential years to calculate annual home range overlap. Polar bears showed annual home range fidelity with a mean ± SE annual home range overlap of 60 ± 4% (*n* = 16, range = 24 to 88%). High annual home range overlap (≥50%) supported the decision to use telemetry data collected after tissue sampling from all bears to determine annual space use of polar bears. All individuals had part of their home range ≤150 km from shore. I classified 27 polar bears as coastal and 22 pelagic. Only one bear switched patterns from coastal to pelagic between the first and second year of tracking; however, in the second year, the bear had 40% of its home range ≤150 km from shore. No pelagic bears switched strategies. Annual home ranges of pelagic polar bears (median = 500,821 km^2, mean ± SE = 521,381 ± 68,932 km^2, n = 22) were significantly larger (Wilcoxon rank sum test, W = 158, P = 0.004) than coastal bears (median = 229,003 km^2, mean ± SE = 285,381 ± 35,083 km^2, n = 27).

Sectioned tissue analysis

Claws had lower δ^{13}C (ANOVA, $F_{(1, 89)}$ = 12.29, P < 0.0001) and higher δ^{15}N (ANOVA, $F_{(1, 89)}$ = 4.27, P = 0.04) than guard hairs. I found no statistical significance in the comparison of hair sections for both δ^{13}C (repeated-measures ANOVA, $F_{(2, 50)}$ = 2.67, P = 0.086) and δ^{15}N (repeated-measures ANOVA, $F_{(2, 50)}$ = 3.06, P = 0.056) (Table 2-2). Significant variation was found in δ^{13}C (repeated-measures ANOVA, $F_{(3,192)}$ = 29.58, P < 0.0001), but not δ^{15}N (repeated-measures ANOVA, $F_{(3,192)}$ = 2.46, P = 0.073), between the claw sections (Fig. 2-2, Table 2-2). For δ^{13}C, all section comparisons were significantly different, except for the comparison between the middle and base section. In coastal bears (n = 27), sections significantly differed in δ^{13}C (repeated-measures ANOVA, $F_{(3,78)}$ = 9.26, P = 0.001) and δ^{15}N (repeated-measures ANOVA, $F_{(3,78)}$ = 4.20, P = 0.008). However, only the comparison between the clipped tip and the side sections was significant (P < 0.007), with the clipped tip having the highest δ^{13}C and δ^{15}N. Pelagic bear (n = 22) claw sections varied in δ^{13}C (repeated-measures ANOVA, $F_{(3,63)}$ = 9.99, P = 0.001), but not δ^{15}N (repeated-measures ANOVA, $F_{(3,63)}$ = 0.12, P = 0.90). Pairwise comparisons showed that the clipped tip was higher in δ^{13}C compared the middle (P = 0.002) and base (P = 0.011) of the side piece, but not the tip (P = 0.36). As well, δ^{13}C was highest in the tip of the side piece (P = 0.011) compared to the middle, but all other comparisons of the side of the claw were insignificant. I did not complete repeated-measures ANOVAs on hair sections of bears with a known space use pattern due to the small sample size (n = 12).

Space Use Model

A total of 49 polar bears were included in the GLM, which examined whether δ^{15}N and δ^{13}C isotopes were related to coastal or pelagic space use. ΔAICc supported a top model including δ^{15}N, class, and home range (Table 2-3). δ^{15}N was related to space use (Fig. 2-3), while δ^{13}C was not. The Hosmer-Lemeshow goodness of fit test showed that the model fit the data (P = 0.21).

Mixing model diet estimation

Due to non-significant variation in hair and unknown growth rates in claws, estimates were only made for claw section, winter (ca. December to March, side of claw, n = *49*), and summer (ca. May to November, guard hair, n = 12) diets. MixSIAR diet estimates indicated that ringed seals made up the largest proportion of the diet for all bears (Fig. 2-4 and 2-5). When examining the population's winter diet at a finer-scale using the side of the claw, I found that the proportion of bowhead whale was at 15.2% in the tip and 20.6% in the base (Fig. 2-4). The diet proportion of bowhead whale in the clipped tip was 11%. The proportion of diet that was ringed seals was 87% in winter and 63.1% in summer for pelagic bears. In coastal bears, ringed seals made up 64.6% of the winter diet, and 62.8% of the summer diet (Fig. 2-5A). Coastal polar bears had 27.2% bowhead whale in their diet during the winter, and 15.7% in the summer. Pelagic bears had 5.8% bowhead whale in their winter diet and 12.8% in their summer diet (Fig. 2-5B). When all bears were pooled (including uncollared bears), the proportion of ringed seals was 72.8% in winter (n = 65) and 58.6% in summer (n = 26). The proportion of bowhead whale was 18.9% in winter and 20.9% in summer. Bowhead whales were the second most consumed prey item. Bearded seal, beluga (*Delphinapterus leucas*), gray whale (*Eschrichtius robustus*), and walrus (*Odobenus rosmarus*) made up the lowest proportion of the diet.

2.4 Discussion

I found individuals showed fidelity to their home ranges between years and this difference in behavior was reflected in $\delta^{15}N$ stable isotope values, highlighting intraspecific variation in diet within a population. While the home ranges of coastal and pelagic bears can overlap, I found evidence that their diets differ. I identified temporal variation in diet by sectioning metabolically inactive tissues and comparing hair and claw tissues. Sectioning of claws demonstrated that finer-scale stable isotope analysis may be a valuable method for examining diet; however, further studies on tissue growth rates are necessary.

I found evidence that $\delta^{15}N$ in claws can be used to assess coastal and pelagic space use patterns in polar bears of the Beaufort Sea. Depleted $\delta^{15}N$ in claws was indicative of coastal space use (Fig. 2-3) and suggests that either coastal bears feed upon a food web with more terrestrially derived nutrients, pelagic bears are nutritionally stressed, and/or that coastal bears were feeding at a lower trophic level (Minagawa and Wada 1984, Hobson et al. 1993, Dunton et al. 2012). Terrestrially derived organic matter from coastal erosion and rivers (e.g. Mackenzie River) incorporates into nearshore food webs, and is $\delta^{15}N$ derived (Parsons et al. 1989, Naidu et al. 2000, Dunton et al. 2012). Therefore, feeding on a nearshore food web would deplete coastal bear $\delta^{15}N$. As well, the diet of pelagic bears is less supplemented by scavenging on bowhead whale carcasses and they experience higher nutritional stress and muscle atrophy in summer than coastal bears (Whiteman et al. 2017, Whiteman et al. 2018). Protein catabolism can elevate $\delta^{15}N$ (Hobson et al. 1993, Hertz et al. 2015), which may enrich $\delta^{15}N$ in pelagic bears. As well, bowhead whales are depleted in $\delta^{15}N$ compared to other prey sources within this study (Hoekstra et al. 2002, Bentzen 2006, Cherry et al. 2011), due to feeding upon planktonic crustaceans (Lowry et al. 2004). Bowhead whale makes up a large proportion of the diet of coastal bears in my study (Fig. 2-5A), as well as others (Rogers et al. 2015, Whiteman et al. 2018). Bowhead whales migrate into the Beaufort Sea during winter, and remain until autumn (Braham et al. 1980). Polar bears may feed upon bowhead whales carcasses that are either left from subsistence hunts or entrapped in the sea ice (Hansen 2004, Bentzen et al. 2007, Herreman and Peacock 2013, Rogers et al. 2015, Laidre et al. 2018). As coastal polar bears remain nearshore, they have an increased chance of encountering subsistence hunt carcasses left along the shore (Pongracz and Derocher 2017, Wilson et al. 2017). These whale carcasses can support large number of bears (Herreman and Peacock 2013), and one whale carcass may replace up to 1,300 ringed seals (Laidre et al. 2018).

Ringed seals are the primary prey of pelagic bears and are at a higher trophic level than bowhead whales (Lowry et al. 1980). For both space use patterns, ringed seals were the main food source, which is consistent with previous research (Bentzen et al. 2007, Thiemann et al. 2008). Pelagic bears may become nutritionally stressed when ringed seals are unavailable, as they cannot rely upon whale carcasses (Whiteman et al. 2018). Pelagic polar bears must travel farther across the moving sea ice to find ringed seals, which may result in the larger home ranges of pelagic bears in this study. Larger home ranges of pelagic bears were also found in the Barents Sea (Mauritzen et al. 2001). As well, pelagic bears have higher movement rates than coastal bears, to accommodate for ice drift (Whiteman et al. 2015).

As seals are an important part of the polar bear diet, it was surprising that bearded seals did not play an important role in the diet for either space use pattern. Studies have found a higher proportion of bearded seal in the diet of Beaufort Sea bears (Bentzen et al. 2007, Thiemann et al. 2008) than in this study which may be due to differences in using fatty acids and stable isotopes to study diet and differences in the sex and age composition of my study animals. Large bodied species, such as bearded seals, provide more blubber for polar bear consumption (Crawford et al. 2015), which may lead to the bears eating less protein from bearded seals than smaller ringed seals. Cherry et al. (2011) found that larger prey (e.g. bearded seals, bowhead whales) contribute more to the lipid-metabolic pathway, while a higher proportion of the protein-metabolic pathway consists of small bodied prey (e.g. ringed seals). Therefore, fatty acids may reveal more large-bodied blubber-rich species, such as bearded seals and whales, than stable isotopes. Diets determined by stable isotopes and fatty acids are known to differ (Kolts et al. 2013). Further, my study did not include adult males due to radio collaring limitations and their diet often includes more large bodied species (e.g. bearded seals) (Thiemann et al. 2008).

While $\delta^{15}N$ was related to polar bear space use patterns, $\delta^{13}C$ was not and this was likely due to multiple factors influencing carbon stable isotopes. $\delta^{13}C$ can be affected by distance to shore (Burton and Koch 1999), benthic and pelagic foraging habitats (Dehn et al. 2006), terrestrial and marine food sources (Ramsay and Hobson 1991), and geographic location (Saupe et al. 1989, Goericke and Fry 1994). Nearshore foraging can enrich $\delta^{13}C$ due to increased ^{13}C uptake by benthic macroalgae (Dunton and Schell 1987, France 1995) and rapid carbon fixation during phytoplankton blooms (Goering et al. 1990, Arrigo and van Dijken 2004). However, pelagic-feeding bowhead whales, which the coastal bears fed on, are depleted in $\delta^{13}C$ as compared to benthic feeding gray whales (Burton and Koch 1999, Dehn et al. 2006).

Another confounding factor is the carbon isotope gradient of decreasing $\delta^{13}C$ from the Chukchi to the Beaufort Sea, and with northward latitudes, that has been recorded in primary producers (Saupe et al. 1989, Goericke and Fry 1994). While bears show spatial fidelity, their movements to different foraging habitats likely influence their stable isotopes. This gradient was reflected in bowhead whales, where bowheads migrating into the Beaufort Sea from the Bering Sea are enriched in $\delta^{13}C$ compared to whales migrating out from the Beaufort Sea (Schell et al. 1989). Spring subsistence hunts will provide coastal bears access to the bowhead whales enriched in δ^{13}C from the Bering Sea; however, if bears are feeding on carcasses leftover from the late autumn, they may be feeding on δ^{13}C depleted bowhead whales. It is unlikely that the other migratory prey sources (e.g. beluga, gray whale, walrus) influenced polar bear stable isotopes significantly due to their low proportions in the diet (Fig. 2-4 and 2-5).

Bayesian mixing models provide estimates of diet based on several assumptions that may bias the model. Mixing models can be influenced by choice of TEF (Bond and Diamond 2011), and it is possible this influenced the diet estimates. However, Rogers et al. (2015) assessed the fit of the ursid-specific TEF from Hilderbrand et al. (1996) used in my study in comparison to a tissue-specific TEF from Caut et al. (2009), and found that the ursid-specific TEF explained polar bear diet well. Further, it is possible that the prey source stable isotope values used within the model biased its output due to temporal and spatial variation within prey species. For example, if ringed seals consumed by polar bears within this study were depleted in δ^{15}N relative to the value (18.3 ± 0.2) provided by Cherry et al. (2011), the estimate of the proportion of other lower trophic level prey foods (e.g. bearded seal) within the diet would be inflated. To avoid biasing results, I selected stable isotope values from prey collected as close in time and space to my samples as possible. Lastly, I assumed that food sources not included in the mixing model make up an insignificant proportion of the diet. These other food sources may have affected my estimates of polar bear diet proportions. However, the influence of some terrestrial food sources on polar bear stable isotopes was negligible (Hobson et al. 2009), and alternative large-bodied marine mammals (e.g. *Phoca largha*) are rare within this region (Lowry et al. 1998).

I found that δ^{13}C stable isotope values varied between claw sections, but δ^{15}N did not (Fig. 2-2, Table 2-2). Unlike Rogers et al. (2015), I did not find variation in δ^{15}N and δ^{13}C stable isotope values across hair sections. My results suggest that polar bears foraging varied while growing their claws, but not during hair growth. However, comparisons between claw sections were primarily significant between the clipped tip and the side sections, and there was little variation between the claw's side sections. This result was consistent when coastal and pelagic bear claw sections were analyzed separately. This highlights the temporal difference between the clipped tip and the side of the claw. It is possible that the clipped tip is from the previous year, depending upon claw length. As differences in stable isotopes between sections was minimal, it is possible that some variation may be due to measurement error.

When eating a consistent diet, stable isotope values should remain about constant across the tissue (Hobson et al. 1996). It is possible that the polar bears in my study were eating a consistent diet or foraging in the same habitats while growing their guard hairs. Alternatively, if the guard hairs grew faster than assumed, variation in diet may have been negligible and the sectioning of the hair too coarse to detect the variation. To improve this technique, I suggest further studies on hair and claw stable isotopes and their growth rates in captive and wild polar bears, both between and within individuals, with larger sample sizes, under different nutritional states and times of the year.

Space use patterns and foraging behaviors may influence how individuals of a population cope with climate mediated shifts in Arctic marine ecosystems. Polar bears with coastal and pelagic space use patterns may experience different access to prey as suitable sea ice habitat for hunting seals disappears. The number of coastal polar bears is increasing (Schliebe et al. 2008, Pongracz and Derocher 2017) even though the population as a whole has declined (Bromaghin et al. 2015). Eventually, pelagic polar bears may be forced to use nearshore areas for scavenging opportunities or regions even further north to follow the retreating sea ice. Human-based resources, such as bowhead whale carcasses, may increase in importance for this population. Monitoring changes in diets and space use patterns of apex predators, such as polar bears, may give us insight into shifts in ecosystems dynamics within the Arctic.

Table 2-1 The mean ± SE δ^{15}N and δ^{13}C values from muscle tissue of Beaufort Sea polar bear (*Ursus maritimus*) prey species used for diet reconstruction: ringed seal (*Pusa hispida*), bearded seal (*Erignathus barbatus*), and beluga whales (*Delphinapterus leucas*) (Cherry et al. 2011), bowhead whale (*Balaena mysticetus*) (Hoekstra et al. 2002), gray whale (*Eschrichtius robustus*) (Dehn et al. 2006), and walrus (*Odobenus rosmarus*) (Bentzen 2006)

Species	*n*	Mean δ^{15}N (‰) ± SE	Mean δ^{13}C (‰) ± SE
Ringed seal	45	18.3 ± 0.2	-20.6 ± 0.1
Bearded seal	10	16.8 ± 0.3	-17.8 ± 0.4
Bowhead whale	84	14.3 ± 0.3	-20.8 ± 0.3
Beluga	11	17.7 ± 0.2	-18.1 ± 0.1
Gray whale	17	12.0 ± 0.2	-17.3 ± 0.2
Walrus	9	13.3 ± 0.2	-17.0 ± 0.2

Table 2-2 Mean ± SE and range for $\delta^{13}C$ and $\delta^{15}N$ of polar bear (*Ursus maritimus*) claw samples (*n* = 65) and hair samples (*n* = 26) collected from the Beaufort Sea in 2007-2011

Tissue	**Mean $\delta^{15}N$ ± SE**	**$\delta^{15}N$ Range**	**Mean $\delta^{13}C$ ± SE**	**$\delta^{13}C$ Range**
Claw				
Clipped Tip	20.82 ± 0.10	19.11 to 22.66	-17.56 ± 0.06	-18.45 to -15.56
Tip	20.79 ± 0.11	19.12 to 22.96	-17.76 ± 0.07	-18.92 to -15.40
Middle	20.69 ± 0.11	19.15 to 22.89	-17.89 ± 0.06	-18.95 to -16.10
Base	20.67 ± 0.12	18.46 to 22.50	-17.89 ± 0.07	-18.94 to -16.23
Hair				
Tip	20.43 ± 0.15	18.13 to 21.34	-17.52 ± 0.07	-18.32 to -16.71
Middle	20.34 ± 0.09	19.21 to 21.21	-17.44 ± 0.08	-18.18 to -16.64
Base	20.40 ± 0.17	17.59 to 21.49	-17.32 ± 0.07	-17.94 to -16.76

Table 2-3 The estimate, standard error, *Z*-value, and *P*-value for significant coefficients included in the binomial generalized linear model used to predict space use (coastal or pelagic) for polar bears (*Ursus maritimus*) in the Beaufort Sea from 2007 to 2011. Class was divided into three levels: adult females with cubs (AFwC), adult females without cubs or with two-year old cubs, and subadults

Coefficients	**Estimate**	**Standard Error**	***Z* value**	***P* value**
Intercept	-45.38	14.75	-3.08	0.0021
$\delta^{15}N$	1.92	0.65	2.95	0.0032
Class – AFwC	3.46	1.59	2.18	0.030
Class – Subadult	3.74	1.65	2.26	0.024
Home Range	7.71×10^{-6}	2.98×10^{-6}	2.59	0.0095

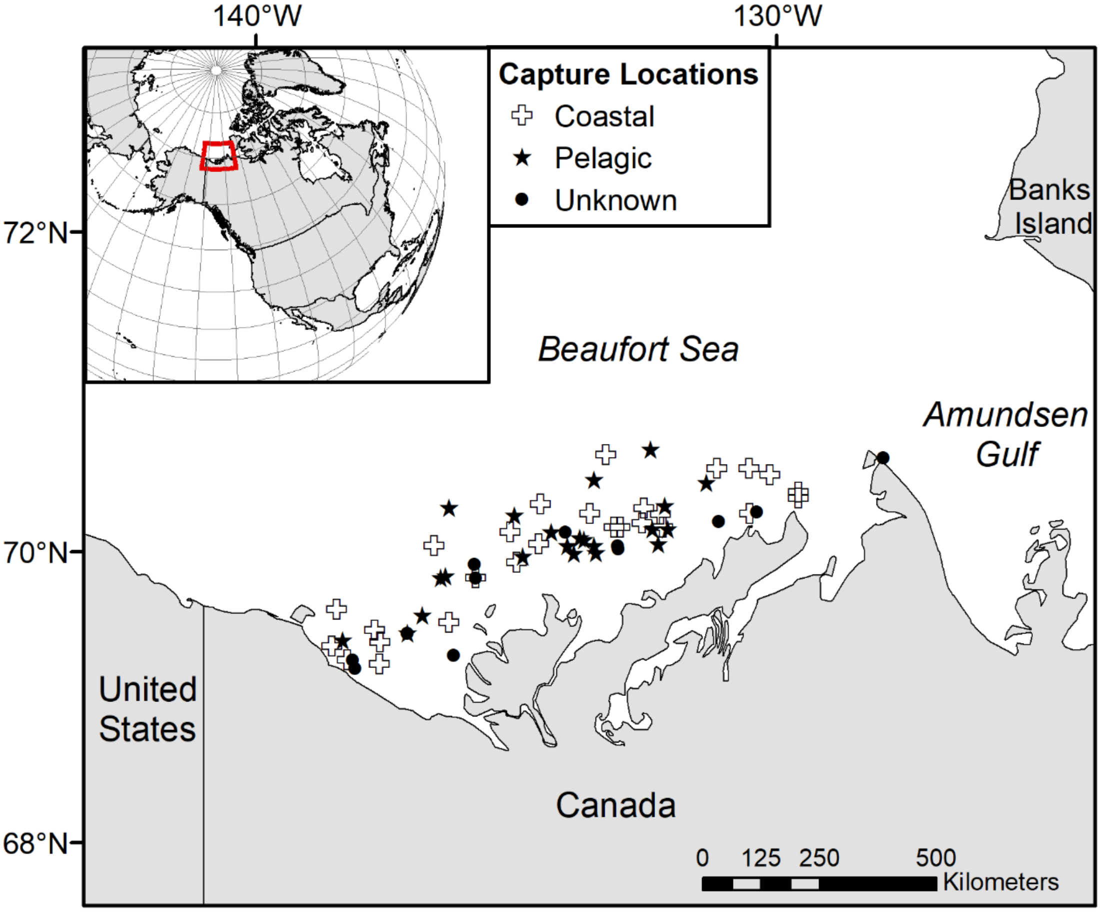

Figure 2-1 Study area with capture locations of polar bears (*Ursus maritimus*) of coastal (cross), pelagic (star) or unknown (circle) space use patterns from the Canadian Beaufort Sea population in 2007 to 2011

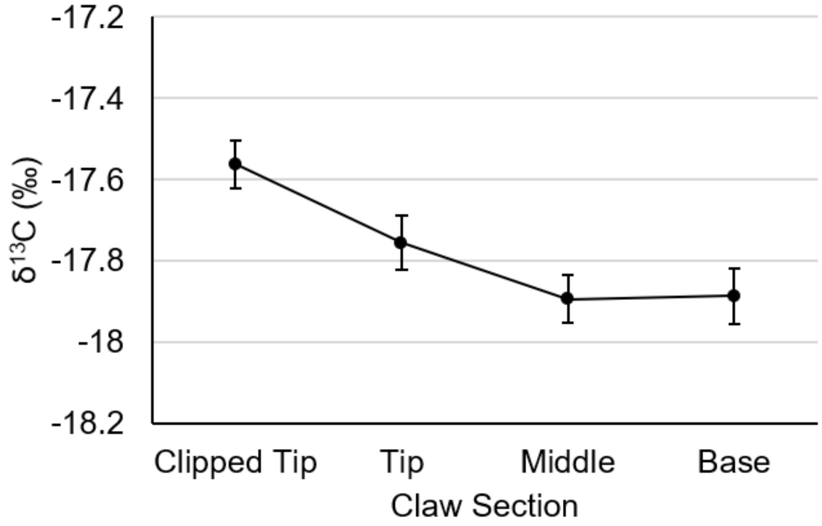

Figure 2-2 Mean δ^{13}C, with standard error bars, of sectioned polar bear (*Ursus maritimus*) claws (*n* = 65) sampled from the Beaufort Sea in 2007 to 2011. Claws sections include a clipped tip, and sections of the claw's side: tip, middle and base

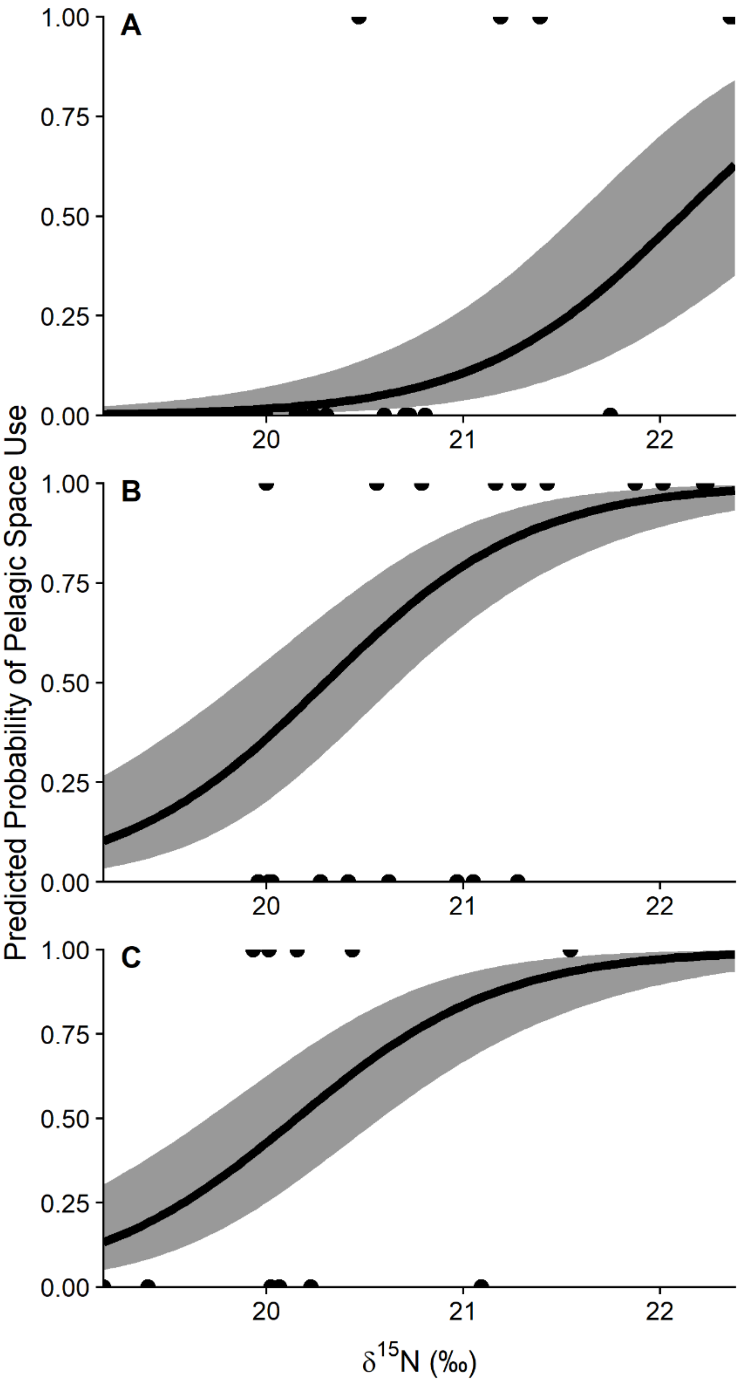

Figure 2-3 Predicted probability of A) adult female, B) adult female with cubs, and C) subadult Beaufort Sea polar bears (*Ursus maritimus*) utilizing pelagic (predicted probability > 0.5) or coastal (predicted probability ≤ 0.5) space use for $\delta^{15}N$. Semi-circle represent actual values of pelagic (1) and coastal (0) bears

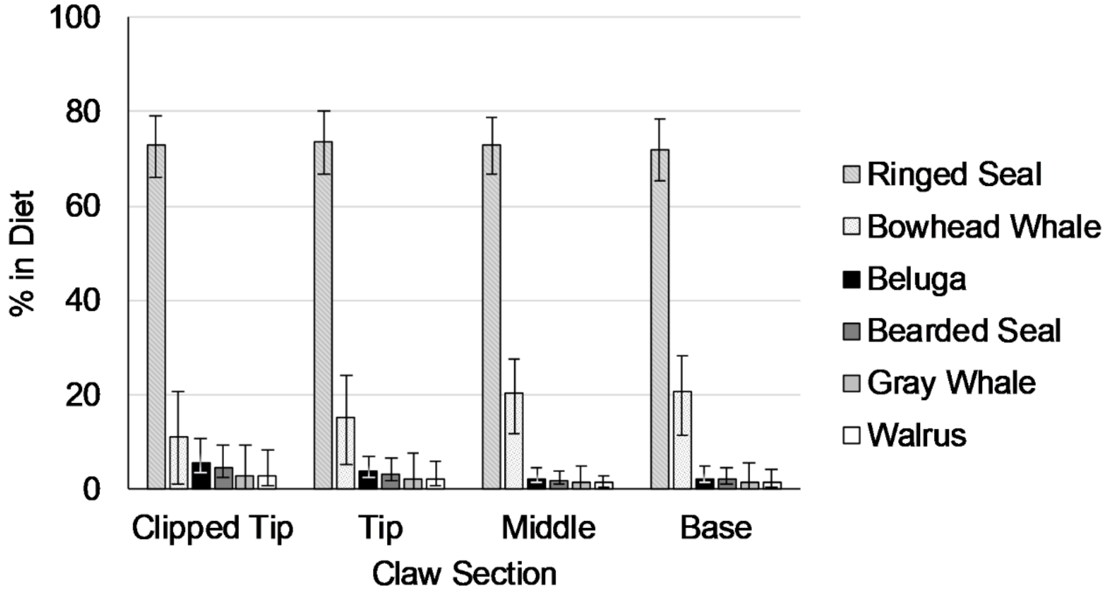

Figure 2-4 Diet estimates from claw sections (*n* = 65) for all polar bears (*Ursus maritimus*) from 2007 to 2011 in the Beaufort Sea, with 95% credible intervals. Diet estimates were produced using MixSIAR Bayesian mixing models

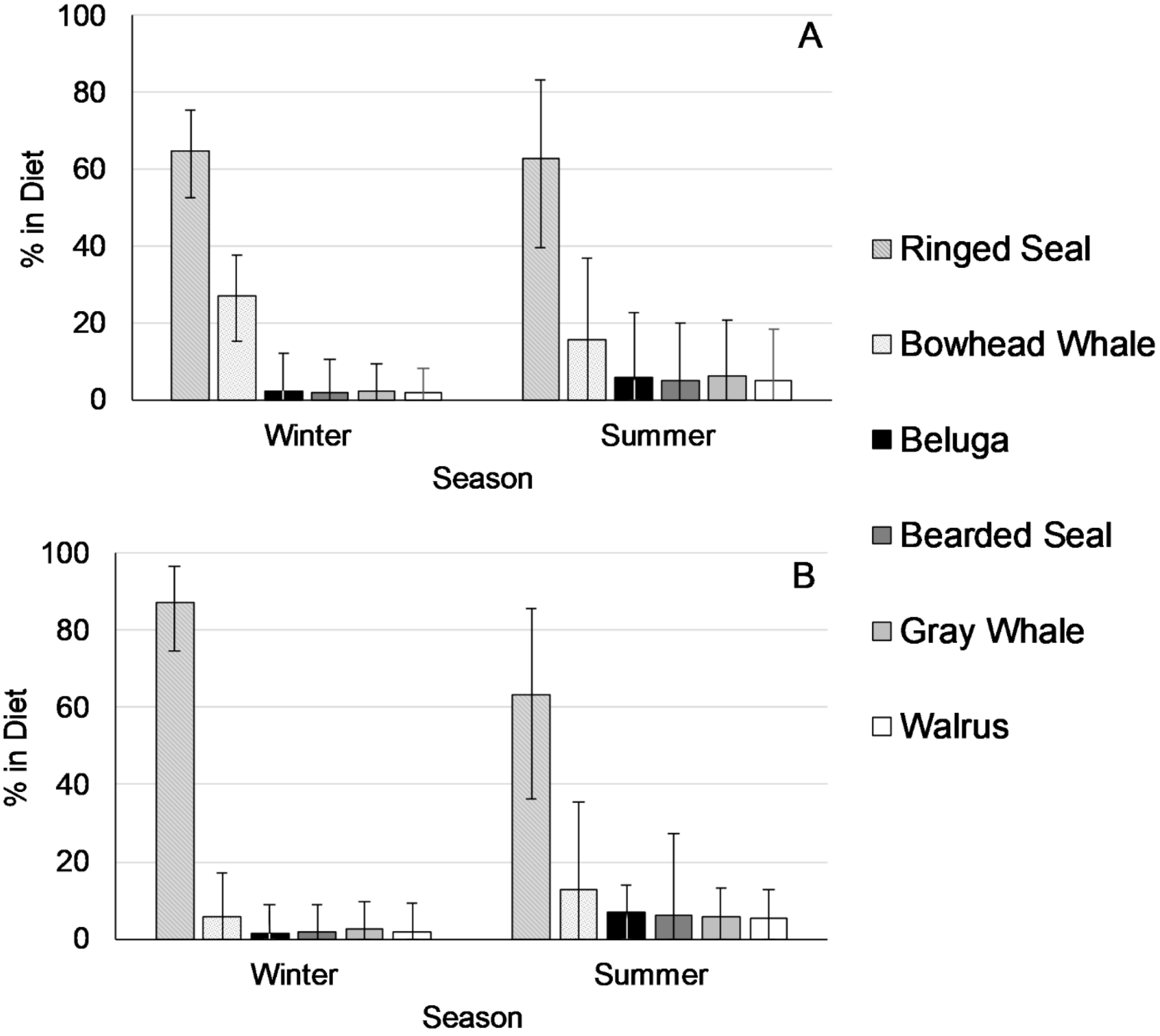

Figure 2-5 Diet estimates for polar bears (*Ursus maritimus*) from 2007 to 2011 in the Beaufort Sea, with 95% credible intervals. Separate tissue was analyzed for each season: winter was represented by the side of claws, and summer was represented by guard hair. Estimates were produced using MixSIAR mixing models for A) coastal (winter: *n* = 29, summer: *n* = 8) bears and B) pelagic (winter: *n* = 21, summer: *n* = 4) bears

CHAPTER 3 – MONITORING ECOSYSTEM DYNAMICS IN THE BEAUFORT SEA USING STABLE ISOTOPES IN POLAR BEARS (*URSUS MARITIMUS*)

3.1 Introduction

Fluctuations in the environment can cause shifts in ecosystem structure and function, resulting in species altering their foraging and habitat use in response to variation in resources (Stenseth et al. 2002, Post et al. 2009). Such alteration or plasticity in diet is driven by optimal foraging, in which resource selection by an individual attempts to maximize energy gain at a reduced search and handling cost (MacArthur and Pianka 1966, Pyke et al. 1977). Food sources with low availability may be difficult to encounter, resulting in animals switching to resources that are more abundant and accessible (Randa et al. 2009, Jaworski et al. 2013). Therefore, shifts in diet may indicate changes in the availability and distribution of resources within the ecosystem (Montevecchi and Myers 1996, Zhou et al. 2008). Dietary shifts in high trophic level species may have pronounced effects upon the ecosystem (McLaren and Peterson 1994, Estes et al. 1998, Ripple and Beschta 2004). As such, monitoring the diets of apex predators can be used both to indicate changes within the community and to understand the effects of environmental fluctuations on the ecosystem. Studies on predator diets have documented alterations to community composition and prey population density, and have been supported by research on shifts in population dynamics and distributions of prey (Montevecchi and Myers 1995, Montevecchi and Myers 1996, Rose 2005, Carroll et al. 2013, Young and Ferguson 2014, Crawford et al. 2015).

Sea ice loss due to climate change is modifying the structure and dynamics of Arctic marine ecosystems (Hansell et al. 1998, Comeau et al. 2011, Post et al. 2013). Temperatures within the Arctic are increasing faster than other areas (Holland and Bitz 2003, Wood et al. 2013), resulting in rapid and accelerating reductions in sea ice extent and thickness (Stroeve et al. 2007, Stroeve et al. 2014, Lang et al. 2016, Stern and Laidre 2016). For several organisms within this ecosystem, including polar bears (*Ursus maritimus*) and ringed seals (*Pusa hispida*), sea ice is critical to various aspects of their life history (Smith 1980, Smith and Hammill 1981, Laidre et al. 2008).

Polar bears are apex predators dependent on sea ice to catch ringed seals and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980, Pilfold et al. 2012). Polar bears accumulate most of their energy from adult seals and newborn pups during a hyperphagic spring period and rely on their energy reserves after the ice breaks up during a fasting period in late summer/fall (Lunn and Stirling 1985, Robbins et al. 2012). Loss of sea ice reduces polar bear's access to seals (Stirling and Derocher 1993, Stirling et al. 1999, Derocher et al. 2004) and decreases in sea ice are associated with lower seal productivity (Stirling and Øritsland 1995, Ferguson et al. 2005, Harwood et al. 2012b), potentially affecting the predator prey dynamics of these two species.

Reduced available sea ice limits opportunities for polar bears to hunt seals and as a result, polar bears may exploit alternative food sources, such as seabirds and waterfowl (Prop et al. 2015, Dey et al. 2016). However, terrestrial food sources may not provide adequate nutrition for polar bears compared to lipid-rich marine mammals prey (Hobson and Stirling 1997, Rode et al. 2015b). Whales may supplement polar bear diets, as they are a large source of protein and fats that may sustain many bears (Laidre et al. 2018). Polar bears may hunt belugas (*Delphinapterus leucas*), which may be scavenged or hunted from openings in the sea ice (Lowry et al. 1987a, Smith and Sjare 1990, Thiemann et al. 2008). In the southern Beaufort Sea, scavenging of bowhead whale (*Balaena mysticetus*) carcasses left after subsistence hunts has increased as the open water period becomes longer (Bentzen et al. 2007, Rogers et al. 2015, Atwood et al. 2016). Within the Beaufort Sea, climate variation is linked to changes in diet, with more bowhead whales consumed in years with longer open water periods (McKinney et al. 2017).

Shifts in diet can be documented by changes in an individual's nitrogen and carbon stable isotope values over time (Hobson and Clark 1992, Hobson et al. 1996) and they have been used to examine seasonal and annual diet variation in polar bears (Bentzen et al. 2007, Rogers et al. 2015, Tartu et al. 2016). However, these studies only examined short periods or parts of the population, which may not capture diet variation on a population basis.

This study examines nitrogen and carbon stable isotopes in guard hairs of northern (NB) and southern (SB) Beaufort Sea polar bears from 2003 to 2011. The objectives of this study are to: 1) quantify diet using stable isotope values, 2) relate stable isotope values to subpopulation demographics (age, sex, and reproductive status), sea ice dynamics, climate indices, and ringed seal ovulation rate, and 3) assess annual variation in diet using diet proportions and niche widths of NB and SB polar bears.

3.2 Methods

Study Area

The study area included the region of the Beaufort Sea north of the Yukon and Northwest Territories, Canada, as well as in the Amundsen Gulf (Fig. 3-1). Within the Beaufort Sea, sea ice begins to breakup in May in the Cape Bathurst polynya, an area of open water off Cape Bathurst at the mouth of the Amundsen Gulf (Barber and Hanesiak 2004, Galley et al. 2016). In September, the Beaufort Sea's open water season typically ends, and freeze-up begins (Galley et al. 2008, Galley et al. 2016). Sea ice is circulated through the Beaufort Sea by the Beaufort gyre (McLaren et al. 1987).

Two polar bear subpopulations occur in the Beaufort Sea. While the subpopulations can intermix, the northern Beaufort Sea polar bears primarily use the northeastern Beaufort Sea, and the southern Beaufort Sea bears use the southwest side eastward to Barrow, Alaska. When the sea breaks up, polar bears either migrate north following the sea ice retreat (Amstrup et al. 2000), or move to land (Gleason and Rode 2009, Pongracz and Derocher 2017).

Sampling

Samples were collected in late April to early May in 2004 to 2012. Polar bears were live-captured from helicopter, within 150km of the coast, using standard immobilization techniques (Stirling et al. 1989) as part of a monitoring study (Bromaghin et al. 2015). Guard hairs were shaved from the skin on the rump adjacent to the side of the tail using a scalpel, and all underfur was removed from the sample. Bears were aged using a vestigial premolar, and grouped as subadults (3 to 4 years) or adults (≥ 5 years) (Hensel and Sorensen 1980). Straight-line body length (SLEN, tip of nose to end of tail bone) and axillary girth (AXG, body circumference behind forelimbs) were measured to the nearest cm. Body mass (kg) was estimated following Thiemann et al. (2011), using SLEN and AXG measurements:

$$[1]\ M=0.00006039 \times AXG^{1.762} \times SLEN^{1.249}$$

A 2:1 chloroform:ethanol solution was used to wash the hair samples, followed by rinsing with deionized water. Samples were air dried and packed into tin capsules before carbon and nitrogen stable isotope analysis. The stable isotope ratios were expressed using the delta (δ) notation, measured in parts per thousand (‰):

$$[2]\ \delta X\ (‰)= \frac{R_{sample}-R_{standard}}{R_{standard}} \times 1000$$

where X represents the element's heavier isotope (^{15}N or ^{13}C), and the ratio of heavy to light nitrogen ($^{15}N/^{14}N$) or carbon ($^{13}C/^{12}C$) stable isotopes is represented by R for both the polar bear guard hair sample (R_{sample}) or the standard ($R_{standard}$; nitrogen – atmospheric nitrogen, carbon – Pee Dee Belemnite).

Data Analysis

Polar bear hair growth occurs between approximately May to October/November (Amstrup 2003). My sampling was completed before the moult and likely represents diet from the previous year (Rogers et al. 2015). To account for this in the models, all environmental variables were examined for the year of hair growth, rather than the sampling year. Bears were grouped by age (subadults and adults), and by class, a combination of sex and reproductive status (males, females, females with cubs up to two years old). As cub presence for females without cubs at the time of capture was unknown during hair growth, the females category could include solitary adult females, females that weaned two-year old cubs and did not breed, and females that may have lost offspring.

I used sea ice concentrations from Advanced Microwave Scanning Radiometer - Earth Observing System (AMSR-E) daily satellite images obtained from National Snow and Ice Data Center (Boulder, Colorado). I derived the following metrics for both the SB and NB: break-up date, freeze-up date, and open water duration. Break-up date was defined as the first day in which sea ice concentration dropped below 50%, 60%, 70%, 80%, or 90%, and freeze-up date was the first day in which sea ice concentration remained above these percentages. Multiple percentages were used to determine the cut-off that was the best fit in the models. Below 50% sea ice concentration, polar bears will typically abandon the sea ice and retreat to land (Stirling et al. 1999, Durner et al. 2006). I chose to examine the other percentages as foraging opportunities may vary with sea ice concentration. The open water period was the duration between break-up and freeze-up dates.

Three climate indices were included in the models: the Arctic Oscillation (AO), the Pacific Decadal Oscillation (PDO) and the Arctic Ocean Oscillation (AOO). The AO index is a pattern of sea level pressure anomalies in high latitudes (Rigor et al. 2002). The PDO is a pattern characterized by sea surface temperature anomalies, and fluctuates between warm and cool phases (Mantua and Hare 2002). Both the AO and the PDO affect the strength of the Beaufort Sea gyre, as well as sea ice thickness, retention, and transport within the Beaufort Sea (Rigor et al. 2002, Lindsay and Zhang 2005, Stroeve et al. 2011). The AOO focuses on wind-driven sea surface height circulation regimes in the Arctic, measuring both direction (cyclonic and anticyclonic) and strength of the circulation (Proshutinsky and Johnson 1997b, Proshutinsky et al. 2015). The AOO affects the amount of freshwater within the Beaufort Sea, as well as sea ice drift (Proshutinsky et al. 2015). I determined the annual, winter (January – March), spring (April – June), summer (July – September) and autumn (October – December) means for both the AO and PDO. AOO was used as a mean annual measure.

Air temperatures were obtained from Environment and Climate Change Canada weather stations in the Northwest Territories, Canada, at Sachs Harbour for the NB and Tuktoyaktuk for the SB (Fig. 3-1). Mean air temperature was determined for each station for winter, spring, summer, and autumn. Air temperature is correlated with sea surface temperatures, which influence sea ice and water conditions within the Beaufort Sea (Wood et al. 2013), and may influence food webs (Jarvela and Thorsteinson 1999).

Lastly, I included ringed seal ovulation rates (%) determined by Harwood et al. (2012b) for the eastern Amundsen Gulf, which describes ringed seal productivity in the Beaufort Sea. Ovulation rates were matched to the year of polar bear hair growth. Ovulation rate has been correlated to seal body condition and recruitment (Harwood et al. 2012b), as well as polar bear predation events (Pilfold et al. 2015).

Before modeling, I compared factors using Pearson correlation coefficients and excluded factors with a coefficient of >0.7 based on minimizing Akaike Information Criterion for small sample size (AIC_c) values. Only the temporal AO and PDO factor (annual, winter, spring, summer, or autumn), as well as percentage cut-offs (50%, 60%, 70%, 80%, or 90%) for break-up date and open water duration, that minimized AIC_c values were included in the candidate model. I determined models for both carbon and nitrogen stable isotopes with year as a random effect. Carbon stable isotopes were transformed to positive by adding 18.5 and modeled using a generalized linear mixed-effects model (GLMM) with a gamma distribution and a log link. Nitrogen models were modeled as a linear mixed-effects model (LMM). Stepwise model selection was used to determine the top models. Subpopulation, class, and age were retained in all models. Mass was $\log_{10}$ transformed. Model fit was assessed using AIC_c, and the most parsimonious model was selected for in cases with multiple models of $AIC_c < 2.00$. Residual plots were used to determine whether the models met assumptions. Levene's test for homogeneity of variance was used to determine whether the model met the assumption of homoskedasticity. The significance level was $\alpha \leq 0.05$.

Bayesian mixing models, with uninformative priors, were implemented using MixSIAR version 3.1 (Stock and Semmens 2016) to determine the proportion of prey species in the diet of SB and NB polar bears. I obtained ringed seal, bearded seal, bowhead whale and beluga muscle $\delta^{15}N$ and $\delta^{13}C$ means from the literature (Cherry et al. 2011), and used the discrimination factor of Hilderbrand et al. (1996) calculated for all tissues in American black bears (*U. americanus*). Only the main prey of polar bears were included in the model as other food sources likely do not significantly contribute to their stable isotope values (Bentzen et al. 2007, Hobson et al. 2009) and would reduce model determination.

Niche comparisons were completed using SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.3, which uses standard ellipses area as a Bayesian estimate (SEA_b) or corrected for sample size (SEA_c) to estimate niche width of groups (Jackson et al. 2011). I compared niche widths of polar bears in each sampling year. The model was run with 2×10^6 iterations. NB and SB polar bear subpopulation niche widths were compared using the Bayesian total area (TA) of the convex hull, as well as Bayesian estimates for $\delta^{13}C$ and $\delta^{15}N$ range (Layman et al. 2007, Jackson et al. 2011). The association between SEA_b and ringed seal ovulation rate was assessed using Spearman's rank correlation.

3.3 Results

Stable isotope models

Polar bear samples (n = 291) included individuals from the SB (n = 177) and NB (n = 114). The mass of NB bears ranged between 144 to 583 kg, while SB bears ranged from 123 to 647 kg (Table 3-1). Mass differed significantly between classes (two-way ANOVA: $F_{(4, 281)} = 172.14$, $p < 0.001$) but not subpopulations ($F_{(1, 281)} = 0.99$, $p = 0.32$), and their interaction was not significant ($F_{(4, 281)} = 0.72$, $p = 0.58$). For all bears within the study, the mean ± standard deviation for $\delta^{13}C$ values was -17.1 ± 0.45‰ (SB: -18.1 to -15.4‰; NB: -18.1 to -15.9‰), while $\delta^{15}N$ was 20.8 ± 0.67 (SB: 18.9 to 22.4‰; NB: 18.6 to 22.9‰).

The top $\delta^{13}C$ model included seven covariates: age, class, subpopulation, $\log_{10}$(mass), 80% break-up date, ringed seal ovulation rate, and autumn air temperature (Table 3-2 & 3-3). $\delta^{13}C$ decreased with increasing autumn air temperature, decreasing $\log_{10}$(mass), earlier 80% sea ice break-up dates, and higher ringed seal ovulation rates. The top $\delta^{15}N$ model included five covariates: age, class, subpopulation, summer AO, and 90% break-up date (Table 3-2 & 3-3). $\delta^{15}N$ decreased with later 90% break-up dates, and lower summer AO values. NB bears had higher $\delta^{13}C$ and lower $\delta^{15}N$ values than SB bears (Table 3-1 & 3-3). Both models indicated that age did not affect stable isotope values; however, class was significant in both models (Table 3-3). Females with cubs had lower $\delta^{13}C$ and $\delta^{15}N$ compared to the other two classes.

Diet estimation

Ringed seal made up the highest proportion of the diet for all bear classes and years (Fig. 3-2 & 3-3). In both subpopulations, polar bear classes showed similar diets (Fig. 3-2). Females consumed the highest proportion of ringed seal, followed by subadult males. Adult males had the lowest proportion of ringed seal, and higher proportions of bearded seal and beluga compared to other classes. Bearded seal was consumed the least by adult females with cubs. Adult females with cubs consumed more bowhead whale than the other classes, followed by subadult males. Diet proportions varied between years for both SB and NB subpopulations (Fig. 3-3). After 2004, there appears to be a trend in increasing ringed seal consumption for both subpopulations.

Niche comparison

Niche width, as represented by SEA_b (‰^{2}), varied between years and subpopulations (Fig. 3-4). In the NB, niche width peaked in 2004 and was smallest in 2011. In the SB, niche width also appeared to be highest in 2004 and decreased between 2005 to 2010; however, the credible intervals for 2006-2010 in the SB were more uncertain about this trend than for the NB. In the NB, SEA_b of 2004 and 2005 did not overlap with the 2011 niche (Fig. 3-4). SEA_c was similar to the SEA_b mode for all years in the NB; however, SEA_c estimated a larger niche width than SEA_b for 2006-2010 in the SB. SEA_b was negatively correlated with ringed seal ovulation rate ($r_s = -0.70$, $p = 0.023$).

Niche width, represented by total convex hull area, was larger in the SB than the NB. The Bayesian estimate of both $\delta^{13}C$ (NB: 0.56, SB: 1.16) and $\delta^{15}N$ (NB: 0.95, SB: 1.0) range was larger in the SB than the NB. The probability that $\delta^{15}N$ range was smaller in the NB was 0.64, while the probability that $\delta^{13}C$ range was smaller was 0.90.

3.4 Discussion

For both NB and SB polar bear subpopulations, variation in stable isotopes was linked to both intrinsic and extrinsic factors, of which the latter likely affect prey population dynamics and accessibility. Polar bear diet differed between subpopulations and years. Variation in niche widths between years for NB and SB subpopulations suggest that polar bears forage adaptively in response to availability, accessibility and distribution of resources.

Ringed seal ovulation rate was negatively correlated with polar bear $\delta^{13}C$, which suggests that foraging patterns were dependent upon juvenile ringed seal abundance. Polar bears prefer feeding upon fat, which is high in calories but depleted in δ^{13}C compared to muscle (Stirling and McEwan 1975, Best 1985, Cherry et al. 2011). However, in years with fewer available juvenile ringed seals, bears may be less selective in tissue consumption. Therefore, as ringed seal ovulation rate increases, polar bears may increase blubber consumption and reduce intake of protein and thereby deplete guard hair δ^{13}C. However, ringed seal ovulation rate did not significantly influence δ^{15}N values. Late sea ice break-ups reduce hunting success and increase predation risk by polar bears for the seals, which may result in low ringed seal ovulation rates (Harwood et al. 2012b). Delayed sea ice break-up increases the period that polar bears can hunt on the ice for seals (Stirling et al. 1999, Durner et al. 2006, Pilfold et al. 2015, Nguyen et al. 2017). Therefore, while juvenile ringed seal availability may be reduced in years with low ovulation rates, adult ringed seals may occur more frequently proportionately in the diet during years with later sea ice break-ups or low pup availability (Pilfold et al. 2015, Reimer et al. 2018). Increased sea ice availability may allow polar bears to continue foraging upon ringed seals, instead of lower trophic level prey species, such as bowhead whale carcasses.

Sea ice dynamics within the Beaufort Sea are linked to climate indices (Rigor et al. 2002, Lindsay and Zhang 2005, Stroeve et al. 2011, Proshutinsky et al. 2015), and sea ice availability is important for polar bear foraging. Neither the PDO nor the AOO climate indices were significant within either model; however, I found that high-index summer AOs were correlated with increases in δ^{15}N values. AO conditions are related to sea ice dynamics (Wang and Ikeda 2000, Rigor et al. 2002, Stroeve et al. 2011), and therefore, influence accessibility of ringed seals to polar bears. Low AO summer conditions result in reduced sea ice near the coast due to wind driving sea ice movement and transferring warm air over the ocean, while high-index summer AO conditions result in sea ice persistence along the coast (Rigor and Wallace 2004). Therefore, under a high AO summer, sea ice would be retained and provide a hunting platform for polar bears to prey on seals or beluga whales, increasing their δ^{15}N values. As a caveat, space use patterns of bears within this study were not available, and therefore, shifts in space use patterns may account for some variation within stable isotopes. For example, if bears switch to using pelagic areas, it is likely that their δ^{15}N will become enriched due to reduced bowhead whale and increased ringed seal within the diet.

The ability of polar bears to access and hunt seals is dependent upon the presence of sea ice (Stirling and Archibald 1977, Smith 1980, Thiemann et al. 2008). Air temperature is linked to sea ice availability and sea surface temperatures (Galbraith and Larouche 2011). High autumn air temperatures, which likely influence freeze-up dynamics, were correlated with low δ^{13}C values within polar bears. When air temperatures are higher, polar bears may remain north for longer periods, following the sea ice distribution (Amstrup et al. 2000), and feed upon a low δ^{13}C food web (Goericke and Fry 1994). Alternatively, bears may move to land earlier in warm conditions and feed upon bowhead whales (McKinney et al. 2017, Pongracz and Derocher 2017), which have blubber that is low in δ^{13}C (Cherry et al. 2011). Warm temperatures influence the date of sea ice break-up (Galbraith and Larouche 2011), which was also correlated to polar bear stable isotope values.

The date of sea ice break-up significantly influenced δ^{13}C and δ^{15}N values; however, the threshold sea ice concentration percentage that fit the model best varied between isotopes. As δ^{13}C typically indicates food sources and foraging habitat (Marshall et al. 2007), while δ^{15}N values provide information on trophic level (Minagawa and Wada 1984), the difference in thresholds suggests that sea ice concentration thresholds for break-up differentially affect aspects of polar bear foraging.

Later 90% sea ice concentration break-up dates correlated with decreasing δ^{15}N values, which may be due to reduced fasting or protein consumption. Severe fasting events may elevate δ^{15}N due to protein catabolism (Hobson et al. 1993, Hertz et al. 2015, Doi et al. 2017). SB polar bears prefer sea ice concentrations of 70-90%, which may be due to hunting success and avoidance of energetically expensive swimming events (Durner et al. 2004). As later sea ice break-up dates allow for increased seal hunting opportunities, starvation would be less likely for individuals, resulting in decreased δ^{15}N. In years with early break-ups, polar bears may increase terrestrial foraging, but alternative food sources (e.g. vegetation) do not provide sufficient nutrition to prevent starvation (Rode et al. 2015b). However, the relationship between stable isotope values and fasting varies based on factors that affect metabolic pathways, including body condition before fasting commences (Polischuk et al. 2001, Rode et al. 2016). In addition, increased protein consumption relative to lipids can elevate δ^{15}N values (Rode et al. 2016). Polar bears prefer fat as it is high in calories (Best 1985). Therefore, in years with later sea ice break-ups, polar bears may consume more fat and less protein when ringed seals are more accessible.

Increasing δ^{13}C was related to later 80% sea ice concentration break up dates, which likely result in a greater contribution of sympagic (associated with sea ice) sources to the polar bear diet. Brown et al. (2018) found that most carbon within a polar bear diet was from sympagic, rather than pelagic, sources. Sympagic algae are δ^{13}C-enriched compared to pelagic (Wang et al. 2014). Therefore, later sea ice break-ups may result in more δ^{13}C-enriched sympagic carbon, resulting in higher δ^{13}C within polar bears. In addition, polar bears in the Beaufort Sea move either northward to multiyear ice or towards land during break-up (Amstrup et al. 2000, Pongracz and Derocher 2017). Later sea ice break-up may result in bears remaining longer in the south over the continental shelf where ringed seal density is higher (Stirling et al. 1977, Frost et al. 2004), which may result in polar bears feeding in an area where the food web is enriched in δ^{13}C (Goericke and Fry 1994). As well, later sea ice break-ups correlate with reduced seal blubber thickness and productivity (Harwood et al. 2012b), which may result in bears having less δ^{13}C-depleted blubber to feed upon with each seal kill.

The model found that NB bears had lower δ^{13}C and higher δ^{15}N values than SB bears. This difference is consistent with the carbon isotope gradient at the base of the food chain, in which δ^{13}C decreases both eastward and northward (Saupe et al. 1989, Schell et al. 1989, Goericke and Fry 1994). As well, depleted δ^{13}C may indicate increased foraging within a pelagic food web for NB polar bears (Iken et al. 2005, St Louis et al. 2011). Benthic biomass decreases eastward within the Beaufort Sea (Dunton et al. 2005); therefore, NB bears may be exposed to a more pelagic food web. In addition, NB bears feed upon more ringed seals (Fig. 3-2), which are more abundant further north than bearded seals (Stirling et al. 1982) and were depleted in δ^{13}C compared to the other prey species within my study (Cherry et al. 2011). Therefore, carbon stable isotope patterns at the base of the food chain, as well as higher intake of ringed seals, may result in NB bears having depleted δ^{13}C relative to SB polar bears.

Lower δ^{15}N values in SB bears are likely due to SB bears remaining onshore for longer periods due to availability of bowhead whale carcasses (Atwood et al. 2016), which are leftover from subsistence hunts in Alaska and are depleted in δ^{15}N due to feeding on invertebrates (Lowry et al. 2005, Cherry et al. 2011). Fewer carcasses would be available to NB bears, as Canada has limited bowhead whale hunting (Moshenko et al. 2003). Carcasses from whales that perished naturally or are struck and lost may be available to polar bears of both subpopulations, although these carcasses are documented in low numbers (Clarke et al. 2014, DFO 2014). Whale carcasses may supplement the polar bear diet; however, carcasses are an unreliable food source and may not sustain populations in future years (Laidre et al. 2018). Higher δ^{15}N values may be due to increased nutritional stress within NB bears. However, fasting is more prevalent within SB bears (Rode et al. 2018), suggesting that scavenging on whale carcasses is the driver of depleted δ^{15}N.

While stable isotope values and diet proportions varied between the two subpopulations, the pattern of prey consumption by each class was similar. Consistent with research upon these subpopulations (Bentzen et al. 2007, Thiemann et al. 2008), ringed seal made up the largest proportion of the diet. NB bears consumed more ringed seal and beluga. Adult males had the lowest proportion of ringed seal, consuming more bearded seal and beluga than the other classes (Fig. 3-2). Adult male polar bears are larger than females and subadults, and the male's size allow them to prey upon larger species (Thiemann et al. 2007, Thiemann et al. 2008, Cherry et al. 2011). Contribution of bearded seal and beluga was similar to studies within the Beaufort Sea (Bentzen et al. 2007, Thiemann et al. 2008). Variation in bowhead whale consumption among the classes was low, ranging from 0.11 to 0.27, and was similar to other studies (Bentzen et al. 2007, Cherry et al. 2011). Adult males and solitary females consumed slightly less bowhead whale than other classes (Fig. 3-2). Hunting efficiency of subadults is lower than adults (Stirling and Latour 1978) so scavenging by subadults may be a more important source of energy. Females with cubs have high energy demands and scavenging on bowheads offers a reliable high caloric food source.

In both subpopulations, there was a trend of increasing ringed seal proportions within the diet from 2004 to 2011 (Fig. 3-3). High proportions of ringed seal within the diet may be due to a decline in availability of other food sources, but is likely due to an increase in the seal population. In the early 2000s, ringed seal body condition and productivity declined (Harwood et al. 2012b, Nguyen et al. 2017). Polar bear diets reflect this decline, with 2003 and 2004 having lower diet proportions of ringed seal relative to later years. After 2005, ringed seal ovulation rates and the number of seal pups in the subsistence harvest increased (Harwood et al. 2012b). Both the rebounding reproductive indices and polar bear diet proportions indicate ringed seal population growth after 2005.

Niche width estimates for both polar bear subpopulations were related to ringed seal availability. In years of ringed seal reproductive failure, polar bears may have larger niche widths, with a peak of niche width size in 2004. Polar bears are opportunistic foragers and utilize different prey sources in years of reduced ringed seal availability (Lunn and Stirling 1985, Derocher et al. 1993b). In years of ringed seal reproductive failure, polar bears may scavenge more or hunt more challenging prey (e.g. beluga). As well, polar bears may increase their predation on bearded seals when ringed seals are less abundant. Bearded seals may not be affected by the same environmental factors as ringed seals, and have maintained their productivity over time within the nearby Bering and Chukchi seas (Crawford et al. 2015). However, current population estimates and trends for seals within the Beaufort Sea are unknown.

By quantifying diet using stable isotope analysis, I demonstrate that polar bear diet is linked to large scale climatic indices that affect sea ice conditions, sea ice break-up, as well as other extrinsic and intrinsic factors. This complexity should be considered when interpreting polar bear diet from stable isotopes within a changing ecosystem. Polar bears forage in response to changes within their environment, with niche widths and diet proportions showing similar trends to prey population dynamics. Monitoring the impacts of climate change on Arctic marine ecosystems represents a significant challenge in light of forecasted declines in sea ice (Holland et al. 2006, Stroeve et al. 2007), and documenting the trends in diets of high trophic level species will likely be an important tool to investigate changes in ecosystem structure and function.

Table 3-1. Sample size (n) and mean guard hair δ^{13}C and δ^{15}N stable isotope values (‰) with standard deviations (SD) for each class in the southern (SB) and northern (NB) Beaufort Sea polar bear (*Ursus maritimus*) subpopulations.

Subpopulation	Group	n	Mass (mean ± SD)	δ^{13}C (mean ± SD)	δ^{15}N (mean ± SD)
SB	Adult female with cubs	22	188 ± 23	-17.4 ± 0.4	20.7 ± 0.4
	Adult female	61	200 ± 33	-17.1 ± 0.4	20.7 ± 0.6
	Adult male	56	367 ± 84	-17.0 ± 0.4	20.6 ± 0.6
	Subadult female	22	165 ± 29	-17.2 ± 0.4	20.6 ± 0.6
	Subadult male	16	244 ± 40	-17.2 ± 0.4	20.6 ± 0.5
	All	177	251 ± 97	-17.1 ± 0.4	20.6 ± 0.6
NB	Adult female with cubs	12	209 ± 15	-17.4 ± 0.5	20.3 ± 1.0
	Adult female	52	195 ± 29	-17.3 ± 0.4	21.1 ± 0.6
	Adult male	31	385 ± 79	-16.8 ± 0.4	21.0 ± 0.7
	Subadult female	10	166 ± 20	-17.4 ± 0.5	21.1 ± 0.7
	Subadult male	9	249 ± 86	-17.0 ± 0.4	20.8 ± 0.8
	All	114	250 ± 99	-17.2 ± 0.5	21.0 ± 0.7

Table 3-2. Model selection to assess biological and environmental variables affecting δ^{13}C and δ^{15}N of northern and southern Beaufort Sea polar bears (*Ursus maritimus*). Top ten models are shown, ranked by AIC$_c$. POPN = subpopulation, MASS = log of mass, BU = breakup, RS = ringed seal ovulation, AT = air temperature, AO = Arctic oscillation index, PDO = Pacific decadal oscillation index, AOO = Arctic ocean oscillation index. ":" denotes interaction between variables.

Response	Rank	Model	K	AIC$_c$	ΔAIC$_c$	AIC$_c$ Wt
δ^{13}C	1	AGE + CLASS + POPN + MASS + BU + RS + AT	11	272.03	0.00	0.41
	2	AGE + CLASS + POPN + MASS + RS + BU + AT + AT:BU	12	273.47	1.44	0.20
	3	AGE + CLASS + POPN + MASS + PDO + BU + RS + AT	12	273.58	1.55	0.19
	4	AGE + CLASS + POPN + MASS + AO + PDO + BU + RS + AT	13	275.76	3.73	0.06
	5	AGE + CLASS + POPN + MASS	8	276.61	4.58	0.04
	6	AGE + CLASS + POPN + MASS + BU + RS	10	277.41	5.37	0.03
	7	AGE + CLASS + POPN + MASS + BU	9	278.26	6.22	0.02
	8	AGE + CLASS + POPN + MASS + RS + AT	10	278.28	6.25	0.02
	9	AGE + CLASS + POPN + MASS + BU + AT	10	278.93	6.89	0.01
	10	AGE + CLASS + POPN + RS	9	280.86	8.83	0.01
δ^{15}N	1	AGE + CLASS + POPN + AO + BU	9	567.65	0.00	0.71
	2	AGE + CLASS + POPN + AO + PDO + BU	10	570.62	2.97	0.16

3	AGE + CLASS + POPN + AO + PDO + BU + RS	11	572.15	4.49	0.08
4	AGE + CLASS + POPN + RS	8	573.84	6.19	0.03
5	AGE + CLASS + POPN + BU	8	576.15	8.50	0.001
6	AGE + CLASS + POPN + AO + PDO + AOO + BU	12	578.34	10.69	0.001
7	AGE + CLASS + POPN + AT	8	580.38	12.73	0.001
8	AGE + CLASS + POPN + AO	8	580.86	13.21	<0.00
9	AGE + CLASS + POPN + AO + PDO + AOO + BU + RS	13	581.86	14.20	<0.00
10	AGE + CLASS + POPN + MASS	8	584.71	17.06	<0.00

Table 3-3. The estimate, standard error, t-value and P-value for coefficients included in the top model for carbon and nitrogen guard hair stable isotopes of polar bears (*Ursus maritimus*) from the northern (NB) and southern (SB) Beaufort Sea subpopulations, 2003-2011. AT = air temperature, AO = Arctic oscillation index.

Model	Variables	Estimate	Standard Error	t value	P value
Carbon	Intercept	-0.90	0.48	-1.89	0.060
	Age (Subadult)	0.034	0.05	-0.67	0.50
	Class (Female with cubs)	-0.14	0.055	-2.48	**0.013**
	Class (Male)	0.021	0.063	0.34	0.73
	Subpopulation (SB)	0.41	0.079	5.25	**<0.001**
	$\log_{10}$(mass)	0.23	0.090	2.54	**0.011**
	Break-up (80%)	0.088	0.030	2.96	**0.0031**
	Seal ovulation rate	-0.41	0.091	-4.53	**<0.001**
	Autumn AT	-0.19	0.031	-6.20	**<0.001**
Nitrogen	Intercept	23.75	0.50	47.94	**<0.001**
	Age	0.034	0.091	0.38	0.71
	Class (Female with cubs)	-0.29	0.12	-2.45	**0.015**
	Class (Male)	-0.15	0.076	1.95	0.053
	Subpopulation (SB)	-0.49	0.078	-6.24	**<0.001**
	Summer AO	1.15	0.25	4.50	**<0.001**
	Break-up (90%)	-0.017	0.0031	-5.59	**<0.001**

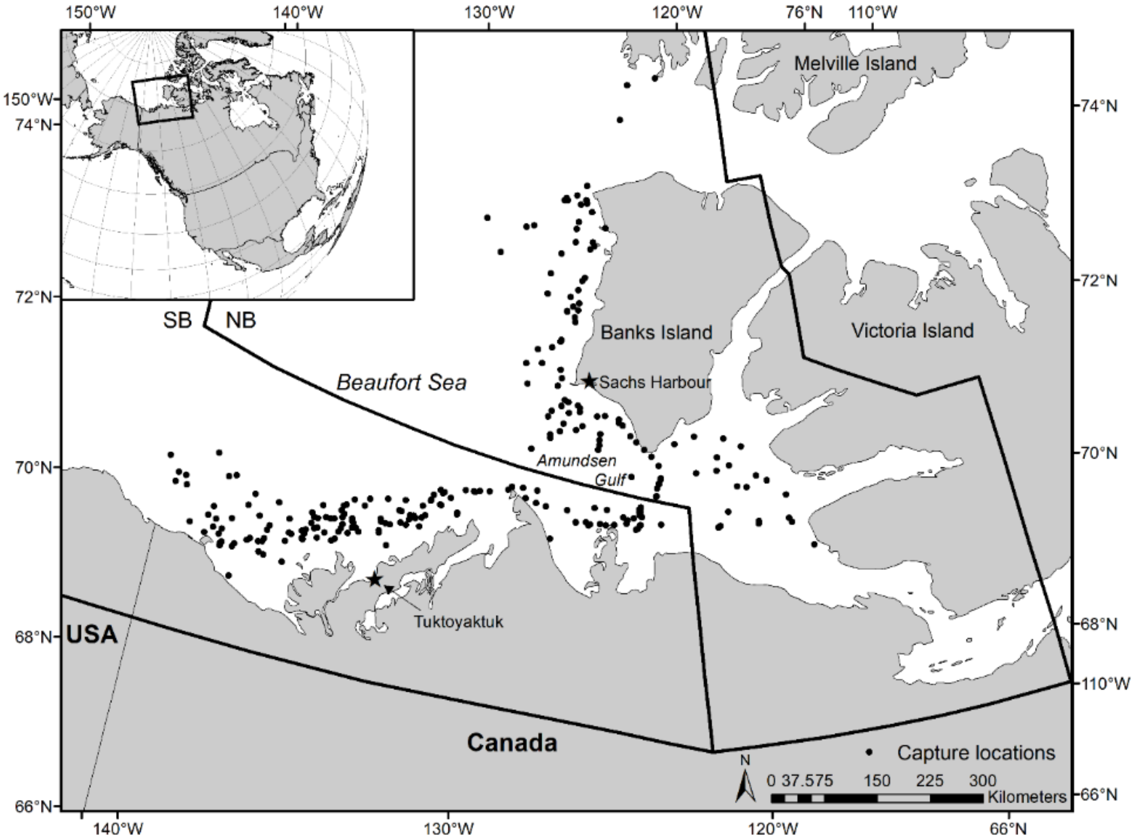

Figure 3-1. Beaufort Sea study area with sampling locations (filled circles; n = 291) of polar bears (*Ursus maritimus*) from the northern (NB) and southern (SB) Beaufort Sea subpopulations, sampled between 2004 to 2012. Subpopulations are based on IUCN 2015 subpopulation boundaries from Wiig et al. (2015). Climate stations at Sachs Harbour and Tuktoyaktuk are represented by stars

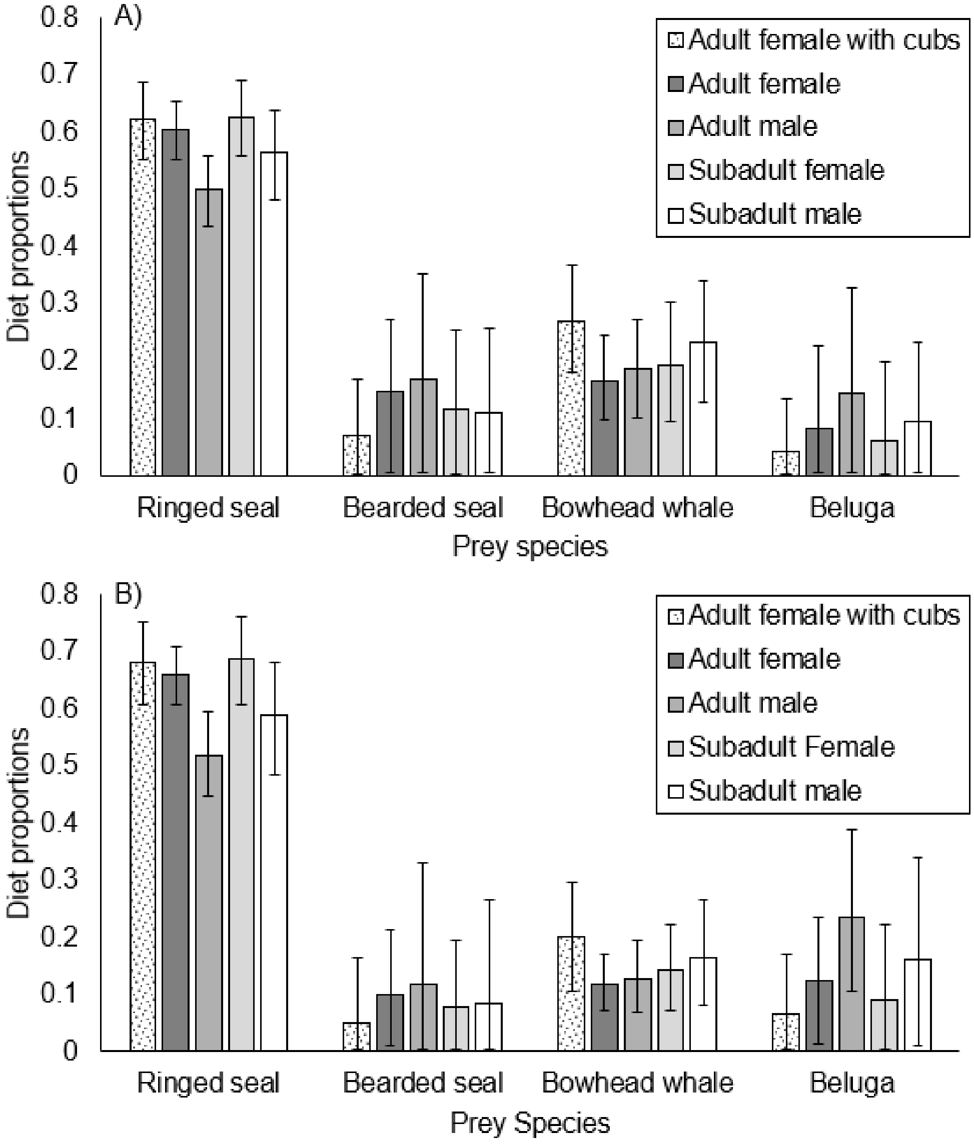

Figure 3-2. A) Diet proportions of southern Beaufort Sea adult females with cubs (n = 22), adult females (n = 61), adult males (n = 56), subadult females (n = 22) and subadult males (n = 16). B) Diet proportions of northern Beaufort Sea adult females with cubs (n = 12), adult females (n = 52), adult males (n = 31), subadult females (n = 10) and subadult males (n = 9). Diet proportions and 95% credible intervals were generated from MixSIAR. Prey sources included in the model include ringed seal (*Pusa hispida*), bearded seal (*Erignathus barbatus*), bowhead whale (*Balaena mysticetus*) and beluga whale (*Delphinapterus leucas*)

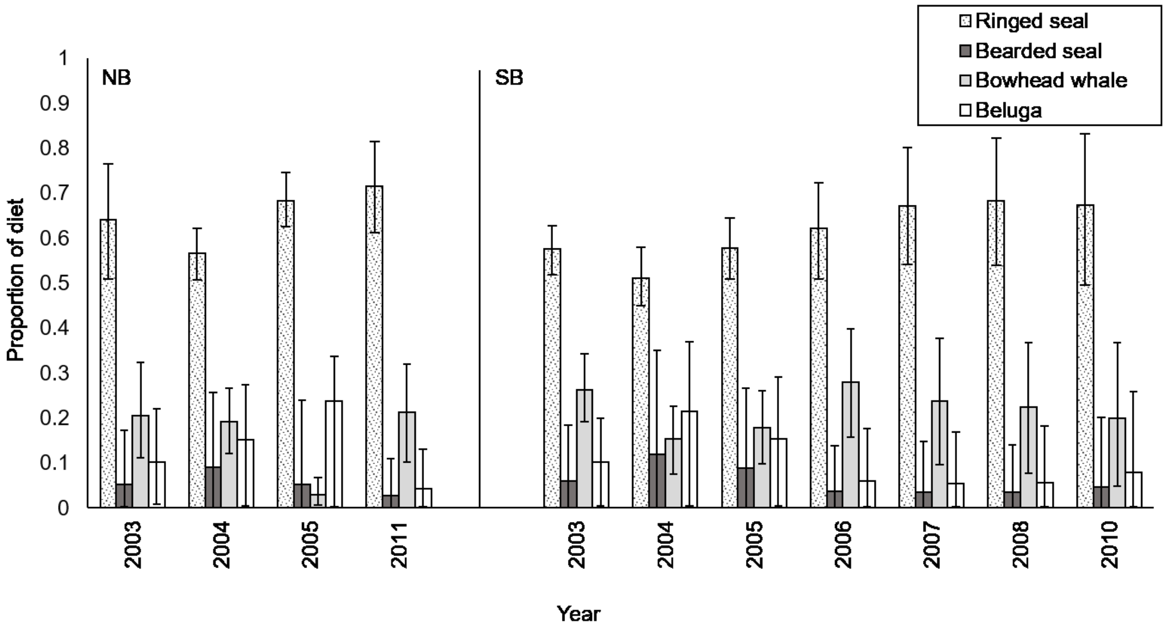

Figure 3-3. Temporal change in diet proportions, with 95% credible interval bands generated by MixSIAR, for polar bears (*Ursus maritimus*) from the northern (NB) and southern (SB) Beaufort Sea subpopulations from 2003-2011. Prey sources included in the model include ringed seal (*Pusa hispida*), bearded seal (*Erignathus barbatus*), bowhead whale (*Balaena mysticetus*) and beluga whale (*Delphinapterus leucas*)

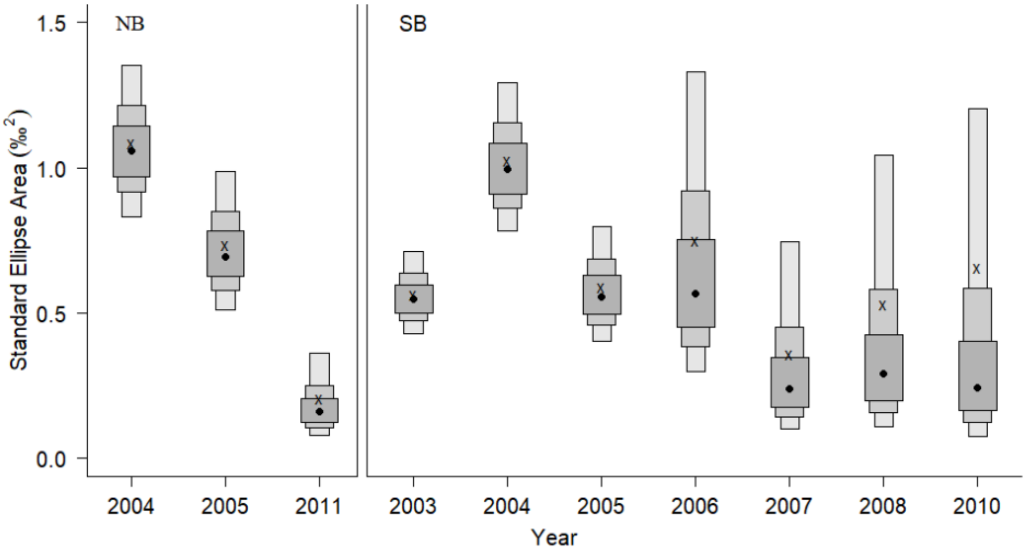

Figure 3-4. Density plot generated from guard hair δ^{13}C and δ^{15}N stable isotope values from northern (NB) and southern (SB) Beaufort Sea polar bears (*Ursus maritimus*) showing the standard ellipse area (‰^{2}) of the Bayesian estimate (SEA$_{b}$) for each sampling year. Black circles represent the mode for each group, and shaded boxes represent the credible intervals of 50%, 75% and 95%. Black x's represent the maximum likelihood estimated standard ellipse area (SEA$_{c}$)

CHAPTER 4 – LONG-TERM SPATIAL AND TEMPORAL VARIABILITY IN RINGED SEAL (*PUSA HISPIDA*) STABLE ISOTOPES IN THE BEAUFORT SEA

4.1 Introduction

Monitoring of Arctic marine ecosystems can be challenging, due to the region's remoteness, large scale, and complexity. However, identifying and assessing shifts in ecosystem dynamics is vital for management and conservation efforts, particularly as the Arctic undergoes large-scale reductions in sea ice due to climate change (Holland et al. 2006, Parkinson 2014, Stroeve et al. 2014, Galley et al. 2016). Reduced sea ice and warmer waters are resulting in changes to the distribution and abundance of species, which in turn alters community composition (Montevecchi and Myers 1996, Rose 2005, Carroll et al. 2013, Young and Ferguson 2014). These shifts in ecosystem dynamics may be monitored by tracking the diets of high trophic level species with stable isotopes because the composition of their diets reflect prey availability (McKinney et al. 2013, Braune et al. 2014, Yurkowski et al. 2016b).

Stable isotopes from assimilated resources are integrated over time into the consumer's tissues, creating a record of their diet (Ben-David and Flaherty 2012). Therefore, a consumer's tissues will have an average isotopic value for food consumed in a time-period, as determined by the tissue's turnover rate (McCutchan et al. 2003, Dalerum and Angerbjorn 2005). Changes in isotopic values over time can reveal changes in diet for an animal (Hobson et al. 1996), which may be due to shifts in foraging behavior or changes in the abundance and distribution of prey.

Marine predators, such as ringed seals (*Pusa hispida*), may play a potential role as indicator species, as their diets can offer insights into shifts in ecological communities. Ringed seals are a circumpolar, ice-dependent species (Reeves 1998), and can be found in both pack and shorefast ice (McLaren 1958). While ringed seals show high site fidelity in the winter and spring, they will range extensively in the late summer (Kelly et al. 2010). Ringed seals are an important prey source for polar bears (*Ursus maritimus*), and polar bear abundance is linked to that of seals (Stirling and Øritsland 1995, Pilfold et al. 2012). As opportunists, ringed seals feed on over 70 species across the Arctic, including fish (e.g. Arctic cod, *Boreogadus saida*; capelin, *Mallotus villosus*) and crustaceans (e.g. amphipods, euphausiids) (McLaren 1958, Lowry et al. 1978, Lowry et al. 1980, Dehn et al. 2007). Arctic marine ecosystems are inherently variable with large interannual variation in environmental conditions that affect marine productivity, as well as the abundance and distribution of species (Arrigo and van Dijken 2004, Rand and Logerwell 2011, Pickart et al. 2013). As ringed seals are generalists, shifts in prey availability will be reflected in their diets, and these variations in diet may be archived in stable isotopes of metabolically inactive tissues such as claws (Ferreira et al. 2011, Carroll et al. 2013).

Ringed seal claws can represent a stable isotope diet record up to approximately ten years, limited by claw wear at the claw's tip from the creation and maintenance of breathing holes (McLaren 1958, Smith and Stirling 1975). Ringed seal claws have alternating light and dark bands which are likely demarcated by moulting, or fasting and foraging cycles (Ferreira et al. 2011). Approximately one year of claw growth is represented by each pair of light and dark annuli, and therefore, can be used to roughly estimate the minimum age of the seal (McLaren 1958, Benjaminsen 1973). The light growth band is likely formed during the hyperphagic summer period, from May to winter (October to January), while the dark band is formed during the period of reduced dietary intake (Ferreira et al. 2011).

Ringed seal diets may reflect changes in abundance and distribution of their prey associated with changing ice conditions due to climate change. Loss of sea ice has been associated with an increase in the proportion of fish in ringed seal diet (e.g. Arctic cod) and reduced invertebrates (e.g. cephalopods) (Crawford et al. 2015). Stable isotopes revealed changes in ringed seal diet correlated with spring air temperatures (Young and Ferguson 2014) and amount of sea ice (Carroll et al. 2013). Warming of the oceans may reduce the number of benthic organisms, which can result in a marine system dominated by pelagic species (Grebmeier et al. 2006). This shift to a system dominated by pelagic species is supported by stable isotope evidence that suggests that ringed seals feed on more pelagic organisms during years with less sea ice (Carroll et al. 2013). Also, ringed seal diets may be affected by changes to fish assemblages, due to changes in water temperature displacing certain species of fish (Crawford et al. 2015). For example, ringed seals fed on more capelin and sand lance (*Ammodytes* sp.), which are shifting their range northwards due to rising ocean temperatures, during warmer years in the Hudson Bay (Rose 2005, Young and Ferguson 2014, Yurkowski et al. 2016b).

I hypothesized that ringed seal claw stable isotope values and niche widths would shift temporally in relation to changes in the climate, sea ice, and temperature, which may change the abundance and availability of prey species. As well, I expected that ringed seal stable isotopes would be related to seal body condition and productivity, as well as geographic location, which would indicate years of abundant resources and spatial distribution of prey. The objectives of this study are to examine $\delta^{13}C$ and $\delta^{15}N$ in ringed seal claw growth bands from 1964 to 2011 to: 1) assess spatial and temporal trends in diet for Beaufort Sea ringed seals, 2) relate stable isotopes to environmental variables and biological trends, and 3) evaluate changes in niche width of ringed seals over time.

4.2 Methods

Sample collection

The study area consisted of the Beaufort Sea and Amundsen Gulf, north of the Yukon and Northwest Territories, Canada (Fig 4-1). This region is almost completely covered by pack and land-fast sea ice in winter, and open water season only lasts a couple of months in the summer (Galley et al. 2008, Galley et al. 2012). The Cape Bathurst Polynya, a large stretch of open water, forms early in the year and is an important source of biological productivity within the area (Arrigo and van Dijken 2004). The

Beaufort Sea gyre drives a clockwise ocean circulation, which moves large quantities of sea ice and freshwater through the region (Proshutinsky et al. 2002). Within this system, increasing easterly winds and sea surface temperatures are resulting in loss of sea ice and changes to sea ice dynamics (Wood et al. 2013). These changes include earlier break-ups, delayed freeze-ups, thinner sea ice cover, and reduced old sea ice concentration (Galley et al. 2008, Frey et al. 2015, Galley et al. 2016).

Ringed seal claws were opportunistically collected from polar bear kill-sites within 150 km of shore while conducting polar bear monitoring studies in 1974 to 2011 (Fig 4-1). Front flippers and jaws were collected from the kill-sites, if available, for age and sex determination. Samples were frozen at -20°C until analysis. Observations of age class and sex of the seal were recorded if possible. Age of the seal was obtained or verified using canine teeth (Stewart et al. 1996), and growth bands on claws (McLaren 1958). Seals were classified as juven`iles (1-6 years) or adults (≥7 years). Species and sex of the samples were verified using DNA analysis by Wildlife Genetics International (Nelson, British Columbia). All sampling was approved by the University of Alberta Biosciences Animal Care and Use Committee.

Digit I or II claws were cut from front flippers, and excess tissue was cleaned off using a scalpel. Claws were soaked in water until the dermis and cuticle skin softened and loosened from the unguis. Claws are made of keratin, and therefore, are lipid-poor tissues (Newsome et al. 2010). However, to prevent ^{13}C depletion due to lipid contamination from handling, claws were cleaned using a 2:1 chloroform:methanol solution, and rinsed with distilled water. For each claw, the number of dark and light annuli were recorded, and the age of the claw estimated using claw growth bands by two observers. The year in which each claw band was grown was determined by subtracting the growth band's position along the claw (the number of growth bands from the base of the claw) from the year of collection from the kill-site. Claws were sectioned by light growth bands using a rotary tool, set to 14000 rev/min, that powdered the claw.

Stable isotope analysis

All nitrogen and carbon stable isotope analyses were completed by the Great Lakes Institute for Environmental Research facility at the University of Windsor. The delta (δ) notation, measured in parts per thousand (‰), is used to express the stable isotope ratios:

$$[1]\quad \delta X\,(‰) = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

where X is the heavy isotope of the element (^{15}N or ^{13}C), and R is the ratio of heavy to light isotopes for nitrogen ($^{15}N/^{14}N$) or carbon ($^{13}C/^{12}C$) for the ringed seal claw sample (R_{sample}) or the standard ($R_{standard}$; $\delta^{13}C$ values – Pee Dee Belemnite, $\delta^{15}N$ – atmospheric nitrogen).

Before analysis, I corrected all ringed seal $\delta^{13}C$ values for the Ocean Suess Effect. The Ocean Suess Effect refers to increasing amounts of ^{13}C-depleted anthropogenic CO_2 causing a depletion in $\delta^{13}C$ in dissolved inorganic carbon within oceans (Revelle and Suess 1957, Keeling 1979). The Ocean Suess

Effect correction factor was applied to the $\delta^{13}C$ of all seal claw samples, using the following formula from Misarti et al. (2009):

[2] Suess effect correction factor=$a^{b\times0.027}$

where the variable *a* is the maximum annual rate of decrease in $\delta^{13}C$, which is -0.014 in the North Pacific (Quay et al. 1992); the variable *b* is the year in which the claw band was grown, minus 1850 (i.e. the year the Industrial Revolution began).

Statistical analyses

Ringed seal stable isotopes were compared between individuals of known sex and age classes using one-way ANOVAs to determine whether the populations could be pooled. Unless a natal tip is present, claw annuli counts only provide the age of the claw, not the individual's age. Therefore, only the newest annulus' isotopes were compared between age classes, to avoid incorrect assignment of a seal's older annuli to an age class. Shapiro-Wilk tests and Levene's tests were used to assess normality and homogeneity of variances respectively, for both carbon and nitrogen isotopes.

Linear mixed-effects models, accounting for temporal pseudoreplication within an individual, were used to assess patterns in the claw growth band stable isotopes, with either $\delta^{13}C$ or $\delta^{15}N$ as the response variable (Crawley 2012). Stepwise model selection was completed using Akaike's Information Criterion for small sample sizes (AIC_c) to determine a top model. When $AIC_c < 2$, the most parsimonious model was selected. Significant variables from the climate index model were carried into the environmental and biological models. Before model selection, I assessed multicollinearity between explanatory variables using Pearson correlation coefficients and excluded factors within the same model that had coefficients > 0.7. Durbin-Watson tests were used to assess each model's residuals for temporal autocorrelation.

I first created a climate index model on the full dataset, which included samples from all years in the study (1964-2011). The climate index model included the Pacific Decadal Oscillation (PDO), the Arctic Oscillation (AO), and the Arctic Ocean Oscillation (AOO), all of which influence sea ice dynamics (Rigor et al. 2002, Lindsay and Zhang 2005, Stroeve et al. 2011, Proshutinsky et al. 2015). As the Beaufort Sea is highly seasonal, I provided both annual and seasonal means for both the PDO and AO. Seasons were classified as follows: spring (April – June), summer (July – Sept), Autumn (Oct – Dec) and winter (Jan – Mar). Before inclusion in the candidate model, I assessed which PDO and AO season to include based on minimizing AIC_c values.

The climate index model was followed by an environmental model which included sea ice and temperature. The model was restricted in time to between 1982-2011, which is when satellite data on sea ice concentration and sea surface temperature became available. As well, 1986 data was excluded due to lack of air temperature data from August – November. I determined annual sea ice break-up and freeze-up dates, as well as open water duration, using SSM/I satellite sea ice concentration data (National Snow and Ice Data Center, Boulder, Colorado, USA; http://nsidc.org/), clipped to the study area (Fig 4-1). Daily mean sea ice concentrations were calculated to determine break-up and freeze-up dates.

The break-up date was defined as the first ordinal date in which sea ice concentration was <50%, while the freeze-up date was the first ordinal date in which sea ice concentration remained above that threshold. Open water duration was the difference between the break-up and freeze-up dates. In addition, I determined the sea surface temperature (SST) and air temperatures for the Beaufort Sea. SSTs were obtained from the NOAA optimum interpolation SST v2 data set (NOAA/OAR/ESRL PSD, Boulder, Colorado, USA; https://www.esrl.noaa.gov/psd/) and resampled to match the SSM/I sea ice concentration resolution. The mean SSTs for summer were determined for the study area. Mean air temperatures for each season were calculated from the Environment and Climate Change Canada historical climate data set (http://climate.weather.gc.ca/). I used two climate stations (Sachs Harbour Climate: 71.99 N, 125.25 W; Sachs Harbour A: 71.99 N, 125.24 W), as not all years had data at each station. To determine whether the data from both stations could be pooled, I used a paired t-test and compared overlapping years.

I compared ringed seal productivity and body condition to stable isotope values in a biological model that was restricted between 1992 to 2006 due to limited availability of ringed seal biological measures within the literature. I included annual ovulation rates of adult females ringed seals and annual percentage of ringed seal pups in the harvest as measures of productivity from Harwood et al. (2012b). As well, I included a proportional width index (PWI), which is a measure of ringed seal teeth growth layers that is correlated with ringed seal productivity from Nguyen et al. (2017). A measure of the population's body condition, based on a length-mass-blubber depth index of adult female ringed seals, was included from Harwood et al. (2012b). I included body condition in the model as either low (below overall median) or high (above overall median), with the assumption that the sampled seals reflect the overall population's health within the Beaufort Sea.

To assess the effects of geographic location of the kill-site, $\delta^{13}C$ and $\delta^{15}N$ were compared to the ringed seal kill site's longitude, latitude, bathymetry, and distance from shore, using a linear mixed-effects regression. Ringed seals show inter-annual site fidelity during the spring and early summer, ranging only up to 2 km^2, and may remain in the same home range area for up to 10 months each year (Kelly et al. 2010). As the samples were collected in April and May, I assumed that the location of the kill-site would approximately reflect the area that the ringed seal most commonly uses during the formation of the light growth bands. As the dates of samples with geographic locations did not completely overlap the sampling periods for the climate, environmental or biological models, I analyzed the location data without carrying over terms from the previous models. The distance to shore was measured from the kill site to the closest coastline. Bathymetry at the kill site location was determined using the International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0 (Jakobsson et al. 2012).

To determine the niche width of ringed seals, I used SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.3 (Jackson et al. 2011). I compared ringed seal stable isotopes between the 1960s, 1970s, 1980s, 1990s, and 2000s. SIBER requires at least three samples per group for calculations. Claw growth bands are often not grown within the same decade, and therefore, a mean value cannot always be associated with a specific decade of growth. As well, variation in stable isotopes is expected to be higher between individuals than within an individual, and pseudoreplication is not accounted for within SIBER. Therefore, I randomly selected one band from each ringed seal claw to represent that individual's stable isotopes, and grouped the samples into decades based on the year that growth band was assumed to be produced. Within SIBER, niche width is represented by standard ellipse area (SEA), and several measures of niche width are calculated, including SEA, SEA_c (SEA corrected for sample size), SEA_b (Bayesian estimate of SEA), and total area of the convex hull.

4.3 Results

In total, 94 ringed seal (24 female, 26 male, and 44 unknown) claws were collected, and a total of 714 growth bands analyzed for stable isotopes, ranging from 1964 to 2011 (Fig 4-2). The oldest seal in the study, based on tooth age, was 41 years. The maximum number of light growth bands counted on a ringed seal claw was 12, with an average claw age of 7.8 years. Most samples were taken from adult seals (25 juveniles, 68 adults), based on claw and tooth age. No difference in carbon and nitrogen stable isotopes was found between known sexes or age classes ($p > 0.05$); therefore, samples were pooled for analyses. When the population was pooled, the mean Suess-corrected $\delta^{13}C$ was -17.9 ± 0.6 (range: -20.15 to -15.63), while $\delta^{15}N$ was 17.6 ± 1.0 (range: 14.57 to 20.24).

The climate model included 94 ringed seals (714 growth bands). The variables included in the $\delta^{13}C$ climate model included autumn PDO, summer AO and AOO, while the $\delta^{15}N$ climate model included autumn PDO, summer AO and AOO (Table 4-1 and 4-6). The top $\delta^{13}C$ climate model only included AOO (Table 4-3 and 4-4), with $\delta^{13}C$ increasing with cyclonic circulation regimes. AIC_c indicated that the best fitting $\delta^{15}N$ climate model was the null.

The environmental model included 74 seals (474 growth bands). Air temperatures were not significantly different between the two climate stations ($t_{(13)} = -1.60$, $P = 0.13$) so I pooled the stations. The $\delta^{13}C$ environmental model included summer SST, spring air temperature, and AOO (Table 4-2 and 4-3). The top $\delta^{13}C$ environmental model supported by AIC_c included only AOO (Table 4-3 and 4-4). The $\delta^{15}N$ environmental model included summer SST and summer air temperature. The top $\delta^{15}N$ environmental model included only summer SST, with increasing $\delta^{15}N$ at lower summer SSTs (Table 4-5).

The biological model included 39 seals (337 growth bands). The $\delta^{13}C$ biological model included PWI, ovulation, body condition, percentage of pups in the harvest and AOO. Only PWI and AOO remained in the top $\delta^{13}C$ biological model (Table 4-3 and 4-4). AOO did not significantly influence the $\delta^{13}C$ biological model; however, it was left in the model due to its previous significance in the prior models. $\delta^{13}C$ increased with an increasing PWI. The $\delta^{15}N$ biological model included PWI, ovulation, body condition, percentage of pups in the harvest and summer SST. The top $\delta^{15}N$ biological model included percentage of pups in the harvest, and summer SST (Table 4-3 and 4-5). $\delta^{15}N$ increased with higher percentages of pups in the harvest.

The geographic location model included 65 seals (534 growth bands). Longitude of the ringed seal kill site was related to δ^{15}N, and weakly to δ^{13}C (Table 4-3 and 4-6). Eastward longitudes had decreasing δ^{13}C (Fig 4-3) and increasing δ^{15}N. As well, δ^{15}N was related to the distance of the kill site from shore. Ringed seals killed further offshore had higher δ^{15}N than nearshore seals (Fig 4-3). Bathymetry was not related to either δ^{13}C or δ^{15}N.

Total area of the convex hull, SEA, and SEA_c were largest in the 2000s, and smallest in the 1960s. SEA_b varied between decades for ringed seals in the Beaufort Sea (Fig 4-4). Niche width was smallest in the 1960s, and largest in the 2000s. Between the 1970s to 1990s, SEA_b remained relatively consistent, with a possible slight trend in decreasing niche width into the 1990s. The niche widths of the 2000s and 1960s did not overlap; all other decades overlapped (Fig 4-4).

4.4 Discussion

Assessing diet of species is challenging and costly for large, remote regions, such as the Arctic. Stable isotopes in metabolically inert tissues, such as claws, can provide extensive information on diet. A long-term record of stable isotopes may describe changes affected by environmental conditions within the ecosystem to community structure and composition. However, as found in my study, many factors must be considered when inferring dietary shifts from isotopic values.

Circulation regimes within the Arctic influence primary producer dynamics and organic matter composition, which may be reflected in ringed seal δ^{13}C. Within the Beaufort Sea, cyclonic circulation regimes consist of cyclonic sea ice drift, warm and humid temperatures, increased ice melt, and increased sea ice and freshwater export (Proshutinsky and Johnson 1997a, Proshutinsky et al. 1999, Proshutinsky et al. 2002). Nguyen et al. (2017) linked increased ringed seal productivity to a negative AOO, and suggested this relationship was caused by reduced sea ice and warmer waters increasing primary productivity. During phytoplankton blooms, ^{13}C discrimination reduces due to rapid carbon fixation (Goering et al. 1990, Arrigo and van Dijken 2004). In addition, negative AOOs involve the release of low salinity water from the Beaufort Sea (Proshutinsky et al. 2002), which may increase δ^{13}C of dissolved organic carbon due to higher salinity (Gillikin et al. 2006). While δ^{13}C of particulate organic matter increases with sea surface temperature (Goericke and Fry 1994), I did not find that sea surface temperature was related to ringed seal δ^{13}C. Overall, increased uptake of enriched δ^{13}C by primary producers may result in elevated δ^{13}C in ringed seals.

Cyclonic circulation regimes may favour pelagic-dominated communities, which are characterized by depleted δ^{13}C. Conversely, my study found that ringed seals had enriched δ^{13}C in negative AOO years. Bluhm and Gradinger (2008) predicted that reduced sea ice would result in shifts towards a pelagic-dominated community. However, this shift may occur gradually over several years (Dunton et al. 2005). Carroll et al. (2013) attributed changes in stable isotopes within ringed and bearded seals in the Chukchi and Bering seas to be from the shift to a pelagic-dominated community. The Beaufort Sea has lower benthic biomass than the Chukchi or Bering sea (Dunton et al. 2005); therefore, the change to a pelagic-dominated system may not be as drastic. However, reduced sea ice may result in increased productivity and biomass of epontic communities, as thinner sea ice allows more light penetration (Arrigo et al. 2012). These blooms would reduce ^{13}C discrimination, resulting in enriched $\delta^{13}C$ through the food web (Goering et al. 1990, Arrigo and van Dijken 2004). As well, ice particulate organic matter is enriched in $\delta^{13}C$ compared to suspended matter (France et al. 1998). A variety of ecological and environmental factors may influence carbon stable isotopes, which may confound interpretations of diet. Therefore, I propose that future studies compare ringed seal stable isotopes to benthic biomass over time to clarify the relationship.

Sea surface temperatures described ringed seal $\delta^{15}N$ better than large-scale climate circulation patterns, with $\delta^{15}N$ in claw growth bands depleted at high SSTs. Nitrogen is typically indicative of the individual's trophic level (Minagawa and Wada 1984), suggesting that ringed seals consume lower trophic level foods (e.g. invertebrates) at high SSTs. The importance of prey species within the ringed seal diet may switch as temperature shifts alter community composition. In warm years, low trophic level prey species (e.g. zooplankton) proliferate and are more abundant for consumption (Coyle and Pinchuk 2003). The population growth of high trophic level species (e.g. fish) may lag in response to the increased populations of low trophic level species (Krebs et al. 2001). As well, certain species within the Beaufort Sea (e.g. *Boreogadus saida*) show preference to colder waters (Logerwell et al. 2011), and therefore, may be more dominant within the ringed seal diet in cold years.

The relationship between $\delta^{15}N$ and SST does support use of pelagic food webs. Pelagic organisms are often depleted in $\delta^{15}N$ relative to benthic; however, benthic organisms are highly variable in $\delta^{15}N$ (Iken et al. 2005). Increased temperatures may also support the expansion of species ranges into the Beaufort Sea. For example, walleye pollock (*Gadus chalcogrammus*) have extended their range into the Beaufort Sea since the 1970s (Frost and Lowry 1983, Rand and Logerwell 2011). In addition, temperatures may be affecting $\delta^{15}N$ trophic fractionation. In dietary studies with European sea bass (*Dicentrarchus labrax*), high temperatures reduced $\delta^{15}N$ trophic fractionation (Barnes et al. 2007). Within a non-controlled environment, fractionation rates may be variable due to confounding factors; however, lower fractionation may play a role in depleted $\delta^{15}N$ in ringed seals during high SSTs.

While environmental conditions influenced diet, sex and age were not related to an individual's stable isotope value indicating similar foraging habitats and prey between demographics. Resource partitioning may exist between demographic groups to reduce competition for available food sources (Field et al. 2005, Newland et al. 2009) but may not always be detected by stable isotopes. As a caveat within this study, not all individuals were of a known sex and only the age class of the seal was assessed as claw growth bands do not provide an exact age if the natal tip is not present. Ringed seals are opportunistic hunters with a highly variable diet (Lowry et al. 1978, Lowry et al. 1980, Dehn et al. 2007), and variation in foraging between demographic groups occurs based on stable isotopes (Dehn et al. 2005, Young et al. 2010, Young and Ferguson 2014, Yurkowski et al. 2016b) and stomach content analysis (Lowry et al. 1980, Dehn et al. 2007). Based on stomach contents, males consume more zooplankton and less fish than females, and fish consumption increases with age (Lowry et al. 1980, Dehn et al. 2007, Yurkowski et al. 2016b). However, differences in foraging between sexes and ages detected by stomach content analyses were not reflected in stable isotopes within the Canadian Beaufort Sea (Dehn et al. 2007). As well, resource partitioning within ringed seals appears to be highly variable by geographic location (Yurkowski et al. 2016a, Yurkowski et al. 2016b), and may not have occurred within my study area. While no support was found for different foraging strategies between demographic groups, trends in stable isotope values were related to ringed seal population dynamics.

Ringed seal stable isotopes were linked to seal population productivity, with $\delta^{13}C$ increasing at high PWIs and $\delta^{15}N$ increasing with percentage of pups in the harvest. Ringed seal PWIs are related to population productivity (Nguyen et al. 2017), and may represent a measure of somatic growth (Wittmann et al. 2016). During fasting, $\delta^{13}C$ becomes depleted due to the use of ^{13}C-depleted lipids (Polischuk et al. 2001, Williams et al. 2007), and therefore, high $\delta^{13}C$ may be related to increased body condition or growth. Body condition from Harwood et al. (2012b) was not related to $\delta^{13}C$ or $\delta^{15}N$; however, their study focused only on the Amundsen Gulf which may not represent the Beaufort Sea as assumed by my study. As claws were collected from polar bear kill sites, most of the ringed seal blubber was typically consumed and could not be measured to determine seal body condition. The relationship between stable isotopes and ringed seal body condition could be determined using captive seals; this information would be useful in assessing health of wild ringed seal populations.

Enriched $\delta^{15}N$ during years with high percentages of pups in the harvest could indicate foraging at a higher trophic level. Ringed seal diets have shifted to include more fish within the Bering and Chukchi sea, which is linked to healthier and larger individuals (Crawford et al. 2015). Harwood et al. (2012b) found that ovulation rates increased with body condition, which may result in more pups in the harvest. However, elevated $\delta^{15}N$ is also linked to nutritional stress, as ^{14}N is excreted (Hobson et al. 1993), and in seals, lactation can elevate $\delta^{15}N$ (Kurle and Worthy 2001, Sinisalo et al. 2007). Ringed seal pups are highly active and energetically expensive to raise (Lydersen 1995). In my study, no difference in stable isotopes between sexes was found; however, not all samples were of a known sex. Nguyen et al. (2017) found evidence for similar energy budgets between sexes based on PWIs. Therefore, it is likely that elevated $\delta^{15}N$ during years with a higher percentage of pups is due to foraging at a higher trophic level, rather than nutritional stress from raising offspring.

Interpretations of diet may be influenced by the geographic location at which the individual forages. Individuals with kill sites located further east had depleted $\delta^{13}C$ and enriched $\delta^{15}N$. The longitudinal pattern in ringed seal $\delta^{13}C$ likely reflects the trend of $\delta^{13}C$ depletion eastward from the Bering to Beaufort Sea in zooplankton (Saupe et al. 1989, Schell et al. 1998). Previously, this trend has been recorded in migrating bowhead whales (*Balaena mysticetus*) from the Bering to Beaufort Sea (Schell et al. 1989). As well, Dehn et al. (Dehn et al. 2007) found this trend of $\delta^{13}C$ depletion in ringed seals from Barrow, USA to Holman, Canada. A trend in $\delta^{15}N$ depletion eastward within the Beaufort Sea has also been found in zooplankton (Schell et al. 1998), but this was not reflected in ringed seal δ^{15}N which became enriched eastward. Ringed seals may be feeding at a higher trophic level in the eastern Beaufort Sea.

The source of nitrogen within the food web may have resulted in reduced ringed seal δ^{15}N close to shore. Nearshore organisms may have depleted δ^{15}N due to the source of nitrogen being terrestrially derived (Dunton et al. 2012). Coastal erosion and rivers (e.g. Mackenzie River) that empty into the Beaufort Sea are a large source of terrestrially derived organic matter, which is then integrated into nearshore food webs (Parsons et al. 1989, Naidu et al. 2000). Fish inhabiting estuarine waters as compared to coastal waters of the Beaufort Sea were depleted in δ^{15}N (Dunton et al. 2012), and this depletion of δ^{15}N may be reflected in ringed seals. Therefore, both source of organic matter and geographic location of the sample are important to consider when interpreting diet.

Niche width increased from the 1960s to 2000s, indicating that ringed seal diet has diversified. A shift in community composition within Arctic ecosystems has occurred (Frost and Lowry 1983, Jarvela and Thorsteinson 1999, Rand and Logerwell 2011), which may explain the increasing ringed seal niche width. The number of macrobenthic species within the Bering Sea greatly exceeds the Beaufort Sea (Sirenko 2001, Grebmeier et al. 2006), and some of these species may expand their ranges as northern waters warm and sea ice recedes. Some species, such as Bering flounder (*Hippoglossoides robustus*), have already expanded their distributions northward into the Beaufort Sea from the 1970s (Rand and Logerwell 2011). As a result, the prey sources available to ringed seals may have increased over time. The proportion of forage fish (i.e. small pelagic fish) have increased within the ringed seal diet, which resulted in larger niche widths (Yurkowski et al. 2016b, Yurkowski et al. 2018). As well, ringed seals exhibit home range fidelity, but will migrate between the Beaufort and Chukchi Seas during late summer (Kelly et al. 2010, Harwood et al. 2012a). A possible explanation for the trend in increasing niche width is that ringed seals are undergoing further migrations into the Chukchi Sea, and therefore are being exposed to a larger number of prey species.

Overall, ringed seal stable isotopes are influenced by a variety of factors that must be considered when making interpretations about ecosystem changes. Age and sex of the individual were not related to stable isotope value. However, demographics, as well as geographic location and seal body condition, should be considered as possible confounding factors for diet interpretations in future studies. While the Beaufort Sea ecosystem may be shifting towards a pelagic-dominated community (Bluhm and Gradinger 2008), my study found conflicting evidence for this within the ringed seal diet. However, my study provides evidence that ringed seal diets have diversified since the 1960s. Warming temperatures and sea ice loss within the Arctic may result in changes to community composition and structure (Comeau et al. 2011, Post et al. 2013, Wood et al. 2013, Galley et al. 2016). Sea ice loss is expected to continue in the future (Wang and Overland 2009, Overland and Wang 2013, Gascard et al. 2017). Due to their opportunistic diet, ringed seals may be able to adapt to changes within the ecosystem, but this may not be the case for other Arctic species. Therefore, it is important to continue monitoring stable isotopes of ringed seals, as their diet provides an important archive of ecological changes within the Arctic food web.

Table 4-1. Selection of seasonal (Annual, Winter: Jan-Mar, Spring: April-June, Summer: July-Sept, Autumn: Oct-Dec) climate index and air temperature metrics for inclusion into climate and environmental models, respectively, with a response variable of either $\delta^{13}C$ or $\delta^{15}N$ of ringed seal claw growth bands from 1964 to 2011 in the Beaufort Sea. The seasonal metric that minimized AIC_c (bolded) was used within the candidate climate index models.

		AIC_c		
Response Variable	Season	Pacific Decadal Oscillation	Arctic Oscillation	Air Temperature
$\delta^{13}C$	Annual	764.0	654.8	488.7
	Winter	765.6	655.7	488.8
	Spring	767.0	654.4	**487.8**
	Summer	766.1	**652.4**	489.4
	Autumn	**762.0**	656.3	488.8
$\delta^{15}N$	Annual	1084.7	967.0	601.1
	Winter	1087.4	968.7	601.4
	Spring	1088.3	967.6	601.4
	Summer	1085.8	**964.0**	**600.1**
	Autumn	**1083.1**	969.1	601.3

Table 4-2. Selection of correlated environmental metrics, based on minimizing AIC_c, modeled against $\delta^{13}C$ or $\delta^{15}N$ of ringed seal claw growth bands from 1964 to 2011 in the Beaufort Sea. Top terms included within environmental model are bolded. 50% BREAK = first day sea ice concentration <50%, 50% FREEZE = first day sea ice concentration remains >50%, OPEN WATER = duration between 50% BREAK and 50% FREEZE, SUMMER SST = summer (July-Sept) sea surface temperature.

Response Variable	Sea Ice Metric	AIC_c
$\delta^{13}C$	50% BREAK	491.4
	50% FREEZE	492.7
	OPEN WATER	493.6
	SUMMER SST	**486.5**
$\delta^{15}N$	50% BREAK	597.9
	50% FREEZE	600.7
	OPEN WATER	597.0
	SUMMER SST	**595.3**

Table 4-3. Top five climate, environmental, biological and geographic location models based on AIC$_c$ scores for $\delta^{13}C$ and $\delta^{15}N$ of ringed seal claw growth bands. AOO = Arctic Ocean Oscillation, AO = Arctic Oscillation, PDO = Pacific Decadal Oscillation, SST = sea surface temperature, AT = air temperature, PWI = proportional width index, OVULATION = ovulation rate, % PUPS = percentage of pups in harvest, CONDITION = body condition, SHORE = distance to shore (km), and BATHY = bathymetry (m). ':' denotes interaction.

Model	Response	Rank	Model	K	AIC$_c$	ΔAIC$_c$	AICc Wt
Climate	$\delta^{13}C$	1	AOO	7	646.13	0.00	0.70
		2	SUMMER AO	8	649.69	3.57	0.12
		3	AUTUMN PDO + AOO	8	650.57	4.44	0.075
		4	NULL	6	650.72	4.59	0.070
		5	AUTUMN PDO	7	653.83	7.70	0.015
	$\delta^{15}N$	1	NULL	6	963.52	0.00	0.45
		2	SUMMER AO	7	963.98	0.46	0.36
		3	AUTUMN PDO + SUMMER AO	8	968.03	4.50	0.048
		4	AOO	7	968.21	4.69	0.044
		5	AUTUMN PDO	7	968.22	4.70	0.043
Environmental	$\delta^{13}C$	1	AOO	7	483.25	0.00	0.48
		2	NULL	6	485.43	2.18	0.26
		3	SUMMER SST + AOO	8	486.81	3.56	0.081
		4	SPRING AT + AOO	8	487.81	4.56	0.049
		5	SUMMER SST	7	488.08	4.83	0.043
	$\delta^{15}N$	1	SUMMER SST	7	595.25	0.00	0.81

		2	SUMMER AT	7	600.08	4.83	0.073
		3	NULL	8	600.73	5.48	0.053
		4	SUMMER SST:SUMMER AT	7	601.27	6.02	0.040
		5	SUMMER SST + SUMMER AT	7	602.62	7.37	0.020
Biological	$\delta^{13}C$	1	PWI + AOO	8	329.25	0.00	0.35
		2	PWI + % PUPS + AOO	9	330.16	0.91	0.22
		3	PWI + OVULATION + AOO	9	330.53	1.29	0.18
		4	PWI + OVULATION + % PUPS + AOO	10	331.39	2.14	0.12
		5	PWI + CONDITION + AOO	9	333.59	4.35	0.039
	$\delta^{15}N$	1	% PUPS + SUMMER SST	8	402.58	0.00	0.58
		2	SUMMER SST	7	405.50	2.92	0.14
		3	% PUPS + OVULATION + SUMMER SST	9	406.27	3.70	0.092
		4	% PUPS + PWI + CONDITION + SUMMER SST	10	406.35	3.78	0.088
		5	OVULATION + SUMMER SST	8	408.05	5.48	0.038
Location	$\delta^{13}C$	1	LONGITUDE	4	141.57	0.00	0.92
		2	LATITUDE + LONGITUDE	5	146.43	4.86	0.081
		3	LONGITUDE + SHORE	5	153.58	12.01	0.0020
		4	LATITUDE + SHORE	5	153.78	12.21	0.0020
		5	LATITUDE + LONGITUDE + SHORE	6	158.16	16.59	<0.00
	$\delta^{15}N$	1	SHORE + LONGITUDE	5	205.10	0.00	0.99
		2	SHORE + BATHY	5	216.23	11.13	0.004

	3	BATHY + LONGITUDE + LATITUDE	6	217.11	12.01	0.002
	4	SHORE + BATHY + LONGITUDE	6	220.38	15.27	<0.00
	5	SHORE + BATHY + LATITUDE	6	220.88	15.78	<0.00

Table 4-4. The estimate, standard error (SE), t-value, and P-value for variables of the top climate, environmental and biological model influencing Suess-corrected carbon stable isotopes of ringed seal claw annuli in the Beaufort Sea from 1964 to 2011.

Model	Coefficient	Estimate	SE	t-value	P-value
Climate	Intercept	-18.11	0.08	-237.23	<0.001
	AOO (CCR)	0.31	0.10	3.11	0.0041
Environmental	Intercept	-18.29	0.12	-152.20	<0.001
	AOO (CCR)	0.43	0.20	2.18	0.044
Biological	Intercept	-21.79	1.50	-14.49	<0.001
	PWI	12.24	5.21	2.35	0.037
	AOO (CCR)	-0.23	0.15	-1.50	0.16

Table 4-5. The estimate, standard error (SE), t-value and P-value for variables of the top environmental and biological models influencing nitrogen stable isotopes of ringed seal claw annuli in the Beaufort Sea from 1964 to 2011. The climate model estimates are not presented, as the top model was the null model.

Model	Coefficient	Estimate	SE	t-value	P-value
Environmental	Intercept	17.90	0.15	129.31	<0.001
	Summer SST	-0.11	0.043	-2.66	0.025
Biological	Intercept	17.58	0.16	112.14	<0.001
	%Pups	0.39	0.13	2.99	0.014
	Summer SST	-0.19	0.036	-5.24	0.00030

Table 4-6. The estimate, standard error (SE), t-value and P-value for variables in the models examining the effect of location on carbon and nitrogen stable isotopes of ringed seal claw annuli in the Beaufort Sea.

Model	Coefficient	Estimate	SE	t-value	P-value
$\delta^{13}C$	Intercept	-21.86	1.69	-12.96	<0.001
	Longitude	-0.026	0.013	-2.01	0.05
$\delta^{15}N$	Intercept	22.57	2.64	8.55	<0.001
	Distance from Shore (km)	0.0011	0.0046	2.45	0.017
	Longitude	0.044	0.020	2.13	0.037

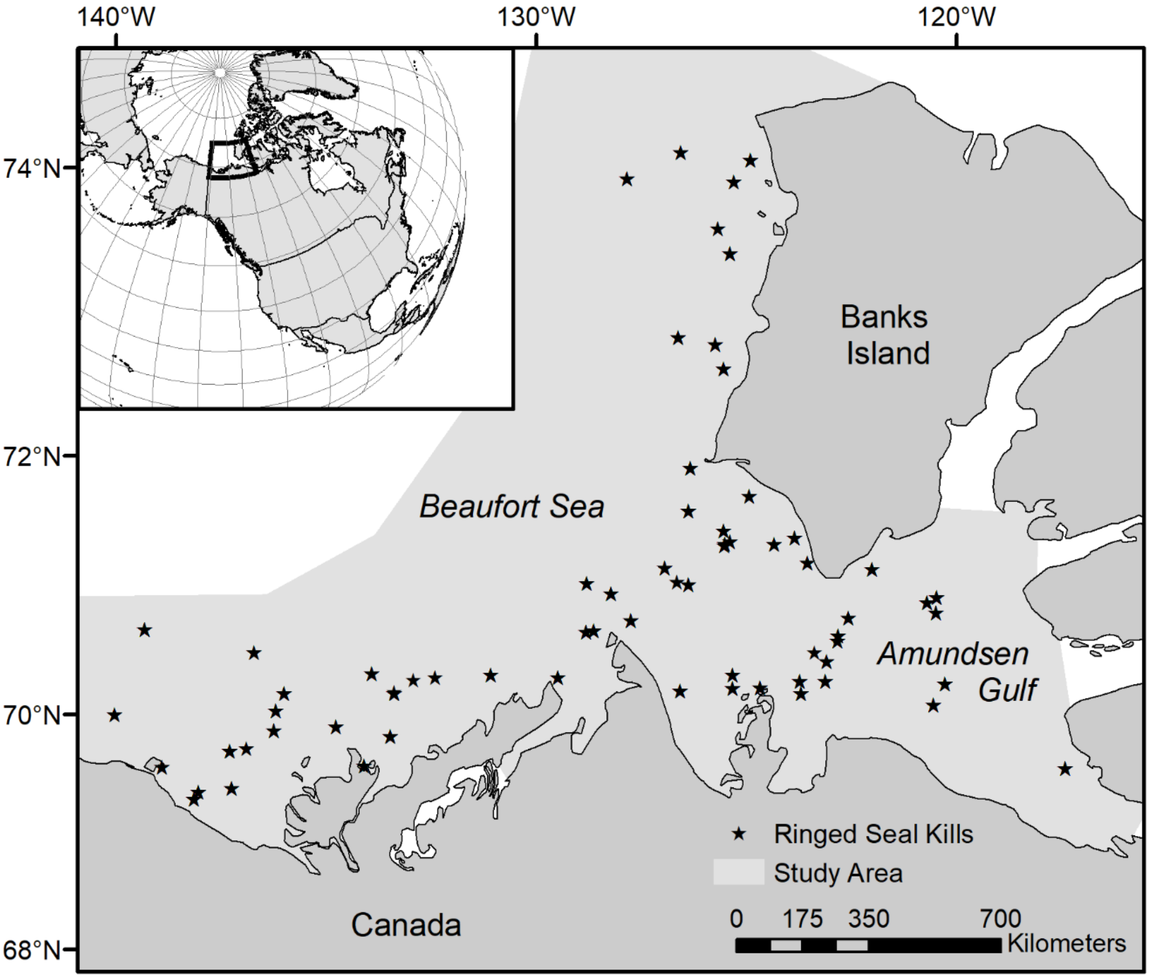

Figure 4-1 Map of the Beaufort Sea, showing locations of ringed seals (n = 69) killed by polar bears between 1974 to 2011. Ringed seal kills (n = 24) without geographic coordinates are not shown. Light gray indicates area where environmental variables were extracted for the study.

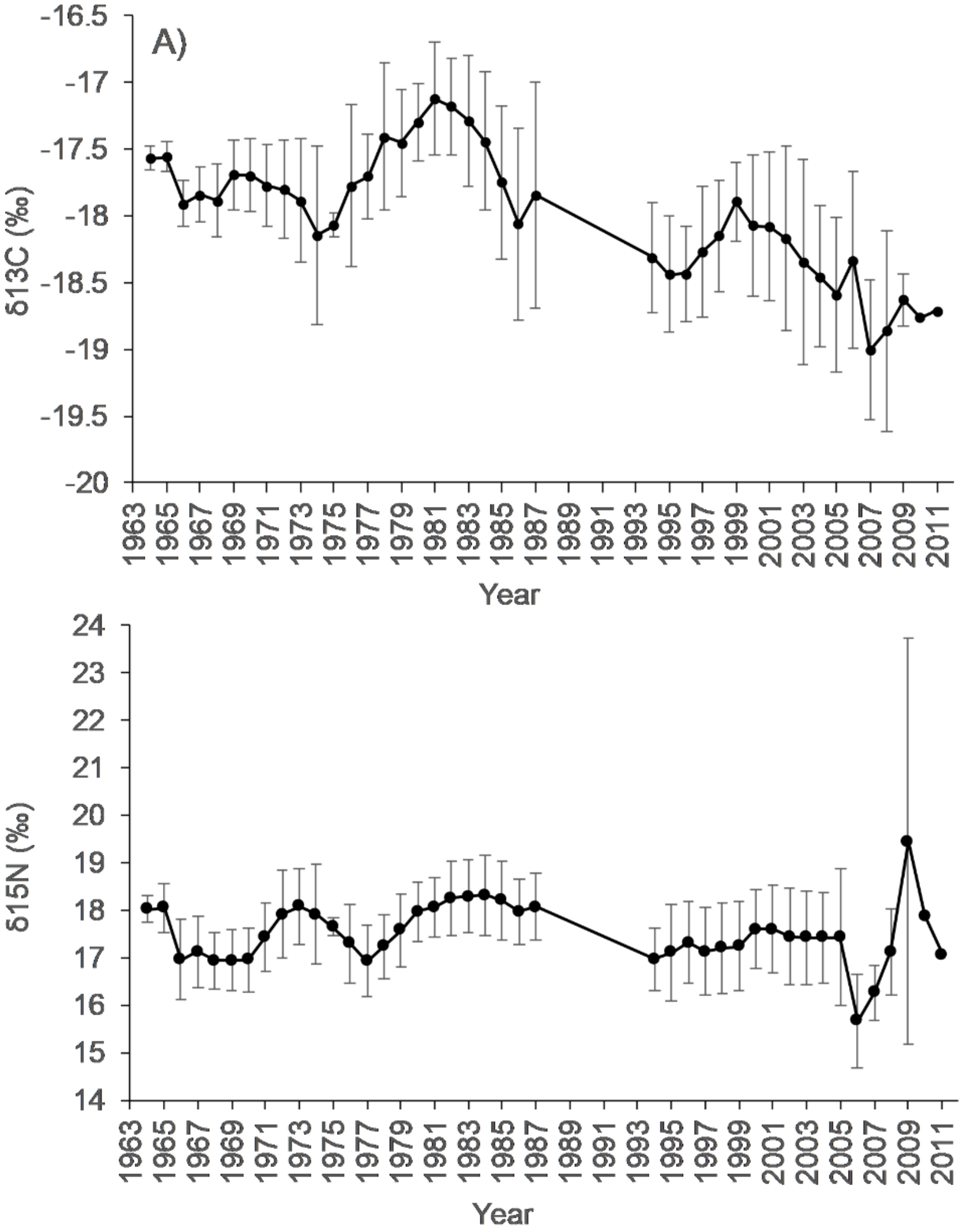

Figure 4-2 Claw growth band stable isotope values of $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) between 1964 to 2011 for ringed seals (n = 93; 714 claw growth bands) within the Beaufort Sea.

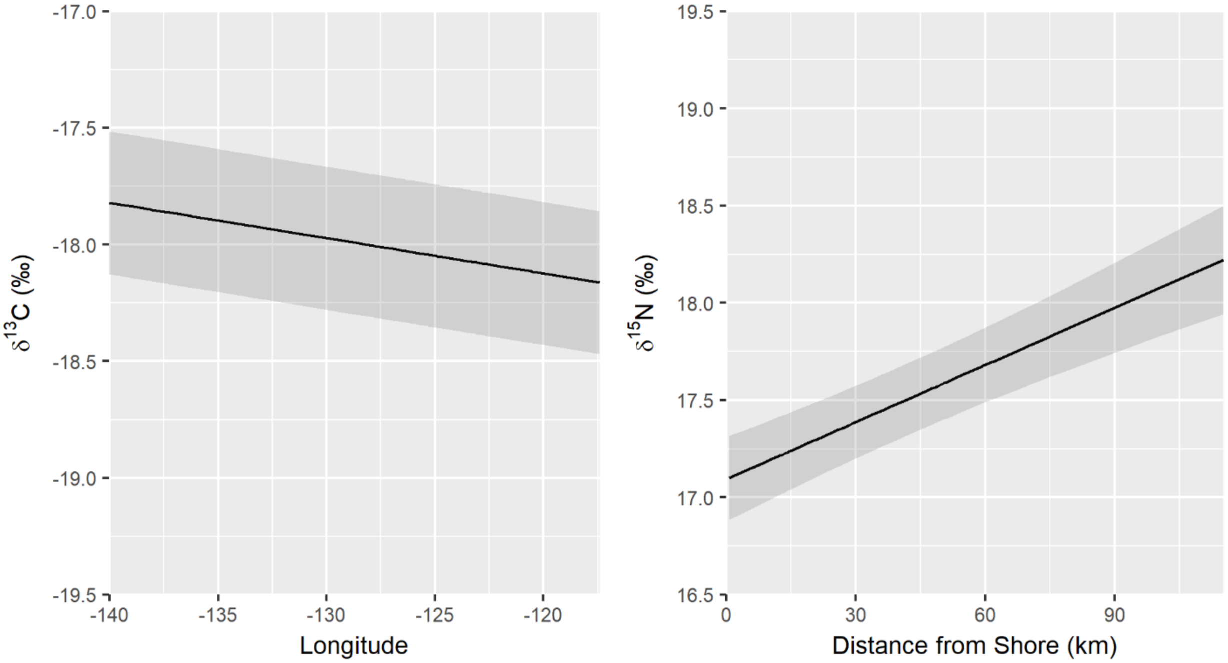

Figure 4-3 Predicted δ^{13}C and δ^{15}N of ringed seal claw bands, based on the longitude (left) and distance from shore (km; right) of the kill site.

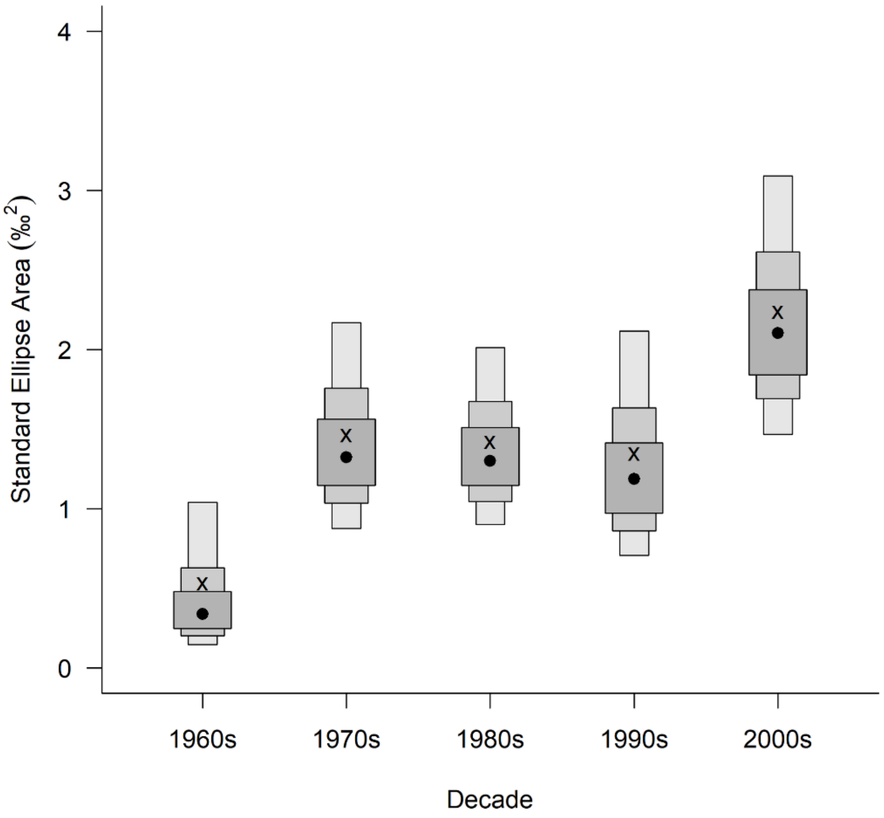

Figure 4-4 Density plot produced by SIBER of the Bayesian estimate of the standard ellipse area (SEA_b; ‰^{2}) for Beaufort Sea ringed seal claw annuli $\delta^{13}C$ and $\delta^{15}N$ stable isotope values. The mode for each decade is represented by the black circle, and credible intervals of 50%, 75% and 95% are represented by the shaded boxes.

CHAPTER 5 – CONCLUSIONS

Sea ice loss is predicted to continue in the future (Stroeve et al. 2007, Overland and Wang 2013), and the Arctic may even experience ice free Septembers as early as 2037 (Wang and Overland 2009). For pagophilic species, this loss of habitat may be devastating. As the sea ice melts, pagophilic species are likely to exhibit modifications in their ecology, such as diet, and may risk extirpation. Available food resources will shift in the future, as species ranges shift (Rand and Logerwell 2011) and habitat loss reduces prey accessibility (Regehr et al. 2010). Dietary changes may have implications of the ecology of polar bears and ringed seals and may provide valuable insights into changing Arctic ecosystems. My research presents an extensive examination of polar bear and ringed seal stable isotopes in the Beaufort Sea, providing valuable baseline data on both species and information on how spatial and temporal variation affects foraging within these species.

Chapter 2 relates SB polar bear stable isotopes to space use and examines whether sectioned metabolically inactive tissues can be used to identify seasonal trends in stable isotopes. This chapter provides the first examination of nitrogen stable isotopes in claws of polar bears and shows that claws can provide information on seasonal diet trends. Within this chapter, the differences in stable isotopes between coastal and pelagic strategies are examined, finding that $\delta^{15}N$ depletion occurs in coastal bears due to coastal bears feeding upon $\delta^{15}N$ depleted nearshore food webs, relying on bowhead whale carcasses and/or experiencing less nutritional stress than pelagic bears. As well, this research highlights the importance of understanding space use patterns when interpreting diet using stable isotopes.

Chapter 3 examines temporal variation in SB and NB polar bear stable isotopes in relation to sea ice dynamics, climate indices and biological factors. Within this study, polar bear diet was related to sea ice dynamics, summer Arctic oscillation, air temperature and seal ovulation rates. In years with fewer available ringed seals, polar bear diets diversified. This work provides the first examination of stable isotopes in the NB subpopulation, as well as the most extensive study of SB stable isotopes. Results from this research may be applied to predict how diet may change in upcoming years under different environmental conditions. Additionally, this work shows that polar bear diets may provide an indication of seal population dynamics.

Chapter 4 investigates spatial and temporal variation in stable isotopes in claw growth bands of ringed seals in the Beaufort Sea. This study uses stable isotope data spanning from 1964 to 2011 and is the most temporally extensive ringed seal stable isotope study to date. Within this chapter, environmental conditions are linked to ringed seal isotopes, with cyclonic circulation regimes enriching $\delta^{13}C$ and seals feeding at a lower trophic level during warmer years. Based on increasing niche width sizes, ringed seals are diversifying their diet, likely as sub-Arctic species invade the Arctic.

As demonstrated by these chapters, stable isotopes provide valuable information on the diet ecology of polar bears and ringed seals, as well as Arctic ecosystem dynamics. Spatial distribution of animals was shown to be important in structuring an individual's diet. As well, numerous environmental and biological conditions influenced stable isotope values within this study. Together, this highlights the importance of understanding and considering the effects of various factors on stable isotopes when interpreting diet and monitoring ecosystem changes. Within this study, metabolically inactive tissues formed a valuable archive of dietary information, that provided a record of ecological change within the Beaufort Sea. Overall, use of these species to monitor the Arctic ecosystem should be continued, and conclusions from their stable isotope values will improve as the effects of environmental variables on stable isotopes are better understood.

Spatial distribution and space use patterns of individuals influence access to resources (Mauritzen et al. 2001, Edwards et al. 2011), and therefore, can play an important role in the diet of an animal. In Chapters 2 and 4, geographic location influenced stable isotope values in both polar bears and ringed seals, respectively. In both species, $\delta^{15}N$ increased offshore. In ringed seals, $\delta^{13}C$ decreased and $\delta^{15}N$ increased with longitude. Likely, the increased $\delta^{15}N$ observed in pelagic polar bears is influenced by offshore ringed seals feeding at a higher trophic level and enriching their $\delta^{15}N$. As well, the $\delta^{13}C$ of ringed seals is likely driven by patterns in primary productivity; however, this did not appear to be reflected in the polar bear stable isotope values possibly due to variable tissue consumption. These results highlight the importance of considering geographic location of an animal when interpreting diet. In best practice, stable isotope values should be interpreted with location or telemetry data; however, this data is not always available (as in Chapter 3). In such cases, it will be important to consider that changes in spatial distributions of animals may be causing variation in diet. For example, in Chapter 3, years with higher dietary proportions of bowhead whale may be a result of increased coastal use in polar bears.

As loss of sea ice continues, the number of polar bears that utilize pelagic or coastal strategies may change. The dietary variation seen in Chapter 3 may reflect these fluctuations in space use patterns, which would influence available food resources. Earlier sea ice break-ups reduce availability of seals to polar bears (Derocher et al. 1993b, Derocher et al. 2004), and therefore, climate change may favour coastal space use. Reduced sea ice will force pelagic bears either further north into the Arctic basin following sea ice distribution or south into coastal areas. Whether a pelagic bear moves north or south likely depends upon individual behavior, resource distribution and environmental conditions. For example, as suggested in Chapter 3, warming temperatures might result in bears moving to land, as evidenced by depleted $\delta^{13}C$. Patterns of space use may be passed on to offspring (Moyer et al. 2006). In the SB, more polar bears are utilizing coastal areas (Schliebe et al. 2008, Pongracz and Derocher 2017), indicating that this may become the dominant space use pattern. As illustrated in Chapter 2, coastal polar bears scavenge on more bowhead whale carcasses, likely from subsistence hunts, than pelagic bears which supports previous evidence on the diets of coastal and pelagic bears within this region (Rogers et al. 2015). This scavenging may offset nutritional stress and muscle atrophy in coastal bears (Whiteman et al. 2015, Whiteman et al. 2017, Whiteman et al. 2018)

Increased scavenging on limited resources may have many consequences, including amplified competition. Using genetic sampling, Herreman and Peacock (2013) identified approximately 228 polar bears at a bowhead whale carcass over a three-month period, which constitutes approximately 15% of the SB population. Based off Bentzen et al. (2007)'s formula to calculate number of bowhead carcasses required to meet a certain proportion of polar bear diet, approximately 17 to 33 carcasses per year are required achieve a diet that consists of 25% bowhead whale for every bear in the entire SB subpopulation (approximately 606 to 1212 bears in 2010) (Bromaghin et al. 2015). However, as Bentzen et al. (2007) notes, this formula may underestimate the number of required carcasses. In Alaska, approximately 40 whales are harvested per year (Suydam et al. 2017). In addition, Laidre et al. (2018) predicts 33 bowhead whale carcasses from the Bering-Chukchi-Beaufort stock may be available every year from natural deaths. However, leftover carcasses may vary in quality and quantity, carcass availability is unpredictable, and subsistence hunt management practices (e.g. disposal in water) may prevent bears foraging upon the carcasses. Bears from the neighboring NB and Chukchi Sea subpopulations may move into these regions to take advantage of the carcasses, and intraspecific competition occurs.

If more polar bears are displaced to coastal regions by sea ice loss, the number of bears relying upon these carcasses could increase, intensifying interspecific competition. As well, grizzly bears (*U. arctos*) use the carcasses, and typically displace polar bears when feeding (Miller et al. 2006, Miller et al. 2015). The coast of the Beaufort Sea is relatively unproductive habitat within the grizzly bear range (Ferguson and McLoughlin 2008). However, as the Arctic warms, productivity of this habitat may increase, and grizzly bears may encroach more into the polar bear range. As such, both inter- and intraspecific competition at whale bone piles may increase with climate change. This may exclude certain polar bear demographics from the bone piles, such as females with cubs, due to avoidance of aggressive encounters (Miller et al. 2015). In such case, particularly if ringed seal hunting opportunities are limited, recruitment rates might drop due to poor cub and maternal nutrition. Alternatively, temporal resource partitioning may occur between demographics to avoid competition at the bone piles, or bears may further seek out alternative food sources.

If polar bears do not have access to sea ice to hunt ringed seals, and bowhead whale carcasses are unavailable, bears will have to seek out alternative resources. Terrestrial resources are typically low in calories compared to the lipid-rich blubber of marine mammals (Stirling and McEwan 1975, Hobson et al. 2009), and large quantities would have to be eaten to fulfil a bear's nutritional needs (Rode et al. 2015b). Anthropogenic food sources may be used to supplement polar bear diet (Lunn and Stirling 1985). More problem bears may occur, as bears enter urban areas to forage for anthropogenic resources. The number of problem bears has increased in Churchill, Manitoba from 1970 to early 2000s (Towns et al. 2009). Human-bear conflicts may result in injuries or fatalities of humans or bears, and management of bears may require deterrents and expensive relocations (Clark et al. 2013). Sea ice freeze-up is related to the occurrence of problem bears (Towns et al. 2009), and climate may play a large role in determining spatial distribution of animals.

Climate, and associated environmental conditions (e.g. sea ice dynamics), influence the diet and stable isotope values of animals, as shown in Chapter 3 and 4. Climate indices were related to the diet of both polar bears and ringed seals within this study, and have been previously linked to aspects of these species' ecology likely due to the effect of climate on sea ice dynamics (Pilfold et al. 2015, Nguyen et al. 2017). As pagophilic species, the ecology of polar bears and ringed seals, and their predator-prey relationship, is linked to sea ice dynamics (McLaren 1958, Stirling and Archibald 1977, Amstrup 2003). Fluctuations in sea ice extent and thickness affects availability of ringed seals to polar bears, forcing bears to land or unproductive multiyear sea ice (Pongracz and Derocher 2017). Ringed seal foraging is associated with the sea ice, particularly along highly productive ice edges, and their spatial distribution will likely follow the sea ice retreat north (Tynan and DeMaster 1997, Freitas et al. 2008a, Freitas et al. 2008b).

Sea ice severity is related to ringed seal population dynamics, which is likely tied to resource availability (Ferguson et al. 2005). In the Hudson Bay, ringed seal recruitment rates were related to timing of sea ice breakup, which is driven by the North Atlantic Oscillation (Ferguson et al. 2005). In years with late sea ice breakups and ice that is heavily compacted, ringed seal populations and recruitment rates declined possibly due to reduced primary productivity (Stirling et al. 1977, Harwood and Stirling 1992, Ferguson et al. 2005, Harwood et al. 2012b). Chapter 4 showed that cyclonic circulation regimes and sea surface temperature, both of which influence sea ice dynamics, were related to ringed seal stable isotopes. Increased reliance of ringed seals upon prey low in calories may occur as sea ice melts and preferred prey populations decline, resulting in lower seal body conditions (Harwood et al. 2000, Harwood et al. 2012b, Harwood et al. 2015). For example, increased feeding upon forage fish, which are depleted in lipids relative to Arctic cod, was linked to decreased body condition in ringed seals (Yurkowski et al. 2016, Ferguson et al. 2017).

With warming temperatures and sea ice loss, ringed seals are likely to be exposed to different prey sources due to shifts in the spatial distribution of seals and prey. As sea ice melts, ringed seals ranges will likely shift northwards following the sea ice distribution (Tynan and DeMaster 1997). During the fall, ringed seals undergo long distance migrations to forage (Harwood et al. 2012a). However, with the sea ice edge retreating north, these excursions may require more energy, and the benefits of long distance migrations to sea ice edges may be outweighed by the energetic costs (Freitas et al. 2008b). Ringed seals in the Beaufort Sea primarily feed upon, but are not limited to, gadidae fish (e.g. *Boreogadus saida, Eleginus gracilis*), mysids, euphausiids and hyperiid amphipods (Lowry et al. 1980, Dehn et al. 2007). However, in the Beaufort since the 1970s, species have expanded their range northward as sea temperatures warm (Rand and Logerwell 2011), increasing the species available for ringed seal consumption. This diversification of seal diet is shown in Chapter 4, with ringed seal niche widths increasing since the 1960s. Other studies have used seal diets to provide evidence of shifts in community composition (Carroll et al. 2013, Young and Ferguson 2014). Warming temperatures may lead to a pelagic-dominated food web (Grebmeier et al. 2006), and Carroll et al. (2013) suggested that patterns in stable isotopes of bearded and ringed seals may be explained by increased pelagic foraging. In the Hudson Bay, capelin (*Mallotus villosus*) are shifting their range northward (Rose 2005), and are becoming increasingly important in the ringed seal diet (Chambellant et al. 2013, Young and Ferguson

2014). This trend in increasing capelin was also captured in the diet of thick-billed murres (*Uria lomvia*) within this region (Gaston et al. 2012).

When monitored long-term, diets of high trophic level species can expose changes within ecological communities, as seen in Chapter 3 and 4. Polar bears may provide valuable information about bearded seal and ringed seal population dynamics, which are understudied in the Beaufort Sea. In addition, their diets may indicate shifts in sea ice dynamics, prey productivity and population dynamics, and ecosystem health, among others. Ringed seals diets can capture changes to community composition of marine biota, which are relatively difficult to study. Concurrently examining polar bears and ringed seals, or with other species (e.g. marine birds), will allow for a fuller picture of ecosystem change. In the future, comparisons between consumer diet proportions and prey population size, spatial distribution and accessibility to predators should be completed. This comparison will allow for a better understanding of whether shifts in a consumer's diet proportions reflect prey population trends, or changes in accessibility of prey to predators.

Records of polar bear and ringed seal tissues, or other high trophic level species, will become valuable resources for identifying ecological changes over the coming years. Metabolically inactive tissues are an archive of ecological information as shown in all chapters of this study and can provide a detailed dietary timeline for an individual as demonstrated in Chapters 2 and 4. Tissues such as claws, and hair can be collected from both museum and living specimens, allowing comparisons between current and historic trends. In addition, these tissues can be relatively inexpensive to collect, and some tissues, such as hair, can be collected non-invasively (e.g. barbed wire hair snares). For example, as shown in Herreman and Peacock (2013), barbed wire snares can be set up around bowhead whale carcasses to capture polar bear hair. While use of these tissues is promising, future stable isotope studies would benefit from improved understanding of tissue growth rates, allowing accurate aging and backdating of tissues.

Tissue growth rates can vary seasonally and may vary with metabolic rate (Hilderbrand et al. 1996, Belant et al. 2006). Claw growth rates for polar bears were estimated previously to be 3-6mm/month during summer; however, this study only consisted of three bears from spring to autumn (Holladay 1988). Polar bear hair growth is assumed to match with the moulting period (Amstrup 2003, Cardona-Marek et al. 2009, Rogers et al. 2015). In ringed seals, claw growth bands are likely caused by foraging cycles (Ferreira et al. 2011). While growth rates for these tissues can be estimated, further measurements on these tissues would advance the use of stable isotopes within both species, allowing us a better understanding of how physiological conditions (e.g. hormone cycles) affect tissue growth.

For both species, tissue growth rates could be assessed using studies on both captive and wild animals. Upon capture, claws could be marked following recommendations by Ethier et al. (2010) and if the individual is recaptured, claw growth can be measured. Understanding of claw growth rates would be most insightful if these mark-recapture studies are combined with synchronous data on movement, and biological factors such as body condition. Further, tissue growth could be measured in captive animals, which would allow assessment of how different feeding conditions or physiological conditions affect claw growth rates.

In addition, controlled feeding studies using captive animals could be performed for both species. Controlled feeding studies are important as they allow determination of turnover rates of metabolically active tissues and discrimination factors (Newton 2016). While feeding studies on captive polar bears and ringed seals have been completed, these studies were limited in sample size (Hobson et al. 1996, L'Hérault et al. 2018). Further controlled feeding studies on these species with larger sample sizes should be conducted, with an examination of how biological conditions affect isotopic discrimination. For example, age may play a role in discrimination factors, with δ^{13}C value increasing (L'Hérault et al. 2018) or decreasing (Lecomte et al. 2011) in juveniles. Completion of these studies would reduce the number of assumptions required when completing stable isotope studies and will result in higher accuracy of dietary studies.

Sea ice has declined in extent and thickness from the 1950s (Kwok and Rothrock 2009), and is expected to continue into the future (Overland and Wang 2013). Across the Arctic, temperatures are increasing (Hinzman et al. 2005, Lang et al. 2016). These changes have many potential implications, such as a loss of habitat (Wauchope et al. 2016), phenological mismatches (Wrona et al. 2016), shifts in species' distributions (Poloczanska et al. 2013), loss of ecosystem services (Oechel et al. 1993) and spread of disease (Parkinson and Butler 2005). Stable isotope analysis is a promising tool for examining ecological changes, particularly as the connections between environmental conditions and stable isotopes are clarified. Climate change is having large scale effects upon ecosystems (Post et al. 2009, Post et al. 2013), and therefore, monitoring of ecosystems will be crucial to manage the effects of climate change.

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