Polar bear (*Ursus maritimus*) foraging, spatial, and energetics ecology in the changing Arctic

by

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Abstract

Climate warming in the Arctic has resulted in rapid and extensive changes to sea ice dynamics and profound ecological impacts, including changes to the timing of life history events, community structure, and food web dynamics. Sea ice-dependent species such as polar bears (*Ursus maritimus*) are particularly vulnerable to Arctic warming and can be useful for monitoring changing ecosystem dynamics. In this dissertation, I examine multiple aspects of polar bear ecology at different spatiotemporal scales in two declining populations to assess the underlying factors affecting population dynamics.

To examine foraging ecology, I analyzed stable isotopes in Western Hudson Bay (WH) polar bear hair samples (1993-1994, 2004-2016) to assess intra-population variation, temporal dynamics, and relationships to sea ice dynamics. Here, I showed that adult males had the broadest diets while adult females and subadults had smaller isotopic niches, potentially increasing their sensitivity to reduced prey availability. Population isotopic values varied over time in relation to the length of the open-water period, reflecting a dietary niche shift and/or changes to ecosystem baseline isotopic values in response to climate warming.

Secondly, I examined patterns in the spatial ecology of Southern Beaufort Sea (SB) polar bears from 2007-2011. I found broad similarities in population habitat preferences for intermediate to high sea ice concentration and seasonal movements in response to sea ice phenology. I also documented variation within the population, such that adult females with cubs-of-the-year used lower quality habitat, likely to protect dependent young. Subadult males also used lower quality habitat, which may be a mechanism to reduce intra-specific competition and/or kleptoparasitism. Monitoring habitat use can identify vulnerable demographic groups and shifts in population distribution as polar bears experience declines in optimal sea ice habitat.

Thirdly, I analyzed the movements of an individual bear that displayed exceptionally long-distance travel from the SB population to the Chukchi Sea population (2009-2011). I compared two methods for calculating home range size and provided evidence that the Brownian bridge movement model is less biased than minimum convex polygons. Such long-distance movements and long-distance swimming events may become more common as sea ice habitat declines. As polar bear populations are relatively discrete, these movements may have implications for gene flow and population boundaries in the changing Arctic.

Lastly, I used a novel technique to estimate WH population energy density and storage energy from abundance, age/sex structure, and body condition measurements (1985-2018). Here, I showed that energy metrics for most demographic classes declined over time in relation to earlier sea ice breakup, most significantly for solitary adult females and yearlings, demonstrating their vulnerability to nutritional stress. Additionally, population energy values declined over time in relation to earlier sea ice breakup and longer lagged open-water periods, suggesting multi-year effects of sea ice decline on WH polar bear physiological condition. Overall, this thesis provides insights into the ecological mechanisms influencing polar bear population responses to climate warming, and highlights the utility of multiple monitoring techniques for understanding changing ecological dynamics.

Preface

Chapter 2 of this thesis has been published as: Johnson AC, Hobson KA, Lunn NJ, McGeachy D, Richardson ES, Derocher AE (2019). Temporal and intra-population patterns in polar bear foraging ecology in western Hudson Bay. *Marine Ecology Progress Series* 619:187–199. doi:10.3354/meps12933. I designed the models, analyzed the data, and wrote the manuscript. A.E. Derocher provided supervisory guidance and contributed to manuscript writing. K.A. Hobson, N.J. Lunn, and E.S. Richardson contributed editorial advice on the manuscript. D. McGeachy extracted and processed sea ice data and contributed editorial advice on the manuscript.

Chapter 3 is currently in revision as: Johnson AC, Derocher AE (2020). Variation in habitat use of Beaufort Sea polar bears. *Polar Biology*. I was responsible for creating the models, analyzing and interpreting the data, and writing the manuscript. A.E. Derocher provided supervisory guidance and contributed to manuscript writing. Additionally, Jodie Pongracz and Charlene Nielsen assisted with environmental data extraction.

Chapter 4 of this thesis has been published as: Johnson AC, Pongracz, JD, Derocher AE (2017). Long-distance movement of a female polar bear from Canada to Russia. *Arctic* 70:121–128. doi:10.14430/arctic4641. I designed the models, analyzed the data, and wrote the manuscript. A.E. Derocher provided supervisory guidance and contributed to manuscript writing. J.D. Pongracz assisted with data processing and manuscript writing.

Chapter 5 is submitted as: Johnson AC, Reimer JR, Lunn NJ, Stirling I, McGeachy D, Derocher AE (2020). Influence of sea ice dynamics on population energetics of Western Hudson Bay polar bears. *Functional Ecology*. I designed the models, analyzed the data, and wrote the manuscript. A.E. Derocher provided supervisory guidance and contributed to manuscript writing. J.R. Reimer contributed to model design and manuscript writing. N.J. Lunn and I. Stirling provided editorial comments on the manuscript. D. McGeachy extracted and processed sea ice data and contributed to writing the manuscript.

All capture and handling techniques were in accordance with the Canadian Council on Animal Care (www.ccac.ca) guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee and Environment and Climate Change Canada's Western and Northern Animal Care Committee. Research was conducted under wildlife research permits issued by the Government of Manitoba and the Parks Canada Agency.

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Chapter 1

1 Introduction

1.1 Ecological processes

Foraging, habitat use, and energetics are ecological processes that influence life history events and have consequences for individual fitness and population dynamics. Foraging behaviour is influenced by natural selection and affects the likelihood of survival and reproduction (Krebs 2001). Optimal foraging theory predicts the selection of foraging behaviour that optimizes energy intake while reducing foraging costs (Emlen 1966, MacArthur and Pianka 1966, Pyke et al. 1977). The timing of life history events is often linked to the seasonal availability of food resources (Post and Forchhammer 2008), and similarly, the availability of prey resources influences the foraging ecology of predators (Lemke 1984, Westphal et al. 2006). Conversely, predation influences population dynamics and distribution of prey species (Krebs 2001, Borrvall and Ebenman 2006). Thus, changes to apex predator population dynamics have the potential to cascade through ecosystems (Pace et al. 1999, Schmitz et al. 2000, Frank et al. 2005) and affect trophic interactions and ecosystem stability (de Ruiter et al. 1995, Neutel et al. 2002, Rall et al. 2010), highlighting the importance of understanding food web ecology.

The geographic distribution of a species is linked to resource availability and the habitat selection of individuals (Brown and Orians 1970, Krebs 2001). Spatial connectivity between habitats and dispersal of individuals link populations and promotes gene flow (Slatkin 1987, Ranta et al. 1997, Krebs 2001). Habitat selection is a hierarchical process that begins at broad spatial scales and spans through progressively narrower scales of habitat choices (Johnson 1980, Krebs 2001). This selection of habitat is affected by energetic requirements, habitat quality, population density, and intra-specific competition, with consequences for survival and reproduction (Alonso et al. 1997, Krebs 2001, Jetz et al. 2004). Furthermore, some species display seasonal migrations in response to environmental and resource fluctuations (Levey and Stiles 1992, Dingle and Drake 2007). Changes in species distributions can occur as a result of altered resource availability and environmental conditions, and have implications for community structure and trophic interactions (Cheung et al. 2009, Van Der Putten et al. 2010, Wassmann et al. 2011, Doney et al. 2012). As such, monitoring spatial ecology can assist in understanding ecological responses to habitat change.

Lastly, predator-prey interactions result in the transfer of energy through trophic levels in a food web (Krebs 2001). Bioenergetics research can examine energy dynamics at the individual scale (Bailey and Mukerji 1977, Cressa and Lewis 1986), population-wide (Markussen and Øritsland 1991, Ryg and Øritsland 1991), and across trophic levels (Sakshaug et al. 1994). Individual energetic balances are influenced by energetic intake (predation) as well as energetic expenditure (e.g., metabolism, maintenance, movements, growth, and reproduction) (Krebs 2001, Molnár et al. 2009, Pagano et al. 2018). The accumulation of energetic reserves has consequences for individual fitness by affecting reproduction and survival (Jakob et al. 1996, Sciullo et al. 2016). Furthermore, changes in the energetic balances of individuals lead to alterations in population dynamics (Yodzis and Innes 1992, Humphries et al. 2004, Pagano et al. 2020), and thus demonstrates the importance of monitoring ecological energetics to improve our understanding of the mechanisms underlying population change.

The integration of foraging, spatial, and energetics research can provide insights into ecological dynamics in changing environments. Monitoring these ecological processes can identify the factors influencing population dynamics in response to anthropogenic change and have implications for wildlife management and conservation.

1.2 Anthropogenic climate change

Anthropogenic greenhouse gas emissions have led to large changes in the Earth's climate system including ocean acidification due to uptake of carbon dioxide, decreased spring snow cover and glacier/ice sheet masses, and increased permafrost temperatures (IPCC 2014, 2019). In addition to climate change, habitat destruction and loss are key anthropogenic factors threatening species persistence and global biodiversity (Wilcove et al. 1998, Brook et al. 2008, Mantyka-Pringle et al. 2012, Scheffers et al. 2016). Understanding species responses to anthropogenic factors can help inform management efforts and improve predictions about ecosystem dynamics in future conditions. There are a broad range of ecological responses to anthropogenic change (Post et al. 2009, 2013, 2019). In particular, temperature is a major factor influencing the timing of life history events for many species, and as such, climate warming can lead to altered phenology and disconnects between trophic levels, with consequences for predator-prey dynamics (Visser and Both 2005, Post and Forchhammer 2008, Van Der Putten et al. 2010). Climate change can affect phenology through shifts in seasonal resource abundance (Visser and Both 2005, Post and Forchhammer 2008), asynchrony between juvenile development and prey availability (Hoegh-Guldberg and Bruno 2010, Søreide et al. 2010), and changes to the timing of migration events (Reist et al. 2006). In addition, changes to ecosystem composition resulting from climate change-induced range shifts or species extirpation (Cheung et al. 2009, Van Der Putten et al. 2010, Doney et al. 2012) can influence predator-prey interactions and food web dynamics (Mahan and Yahner 1999, Bluhm and Gradinger 2008, Hoegh-Guldberg and Bruno

2010, Gaston et al. 2012). Lastly, population vital rates are affected by habitat loss, which can result in abundance declines (Fahrig 2003, Scheffers et al. 2016). Overall, these ecological responses to anthropogenic climate change have implications for ecosystem composition, function, and stability (de Ruiter et al. 1995, Neutel et al. 2002, Rall et al. 2010, Molinos et al. 2015). Species that are specialized will likely be more vulnerable to habitat alteration than generalists (Davies et al. 2004). It is important to monitor ecosystem dynamics as individuals, populations, and species respond to anthropogenic changes, especially in rapidly changing ecosystems.

1.3 Arctic marine ecosystem

The Arctic marine ecosystem is characterized by seasonal variation in light availability and primary production, with a reliance upon sea ice algae as the base of the food web (Gosselin et al. 1997, Arrigo 2014, Leu et al. 2015). This ecosystem consists of relatively short food chains with few species, which increases sensitivity to changes in the abundance of species at key trophic levels (Murphy et al. 2016). The Arctic is warming at a faster rate than the global mean in response to anthropogenic greenhouse gas emissions (Franzke et al. 2017, IPCC 2019). As a result, sea ice extent, duration, and thickness have experienced rapid and extensive declines (Comiso 2012, Parkinson 2014, Stroeve and Notz 2018, Hwang et al. 2020). The timing of sea ice dynamics have also been affected by Arctic warming, resulting in earlier breakup and later freeze-up (Stirling and Parkinson 2006, Stern and Laidre 2016, Stroeve and Notz 2018). In addition, there have been reductions in the amount of multiyear ice and a shift towards a predominance of thin, first-year ice that is more sensitive to melting (Rigor and Wallace 2004, Belchansky et al. 2005, Stroeve et al. 2012). These environmental changes have led to a positive feedback loop (Arctic amplification) where sea ice melts, open-water areas expand, surface albedo declines, and the Arctic ocean absorbs more solar radiation, limiting future ice growth (Serreze and Francis 2006, Screen and Simmonds 2010, Stroeve et al. 2012).

Species that are most affected by warming are sea ice-dependent - such as Arctic marine mammals - due to their reliance on sea ice for various life history events (Laidre et al. 2008, Post et al. 2009, Søreide et al. 2010). The Arctic marine ecosystem has responded to altered sea ice dynamics with changes to the timing of primary productivity blooms, which can lead to trophic mismatches between primary producers and zooplankton, and has implications for food web dynamics (Hansen et al. 2003, Laidre et al. 2008, Søreide et al. 2010, Leu et al. 2011). In addition, sea ice decline results in habitat loss for sea ice algae, which will affect the foraging ecology of higher trophic levels (Søreide et al. 2010, Leu et al. 2011, Wassmann et al. 2011). Furthermore, climate warming affects Arctic marine community structure through shifts in the ranges of lower trophic species, such as the northward expansion of warm-water copepods and subarctic/boreal fish species (Beaugrand et al. 2002, Gaston et al. 2003, Wassmann et al. 2011, Young and Ferguson 2014, Kortsch et al. 2015). The Arctic is predicted to be seasonally ice-free in September before 2050 (Thackeray and Hall 2019, Hwang et al. 2020), which will have consequences for ecosystem structure and stability, and highlights the importance of monitoring ecological responses (particularly for sea ice-dependent species) to Arctic warming.

1.4 Polar bears

Polar bears (*Ursus maritimus*) have a circumpolar distribution in the Arctic and are dependent upon sea ice, which provides a platform for foraging, travelling, and reproduction (Stirling and Archibald 1977, DeMaster and Stirling 1981, Stirling et al. 1993). Approximately

150,000 years ago, polar bears evolved from brown bears (*U. arctos*) (Lindqvist et al. 2010) and adapted to survive as a top predator specialized on Arctic marine mammals (Kurtén 1964, Stirling and Derocher 1993, Derocher et al. 2004). Sea ice provides access to their main prey, ice-associated seals, particularly ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980, DeMaster and Stirling 1981). The timing of sea ice breakup and formation are influential in the phenology of polar bear life history as they experience seasonal fluctuations in prey availability. Spring is a critical hunting period wherein polar bears undergo hyperphagia and forage on abundant and naïve ringed seal pups (Stirling and McEwan 1975, Stirling and Archibald 1977, Stirling and Øritsland 1995). After sea ice breakup, polar bears either travel north to less-productive multiyear sea ice or are forced ashore where they fast until freeze-up (DeMaster and Stirling 1981, Amstrup et al. 2000, Pongracz and Derocher 2017). The preferred habitat of polar bears is annual sea ice over the productive continental shelf (Derocher et al. 2004, Durner et al. 2009). Polar bears have large home ranges and do not display territorial behaviour, likely due to unpredictable resource distribution in the Arctic marine environment (Ramsay and Stirling 1986, Ferguson et al. 1999, Pilfold et al. 2014). Yet, spatial segregation exists based on age, sex, and reproductive status (Latour 1981, Derocher and Stirling 1990, Stirling et al. 1993). Polar bears must rely on accumulated energetic reserves to survive extended fasting periods on land of 4-5 months (Stirling and McEwan 1975, Nelson et al. 1983, Lunn and Stirling 1985, Derocher et al. 1990) and up to 8 months for adult females in maternity dens (Ramsay and Stirling 1988, Atkinson and Ramsay 1995).

Due to their reliance on sea ice, polar bears are particularly sensitive to sea ice loss (Stirling et al. 1999, Stirling and Derocher 2012) and various populations have experienced declines in optimal sea ice habitat (Durner et al. 2009, Stern and Laidre 2016). Earlier breakup and longer ice-free periods have been associated with reduced body condition (Obbard et al. 2016, Sciullo et al. 2016, Laidre et al. 2020), declines in reproductive and survival rates (Stirling et al. 1999, Regehr et al. 2007, Rode et al. 2010), and reduced abundance (Lunn et al. 2016, Obbard et al. 2018). As a top predator in the Arctic and a species whose ecology is associated with sea ice dynamics, polar bears can act as an indicator species to monitor ecological responses to climate warming (Rode et al. 2018). Furthermore, polar bears are threatened by predicted future Arctic warming (Wang and Overland 2009, Castro de la Guardia et al. 2013, Regehr et al. 2016), indicating the importance of understanding the ecological responses of this species to climate warming to inform management and conservation actions.

1.5 Study areas

There are 19 populations of polar bears in four ecoregions: Divergent, Convergent, Seasonal ice, and Archipelago (Amstrup et al. 2007). The Western Hudson Bay (WH) and Southern Beaufort Sea (SB) populations are two of the most well-researched due to long-term research programs spanning several decades (Stirling and Archibald 1977, Amstrup et al. 2000, Lunn et al. 2016, Rode et al. 2018). The WH population occurs in the Seasonal ice ecoregion in Hudson Bay (Amstrup et al. 2007) (Fig. 1.1), a shallow inland sea that is ice-covered from January to April (Maxwell 1986, Jones and Anderson 1994). When the sea ice melts in late summer, WH bears are forced ashore where they fast for 4-5 months until ice freeze-up (Lunn and Stirling 1985). Meanwhile, the SB population is in the Divergent ice ecoregion (Amstrup et al. 2007) (Fig. 1.1). The southern Beaufort Sea has a narrow continental shelf and the Beaufort Gyre, wind, and currents influence sea ice drift (Proshutinsky et al. 2002, Bromaghin et al. 2015, Pongracz and Derocher 2017). The southern Beaufort Sea has a seasonal open-water lead that is biologically productive and forms at the boundary between shorefast nearshore ice and offshore pack ice (Stirling et al. 1993, Pilfold et al. 2014). This region is ice-covered in late autumn through winter, and when the ice melts in summer, SB bears either come ashore to fast or travel north to multiyear sea ice (Amstrup et al. 2000, Pongracz and Derocher 2017). Both the WH and SB populations have experienced declines in optimal sea ice habitat (Stern and Laidre 2016), which is predicted to continue (Wang and Overland 2009, 2012, Stroeve and Notz 2018).

1.6 Dissertation outline

The overall objective of this thesis is to examine intra-population and inter-annual trends in polar bear ecological processes in relation to sea ice dynamics to further our understanding of the ecological mechanisms underlying population responses to rapid and extensive habitat change. In Chapter 2, I examine patterns in foraging ecology within the WH population, temporal trends from 1993-2016, and the relationship between foraging ecology and sea ice dynamics. This chapter discusses the link between inter-annual variation in foraging ecology and longer open-water periods, as well as highlights the narrower diets and vulnerability of adult females and subadults to future changes in prey availability. In Chapter 3, I assess variation in habitat use and selection between adult and subadult polar bears in the SB population. This study provides insights into population spatial ecology as sea ice habitat declines, as well as discusses the vulnerability of different demographic groups to changes in habitat quality and prey availability. In Chapter 4, I investigate the movements of an individual that displayed exceptionally long-distance travel from the SB population to the Chukchi Sea population. This chapter discusses polar bear spatial ecology and population connectivity, with implications for gene flow and population boundaries as polar bears experience habitat loss. This chapter also examines long-distance swimming events and compares techniques for estimating home range size. In Chapter 5, I estimate WH population energy density and storage energy, examine inter-annual dynamics of population energy from 1985-2018, determine intra-population variation in energetic patterns, and examine the relationship between energy patterns and environmental dynamics. This chapter discusses the implications of energetic declines for vulnerable demographic groups as well as the link between nutritional stress and Arctic warming. This chapter also highlights multi-year, cumulative impacts of environmental change on the WH population. Finally, in Chapter 6, I discuss the significance of these studies for the field of Arctic ecology, outline the relevance of this dissertation for management and conservation of the WH and SB polar bear populations, and suggest future research to improve our understanding of ecological responses to climate warming.

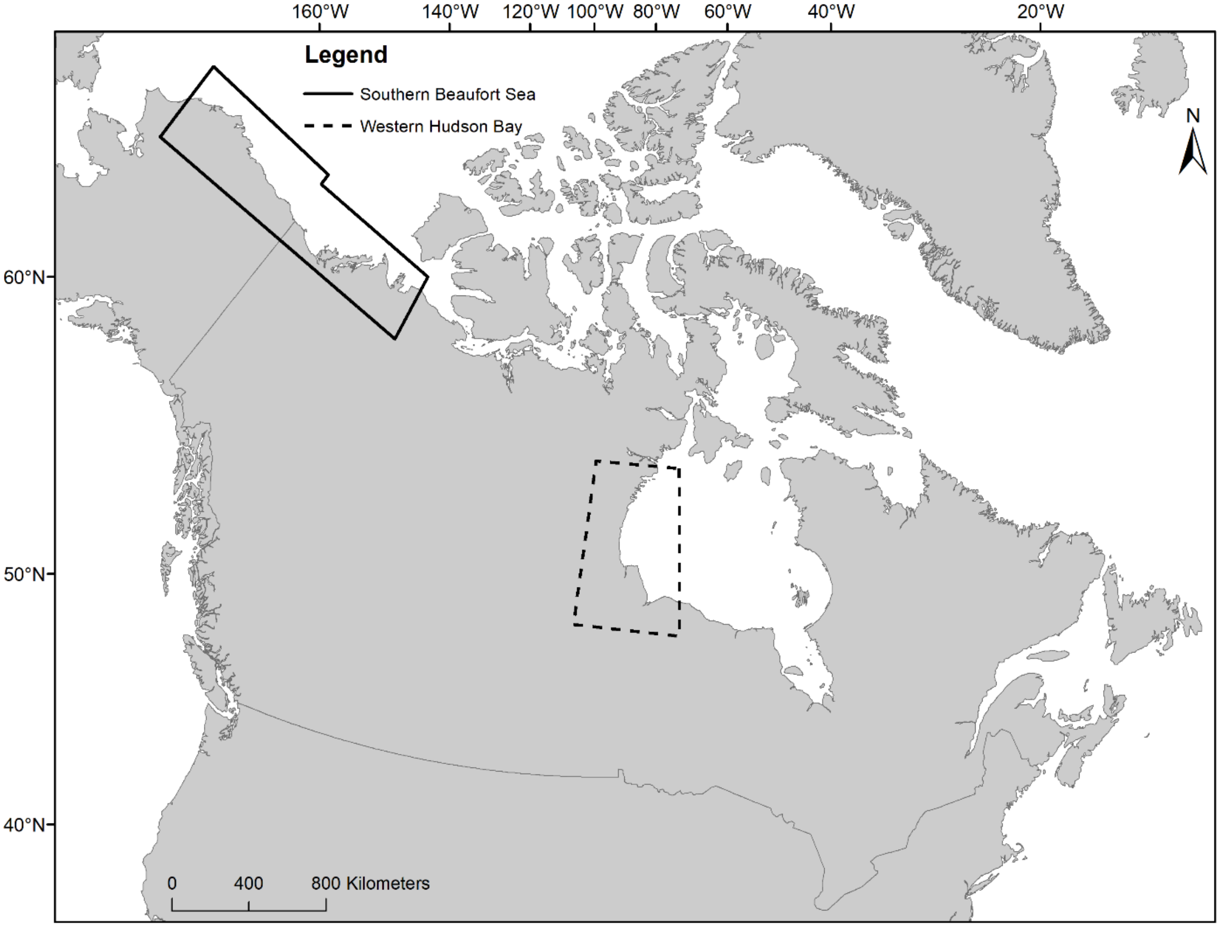

Figure 1.1: The study areas for the Western Hudson Bay polar bear population (dashed black lines; Chapters 2, 5) and the Southern Beaufort Sea population (solid black lines; Chapters 3, 4).

Chapter 2

2 Temporal and intra-population patterns in polar bear foraging ecology in western Hudson Bay

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2.1 Introduction

The Arctic has experienced rapid warming at a rate 2-3 times the global mean (Post et al. 2009, Franzke et al. 2017), which has resulted in significant and continuing sea ice decline (Comiso 2012, Stern and Laidre 2016). Climatic change is expected to affect the structure and function of Arctic marine ecosystems (Van Der Putten et al. 2010), and species whose life history is dependent on sea ice habitat are particularly vulnerable to continued warming (Laidre et al. 2008, Post et al. 2009, Søreide et al. 2010). Arctic marine mammals depend upon sea ice to varying degrees for various aspects of their life history and are therefore sensitive to climate change-induced sea ice loss (Laidre et al. 2008).

Ecological responses to climate change that may affect Arctic marine mammals fall into three broad categories: alterations in species composition, phenology, and primary productivity. First, changes to ecosystem composition are mainly due to range shifts or species extirpation in response to increasing temperatures (Van Der Putten et al. 2010). Arctic sea ice loss has led to altered distributions of some ice-associated marine mammals with subarctic species expected to expand their ranges northward (Laidre et al. 2008), which can influence food web dynamics (Bluhm and Gradinger 2008, Gaston et al. 2012). Secondly, climate change can affect the timing of life history events, which may lead to a disconnect between trophic levels, with implications for foraging ecology and predator-prey dynamics (Van Der Putten et al. 2010). Arctic sea ice decline alters the phenology of primary productivity, which can lead to a trophic mismatch with zooplankton grazers, with cascading effects on higher trophic level species such as marine mammals (Laidre et al. 2008, Søreide et al. 2010). Further, loss of sea ice may result in declines in sympagic algae that produce up to 57% of overall Arctic marine primary productivity with links through the food web to marine mammals (Brown et al. 2018). Lastly, sea ice decline has resulted in a longer open-water season and an increase in Arctic annual primary productivity due to the longer growing season for pelagic phytoplankton (Arrigo et al. 2008). Because sympagic algae form the base of the Arctic marine food web, loss of sea ice will alter where marine productivity occurs in the Arctic and may affect the foraging ecology of higher trophic levels (Søreide et al. 2010, Leu et al. 2011, Brown et al. 2018). Understanding marine mammal foraging in response to climate change can provide insights into Arctic food web shifts and ecosystem dynamics.

Hudson Bay is near the southern limit of polar bear (*Ursus maritimus*) distribution and has experienced the effects of climate warming before many other Arctic areas (Stirling et al. 1999, McKinney et al. 2009, Lunn et al. 2016). The Hudson Bay ecosystem has undergone rapid change due to changing sea ice phenology, including a shorter on-ice foraging period and longer onshore fasting period for polar bears (Stirling et al. 1999, Thiemann et al. 2008, Castro de la Guardia et al. 2017). As top predators, polar bears may shift their diet in response to the availability of ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), both ice-dependent species, and open-water seals (e.g., harbour seals [*Phoca vitulina*]) due to variation in sea ice conditions (Thiemann et al. 2008, Young and Ferguson 2014). Long-term life history data has documented decreased body condition, survival, reproduction, and abundance in the Western Hudson Bay population (WH) in recent decades (Stirling et al. 1999, Regehr et al. 2007, Lunn et al. 2016), suggesting that it may be experiencing climate-related changes in foraging ecology.

In western Hudson Bay, earlier sea ice breakup and longer ice-free periods threaten the persistence of polar bears (Regehr et al. 2007, Castro de la Guardia et al. 2013, Stern and Laidre 2016) because they are highly specialized predators that rely on the sea ice for movement and access to energy rich, ice-associated seals, especially during the spring, which is an important season for foraging before fasting during the open-water period (Stirling and Archibald 1977). In Hudson Bay, ringed seals are the primary prey of polar bears and also depend on sea ice habitat, while bearded seals, harp seals (*Pagophilus groenlandicus*), harbour seals, and beluga whales (*Delphinapterus leucas*) are occasional prey (Thiemann et al. 2008). Because polar bears depend on sea ice as a platform from which to forage, an increase in the duration of the open-water period can influence their foraging ecology and therefore body condition, survival, reproduction, and population persistence (Stirling et al. 1999, Regehr et al. 2007, Lunn et al. 2016). The open-water period is an important monitoring metric for polar bears because of their dependence upon sea ice habitat; over the past 3.5 decades, the open-water period in western Hudson Bay has increased by > 4 wk (Stern and Laidre 2016).

We used biomarkers of diet to study the foraging ecology of WH polar bears during the critical spring/early summer period when they are largely inaccessible. Stable isotope analysis (SIA), primarily involving the use of stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope ratios, has been used to study foraging ecology (e.g., Hilderbrand et al. 1996, Young and Ferguson 2014), trophic interactions (Hobson and Welch 1992), and to estimate the diet of polar bears (Cherry et al. 2011, Rogers et al. 2015). In marine systems, $\delta^{15}N$ values increase trophically (DeNiro and Epstein 1981), whereas $\delta^{13}C$ values indicate benthic versus pelagic and nearshore versus offshore sources of primary production (Hobson and Welch 1992). Guard hair (outer layer of hair) $\delta^{13}C$ and $\delta^{15}N$ values can provide insights into the foraging ecology of bears (Hilderbrand et al. 1996, Hobson et al. 2000), reflecting the spring/early summer molt period when polar bear hair is produced (St. Louis et al. 2011). Changes in environmental conditions can alter baseline isotopic values in marine systems and these changes can be passed onto higher trophic levels (Lowther et al. 2017). As such, stable isotope analyses, especially when applied through time, can reveal changes in ecosystem responses to perturbations such as climate change. Despite long-term monitoring of polar bears in Hudson Bay, the investigation of diet and linkages to the food web have not been examined using WH polar bear hair stable isotopes.

We used $\delta^{15}N$ and $\delta^{13}C$ analysis for WH polar bears to determine (1) whether there are within-population dietary differences related to age and sex; (2) whether polar bear foraging ecology has changed over time from samples collected in 1993-1994 and 2004-2016; and (3) if there is a relationship between temporal variation in foraging ecology and changes in sea ice phenology.

2.2 Methods

2.2.1 Study area

Hudson Bay (Fig. 2.1) is a shallow inland sea (Jones and Anderson 1994) that is ice-covered from January-April but ice-free from August-October/November (Maxwell 1986, Castro de la Guardia et al. 2017). Three polar bear populations occur in Hudson Bay: Foxe Basin, Southern Hudson Bay, and WH (Peacock et al. 2010). The three populations overlap on the sea ice during the ice-cover period, but are largely segregated from one another during the ice-free period due to fidelity to terrestrial summering areas (Peacock et al. 2010).

2.2.2 Sample collection and preparation

Polar bears were captured in Wapusk National Park and adjacent areas in Manitoba, Canada from August to early October in 1993-1994 and 2004-2016. They were located by helicopter, captured using standard chemical immobilization techniques (Stirling et al. 1989), and individually marked using numbered ear tags and permanent lip tattoos. Sex and reproductive status were recorded, and age was determined from counts of cementum annuli within an extracted vestigial premolar (Calvert and Ramsay 1998) or in the field for dependent offspring based on tooth eruption patterns. We classified adults as ≥ 5 yr old and subadults as 3-4 yr old. Dependent offspring (cubs-of-the-year, yearlings, and 2 yr old cubs captured with mother) and juveniles (< 3 yr old) were excluded from analyses because of the complexities of maternal transfer (Polischuk et al. 2001) and dependence on maternal dietary input (Stirling 1974). Adult females with and without cubs were analyzed separately to assess if there was a difference in stable isotope values between these two groups. Thus, there were five age/sex classes used in the analyses: adult males, adult females with young, solitary adult females, subadult females, and subadult males. Guard hair samples for SIA were collected from a shaved patch on the rump approximately 15 cm lateral to the tail. We obtained 806 hair samples from 559 individual polar bears (Table A.1). The mean (± SE) number of samples yr^{-1} was 54 ± 6.0 (range: 17-106). There were 397 females and 409 males, with 699 adults and 107 subadults. All capture and handling methods were conducted in accordance with the Canadian Council on Animal Care (www.ccac.ca) guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee and Environment and Climate Change Canada's Western and Northern Animal Care Committee. Research was conducted under wildlife research permits issued by the Government of Manitoba and by the Parks Canada Agency.

Surface contaminants (e.g., fat, skin, dirt) on the guard hair samples were removed with a clean scalpel and the hair was then washed in 500 ml milli-Q water with 6 drops of Ivory dish soap at 40°C, rinsed thoroughly, and then dried overnight. Each dried sample was cut into small pieces from which 1 mg was placed into a tin capsule (Rogers et al. 2015). Values of $\delta^{13}C$ and $\delta^{15}N$ were determined via combustion in a EuroVector EA3028-HT elemental analyzer (EuroVector) at 1030°C coupled to a GV Instruments IsoPrime (Manchester) continuous-flow isotope ratio mass spectrometer. Internal laboratory standards NIST 8415 whole egg powder standard reference material ($\delta^{15}N$ = 6.89‰, $\delta^{13}C$ = -23.99‰) were placed for every 20 unknowns in sequence. Values are reported in the standard δ-notation relative to atmospheric nitrogen (Air) and Vienna Pee Dee belemnite limestone for $\delta^{15}N$ and $\delta^{13}C$, respectively. Based on within-run replicate measurements of standards, we estimate analytical precision to be ± 0.2‰ for $\delta^{15}N$ and ± 0.1‰ for $\delta^{13}C$. SIA was conducted at the Biogeochemical Analytical Service Laboratory at the University of Alberta, Edmonton, Canada.

2.2.3 Age- and sex-related patterns

We used Kruskal-Wallis tests to determine whether there were significant differences in $\delta^{15}N$ and $\delta^{13}C$ values among age/sex classes and post hoc Dunn's tests when significant differences were detected.

The package Stable Isotope Bayesian Ellipses in R (SIBER) was used to compare isotopic niche size and overlap among age/sex classes (Jackson et al. 2011, Young and Ferguson 2014, Yurkowski et al. 2016). Isotopic niches are a subset of ecological niches and can be used to study differences in foraging ecology between groups (Layman et al. 2007, Jackson et al. 2011). We used the isotopic niche size to indicate the diversity of prey in the predator's diet, where a larger isotopic niche size reflects a broader prey diversity (Jackson et al. 2011, Yurkowski et al. 2016). For each group, approximately 40% of the isotopic data was encompassed to create the standard ellipse with a standard ellipse area corrected for small sample sizes (SEA_C) to plot the isotopic niche (Jackson et al. 2011, Young and Ferguson 2014, Yurkowski et al. 2016). We then calculated the percentage overlap in isotopic niches between groups (Jackson et al. 2011, Young and Ferguson 2014, Yurkowski et al. 2016). We estimated the isotopic niche size using a Bayesian technique (iterations: 50 000; burn-in: 10 000; thin: 10; Markov chain Monte Carlo [MCMC] chains: 2; covariance matrix prior: inverse Wishart; means prior: vague normal) to determine the mode standard ellipse area and 95% credible interval (SEA_B) (Jackson et al. 2011, Yurkowski et al. 2016). Lastly, we quantitatively compared isotopic niche sizes among age/sex classes and among years by calculating the probability that a group's posterior distribution of ellipse area was smaller than that of the other groups (i.e., the proportion of posterior distributions that were smaller) (Yurkowski et al. 2016). Unlike previous methods of estimating the isotopic niche width that were sensitive to sample size bias (i.e., convex hull), the standard ellipse area is calculated using a Bayesian technique and thus allows for robust quantitative comparisons between groups with different sample sizes (Jackson et al. 2011).

2.2.4 Temporal patterns

We used linear regression to assess the relationship between $\delta^{15}N$ values and year. Due to the observed pattern of a decrease then increase in $\delta^{13}C$ values, we used a broken stick regression to determine the breakpoint in $\delta^{13}C$ values over time; linear regression analyses were conducted to examine the relationship between $\delta^{13}C$ values and year before and after the breakpoint. To determine if the effect of year differed among age/sex classes, we used multiple linear regression to analyze the relationship between $\delta^{15}N$ and $\delta^{13}C$ values and age/sex class, year, and the interaction of these 2 factors. In addition, we used SIBER to compare the population's isotopic niches for each year from 1993-1994 and 2004-2016 to further evaluate trends in foraging over time. SIBER was also used to compare the yearly isotopic niches for adult females and adult males separately.

2.2.5 Relationship between bear isotopic values and sea ice cover

We calculated annual dates of sea ice breakup and freeze-up for the WH management zone portion (Fig. 2.1) of Hudson Bay from 25 × 25 km resolution passive microwave satellite raster imagery from the National Snow and Ice Data Center in Boulder, Colorado (Cavalieri et al. 1996). Date of breakup was defined as the first ordinal date in spring on which sea ice concentration was $\leq 50\%$ for 3 consecutive days and date of freeze-up as the first ordinal date in autumn on which sea ice concentration was $\geq 10\%$ for 3 consecutive days (Etkin 1991, Stirling et al. 1999, Lunn et al. 2016). We derived the variable 'open-water period' as a proxy for the length of time bears spend onshore by subtracting date of breakup from date of freeze-up and then subtracting 25 d because bears typically come ashore 20-30 d after the 50% breakup date (Stirling et al. 1999, Castro de la Guardia et al. 2017). Pearson's correlation analyses were used to examine the relationship between foraging ecology (mean yearly $\delta^{15}N$ values, mean yearly $\delta^{13}C$ values, or yearly isotopic niche sizes) and the sea ice variable (length of the open-water period).

We used Shapiro-Wilk's tests for normality of all variables. When non-normally distributed (Shapiro-Wilk $p \leq 0.05$), non-parametric tests were used if standard transformations ($\log_{10}$ and square root) did not normalize the data: Kruskal-Wallis tests were used to analyze $\delta^{15}N$ and $\delta^{13}C$ values among age/sex classes, while $\log_{10}$ transformation was used to normalize yearly isotopic niche size. All statistical analyses were conducted in R v.3.4.0 (R Core Team 2017).

2.2.6 Stable isotope mixing models

We created stable isotope mixing models to estimate the contributions of various prey species to the diet of WH polar bears (Inger et al. 2006, Cherry et al. 2011, Rogers et al. 2015). Mixing models were created using the package Bayesian Mixing Models in R (MixSIAR), which uses Bayesian methods to estimate possible diet combinations as probability distributions (iterations: 1 000 000; burn-in: 500 000; thinned by 500) (Stock and Semmens 2016). We obtained prey isotopic information from published data on species that constitute WH polar bear diet (Thiemann et al. 2008): ringed seal muscle (mean ± SD of adults and pups from 2006: $\delta^{15}N = 13.8 \pm 0.7‰$, $\delta^{13}C = -20.0 \pm 0.5‰$), harbour seal muscle (pups from 1999-2006: $\delta^{15}N = 16.3 \pm 1.0‰$; $\delta^{13}C = -19.7 \pm 0.8‰$), bearded seal muscle (pups from 2005-2006: $\delta^{15}N = 16.8 \pm 0.9‰$;

$\delta^{13}C = -18.1 \pm 0.3‰$) (Young et al. 2010), and harp seal muscle (from 1996: $\delta^{15}N = 13.5 \pm 0.7‰$; $\delta^{13}C = -18.0 \pm 0.5‰$) (Hammill et al. 2005). Muscle was used because it was the most common tissue type available for prey stable isotope data and the protein from prey muscle tissue would be routed to the polar bear protein metabolic pathway (Cherry et al. 2011). Trophic enrichment factors (TEFs) were included in mixing models to account for the difference in isotope values between a predator's tissue and its diet (Rode et al. 2016). Diet-to-hair TEFs of 4.5 ± 1.51‰ (SD) for $\delta^{15}N$ (brown bears *Ursus arctos*; Rode et al. 2016) and 2.23 ± 1.86‰ for $\delta^{13}C$ (estimated using the package Stable Isotope Discrimination Estimation in R [SIDER]; Healy et al. 2018) were used in the mixing models.

2.3 Results

2.3.1 Age- and sex-related patterns

Values of $\delta^{15}N$ were significantly different among age/sex classes (Kruskal-Wallis $\chi^2 = 406.0$, df = 4, $p \leq 0.001$). There was a significant difference in $\delta^{15}N$ values between all comparisons of age/sex classes except between subadult females and subadult males. Adult males had significantly higher hair $\delta^{15}N$ values than all other classes, solitary adult females had significantly higher $\delta^{15}N$ values than subadults, and adult females with young had significantly lower $\delta^{15}N$ values than all other classes (Table 2.1; Table A.2). Similarly, $\delta^{13}C$ values were significantly different among age/sex classes (Kruskal-Wallis $\chi^2 = 46.9$, df = 4, $p \leq 0.001$). Adult males had significantly higher $\delta^{13}C$ values than all other classes while there were no significant differences in $\delta^{13}C$ values among the other age/sex classes (Table 2.1; Table A.3).

There was variation in percentage overlap of isotopic niches between age/sex classes. Adult females with and without young overlapped to a high degree (79%). However, adult females with young overlapped less with adult males (50%) than did solitary adult females (75%). Adult males overlapped the least with subadults (43-44%), whereas subadult males and subadult females overlapped the most with each other (81%) (Fig. A.1, Table A.4). Isotopic niche sizes of adult males and adult females (solitary and with young) were larger (0.7-0.8‰^{2}) than isotopic niche sizes of subadult males and subadult females (0.5‰^{2}) (Table 2.1; Fig. A.1). All age classes had a high probability of their isotopic niche size being smaller than adult males: adult females with young (72%), solitary adult females (97%), subadult males (99.8%), and sub adult females (99.9%) (Fig. A.1). The probability of the isotopic niche size of solitary adult females being smaller than adult females with young was high (91%). Solitary adult females and adult females with young had a high probability of their isotopic niche size being larger than subadult males (93 and 99%, respectively). Similarly, solitary adult females and adult females with young had a high probability of their isotopic niche size being larger than subadult females (95 and 99.7%, respectively). Lastly, the probability of the isotopic niche size of subadult females being smaller than subadult males was intermediate (49%).

2.3.2 Temporal patterns

There was a significant increase in δ^{15}N values from 1993 (mean ± SD: 18.8 ± 0.5‰) to 2016 (19.5 ± 0.7‰), with a peak in 2014 (19.7 ± 0.6‰) (Fig. 2.2A; linear regression, $R^2 = 0.07$, $F_{1,804} = 57.2$, $p < 0.001$). A similar pattern was noted when data from 2004-2016 were analyzed separately. The broken stick regression indicated a breakpoint in δ^{13}C values in 2011: δ^{13}C values decreased significantly from 1993 (-16.2 ± 0.3‰) to 2011 (-17.7 ± 0.2‰) (Fig. 2.2B;

linear regression, $R^2 = 0.5$, $F_{1,575} = 521.8$, $p < 0.001$) then increased significantly from 2011 to 2016 (-17.0 ± 0.3‰) (Fig. 2.2B; linear regression, $R^2 = 0.2$, $F_{1,294} = 94.3$, $p < 0.001$). We found that while $\delta^{15}N$ and $\delta^{13}C$ values varied significantly over time (multiple linear regression, $R^2 = 0.46$, $F_{7,798} = 96.04$, $p < 0.001$, and $R^2 = 0.27$, $F_{7,798} = 41.93$, $p < 0.001$, respectively), there were no significant interactions for the effects of age/sex class and year on $\delta^{15}N$ ($p > 0.05$) or $\delta^{13}C$ values ($p > 0.05$), and therefore the effect of year did not differ among age/sex classes.

Isotopic niche sizes differed among years: isotopic niche size was highest in 2005, 2006, and 2008, and was lowest in the 1990s and 2011-2013 (Figs. A.2, A.3). Years 1993 and 1994 had high probabilities of their isotopic niche sizes being smaller than most years (> 69%, except when compared to each other and 2011-2013) (Table A.5). Similarly, 2011-2013 had high probabilities of their isotopic niche sizes being smaller than most years (> 60%, except when compared to each other, 1993, and 1994). In contrast, 2005, 2006, and 2008 had high probabilities of their isotopic niche sizes being larger than most years (> 95%, except when compared to each other). The isotopic niche sizes of adult females were largest in 2005, 2006, and 2010, and smallest in 2013 (Figs. A.4, A.5). Similarly, the isotopic niche sizes of adult males were largest in 2004 and 2005, and smallest in the 1990s and 2013 (Figs. A.4, A.5).

2.3.3 Relationship between bear isotopic values and sea ice cover

The mean yearly bear $\delta^{13}C$ values were significantly negatively correlated with the length of the open-water period (Pearson's correlation, $t = -2.4$, $p = 0.03$, $r = -0.6$; Fig. 2.3). The mean yearly bear $\delta^{15}N$ values and the mode yearly SEA_B values (i.e., isotopic niche sizes) were not significantly correlated with the length of the open-water period (Pearson's correlation, $p > 0.05$).

2.3.4 Stable isotope mixing models

Ringed seals (49%) comprised the majority of the overall population diet, followed by harbour seals (20%), bearded seals (19%), then harp seals (12%). Ringed seals were the largest component of the diet for adult females with young (67%), solitary adult females (51%), subadult females (59%), and subadult males (53%), as well as a relatively large part of the diet of adult males (28%) (Table 2.2). Harbour seals were the largest part of the diet of adult males (32%) and were relatively high contributions to the diet of solitary adult females (20%), subadult females (16%), and subadult males (18%). Adult males had higher proportions of bearded seals (29%) than the other age/sex classes (< 20%). Harp seals were generally low in the diet for all age classes (< 14%).

Ringed seals were estimated to be lowest in bear diet in the 1990s (17-21%) and highest in 2008 (72%) (Fig. 2.4, Table A.6). Harbour seals comprised lower proportions of the diet in the 1990s (3%), then increased in the diet over time after 2009 (> 15%). Bearded seals comprised a large part of the diet in the 1990s (23-24%), decreased in 2004-2007 (< 20%), then increased in 2008 (26%) and 2013 (29%). Harp seals contributed a larger proportion to the diet in the 1990s and 2004-2005 (29-56%) but were a smaller proportion of the diet in most years (< 22%).

2.4 Discussion

We found significant variation in polar bear hair $\delta^{15}N$ and $\delta^{13}C$ values both within the WH and over time from 1993-2016, as well as a correlation between $\delta^{13}C$ values and sea ice dynamics. Our results suggest that (1) the food web baseline (i.e., primary producer) isotope values have changed, (2) the Hudson Bay ecosystem has changed (e.g., food web reorganization), (3) there have been alterations in polar bear foraging ecology, and/or (4) there have been changes to polar bear fasting.

2.4.1 Age- and sex-related patterns

Adult males had the highest $\delta^{15}N$ (median 0.5-1‰ higher) and $\delta^{13}C$ values (median 0.2-0.3‰ higher), and largest isotopic niche size compared to the other age/sex classes, as well as the lowest amounts of isotopic niche overlap with the other classes. Higher hair $\delta^{15}N$ values may result from differences in diet; for example, the consumption of bearded seal pups in western Hudson Bay, which have higher $\delta^{15}N$ values (muscle mean: 16.8‰) than other prey (Young et al. 2010). Similarly, the higher $\delta^{13}C$ values of adult male polar bears suggests they are consuming higher proportions of prey with a benthic source, such as bearded seals (McKinney et al. 2009). These results are consistent with Thiemann et al. (2008, 2011a), who used quantitative fatty acid signature analysis of WH polar bears and showed that adult males consumed more bearded seals than other age/sex classes. Similarly, our mixing model estimated that adult males consumed more bearded seals and harbour seals than the other age/sex classes. Additionally, bearded seals and harbour seals use broken ice areas (Cameron and Boveng 2009, Bajzak et al. 2013), which is habitat used more by adult male polar bears, and adult males hunt larger prey than other bears (Stirling and Derocher 1990). Furthermore, spatial differences between males and females may have influenced isotopic values, whereby the use of coastal/nearshore areas by adult males in the summer may have increased their $\delta^{15}N$ and $\delta^{13}C$ values relative to females in inland areas. We also found that adult males had a larger isotopic niche size than other bears. A similar finding was noted by Thiemann et al. (2011a) and indicates that adult males have a more generalist and broader foraging strategy than adult females and subadults that rely mainly on ringed seals. A more generalist foraging strategy may enable adult males to hunt a larger range of prey than other age/sex classes and allow them to alter foraging behaviour in response to changes in prey availability (Thiemann et al. 2011a). In contrast, as a consequence of having a narrower range of prey in their diet, adult females and subadults may be at greater risk from changes in prey availability due to sea ice loss (Thiemann et al. 2011a). Lastly, adult males may have higher $\delta^{15}N$ values because during the spring breeding season their primary activity is mating (Stirling et al. 2016) so they hunt less and are more dependent on fasting, which, in extreme cases, can increase $\delta^{15}N$ values (Hobson et al. 1993).

Adult female reproductive status influenced both $\delta^{15}N$ values and isotopic niche size, most likely as a result of the physiological demands of gestation and lactation. Solitary females may have mated in the spring and were potentially pregnant during the fall capture. Reproductive female black bears (*Ursus americanus*) have more than twice the rate of protein loss as nonreproductive females (Harlow et al. 2002); thus, pregnant female polar bears in our study may have consumed more muscle to increase their protein intake to support reproduction, leading to an increase in their hair $\delta^{15}N$ values. Lactation by females with cubs may also lead to lower $\delta^{15}N$ values (Polischuk et al. 2001). Alternatively, the significantly higher $\delta^{15}N$ values of solitary females (19.3‰) suggests that they are feeding at a higher trophic level than females with young (18.8‰). However, there was no significant difference in $\delta^{13}C$ values between adult females with or without young, suggesting little variation in the carbon sources of the prey consumed; that is, similar proportions of benthic-feeding prey (bearded seals) versus pelagic-feeding prey (ringed, harbour, and harp seals) (McKinney et al. 2009). Therefore, the variation in $\delta^{15}N$ values between females with and without cubs may reflect differences in the proportion of pelagic-feeding species in their diets. For example, ringed seal pups have the lowest $\delta^{15}N$ values of western Hudson Bay seal species (Young et al. 2010) and female polar bears with cubs rely on ringed seal pups (Stirling et al. 1993), which would result in their having lower hair $\delta^{15}N$ values. This is supported by our mixing model result that adult females with young consumed higher proportions of ringed seals than solitary females, while solitary females consumed more harbour seals than adult females with young. Furthermore, adult females with young had a larger isotopic niche size (indicating a more generalist foraging strategy) than solitary adult females. The number and age of the cubs may influence the mother's habitat use and foraging behaviour due to different energetic requirements and hunting abilities of the accompanying cubs (Stirling 1974, Stirling et al. 1993, Sciullo et al. 2017). Future research on isotopic patterns of family groups (females with different numbers of cubs and cubs of different ages) would improve our understanding of variation in foraging ecology within WH. Females with cubs may have a wider range of foraging strategies (e.g., scavenging), which would increase dietary variation (Thiemann et al. 2011a, Sciullo et al. 2017). In contrast, solitary adult females had smaller isotopic niche sizes, suggesting that they targeted particular resources (Yurkowski et al. 2016). These females would not be constrained by cubs and could therefore forage optimally to maximize energy gain without needing to avoid infanticidal males (Stirling et al. 1993) or open water. Lastly, larger overlap between solitary adult females and adult males in isotopic niches and diet suggests similarities in foraging ecology. In contrast, the lower amount of isotopic niche and dietary overlap between adult females with young and adult males is consistent with their occupying different areas and isotopic niche spaces.

Differences in isotopic values between adults and subadults suggests that WH polar bears differ in their foraging ecology based on age class, provided isotopic discrimination between diet and hair is independent of age. The intermediate $\delta^{15}N$ values for subadults (males: 19.0‰;

females: 19.1‰) suggests that they may have fed at lower trophic levels than adult males (19.8‰), potentially reflecting increased predation of juvenile ringed seals (which have midrange δ^{15}N values; mean: 13.8‰) (Young et al. 2010). The smaller isotopic niches of subadult polar bears suggest they are limited in their prey, likely because of their lack of hunting experience. Thiemann et al. (2011a) also found that subadults had narrower diets than adults and suggested that subadults foraged mainly on ringed seals, with little scavenging on other prey. In contrast, adults had larger isotopic niches than subadults, indicating that they had greater variation in foraging ecology. The larger isotopic niche of adults may be the result of the spatial separation and thus prey differences between adult females and males (Stirling et al. 1993) as well as the ability of adults to adopt different foraging strategies in response to changes in prey availability (Thiemann et al. 2011a). Subadult females and subadult males had high isotopic niche overlap with each other, which indicates that they occupy similar isotopic niche spaces. Subadults had the greatest amount of isotopic niche overlap with solitary adult females and secondly with adult females with young, which is similar to Thiemann et al.'s (2011a) results and our mixing model estimates that these groups rely heavily on ringed seals. In contrast, there was low overlap between subadults and adult males, which may be because adult males kleptoparasitize subadults (Stirling 1974), and subadults may therefore avoid adult males, resulting in different isotopic niche spaces.

2.4.2 Temporal patterns and sea ice

The Hudson Bay ecosystem underwent a regime shift after the mid-1990s as a consequence of warming-induced distribution shifts of forage fish (Gaston et al. 2003, 2012). Subsequent dietary shifts from Arctic cod (*Boreogadus saida*) towards subarctic species such as capelin (*Mallotus villosus*) and sandlance (*Ammodytes* sp.) have been observed in lower trophic level predators such as thick-billed murres (*Uria lomvia*) (Gaston et al. 2003) and ringed seals (Young and Ferguson 2014, Yurkowski et al. 2016). Similarly, the lengthening of the open-water period due to sea ice decline in the Arctic supports an increase in subarctic marine mammals such as harbour seals (Florko et al. 2018).

The variation in the WH polar bear population's yearly isotopic niche size may reflect differences in the diversity of polar bear prey over time. Larger isotopic niches in 2005, 2006, and 2008 suggest that a larger variety of prey were consumed. The larger isotopic niche sizes corresponded with higher proportions of harbour/harp seals in the diet of female polar bears in 2004/2005 (Sciullo et al. 2017), similar to our mixing model results of higher proportions of harbour seals in 2005, harp seals in 2005/2006, and bearded/ringed seal in 2008 relative to most other years. We found that WH polar bears had smaller isotopic niche sizes in the 1990s and 2011-2013, which indicates lower prey diversity. Similarly, our mixing model results and Sciullo et al. (2017) indicate that certain species dominated the diet in those years (ringed seals in 2011/2012 and bearded/harp seals in 2013). The isotopic niche sizes of adult females and adult males showed a similar pattern as the overall population, with larger isotopic niches in the early 2000s followed by a decline until 2013. We found that adult females had larger isotopic niches than males in 2010, while Sciullo et al. (2017) also reported that adult female diet had an increase in bearded and harp seals in 2010. While we found the overall population's isotopic niche size increased slightly after 2013, the isotopic niche sizes of adult females and adult males both initially increased in 2014 but then declined, suggesting a decrease in dietary variation in more recent years.

Temporal changes in hair stable isotope values may be associated with 4 different processes that are not necessarily mutually exclusive: (1) changes in the food web baseline isotope values (primary producers); (2) ecosystem changes (e.g., reorganization of the food web); (3) alterations in polar bear foraging ecology; and/or (4) changes in the duration and intensity of fasting. However, data required to conclusively differentiate between these hypotheses is lacking. Nonetheless, we found that isotopic values in WH polar bears changed from the early 1990s to 2016. First, the observed increase in hair $\delta^{15}N$ values may reflect an increase in the baseline (primary producer) $\delta^{15}N$ values over this period (McKinney et al. 2009, Yurkowski et al. 2016, Lowther et al. 2017). For example, Yurkowski et al. (2016) showed that $\delta^{15}N$ values in ringed seal muscle throughout the Arctic increased from 1990 to 2011 (e.g., from 16.1 to 17.3‰ in Resolute, Nunavut, Canada), which was attributed to the effect of sea ice variability on prey availability. Increased polar bear $\delta^{15}N$ values may thus have been driven by prey $\delta^{15}N$ value increases or may have been similarly influenced by changes to prey availability. Alternatively, increasing $\delta^{15}N$ values of hair may indicate that WH polar bears may be feeding at a higher trophic level more recently (mean in 2014: 19.7‰) than in the early 1990s (mean in 1994: 18.7‰). For instance, harbour seals in western Hudson Bay had higher $\delta^{15}N$ values (mean: 16.3‰) than ringed seals (mean: 13.8‰) (Young et al. 2010) and the increase in polar bear $\delta^{15}N$ values over time may reflect increased consumption of harbour seals. This hypothesis is supported by our mixing model estimates of higher proportions of harbour seals in the diet over time. Changes in sea ice conditions may affect prey availability, as harbour seals increased and ringed seals decreased in WH polar bear diet from 1994 to 1998, which was correlated with earlier breakup (Iverson et al. 2006). Furthermore, harbour seals increased in abundance as sea ice cover declined in western Hudson Bay from 1996 to 2016 (Florko et al.

2018). Lastly, higher $\delta^{15}N$ values have also been associated with fasting (Hobson et al. 1993) and WH polar bears have been reported to be spending more time on land, without access to prey, because of earlier breakup and later freeze-up (Stirling et al. 1999, Regehr et al. 2007, Lunn et al. 2016), potentially leading to an increase in $\delta^{15}N$ values.

Similar to hair $\delta^{15}N$ values, changes in bear hair $\delta^{13}C$ values over time may be the result of shifts in lower trophic level dynamics and/or polar bear foraging ecology (McKinney et al. 2009, Yurkowski et al. 2016, Lowther et al. 2017). The temporal pattern of $\delta^{13}C$ values was more variable than $\delta^{15}N$ and was correlated with the open-water period. Firstly, the highest $\delta^{13}C$ values in the 1990s suggest a focus on benthic-foraging prey (e.g., bearded seals) (McKinney et al. 2009), and high $\delta^{13}C$ values were associated with a shorter open-water period (which would increase access to ice-associated prey). These results correspond with the mixing model estimates of high proportions of bearded seals in the 1990s. Secondly, the decrease in $\delta^{13}C$ values from the 1990s (mean: -16.2‰) to 2010 (mean: -17.7‰) suggests a shift towards more pelagic-foraging prey (McKinney et al. 2009), coinciding with higher proportions of harp seals in WH female diets (Sciullo et al. 2017) and harbour seals from our results in 2010. Thirdly, the increase in bear $\delta^{13}C$ values in 2013 (mean: -16.8‰) indicates more benthic-foraging prey, which corresponds with a decline in ringed seal density and pup recruitment in western Hudson Bay (Young et al. 2015, Ferguson et al. 2017). Similarly, our diet estimates and Sciullo et al. (2017) indicate a decrease in ringed seals and increase in bearded seals in 2013 diets. Lastly, $\delta^{13}C$ values decreased again after 2013 (mean: -17.3‰), suggesting further dietary shifts towards pelagic species. Lower bear $\delta^{13}C$ values were correlated with a longer open-water period, similar to the relationship between lower polar bear $\delta^{13}C$ values and earlier sea ice breakup in western Hudson Bay (McKinney et al. 2009). Further, these results suggest that sea ice decline may drive shifts in polar bear foraging ecology between ice-associated and open-water prey, which will likely continue as the open-water period increases (Thiemann et al. 2008).

The change in the Hudson Bay ecosystem composition over our study period may have influenced the observed temporal patterns in WH polar bear $\delta^{15}N$ values, $\delta^{13}C$ values, isotopic niche size, and dietary estimates. We found that temporal patterns in polar bear isotopic values were related to phenological changes in western Hudson Bay. Sea ice phenology drives ecosystem processes in the Arctic, such as ice-associated algae production (Sibert et al. 2010), with consequences for the foraging ecology of higher trophic levels (Søreide et al. 2010, Brown et al. 2018). Furthermore, sea ice decline and subsequent changes to Arctic primary productivity may lead to a shift from a sea ice-dominated ecosystem towards a pelagic ecosystem (Leu et al. 2011), thus affecting polar bear prey availability and Arctic trophic interactions. The WH population has experienced declines in reproduction, survival, and abundance (Stirling et al. 1999, Regehr et al. 2007, Lunn et al. 2016) and future climate projections predict earlier breakup and later freeze-up (Castro de la Guardia et al. 2013), which have the potential to further alter WH polar bears and Hudson Bay food web dynamics. SIA can be a powerful method for monitoring ecological dynamics in the changing Arctic. However, there are challenges associated with this technique, including the ability to separate shifts in predator diet from changes in lower trophic levels (e.g., baseline shifts or changes in prey species). Polar bear isotopic values may therefore be a useful but complex tool for monitoring changes in Arctic trophic dynamics, which would benefit from additional data on the food web baseline and changes in prey isotopic values over time to better understand ecosystem changes. Climate change-induced sea ice loss is predicted to continue to affect Arctic marine ecosystem structure and biodiversity. Research employing stable isotope analysis at multiple trophic levels will provide more refined means to detect potential changes in food web structure and foraging ecology of individual species in this rapidly changing ecosystem.

Epilogue

Since the publication of Johnson et al. (2019), isotopic analyses of WH polar bears have expanded: Yurkowski et al. (2020) examined multidimensional niche dynamics (mercury, $\delta^{15}N$ values, and $\delta^{13}C$ values) and body fat indices for polar bears as well as relationships to ringed seal niche dynamics. Here, we found a decrease in WH polar bear 3-dimensional niche size over time as well as an increase in $\delta^{13}C$ spacing between polar bears and ringed seals, with potential implications for the strength of this predator-prey relationship.

Table 2.1: Median $\delta^{15}N$ values and $\delta^{13}C$ values ± median absolute deviation (‰) and the isotopic niche sizes (i.e., mode standard ellipse area [SEA_B]) with its 95% credible interval (95% CI) for each age/sex class of Western Hudson Bay polar bears. Significant differences are indicated by superscript letters (groups with different letters were significantly different from each other; Dunn's test $p \leq 0.05$; Tables A.2 & A.3).

Age/sex class	n	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	SEA_B (‰^{2}) (95% CI)
Adult female with young	218	18.8 ± 0.4^a	-17.3 ± 0.5^a	0.8 (0.7, 0.9)
Solitary adult female	117	19.3 ± 0.4^b	-17.3 ± 0.5^a	0.7 (0.5, 0.8)
Adult male	364	19.8 ± 0.5^c	-17.0 ± 0.6^b	0.8 (0.7, 0.9)
Subadult female	62	19.1 ± 0.5^d	-17.2 ± 0.4^a	0.5 (0.4, 0.6)
Subadult male	45	19.0 ± 0.3^d	-17.2 ± 0.5^a	0.5 (0.4, 0.7)

Table 2.2: Mean estimated proportion (%) of each prey item in the diet of each Western Hudson Bay polar bear age/sex class from the stable isotope mixing model (and 95% Bayesian credible intervals).

		Prey contribution to diet (95% CI) (%)			
Age/sex class	n	Ringed seal	Bearded seal	Harbour seal	Harp seal
Adult female with young	218	67 (44, 85)	8.8 (2.3, 23)	11 (3.3, 24)	14 (4.2, 32)
Solitary adult female	117	51 (29, 74)	14 (4.4, 33)	20 (7.0, 40)	14 (4.3, 31)
Adult male	364	28 (12, 48)	29 (12, 55)	32 (13, 55)	11 (3.3, 24)
Subadult female	62	59 (35, 80)	15 (4.4, 35)	16 (5.1, 33)	10 (3.0, 24)
Subadult male	45	53 (28, 75)	20 (6.6, 43)	18 (5.6, 36)	9.2 (2.5, 21)

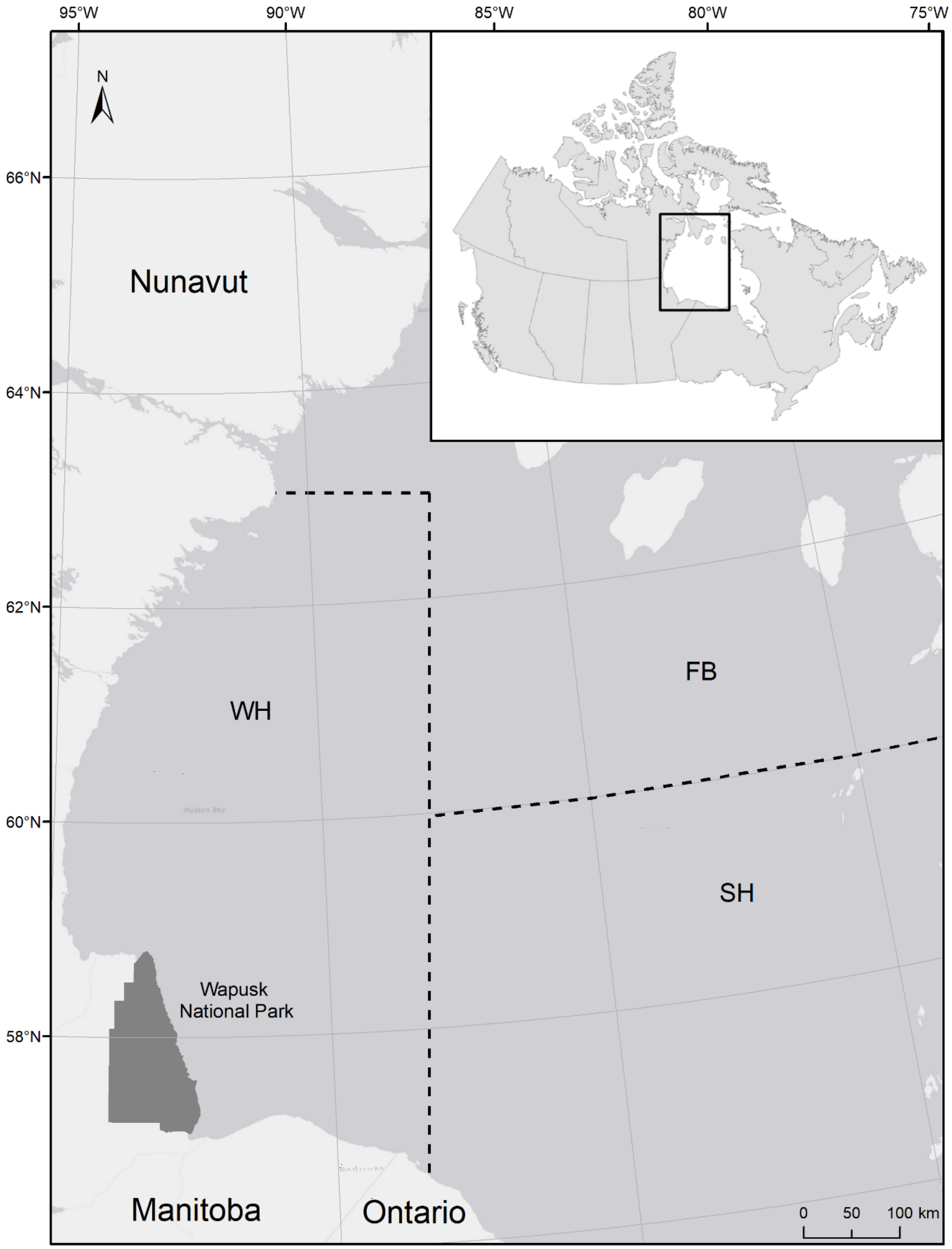

Figure 2.1: Western Hudson Bay, Canada, showing Wapusk National Park and adjacent areas where polar bears were captured in 1993-1994 and 2004-2016. Dashed lines: management boundaries of the Western Hudson Bay (WH), Southern Hudson Bay (SH) and Foxe Basin (FB) polar bear populations (Peacock et al. 2010).

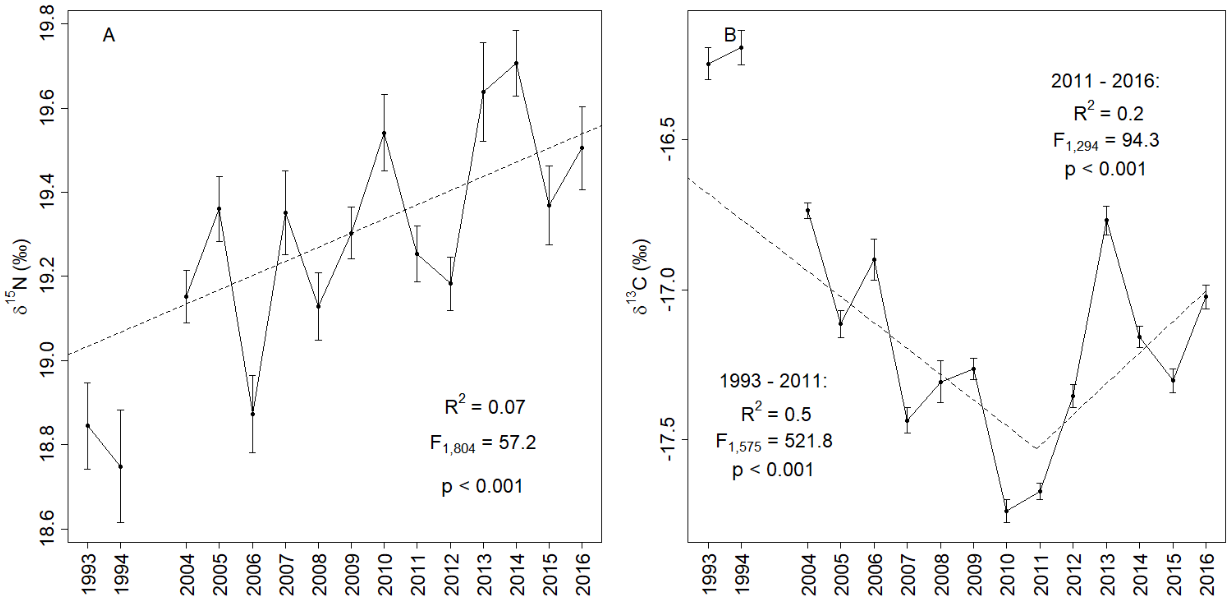

Figure 2.2: Mean (± SE) (A) $\delta^{15}N$ and (B) $\delta^{13}C$ values for Western Hudson Bay polar bears in each year (1993-1994, 2004-2016). Dashed lines: regression line for the relationship between (A) $\delta^{15}N$ values and year and (B) $\delta^{13}C$ values and year before and after the breakpoint in 2011.

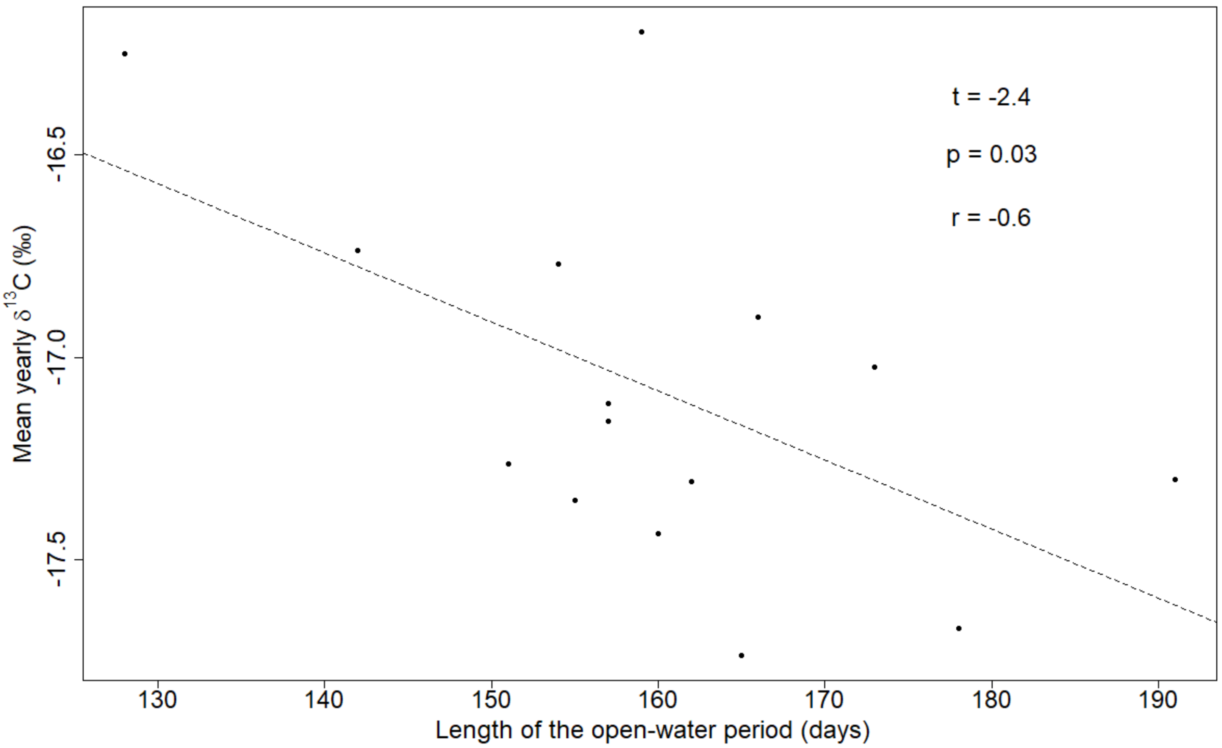

Figure 2.3: Significant correlation between mean yearly $\delta^{13}C$ values for Western Hudson Bay polar bears and the length of the open-water period (Pearson's correlation $p \leq 0.05$).

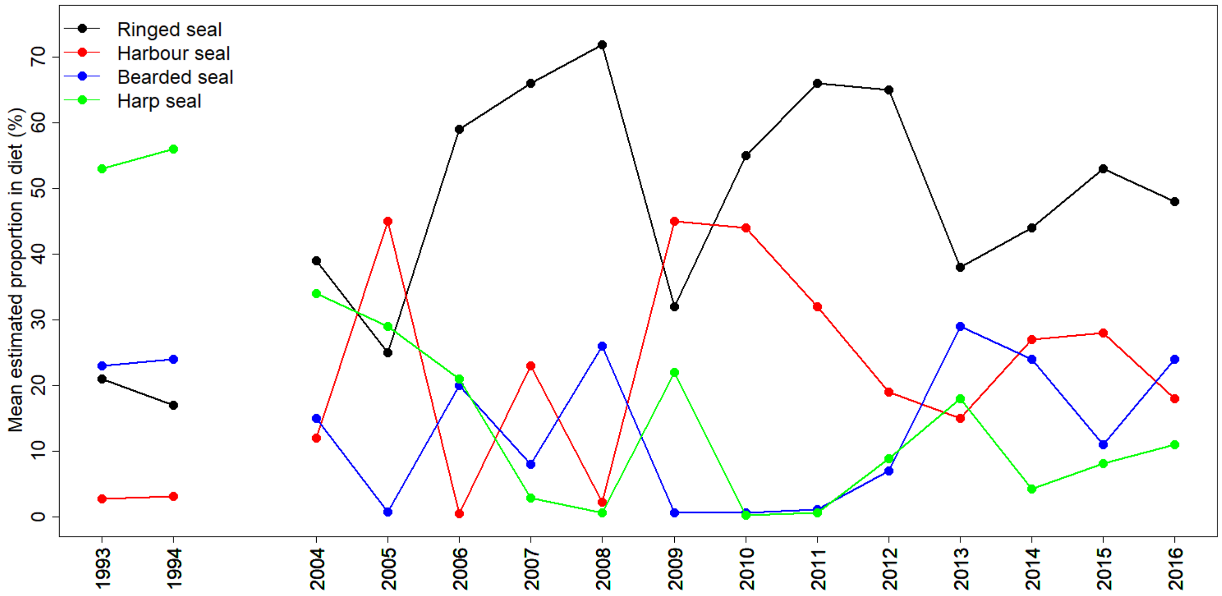

Figure 2.4: Mean estimated proportion (%) of each prey item in the diet of Western Hudson Bay polar bears (all age/sex classes) in each year from the stable isotope mixing model.

Appendices

A.1 Additional tables

Table A.1: Sample sizes of Western Hudson Bay polar bears for each age/sex class in each year (1993-1994, 2004-2016).

Year	Adult female with young	Solitary adult female	Adult male	Subadult female	Subadult male
1993	8	7	6	0	1
1994	12	0	5	0	0
2004	19	5	59	13	10
2005	22	8	32	7	4
2006	20	7	31	4	5
2007	13	3	24	0	0
2008	15	9	16	5	6
2009	23	6	27	11	5
2010	16	8	33	2	3
2011	13	16	27	7	4
2012	9	7	22	4	2
2013	5	6	13	1	1
2014	16	15	27	5	1
2015	13	10	19	2	2
2016	14	10	23	1	1

Table A.2: Dunn's test comparing nitrogen stable isotope ratios ($\delta^{15}N$) (‰) between Western Hudson Bay polar bear age/sex classes. Significant differences between age/sex classes are indicated by asterisks (* indicates significant at $p \leq 0.05$; ** significant at $p \leq 0.001$).

	n	Adult female with young	Solitary adult female	Adult male	Subadult female	Subadult male
Adult female with young	218	–	≤ 0.001**	≤ 0.001**	0.002*	0.016*
Solitary adult female	117		–	≤ 0.001**	0.0108*	0.0079*
Adult male	364			–	≤ 0.001**	≤ 0.001**
Subadult female	62				–	0.3741
Subadult male	45					–

Table A.3: Dunn's test comparing carbon stable isotope ratios ($\delta^{13}C$) (‰) between Western Hudson Bay polar bear age/sex classes. Significant differences between age/sex classes are indicated by asterisks (* indicates significant at $p \leq 0.05$; ** significant at $p \leq 0.001$).

	n	Adult female with young	Solitary adult female	Adult male	Subadult female	Subadult male
Adult female with young	218	–	0.46	≤ 0.001**	0.46	0.18
Solitary adult female	117		–	≤ 0.001**	0.43	0.18
Adult male	364			–	≤ 0.001**	0.015*
Subadult female	62				–	0.24
Subadult male	45					–

Table A.4: Percentage overlap (%) of the isotopic niches between Western Hudson Bay polar bear age/sex classes.

	n	Adult female with young	Solitary adult female	Adult male	Subadult female	Subadult male
Adult female with young	218	–	79	50	63	65
Solitary adult female	117		–	75	71	73
Adult male	364			–	43	44
Subadult female	62				–	81
Subadult male	45					–

Table A.5: Comparison of the isotopic niche sizes among years: the probability that the posterior distribution of ellipse area for the year in the first column was smaller than that of the years in the top row (i.e., the proportion of posterior distributions that were smaller).

	1993	1994	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
1993	–	57%	97%	99.9%	99.9%	77%	99.8%	97%	97%	72%	46%	57%	91%	94%	93%
1994		–	92%	99.9%	99.9%	69%	99%	92%	93%	64%	38%	49%	84%	89%	87%
2004			–	99.9%	99.9%	9%	98%	54%	58%	3%	0.5%	4%	25%	41%	37%
2005				–	66%	0%	12%	< 0.1%	0.1%	0%	0%	< 0.1%	0%	0.1%	< 0.1%
2006					–	0%	6%	0%	< 0.1%	0%	0%	< 0.1%	0%	< 0.1%	< 0.1%
2007						–	99.6%	91%	91%	40%	15%	28%	75%	84%	81%
2008							–	4%	5%	< 0.1%	0%	0.3%	1%	3%	3%
2009								–	54%	3%	0.6%	4%	24%	39%	34%
2010									–	3%	0.6%	4%	22%	36%	32%
2011										–	18%	34%	86%	92%	90%
2012											–	63%	97%	98%	98%
2013												–	88%	92%	91%
2014													–	64%	60%
2015														–	46%

Table A.6: The mean estimated proportion (%) of each prey item in the diet of Western Hudson Bay polar bears (all age/sex classes) in each year from the stable isotope mixing model (and 95% Bayesian credible intervals).

Year	Sample size	Ringed seal	Bearded seal	Harbour seal	Harp seal
1993	22	21 (11, 34)	23 (12, 38)	2.8 (0.1, 10)	53 (37, 67)
1994	17	17 (7.8, 28)	24 (12, 41)	3.1 (0.1, 11)	56 (40, 70)
2004	106	39 (26, 53)	15 (8.0, 26)	12 (5.1, 22)	34 (22, 47)
2005	73	25 (15, 37)	0.8 (0, 2.9)	45 (32, 60)	29 (18, 41)
2006	67	59 (44, 71)	20 (12, 33)	0.5 (0, 1.9)	21 (12, 31)
2007	40	66 (50, 79)	8.2 (2.0, 17)	23 (12, 37)	2.9 (0.1, 9.7)
2008	51	72 (56, 82)	26 (15, 41)	2.3 (0, 8.0)	0.6 (0, 2.7)
2009	72	32 (20, 46)	0.6 (0, 2.3)	45 (32, 60)	22 (13, 33)
2010	62	55 (38, 70)	0.6 (0, 24)	44 (29, 61)	0.3 (0, 1.2)
2011	67	70 (51, 79)	1.1 (0, 4.1)	32 (20, 48)	0.6 (0, 2.4)
2012	44	65 (47, 81)	7.0 (0.5, 18)	19 (7.2, 35)	8.9 (0.6, 19)
2013	26	38 (21, 56)	29 (16, 46)	15 (3.1, 31)	18 (7.3, 31)
2014	64	44 (29, 60)	24 (14, 39)	27 (15, 43)	4.3 (0.2, 12)
2015	46	53 (35, 69)	11 (3.0, 23)	28 (14, 45)	8.1 (0.9, 17)
2016	49	48 (31, 64)	24 (13, 39)	18 (7.2, 31)	11 (3.3, 20)

A.2 Additional figures

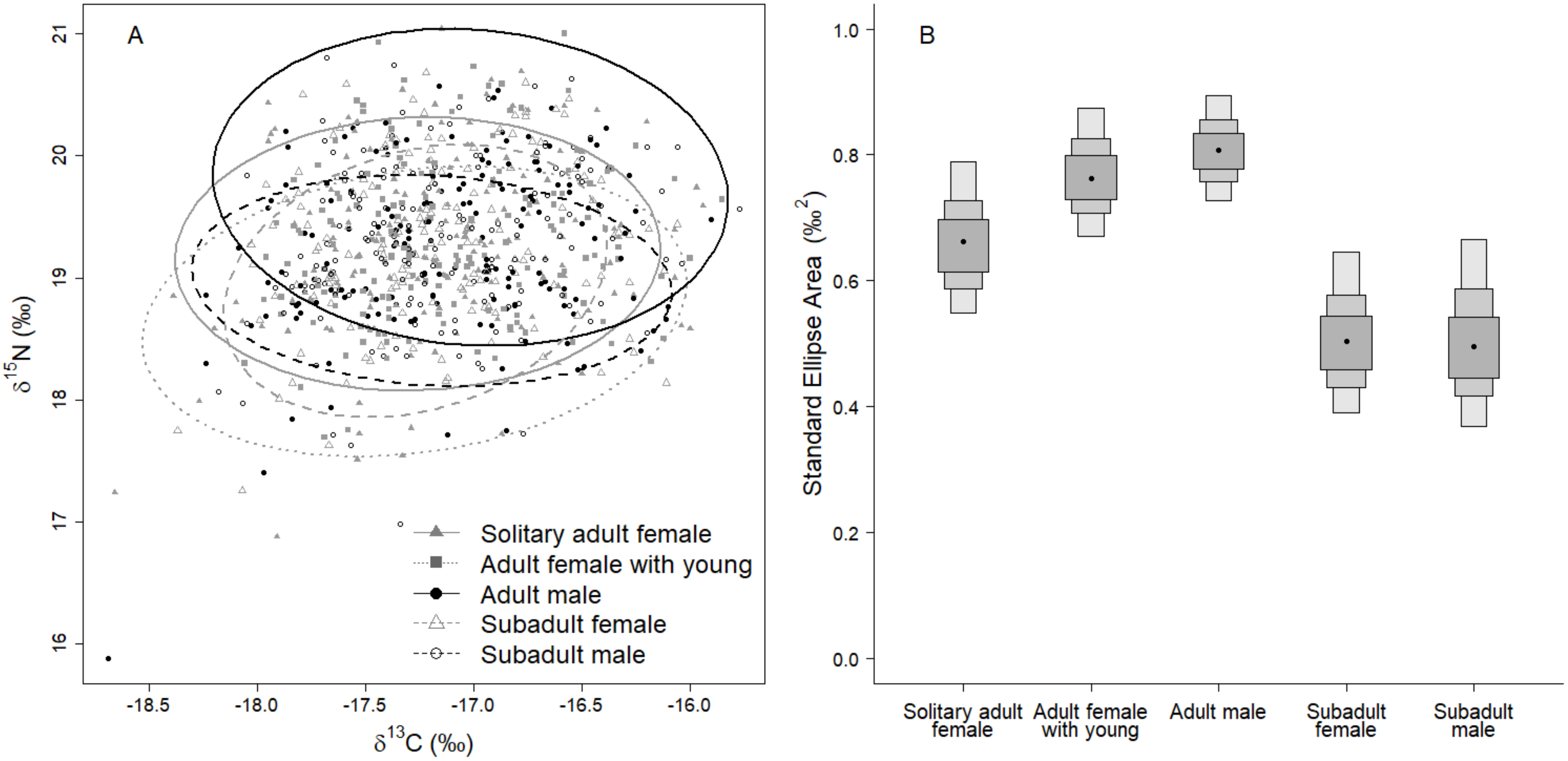

Figure A.1: SIBER (Stable Isotope Bayesian Ellipses in R) ellipses showing the isotopic niches (A) and the isotopic niche sizes (i.e., standard ellipse areas) (B) for each of Western Hudson Bay polar bear age/sex classes.

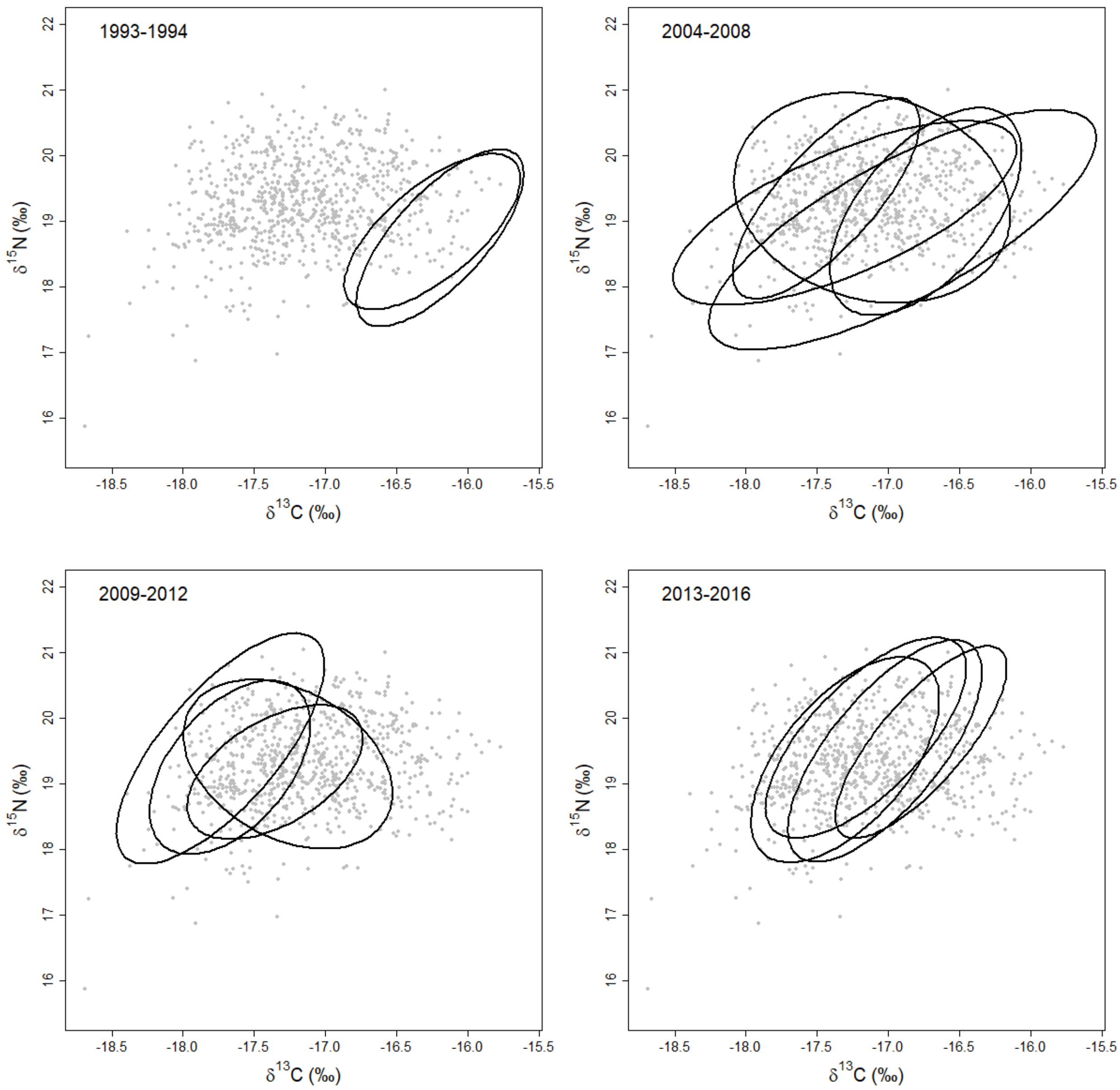

Figure A.2: SIBER (Stable Isotope Bayesian Ellipses in R) ellipses showing the isotopic niches of the Western Hudson Bay polar bear population for each year.

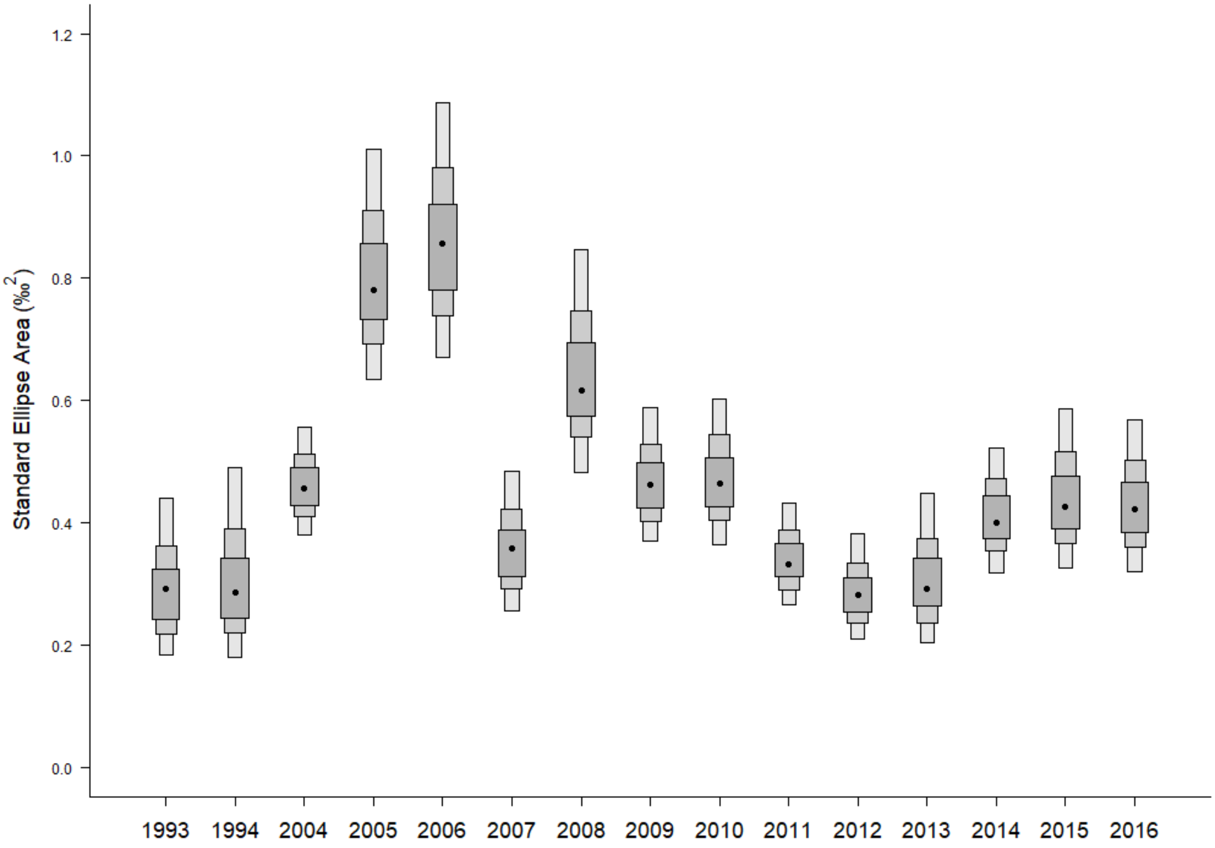

Figure A.3: The yearly isotopic niche sizes (i.e., standard ellipse areas) for Western Hudson Bay polar bears. The boxplots for the standard ellipse areas show the Bayesian credible intervals (dark grey = 50%, medium grey = 75%, and light grey = 95%).

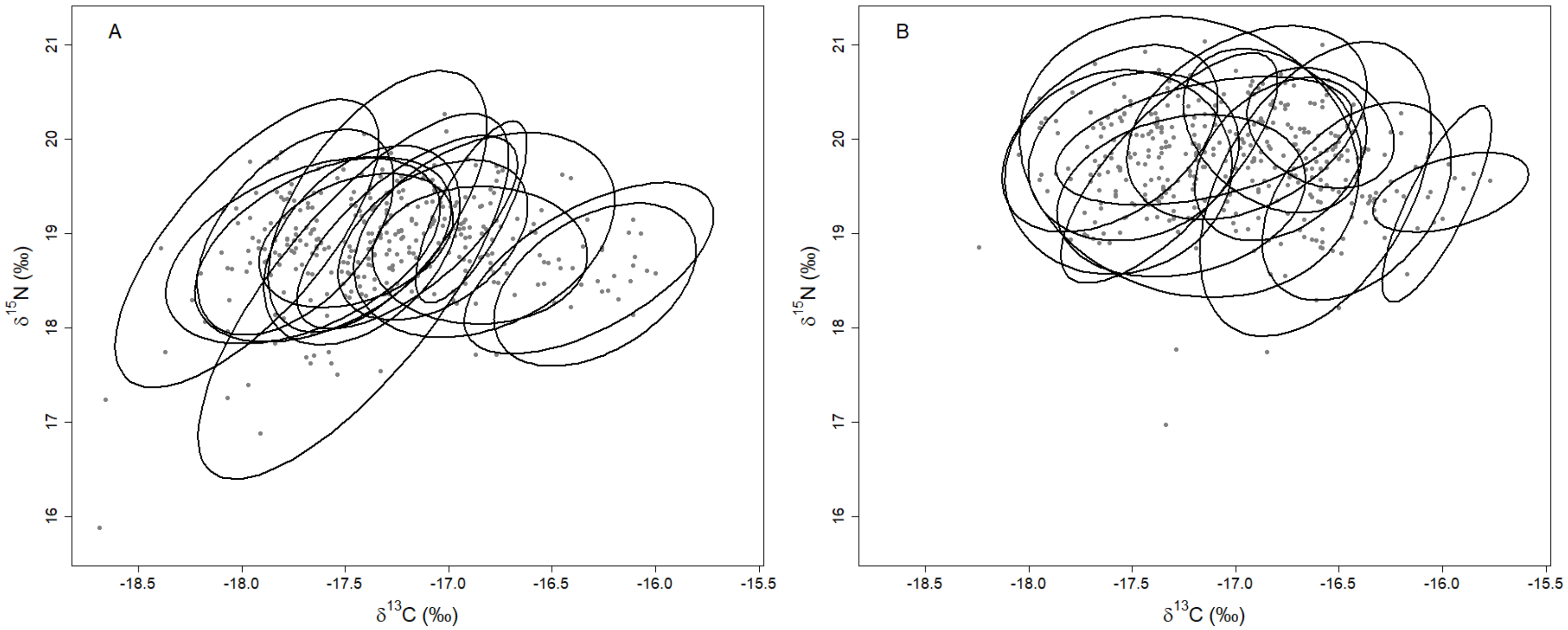

Figure A.4: SIBER (Stable Isotope Bayesian Ellipses in R) ellipses showing the isotopic niches for all adult female (A) and adult male (B) Western Hudson Bay polar bears over time (1993-1994, 2004-2016).

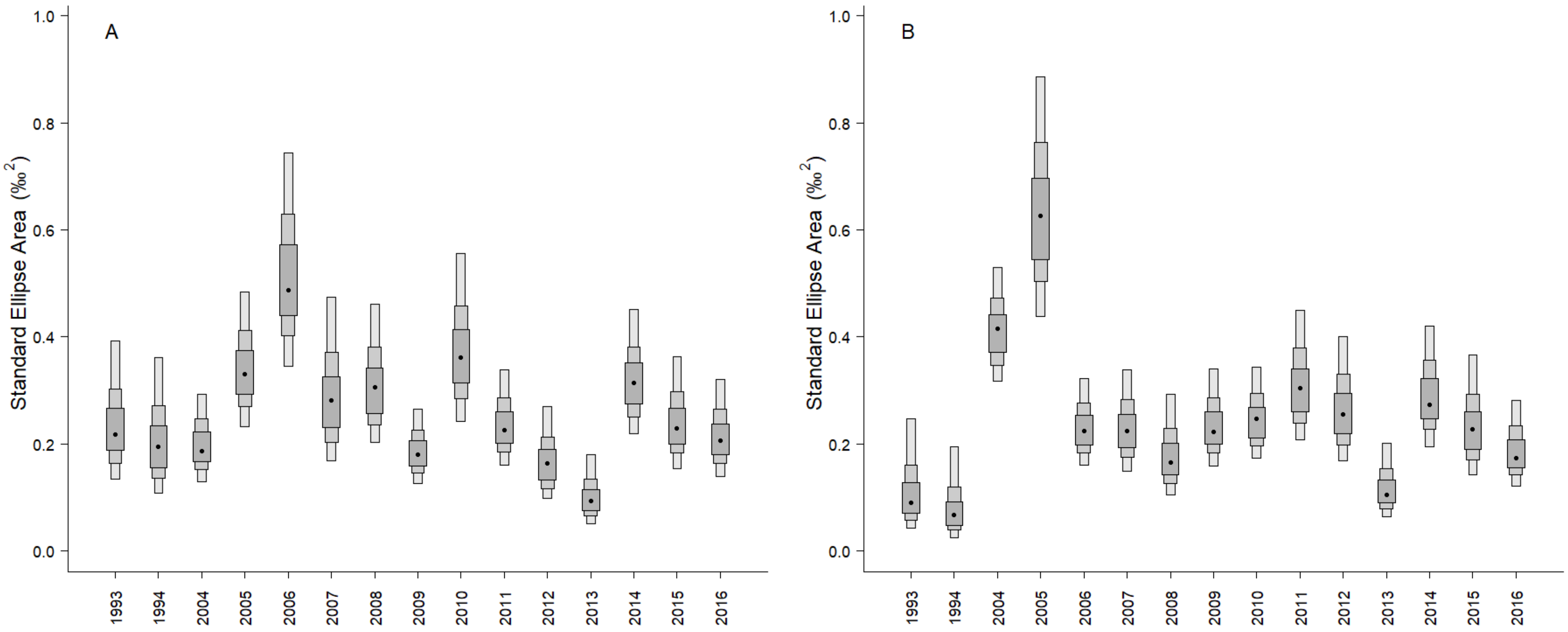

Figure A.5: Isotopic niche sizes (i.e., standard ellipse areas) for all adult female (A) and adult male (B) Western Hudson Bay polar bears. The boxplots for the standard ellipse areas show the Bayesian credible intervals (dark grey = 50%, medium grey = 75%, and light grey = 95%).

Chapter 3

3 Variation in habitat use of Beaufort Sea polar bears

The work presented in this chapter has been submitted and is in revision as: Johnson AC, Derocher AE (2020). Variation in habitat use of Beaufort Sea polar bears. *Polar Biology.*

3.1 Introduction

Habitat loss and fragmentation are key drivers of biodiversity loss (Brook et al. 2008, Mantyka-Pringle et al. 2012) and anthropogenic climate change similarly threatens global biodiversity (Scheffers et al. 2016). Climate change and habitat loss can interact synergistically to negatively affect species (Opdam and Wascher 2004, Brook et al. 2008, Mantyka-Pringle et al. 2012). As changes to habitats are predicted to continue due to climate change (Mantyka-Pringle et al. 2012, IPCC 2014), understanding habitat use and requirements can aid conservation efforts. Habitat use can vary among age classes in many species (Mattson et al. 1987, Reid et al. 1994, Whitehead et al. 2002, Kokurewicz 2004, Crawford et al. 2012). However, habitat use is often modelled with little or no consideration for age or reproductive class, which can result in incomplete assessments of habitat requirements due to variation within populations (Aebischer et al. 1993, Durner et al. 2009, McCall et al. 2016). Understanding variation in habitat use and selection among demographic groups can help identify which groups are more vulnerable to habitat change, and improve predictions about population responses to future change.

The Arctic is warming at a faster rate than the rest of the world (Wassmann et al. 2011, IPCC 2014, Parkinson 2014), resulting in sea ice extent reductions, increased open water duration (Comiso 2002, Parkinson and Cavalieri 2008, Stroeve et al. 2012, Parkinson 2014), earlier sea ice breakup, and later freeze-up (Stirling and Parkinson 2006, Stern and Laidre 2016, Stroeve and Notz 2018). Sea ice is critical habitat for many Arctic species and sea ice decline has negatively affected the population dynamics of various species including many Arctic marine mammals (Laidre et al. 2008, Post et al. 2009, Kovacs et al. 2011). For example, sea ice is essential for polar bears (*Ursus maritimus*) due to its use as a platform for movement and foraging on their main prey (ice-associated ringed seals [*Pusa hispida*] and bearded seals [*Erignathus barbatus*]) (Stirling and Archibald 1977, Smith 1980). Because sea ice affects energy intake and use, polar bear body condition and growth are affected by sea ice availability (Stirling et al. 1999, Rode et al. 2010, Durner et al. 2017). Climate change-induced sea ice decline thus affects the availability of polar bear critical habitat and sea ice loss has been associated with negative effects on polar bear body condition, reproduction, survival, and population abundance (Regehr et al. 2010, Rode et al. 2010, Bromaghin et al. 2015, Lunn et al. 2016). Polar bears are threatened by sea ice declines (Wang and Overland 2009, 2012, IPCC 2014, Regehr et al. 2016) and it is therefore important to understand habitat use and requirements in the warming Arctic.

In particular, the southern Beaufort Sea has undergone significant declines in sea ice concentration by 9.3% decade^{-1} and ice-covered days by 17.5 days decade^{-1} (Stern and Laidre 2016), with associated declines in body condition, reproductive output, survival, and abundance of the Southern Beaufort Sea (SB) polar bear population (Regehr et al. 2010, Rode et al. 2010, Bromaghin et al. 2015). Studies on polar bear habitat use identified selection for intermediate to high sea ice concentrations over the shallow continental shelf, which is a biologically productive region (Durner et al. 2009, Laidre et al. 2018, Lone et al. 2018b). Sea ice can be further categorized as stable landfast ice or active sea ice, which differ in their availability of prey (Stirling et al. 1993, Pilfold et al. 2016, Reimer et al. 2019). Landfast ice is lower-quality foraging habitat where ringed seal pups and adults in birth lairs are hunted by polar bears (Smith and Stirling 1975, Smith 1980, Stirling et al. 1993, Reimer et al. 2019). In contrast, active sea ice is higher-quality foraging habitat along leads between the fast ice and drifting offshore ice, and is the habitat where a larger variety of prey are available, including juvenile/adult ringed seals and bearded seals (Stirling and Archibald 1977, Stirling et al. 1993, Amstrup et al. 2000, Pilfold et al. 2014, Reimer et al. 2019). Adult females with cubs-of-the-year (COY) select landfast ice in spring, likely to protect cubs from the threat of infanticide from adult males, whereas other age classes select active ice (Stirling et al. 1993, Freitas et al. 2012, Pilfold et al. 2014, McCall et al. 2016). Intra-specific competition may also influence distribution within a population and further segregate habitat use due to dominant individuals excluding subordinates from optimal habitat (Egbert and Stokes 1976, Mattson et al. 1987, Pilfold et al. 2014). For example, competition for food resources affects variation in grizzly bear (*U. arctos*) habitat use, whereby adult females and subadults avoid or are excluded from the habitats used by dominant adult males (Egbert and Stokes 1976, Mattson et al. 1987). Similarly, polar bears also differ in their competitive ability as adult males are the largest class and subadults are inexperienced hunters that adults can kleptoparasitize (Stirling et al. 1993, Pilfold et al. 2014). However, knowledge of variation in habitat use within the SB population primarily comes from bear captures and seal kill sites (Pilfold et al. 2014) and observational surveys (Stirling et al. 1993), whereas the use of telemetry to track the movements of different demographic groups of SB polar bears and examine habitat use is lacking.

In this study, we used global positioning system (GPS) satellite-linked telemetry and resource selection functions (RSFs) to examine variation in SB polar bear habitat use between adult females of different reproductive status and male and female subadults. Habitat use was compared between demographic groups and RSFs were used to predict subadult and adult female habitat selection in each season. We hypothesized that habitat selection would vary the most among classes during primary hunting/reproduction seasons (winter and spring). Researching variation in habitat use within the SB can improve our understanding of space use patterns for different demographic groups, with implications for foraging success, energetics, and models of population-wide habitat use.

3.2 Methods

3.2.1 Study area

The study area was located in the southern Beaufort Sea from Pearce Point, Northwest Territories, Canada to Icy Cape, Alaska, USA, and offshore up to 80°N (Fig. 3.1). The clockwise Beaufort Gyre, wind, and currents affect ice drift patterns in this region (Proshutinsky et al. 2002, Bromaghin et al. 2015, Pongracz and Derocher 2017). There is a narrow continental shelf in the Beaufort Sea and primary productivity is driven by sea ice algae (Horner and Schrader 1982). The region is characterized by stable shorefast ice that forms each year, open-water leads that occur in spring at the boundary of the shorefast ice (active sea ice zones), and drifting pack ice farther offshore (Stirling et al. 1993, Pilfold et al. 2014, Pongracz and Derocher 2017). Open-water leads between the shorefast ice and the pack ice are important regions of biological productivity (Stirling et al. 1993, Bromaghin et al. 2015, Moore et al. 2018). When annual sea ice melts in summer, SB polar bears either travel north to multiyear ice in the Polar Basin or move onto land (Amstrup et al. 2000, Atwood et al. 2016, Pongracz and Derocher 2017).

3.2.2 Field sampling

Field work was conducted in April-May of 2007-2010 in the Canadian portion of the southern Beaufort Sea. Subadult male and female (3-4 years old) and adult female (≥ 5 years old) polar bears were immobilized using tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Laboratoires Virbac, Carros, France) following standard procedures (Stirling et al. 1989) and fitted with GPS collars (Telonics, Mesa, AZ) linked to the Argos satellite system (CLS America Inc., Lanham, MD) that collected locations every four hours (Pongracz and Derocher 2017). The programmable releases (CR-2a, Telonics, Mesa, AZ) on the collars were set for 1 year for subadults and 2 years for adults and subadult collars had a corrodible link. Erroneous data, dropped collar data, locations on land, and locations from one adult female that travelled outside the study area to Wrangel Island, Russia (Johnson et al. 2017) were excluded from analyses. Capture and handling protocols followed the Canadian Council on Animal Care guidelines (www.ccac.ca) and were approved by the University of Alberta BioSciences Animal Care and Use Committee.

3.2.3 Habitat use

At each polar bear GPS location, nine environmental covariates were extracted: sea ice concentration (*Ice*; %), distance to 5% sea ice concentration contour (*IceEdge*; km), two types of ice thickness (*FirstYear*, *OldIce*; %), three types of ice floe size (*SmallFloe*, *VastFloe*, *FastIce*; %), distance to land (*DistLand*; km), and depth (*Depth*, m) (Table B.1). These variables were chosen for ecological reasons relevant to polar bears: *Ice* is a key feature that influences polar bear habitat use, *IceEdge* represents the edge of the sea ice, ice thickness/floe type characterizes the seascape and prey availability (nearshore stable fast ice versus active ice) (Stirling et al. 1993, Pilfold et al. 2014), and *DistLand* and *Depth* are important because polar bears prefer shallow, nearshore habitats (Durner et al. 2009, Lone et al. 2018b). Sea ice concentration was obtained from satellite passive microwave data from the National Snow and Ice Data Center (daily SSM/I with a resolution of 25 km; Boulder, CO; Cavalieri et al. 1996; https://nsidc.org/data/NSIDC-0051/versions/1; accessed 09 April 2011) and sea ice thickness/floe size data were obtained from the Canadian Ice Service and extracted from a satellite remote sensor (weekly AMSR-E with a resolution of 6.5 km; Spreen et al. 2008; https://iceweb1.cis.ec.gc.ca/Archive/page1.xhtml; accessed 25 October 2011). ArcGIS was used to calculate *DistLand* for each polar bear location (ArcGIS v.10.6.1, Environmental Systems Research Institute, Redlands, CA). *Depth* at each location was estimated from the International Bathymetric Chart of the Arctic Ocean (IBCAO 2.0, 2 km resolution; Jakobsson et al. 2008).

Use of each environmental covariate was compared among five SB polar bear classes: adult females with COY, adult females with older cubs (yearlings and two-year-old cubs), solitary adult females, subadult females, and subadult males. The environmental variables were non-normally distributed (Shapiro-Wilk test, $p \leq 0.05$) and standard transformations did not improve normality; therefore, Kruskal-Wallis and Dunn's non-parametric tests were used to examine differences in the use of environmental variables among classes in each season.

3.2.4 Resource selection models

RSFs are an effective method for modelling polar bear habitat selection using GPS locations and ecologically relevant environmental covariates, such as sea ice concentration, ice type, and distance to land (Manly et al. 2002, Durner et al. 2009, Rode et al. 2010, Pilfold et al. 2014, McCall et al. 2016). We created separate RSF models for subadults (pooled) and adult females (pooled) in the SB in each season from 2007-2011: winter (December-February), spring (March-May), summer (June-August), and autumn (September-November). A discrete choice modelling approach was used for the RSFs, which involved modelling polar bear selection for the environmental covariates with a used versus available habitat approach (Durner et al. 2009, Laidre et al. 2015, 2018, McCall et al. 2016). The used habitat locations were the polar bear GPS locations (1 location/day selected randomly) while available habitat locations were 75 randomly generated locations within a buffer around each used location (Laidre et al. 2015, 2018, Hauser et al. 2017). The radius of the buffer was based on seasonal mean movement rates between GPS locations for each class to estimate the distance a bear could travel in three days (overall mean hourly movements rates: 2.50 km/h for subadults and 2.07 km/h for adults) (Laidre et al. 2015, 2018). Because it can be expected that selection will be more similar within than between bears, a random-effect term for each individual was included in a generalized linear mixed effects model approach (McCall et al. 2016). The exponential RSFs were modelled with the lme4 package in R (R Core Team 2019) using the logistic regression equation:

Equation 1: $w(x) = \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n)$

where: $w(x)$ is the relative probability of selection, X is the value for the environmental covariates, and β values are the coefficients from the RSF model output. Thirty-four *a priori* RSF models (Table 3.1) were created using combinations of the environmental covariates based on ecological hypotheses: *Ice* (included in every model because it is a key feature in polar bear habitat use), ice thickness/floe type to characterize the seascape, and *DistLand* (Durner et al. 2009, Laidre et al. 2018). Variables were screened for collinearity in each season and models with correlated variables ($|r| > 0.6$) were removed (Table B.2) (Durner et al. 2009, Pilfold et al. 2014). *Ice* was modelled as a quadratic term because polar bears select medium to high concentration (Durner et al. 2009, Pilfold et al. 2014).

3.2.5 Predicted habitat selection

Model selection was conducted using Akaike's Information Criterion (AIC) to select the top model for subadults and adults in each season. The top model for each class in each season was used to predict the relative probability of selection across the landscape in each season using the equation of the top model (Equation 1), β coefficients from each covariate in the top model, and the environmental conditions for a representative day in each season (winter: February 4; spring: May 7; summer: August 6; autumn: November 5) (Durner et al. 2009, McCall et al. 2016). The resulting RSF predictions were then scaled to a relative probability of selection from 0 to 1 to compare predicted selection between subadults and adults (Durner et al. 2009, Laidre et al. 2015).

3.2.6 RSF zones

Predicted RSF values for each age class in each season were placed into 10 equal-area bins that were ranked from 1 to 10 and the percentage of used locations falling into each bin was determined (Durner et al. 2009, 2019). In addition, the percentage of used locations in the upper 20% (i.e., optimal habitat) and upper 50% of RSF zones were calculated and chi-square tests were used to assess differences in the percentage of used locations in each RSF zone between age classes (Durner et al. 2009, 2019). The level of significance was set at $\alpha \leq 0.05$ and statistical analyses were conducted in R v.3.6.0 (R Core Team 2019).

3.3 Results

The four seasonal RSF models were constructed with 1399 locations pooled from 10 subadult males and 11 subadult females, and 2996 locations from 37 adult females (Fig. 3.1). Given that some adult females were tracked for > 1 year, there were 6 adult females with COY, 35 adult females with older cubs, and 5 solitary adult females.

3.3.1 Habitat use

In winter, there were no significant differences in the use of *Ice* and *FastIce* among classes, and no significant differences in any environmental variables between subadult females and subadult males (Dunn's tests, $p > 0.05$; Fig. 3.2; Table B.3). Subadults were significantly closer to land (mean 36 km [$n = 11$]) than adult females with older cubs (mean 60 km [$n = 25$]). Adult females with COY were significantly closer to *IceEdge* (mean 545 km [$n = 6$]) and used areas with significantly less *VastFloe* (mean 0% [$n = 6$]) than all other classes (mean *IceEdge* > 662 km, *VastFloe* > 26% [$n = 36$]). Adult females with COY also used areas with significantly more *SmallFloe* (mean 21% [$n = 6$]) than all classes (mean 12% [$n = 30$]) except subadult males (mean 14% [$n = 6$]).

In spring, adult females with COY used areas significantly closer to land (mean 28 km [$n = 6$]) with significantly more *FastIce* (mean 51% [$n = 6$]) and less *VastFloe* (mean 30% [$n = 6$])

than all other classes (mean *DistLand* > 42 km, *FastIce* < 22%, *VastFloe* > 58% [$n = 59$]) (Dunn's tests, $p \leq 0.05$; Fig. 3.2; Table B.4). Subadult males showed some similarities to adult females with COY by using areas significantly closer to land (mean 42 km [$n = 10$]) with significantly more *FastIce* (mean 22% [$n = 10$]) and less *VastFloe* (mean 58% [$n = 10$]) than adult females with older cubs/subadult females (mean *DistLand* > 50 km, *FastIce* < 12%, *VastFloe* > 69% [$n = 45$]). Subadult males also used significantly lower *Ice* (mean 92% [$n = 10$]) than all classes (mean > 94% [$n = 49$]) except adult females with COY (mean 96% [$n = 6$]). Adult females with older cubs used areas with significantly more *OldIce* (mean 5% [$n = 34$]) than subadults (mean < 2% [$n = 21$]). Solitary adult females used areas with significantly more *SmallFloe* (mean 5% [$n = 4$]) than adult females with older cubs (mean 4% [$n = 34$]) and subadult females (mean 3% [$n = 11$]).

In summer, subadult males used areas with significantly lower *Ice* (mean 64% [$n = 10$]) and were closer to *IceEdge* (mean 25 km [$n = 10$]) than all other classes (mean *Ice* > 74%, *IceEdge* > 36 km [$n = 54$]) (Dunn's tests, $p \leq 0.05$; Fig. 3.2; Table B.5). Adult females with older cubs and subadult females used significantly more *VastFloe* (mean > 55% [$n = 44$]) than other classes (mean < 42% [$n = 20$]). Adult females with COY used significantly more *FastIce* (mean 25% [$n = 6$]) and were significantly closer to land (mean 69 km [$n = 6$]) than other classes (mean *FastIce* < 9%, *DistLand* > 97 km [$n = 58$]).

In autumn, subadults used significantly lower *Ice* (mean 81% [$n = 15$]) than adults (mean > 86%) [$n = 42$] and were significantly closer to *IceEdge* (mean < 130 km [$n = 15$]) than adults (mean > 144 km [$n = 42$]) (Dunn's tests, $p \leq 0.05$; Fig. 3.2; Table B.6). Subadult females used areas farthest from land (mean 177 km [$n = 8$]), with significantly lower amounts of *OldIce* (mean 11% [$n = 8$]) and *VastFloe* (mean 12% [$n = 8$]) compared to all other classes (mean

DistLand < 127 km, *OldIce* > 25%, *VastFloe* > 19% [*n* = 49]). Solitary adult females used areas with significantly more *OldIce* (mean 56% [*n* = 5]) and *VastFloe* (mean 43% [*n* = 5]) than other classes (mean *OldIce* < 34%, *VastFloe* < 25% [*n* = 52]). Adult females with COY were significantly closer to land (mean 57 km [*n* = 6]) than other classes (mean > 110 km [*n* = 51]).

3.3.2 Resource selection models

Ice and *DistLand* were the most common variables retained (in all of the 8 top RSF models), followed by *FastIce* (5 models), *IceEdge* (5 models), *OldIce* (4 models), *SmallFloe* (3 models), *FirstYear* (1 model), and *VastFloe* (1 model) (Table 3.3; Tables B.7-B.14).

Ice was a significant predictor for subadults in winter and summer, and for adults in summer and autumn (Table 3.4). *DistLand* was a highly significant predictor in every season for both age classes. *FastIce* was significant for both classes in winter and spring. *IceEdge* was significant for adults in spring and both age classes in summer/autumn. *OldIce* was significant for subadults in spring while *SmallFloe* was significant for adults in spring/autumn.

3.3.3 Predicted habitat selection

In winter, both adults and subadults selected for nearshore regions over the continental shelf with low *FastIce*, with subadults selecting for lower *Ice* and closer to the coast (~30 km offshore) than adults (~50 km offshore) (Fig. 3.3; Table 3.4). In spring, both classes selected low *FastIce*/*OldIce*, with subadults selecting lower *Ice* and closer to land (~30 km offshore) than adults that selected closer to *IceEdge*, more *SmallFloe*, and farther offshore (~50 km). Both age classes selected closer to *IceEdge* and the farthest offshore in summer (~200 km), as well as closer to *IceEdge* and relatively far offshore (~100 km) in autumn.

3.3.4 RSF zones

A significantly larger proportion of adult locations occurred in the highest RSF zones in winter relative to subadults (Chi-square test, $\chi_1 = 45.14$, $p \leq 0.001$; Fig. 3.4; Table 3.5). In spring, subadults had a larger proportion of locations in the upper 20% of RSF zones than adults (Chi-square test, $\chi_1 = 3.95$, $p = 0.05$), but were not significantly different in the upper 50% of RSF zones (Chi-square test, $\chi_1 = 0.80$, $p = 0.37$). The proportion of locations in the highest RSF zones did not differ significantly between classes in summer (Chi-square test, $\chi_1 = 0.02$, $\chi_1 = 1.28$, $p > 0.05$). In autumn, adults had a larger proportion of locations in the upper 50% of RSF zones (Chi-square test, $\chi_1 = 5.28$, $p = 0.02$), but were not significantly different in the upper 20% of RSF zones (Chi-square test, $\chi_1 = 0.17$, $p = 0.68$).

3.4 Discussion

Understanding variation in habitat use and requirements within populations can be beneficial for managing vulnerable populations experiencing habitat loss. Here, we found broad similarities as well as variation in habitat selection based on age, sex, and reproductive class for SB polar bears. Broadly, SB polar bears selected nearshore habitats with intermediate to high *Ice* over the continental shelf, similar to studies in this and other populations (Durner et al. 2009, Wilson et al. 2014, Laidre et al. 2018, Lone et al. 2018b). *DistLand* was the strongest predictor in all models, which is consistent with polar bear selection for shallow nearshore habitats that are more productive than deeper waters (Pongracz and Derocher 2017, Laidre et al. 2018). *FastIce* was significant in winter and spring (especially for adult females with COY), which is consistent with observations that the fast ice is important habitat for predation on ringed seal pups (Stirling et al. 1993, Freitas et al. 2012). *IceEdge* was important for adult females in spring, indicating selection for the floe edge, while the importance of *SmallFloe* for adults in spring indicates new ice that has formed in an active ice area such as a lead (Pilfold et al. 2014). All bears used areas closer to shore in winter and spring, while ranging farther offshore in areas near *IceEdge* with more *OldIce* in summer and autumn. Our results agree with other studies that have found that SB bears select nearshore habitats in winter/spring and travel farther offshore in summer/autumn to remain with remnant multiyear pack ice (Pilfold et al. 2014, Bromaghin et al. 2015, Pongracz and Derocher 2017). The offshore multiyear pack ice is not optimal polar bear habitat because it is over deeper, unproductive areas and it is energetically expensive for bears to travel longer distances as well as risk long-distance swims as the sea ice retreats (Pilfold et al. 2017, Pongracz and Derocher 2017). If optimal polar bear sea ice habitat continues to decline as predicted (Stern and Laidre 2016, Durner et al. 2019), SB polar bears may spend increasingly longer periods in this unproductive offshore region or more time on land (Bromaghin et al. 2015, Rogers et al. 2015, Pongracz and Derocher 2017). In turn, the SB polar bears have experienced nutritional stress (Amstrup et al. 2006, Stirling et al. 2008a, Cherry et al. 2009, Rode et al. 2018) and declines in body condition, survival, and abundance (Regehr et al. 2010, Rode et al. 2010, Bromaghin et al. 2015) and these challenges may be exacerbated in the future.

While SB bears displayed broadly similar habitat selection, there was variation among age, sex, and reproductive classes, especially in winter and spring. Most notably, adult females with COY displayed the largest differences compared to all other classes and selected nearshore stable landfast ice in spring. The habitat use patterns of females with COY were consistent with the predicted selection for nearshore areas along the edge of the landfast ice in winter, when adults had the highest percentage of locations in the upper 20% RSF zones. In spring, adults had fewer locations in the upper 20% zones, potentially due to the differing selection between females with COY (high *FastIce*) versus other adults (low *FastIce*). Our results are consistent with studies in the SB that found nearshore stable landfast ice is selected by females with COY where they can hunt ringed seal pups and their mothers while balancing protection of their cubs from adult males (Taylor et al. 1985, Stirling et al. 1993, Derocher and Wiig 1999, Pilfold et al. 2014), reduce the risk of hypothermia for cubs (Blix and Lentfer 1979, Lone et al. 2018a), and because young cubs limit the mobility of adult females (Amstrup et al. 2000, Durner et al. 2009). Unfortunately, we are limited in our understanding of adult males because they cannot be collared, but they are the dominant age/sex class likely influencing the distribution of subordinates and have been observed selecting active ice and floe edges (Stirling 1974, Derocher and Stirling 1990, Stirling et al. 1993, Pilfold et al. 2014).

Adult females with older cubs used areas farthest offshore with less *FastIce* and more *VastFloe* in winter/spring, and were predicted to select for areas close to *IceEdge* with more *SmallFloe* in spring, suggesting selection for active ice zones at the floe edge. These active sea ice zones are prime habitat and can provide bears with a wide variety of prey such as bearded seals and adult ringed seals (Stirling et al. 1993, Pilfold et al. 2014, Reimer et al. 2019). Our results are similar to the observations of Stirling et al. (1993) that females with yearlings and two-year-old cubs use the floe edge/active ice and avoid landfast ice habitat. Older cubs are less at-risk of hypothermia (Blix and Lentfer 1979) and hunt more independently than COY (Stirling 1974); therefore, females with older cubs are less restricted in their movements than females with young offspring. There were fewer solitary adult females tracked but they had similar habitat selection for active ice zones. A limitation of our study is our assumption of a three-year reproductive cycle after releasing an adult female and because cub survival is low (Derocher and Stirling 1996), this may have resulted in misclassifying adult females that lost cubs.

In addition to the variation in habitat use among adult females, there were differences between subadults as well. Subadult females used more active sea ice zones than subadult males (farther from shore, more *VastFloe*), similar to females with older cubs/solitary adult females, while still using some landfast zones. The use of both habitat types potentially facilitates hunting or scavenging in high-quality active zones at the edge of the landfast ice near biologically productive open-water leads (Pilfold et al. 2014), while still providing access to safety/refuge in stable zones from threats such as ocean storms and long-distance swimming events (Durner et al. 2009, Pilfold et al. 2017). Furthermore, subadults are inexperienced and less efficient hunters (Stirling 1974, Bromaghin et al. 2015), and as such, intra-specific competition may be influencing the habitat use of subadult females as they may sometimes avoid or be excluded from high-quality habitat used by dominant adults (Mattson et al. 1987, Pilfold et al. 2014). Our results support Stirling et al. (1993) who found that subadult females showed a slight preference for active floe edge habitat, but they also did not avoid the landfast ice as strongly as other classes.

In contrast, subadult males displayed more similar habitat use patterns to adult females with COY by using nearshore stable landfast ice zones in spring. Subadult males may have been using habitat at the edge of the landfast ice as well as hunting/scavenging in adjacent high-quality active ice habitat (resulting in their use of lower *Ice* in spring), which is consistent with Pilfold et al. (2014) who found that subadult males were found in high-quality habitat. Of the demographic groups in our study, subadult males likely compete most directly with adult males, the dominant age/sex class. While older adult males are more successful at mating, subadult males have some mating success (Cronin et al. 2009, Zeyl et al. 2009, Stirling et al. 2016) and may therefore compete with adult males for mating opportunities as well as prey. Adult males may also kleptoparasitize kills made by subadult males (Stirling 1974, Stirling et al. 1993), and subadults can be killed by adult males (Amstrup et al. 2006). The use of lower-quality landfast ice habitat by subadult males may therefore be a mechanism to reduce intra-specific resource competition in the primary hunting/mating season, similar to the avoidance of adult male habitats by subadult grizzly bears (Mattson et al. 1987). These spring habitat use patterns of subadult males differ from observations of SB subadult males that used high-quality active ice zones and avoided stable landfast ice in the 1970s (Stirling et al. 1993). This may be due to differences in study design or a shift in subadult male distribution toward lower-quality habitat as the sea ice has declined.

The Arctic is projected to undergo continued warming and the SB is expected to experience further declines in sea ice habitat (Wang and Overland 2009, 2012, IPCC 2014, Stroeve and Notz 2018). Although an increasing proportion of SB polar bears have been noted to remain on land in the ice-free season (Rogers et al. 2015, Atwood et al. 2016), we found that many travelled north to the less productive multiyear sea ice in summer/autumn, which increases energetic expenditure and the risk of long-distance swims as sea ice declines (Bromaghin et al. 2015, Pilfold et al. 2017, Pongracz and Derocher 2017). In addition, sea ice drift rates have increased, which influences polar bear movements and may have detrimental effects on energy balances (Mauritzen et al. 2003, Durner et al. 2017). Landfast ice and active pack ice areas experience different drift patterns and have different associated energetic costs (Mauritzen et al. 2003, Durner et al. 2017, Blanchet et al. 2020), and the observed differential habitat use among SB demographic groups may therefore result in different energetic impacts in the population.

Furthermore, we found that adult females with COY and subadult males used the lowest-quality habitat in the primary foraging season and they may therefore be most at risk to further declines in habitat. SB subadults have low survival rates (Bromaghin et al. 2015), high fasting rates (Rode et al. 2014), their condition is related to sea ice habitat availability (Rode et al. 2010), and they are more susceptible to unfavourable conditions (Molnár et al. 2010, Pongracz and Derocher 2017), which suggests that subadult males in lower-quality habitat will likely be especially vulnerable to future stressors. As Reimer et al. (2019) noted, bears in sub-optimal habitat may alter their habitat use and make riskier decisions as sea ice continues to decline, and these demographic groups are therefore important to monitor. There is a time lag between the loss of habitat and the ability to detect effects within a population, and the use of lower-quality habitat that has been observed in the SB and other polar bear populations can be an indicator of future demographic change (Laidre et al. 2018, Durner et al. 2019). Long-term research on habitat use of sea ice-dependent species and changes over time can therefore be a useful monitoring tool for vulnerable species experiencing habitat loss. Future studies would benefit from better information on habitat quality as well as larger sample sizes of all demographic classes to improve our understanding of observed patterns.

Table 3.1: List of *a priori* resource selection function models for southern Beaufort Sea polar bears. Covariates included: *Ice* (sea ice concentration), *IceEdge* (distance to 5% sea ice concentration), *FirstYear* (percentage of ice that was first year), *OldIce* (percentage of ice that was multiyear), *SmallFloe* (percentage of floes that were small), *VastFloe* (percentage of floes that were vast), *FastIce* (percentage of floes that were land fast), and *DistLand* (distance to land).

Model	No. covariates	Model structure
1	2	$Ice + Ice^2$
2	3	$Ice + Ice^2 + IceEdge$
3	3	$Ice + Ice^2 + FirstYear$
4	3	$Ice + Ice^2 + OldIce$
5	3	$Ice + Ice^2 + SmallFloe$
6	3	$Ice + Ice^2 + VastFloe$
7	3	$Ice + Ice^2 + FastIce$
8	3	$Ice + Ice^2 + DistLand$
9	4	$Ice + Ice^2 + IceEdge + DistLand$
10	4	$Ice + Ice^2 + FirstYear + DistLand$
11	4	$Ice + Ice^2 + OldIce + DistLand$
12	4	$Ice + Ice^2 + SmallFloe + DistLand$
13	4	$Ice + Ice^2 + VastFloe + DistLand$
14	4	$Ice + Ice^2 + FastIce + DistLand$
15	5	$Ice + Ice^2 + FirstYear + FastIce + DistLand$
16	5	$Ice + Ice^2 + OldIce + FastIce + DistLand$
17	5	$Ice + Ice^2 + SmallFloe + FastIce + DistLand$
18	5	$Ice + Ice^2 + VastFloe + FastIce + DistLand$
19	5	$Ice + Ice^2 + FirstYear + SmallFloe + DistLand$
20	5	$Ice + Ice^2 + FirstYear + VastFloe + DistLand$
21	5	$Ice + Ice^2 + OldIce + SmallFloe + DistLand$
22	5	$Ice + Ice^2 + OldIce + VastFloe + DistLand$
23	6	$Ice + Ice^2 + FirstYear + SmallFloe + FastIce + DistLand$
24	6	$Ice + Ice^2 + FirstYear + VastFloe + FastIce + DistLand$
25	6	$Ice + Ice^2 + OldIce + SmallFloe + FastIce + DistLand$
26	6	$Ice + Ice^2 + OldIce + VastFloe + FastIce + DistLand$
27	6	$Ice + Ice^2 + IceEdge + FirstYear + SmallFloe + DistLand$
28	6	$Ice + Ice^2 + IceEdge + FirstYear + VastFloe + DistLand$
29	6	$Ice + Ice^2 + IceEdge + OldIce + SmallFloe + DistLand$
30	6	$Ice + Ice^2 + IceEdge + OldIce + VastFloe + DistLand$
31	7	$Ice + Ice^2 + IceEdge + FirstYear + SmallFloe + FastIce + DistLand$
32	7	$Ice + Ice^2 + IceEdge + FirstYear + VastFloe + FastIce + DistLand$
33	7	$Ice + Ice^2 + IceEdge + OldIce + SmallFloe + FastIce + DistLand$
34	7	$Ice + Ice^2 + IceEdge + OldIce + VastFloe + FastIce + DistLand$

Table 3.2: Number of used locations for each age class in each season used to create polar bear resource selection functions for the Southern Beaufort Sea in 2007-2011. Note: the total number of subadults/adults does not equal the sum of the number of individuals over the seasons because individuals usually provided data for more than one season.

Season	Number of subadults	Number of subadult used locations	Number of adults	Number of adult used locations
Winter	11	287	26	602
Spring	21	357	37	743
Summer	21	390	36	914
Autumn	15	365	33	737
Total	21	1399	37	2996

Table 3.3: The top model for each season and the *w* (Akaike weight) for subadults and adults. Model number corresponds to Table 3.1. See Tables B.7-B.14 for the top habitat selection models in each season and the associated AIC (Akaike Information Criterion).

	Subadult			Adult		
Season	Model	Covariates	*w*	Model	Covariates	*w*
Winter	24	$Ice + Ice^2 + FirstYear + VastFloe + FastIce + DistLand$	0.37	14	$Ice + Ice^2 + FastIce + DistLand$	0.35
Spring	16	$Ice + Ice^2 + OldIce + FastIce + DistLand$	0.48	33	$Ice + Ice^2 + IceEdge + OldIce + SmallFloe + FastIce + DistLand$	0.59
Summer	33	$Ice + Ice^2 + IceEdge + OldIce + SmallFloe + FastIce + DistLand$	0.34	9	$Ice + Ice^2 + IceEdge + DistLand$	0.66
Autumn	9	$Ice + Ice^2 + IceEdge + DistLand$	0.43	29	$Ice + Ice^2 + IceEdge + OldIce + SmallFloe + DistLand$	0.55

Table 3.4: The β coefficients (β), standard error (SE), and p-values (*p*) from the top models for subadult and adult polar bear resource selection function models in the Southern Beaufort Sea for each season of 2007-2011.

	Subadult				Adult			
Season	Covariates	β	SE	*p*	Covariates	β	SE	*p*
Winter	*Ice*	-0.058	0.035	0.10	*Ice*	0.018	0.030	0.53
	Ice^2	0.0006	0.0003	0.03	Ice^2	-0.0001	0.0002	0.58
	FirstYear	-0.004	0.002	0.08	*FastIce*	-0.010	0.002	≤ 0.001
	VastFloe	0.003	0.002	0.12	*DistLand*	-0.009	0.0009	≤ 0.001
	FastIce	-0.016	0.002	≤ 0.001				
	DistLand	-0.028	0.002	≤ 0.001				
Spring	*Ice*	-0.013	0.018	0.48	*Ice*	0.023	0.016	0.17
	Ice^2	0.0001	0.0001	0.40	Ice^2	-0.0001	0.0001	0.31
	OldIce	-0.024	0.008	0.003	*IceEdge*	-0.0002	0.00009	0.04
	FastIce	-0.011	0.002	≤ 0.001	*OldIce*	-0.004	0.003	0.15
	DistLand	-0.017	0.002	≤ 0.001	*SmallFloe*	0.006	0.003	0.02
					FastIce	-0.009	0.001	≤ 0.001
					DistLand	-0.009	0.001	≤ 0.001
Summer	*Ice*	0.019	0.009	0.03	*Ice*	0.017	0.007	0.01
	Ice^2	-0.0001	0.00008	0.05	Ice^2	-0.00008	0.00005	0.13
	IceEdge	-0.011	0.002	≤ 0.001	*IceEdge*	-0.005	0.0008	≤ 0.001
	OldIce	0.001	0.002	0.62	*DistLand*	-0.003	0.0005	≤ 0.001
	SmallFloe	-0.007	0.006	0.21				
	FastIce	-0.008	0.003	0.006				
	DistLand	-0.004	0.0009	≤ 0.001				

Autumn	*Ice*	0.016	0.011	0.16	*Ice*	0.026	0.010	0.009
	Ice^2	-0.0001	0.00009	0.13	Ice^2	-0.0002	0.00007	0.009
	IceEdge	-0.002	0.0005	≤ 0.001	*IceEdge*	-0.0008	0.0002	0.001
	DistLand	-0.004	0.0006	≤ 0.001	*OldIce*	0.002	0.001	0.15
					SmallFloe	0.005	0.001	≤ 0.001
					DistLand	-0.005	0.0006	≤ 0.001

Table 3.5: The proportion of polar bear locations in the upper 20% and upper 50% of RSF-valued habitat for subadult and adult polar bear resource selection function models in the Southern Beaufort Sea from each season of 2007-2011. Proportions of locations for subadults in each zone were compared with a chi-square test of proportions to adult locations in each zone.

	Subadults	Adults		
Season	Proportion	Proportion	χ^2	*p*
Upper 20%				
Winter	0.14	0.61	45.14	≤ 0.001
Spring	0.38	0.24	3.95	0.05
Summer	0.33	0.31	0.02	0.88
Autumn	0.12	0.15	0.17	0.68
Upper 50%				
Winter	0.70	0.95	19.95	≤ 0.001
Spring	0.92	0.96	0.80	0.37
Summer	0.92	0.86	1.28	0.26
Autumn	0.73	0.87	5.28	0.02

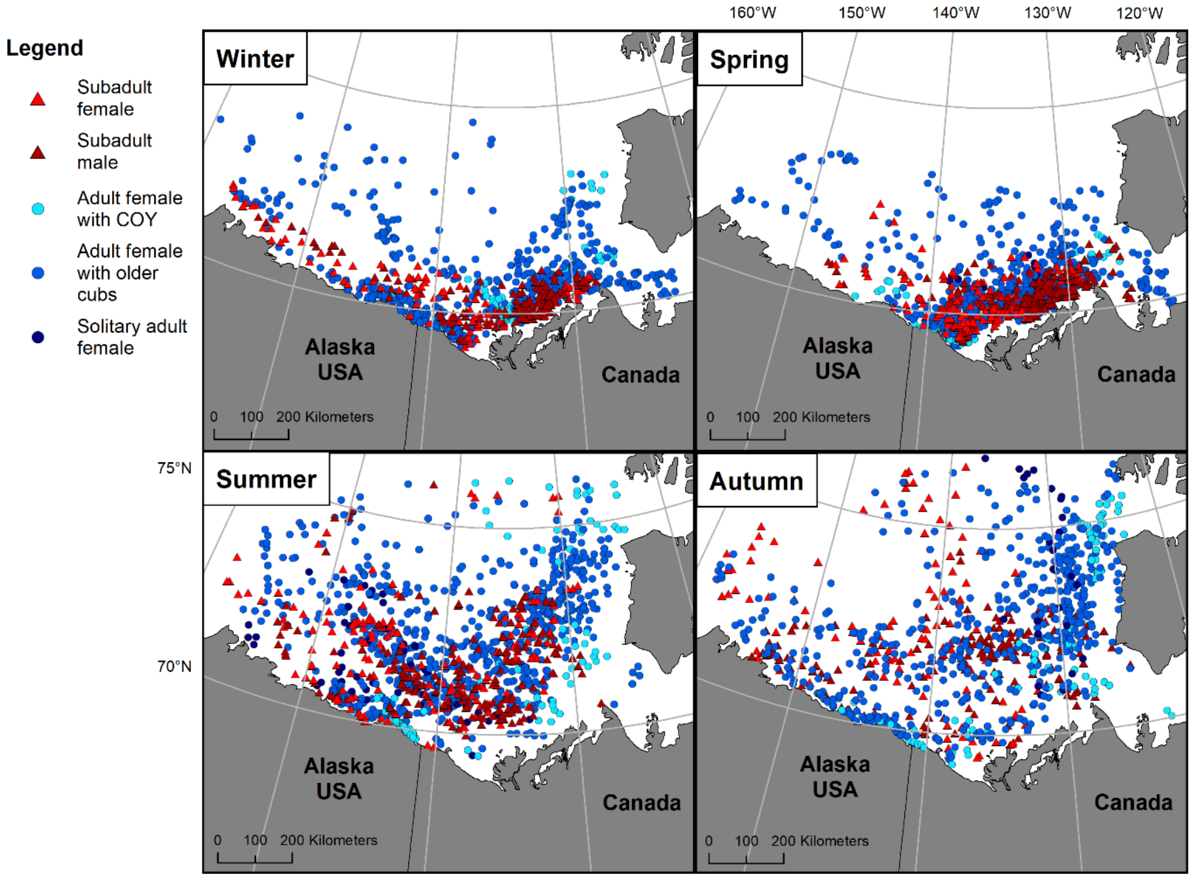

Figure 3.1: Distribution of 21 subadult (female and male) and 37 adult female (with cubs-of-the-year [COY], with older cubs, and solitary) polar bears from GPS collar locations in the Beaufort Sea by season from 2007-2011.

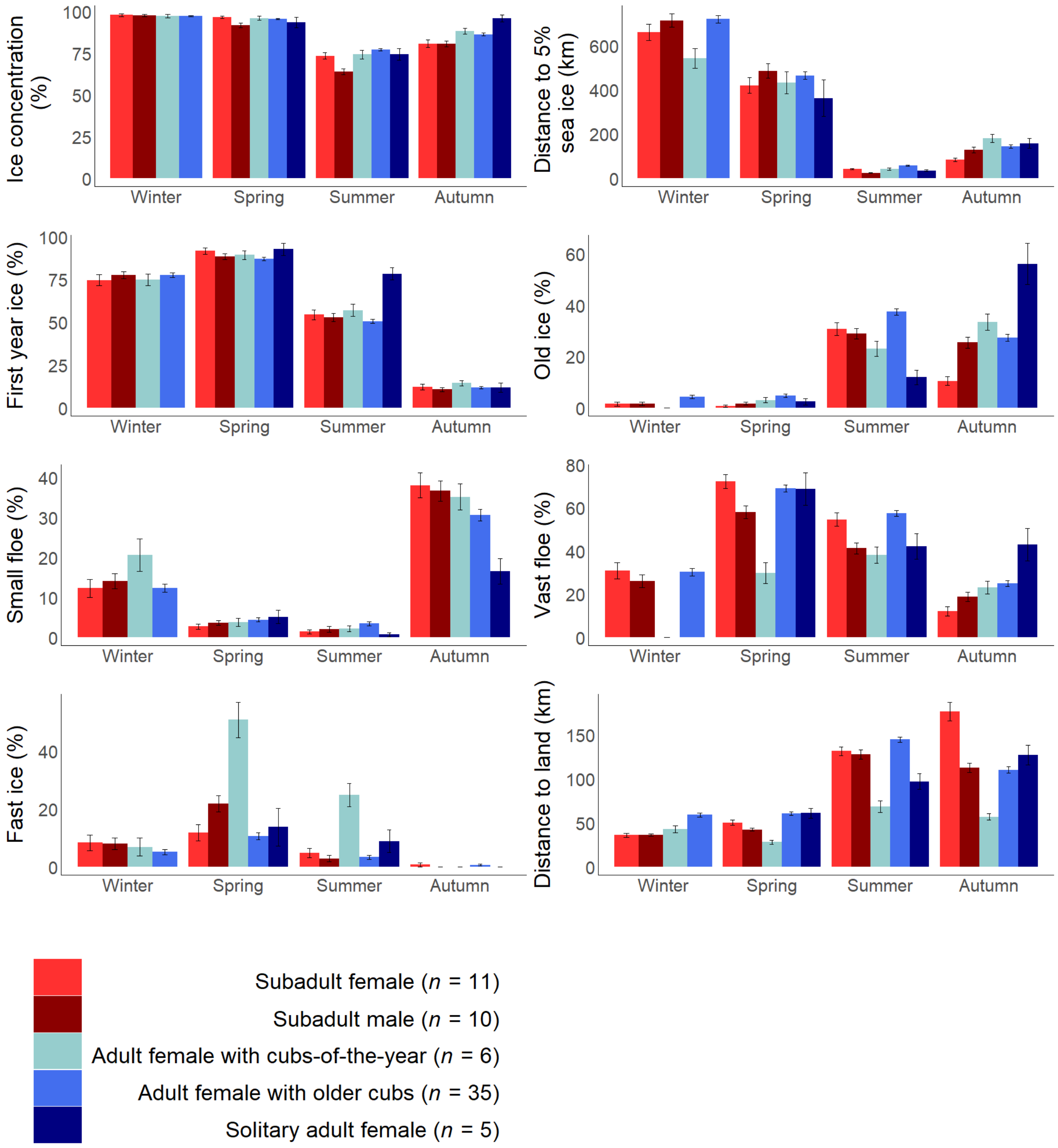

Figure 3.2: The means (± standard error) for the use of each environmental covariate by each class of Beaufort Sea polar bears in each season of 2007-2011. See Tables B.3-B.6 for Dunn's test results comparing the use of environmental variables among classes.

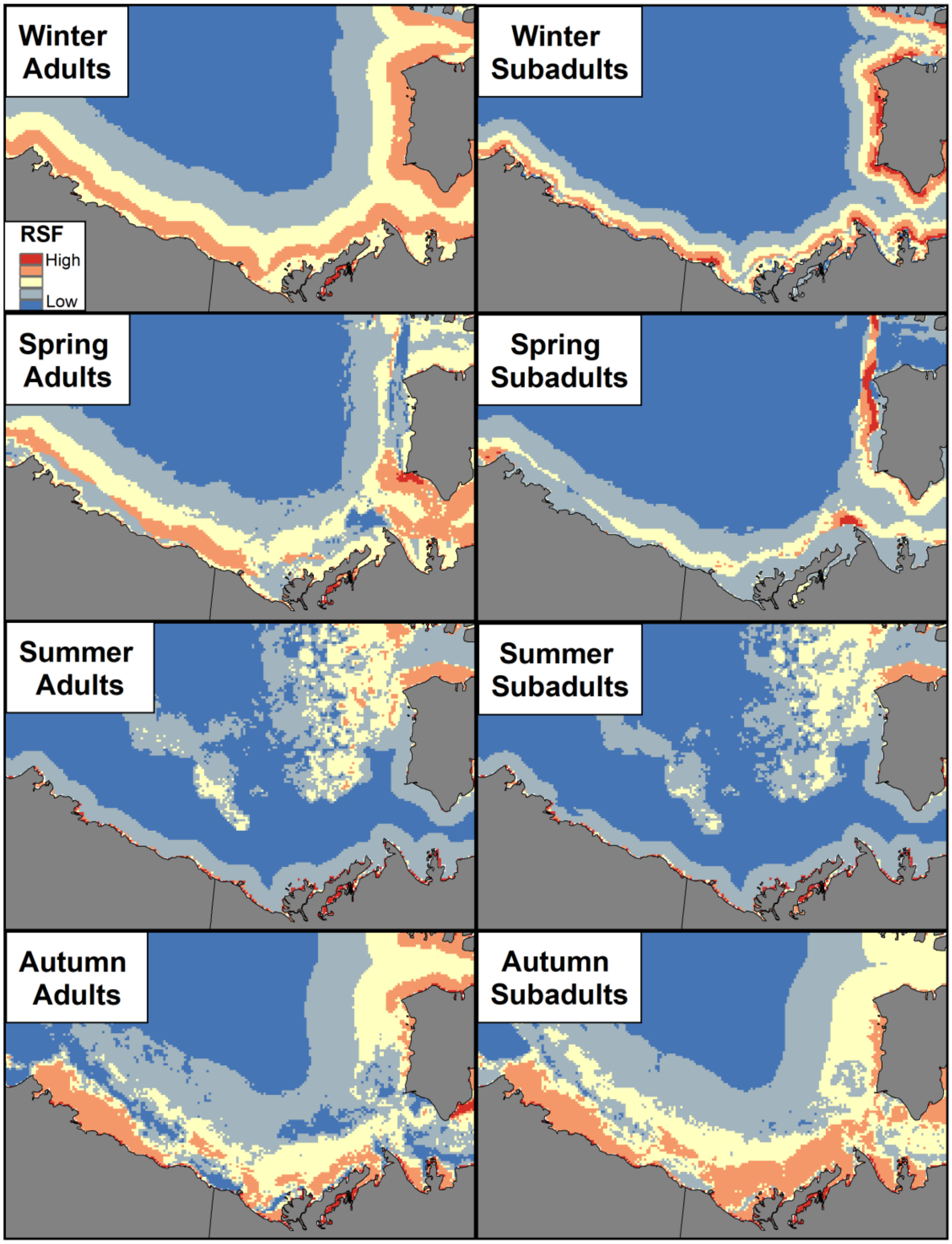

Figure 3.3: Predicted probability of selection from the top resource selection model in each season for adult and subadult polar bears in the Beaufort Sea from 2007-2011.

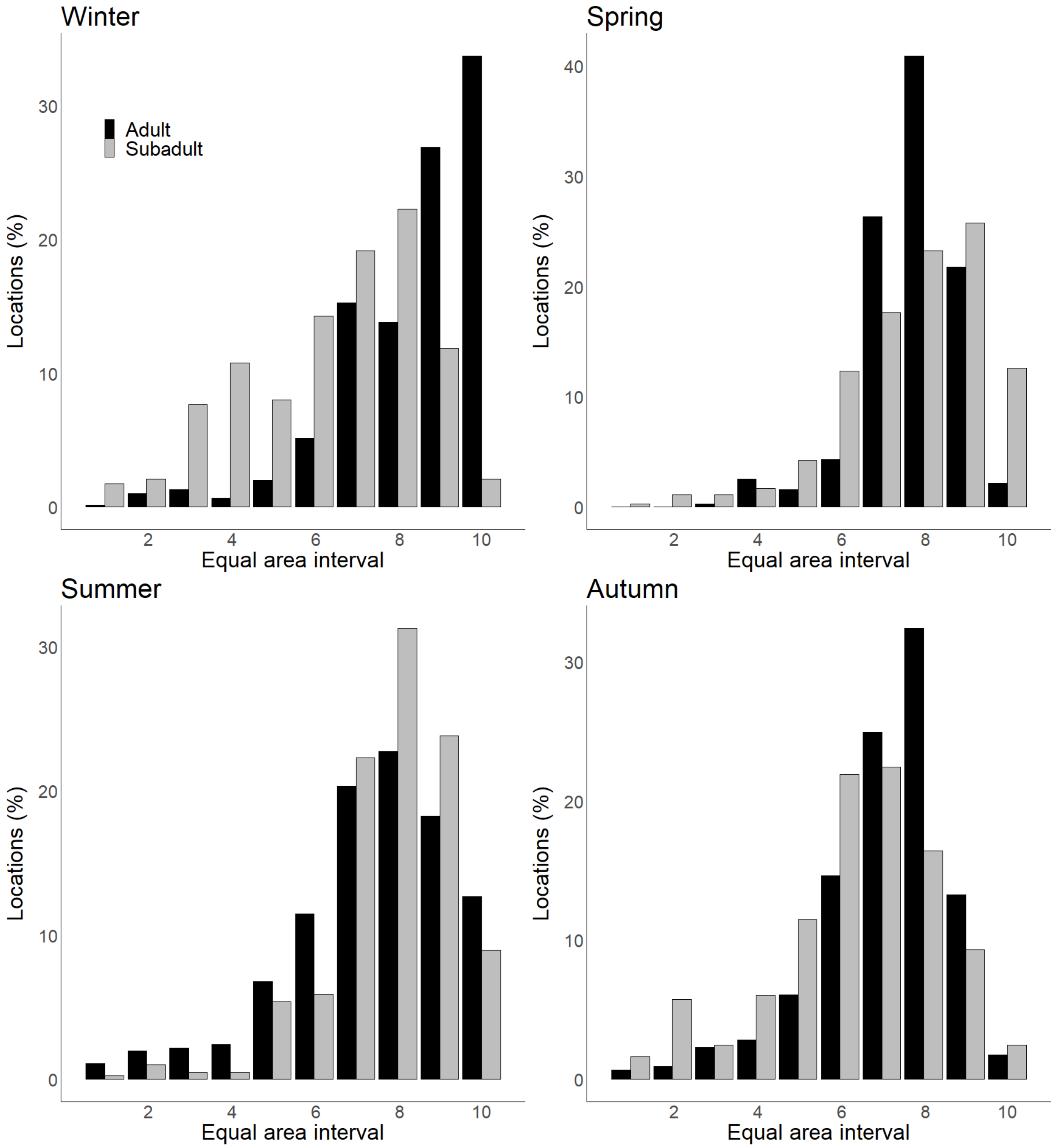

Figure 3.4: Percentages of polar bear telemetry locations within 10 equal area intervals based on RSF values for each age class in each season.

Appendices

B.1 Additional tables

Table B.1: Covariates used in resource selection models for Southern Beaufort Sea polar bear habitat selection.

Covariate	Description	Source
Ice	Sea ice concentration (%)	SSM/I satellite data (25 km resolution)
IceEdge	Distance to 5% sea ice concentration (km)	SSM/I satellite data (25 km resolution)
FirstYear	Percentage (%) of sea ice thickness that was first year ice (30 – 120 cm)	Canadian Ice Service regional charts (6.5 km resolution)
OldIce	Percentage (%) of sea ice thickness that was old ice (multi-year ice)	Canadian Ice Service regional charts (6.5 km resolution)
SmallFloe	Percentage (%) of sea ice floes that were small floes (20 – 500 m)	Canadian Ice Service regional charts (6.5 km resolution)
VastFloe	Percentage (%) of sea ice floes that were vast floes (> 2 km)	Canadian Ice Service regional charts (6.5 km resolution)
FastIce	Percentage (%) of sea ice floes that were landfast ice	Canadian Ice Service regional charts (6.5 km resolution)
DistLand	Distance to land (km)	Calculated in ArcGIS
Depth	Depth (m)	IBCAO bathymetry charts (2 km resolution)

Table B.2: Pearson correlation matrix to test for collinearity of covariates in each season for Southern Beaufort Sea polar bear resource selection function models (2007-2011). See Table B.1 for descriptions of covariates. Spring correlated variables included: *OldIce* and *FirstYear* ($r = 0.75$) and *VastFloe* and *FastIce* ($r = 0.73$). Summer correlated variables included: *OldIce* and *FirstYear* ($r = 0.78$). *Depth* and *DistLand* were correlated in each season ($r \geq 0.79$).

	Variable 2								
Variable 1	*Ice*	*IceEdge*	*FirstYear*	*OldIce*	*SmallFloe*	*VastFloe*	*FastIce*	*Depth*	*DistLand*
Winter									
Ice	1.00								
IceEdge	0.24	1.00							
FirstYear	0.19	0.22	1.00						
OldIce	0.09	0.05	-0.51	1.00					
SmallFloe	-0.17	-0.08	-0.34	-0.12	1.00				
VastFloe	0.11	0.23	0.13	0.22	-0.19	1.00			
FastIce	-0.05	0.06	0.23	-0.12	-0.15	-0.24	1.00		
Depth	-0.04	0.03	0.19	-0.41	0.10	-0.21	0.23	1.00	
DistLand	0.12	-0.01	-0.21	0.46	-0.10	0.26	-0.35	-0.81	1.00
Spring									
Ice	1.00								
IceEdge	0.25	1.00							
FirstYear	0.20	0.06	1.00						
OldIce	0.07	0.05	-0.75	1.00					
SmallFloe	-0.06	0.11	-0.24	-0.01	1.00				
VastFloe	0.12	-0.01	0.15	0.00	-0.16	1.00			
FastIce	0.01	0.02	0.27	-0.20	-0.13	-0.73	1.00		
Depth	-0.11	0.05	0.36	-0.52	0.06	-0.18	0.31	1.00	
DistLand	0.11	-0.05	-0.39	0.55	-0.03	0.31	-0.49	-0.83	1.00

Summer									
Ice	1.00								
IceEdge	0.46	1.00							
FirstYear	0.21	0.02	1.00						
OldIce	0.06	0.15	-0.78	1.00					
SmallFloe	-0.09	-0.07	-0.01	-0.07	1.00				
VastFloe	0.25	0.21	0.02	0.30	-0.27	1.00			
FastIce	0.05	-0.10	0.29	-0.23	-0.04	-0.30	1.00		
Depth	-0.11	-0.40	0.18	-0.32	-0.02	-0.18	0.33	1.00	
DistLand	0.06	0.43	-0.36	0.41	0.01	0.11	-0.34	-0.79	1.00
Autumn									
Ice	1.00								
IceEdge	0.38	1.00							
FirstYear	0.17	0.37	1.00						
OldIce	0.17	0.02	-0.01	1.00					
SmallFloe	0.10	0.14	-0.08	-0.26	1.00				
VastFloe	0.21	-0.04	0.11	0.57	-0.41	1.00			
FastIce	0.03	0.05	0.19	-0.06	-0.06	-0.06	1.00		
Depth	-0.01	0.05	-0.09	-0.13	0.14	-0.12	0.10	1.00	
DistLand	0.02	-0.08	0.02	0.13	-0.17	0.15	-0.11	-0.84	1.00

Table B.3: Dunn's tests comparing use of environmental variables between classes in winter.

Covariate	Class	Class Adult female with COY	 Adult female with older cubs	 Solitary adult female	 Subadult female
Ice	Adult female with older cubs	0.253			
	Solitary adult female				
	Subadult female	0.108	0.154		
	Subadult male	0.270	0.493		0.192
IceEdge	Adult female with older cubs	≤ 0.001			
	Solitary adult female				
	Subadult female	0.039	0.045		
	Subadult male	≤ 0.001	0.414		0.095
FirstYear	Adult female with older cubs	0.028			
	Solitary adult female				
	Subadult female	0.120	0.261		
	Subadult male	0.112	0.190		0.474
OldIce	Adult female with older cubs	0.003			
	Solitary adult female				
	Subadult female	0.069	0.098		
	Subadult male	0.103	0.016		0.343
SmallFloe	Adult female with older cubs	0.044			
	Solitary adult female				
	Subadult female	0.024	0.209		
	Subadult male	0.086	0.381		0.180
VastFloe	Adult female with older cubs	≤ 0.001			
	Solitary adult female				
	Subadult female	≤ 0.001	0.389		
	Subadult male	≤ 0.001	0.082		0.109
FastIce	Adult female with older cubs	0.324			
	Solitary adult female				
	Subadult female	0.436	0.208		
	Subadult male	0.430	0.159		0.499
DistLand	Adult female with older cubs	0.163			
	Solitary adult female				
	Subadult female	0.173	0.004		
	Subadult male	0.265	0.005		0.320

Table B.4: Dunn's tests comparing use of environmental variables between classes in spring.

		Class			
Covariate	Class	Adult female with COY	Adult female with older cubs	Solitary adult female	Subadult female
Ice	Adult female with older cubs	0.219			
	Solitary adult female	0.149	0.244		
	Subadult female	0.238	0.471	0.271	
	Subadult male	0.084	≤ 0.001	0.017	0.003
IceEdge	Adult female with older cubs	0.130			
	Solitary adult female	0.228	0.053		
	Subadult female	0.271	0.287	0.106	
	Subadult male	0.296	0.189	0.113	0.441
FirstYear	Adult female with older cubs	≤ 0.001			
	Solitary adult female	0.180	0.103		
	Subadult female	0.131	0.002	0.429	
	Subadult male	0.067	≤ 0.001	0.492	0.354
OldIce	Adult female with older cubs	0.440			
	Solitary adult female	0.474	0.429		
	Subadult female	0.007	≤ 0.001	0.033	
	Subadult male	0.028	≤ 0.001	0.079	0.186
SmallFloe	Adult female with older cubs	0.279			
	Solitary adult female	0.113	0.036		
	Subadult female	0.308	0.499	0.047	
	Subadult male	0.470	0.140	0.096	0.220
VastFloe	Adult female with older cubs	≤ 0.001			
	Solitary adult female	≤ 0.001	0.315		
	Subadult female	≤ 0.001	0.500	0.327	
	Subadult male	≤ 0.001	≤ 0.001	0.156	0.004
FastIce	Adult female with older cubs	≤ 0.001			
	Solitary adult female	≤ 0.001	0.393		
	Subadult female	≤ 0.001	0.455	0.421	
	Subadult male	≤ 0.001	≤ 0.001	0.135	0.009
DistLand	Adult female with older cubs	≤ 0.001			
	Solitary adult female	≤ 0.001	0.077		
	Subadult female	≤ 0.001	0.187	0.041	
	Subadult male	≤ 0.001	≤ 0.001	0.002	0.025

Table B.5: Dunn's tests comparing use of environmental variables between classes in summer.

		Class			
Covariate	Class	Adult female with COY	Adult female with older cubs	Solitary adult female	Subadult female
Ice	Adult female with older cubs	0.495			
	Solitary adult female	0.411	0.392		
	Subadult female	0.153	0.069	0.291	
	Subadult male	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001
IceEdge	Adult female with older cubs	≤ 0.001			
	Solitary adult female	0.250	0.002		
	Subadult female	0.004	0.008	0.087	
	Subadult male	0.036	≤ 0.001	0.017	≤ 0.001
FirstYear	Adult female with older cubs	0.009			
	Solitary adult female	≤ 0.001	≤ 0.001		
	Subadult female	0.040	0.372	≤ 0.001	
	Subadult male	0.063	0.235	≤ 0.001	0.383
OldIce	Adult female with older cubs	≤ 0.001			
	Solitary adult female	0.015	≤ 0.001		
	Subadult female	0.015	0.011	≤ 0.001	
	Subadult male	0.054	≤ 0.001	≤ 0.001	0.241
SmallFloe	Adult female with older cubs	0.403			
	Solitary adult female	0.091	0.082		
	Subadult female	0.138	0.102	0.282	
	Subadult male	0.172	0.140	0.238	0.425
VastFloe	Adult female with older cubs	≤ 0.001			
	Solitary adult female	0.167	0.011		
	Subadult female	≤ 0.001	0.498	0.019	
	Subadult male	0.297	≤ 0.001	0.264	≤ 0.001
FastIce	Adult female with older cubs	≤ 0.001			
	Solitary adult female	≤ 0.001	0.042		
	Subadult female	≤ 0.001	0.217	0.125	
	Subadult male	≤ 0.001	0.403	0.043	0.205
DistLand	Adult female with older cubs	≤ 0.001			
	Solitary adult female	0.008	≤ 0.001		
	Subadult female	≤ 0.001	0.083	≤ 0.001	
	Subadult male	≤ 0.001	0.002	0.006	0.132

Table B.6: Dunn's tests comparing use of environmental variables between classes in autumn.

		Class			
Covariate	Class	Adult female with COY	Adult female with older cubs	Solitary adult female	Subadult female
Ice	Adult female with older cubs	0.007			
	Solitary adult female	0.172	0.014		
	Subadult female	≤ 0.001	0.010	≤ 0.001	
	Subadult male	≤ 0.001	0.004	≤ 0.001	0.434
IceEdge	Adult female with older cubs	0.018			
	Solitary adult female	0.049	0.003		
	Subadult female	≤ 0.001	0.013	≤ 0.001	
	Subadult male	≤ 0.001	0.002	≤ 0.001	0.478
FirstYear	Adult female with older cubs	0.014			
	Solitary adult female	0.211	0.424		
	Subadult female	0.003	0.091	0.218	
	Subadult male	≤ 0.001	0.025	0.179	0.419
OldIce	Adult female with older cubs	0.088			
	Solitary adult female	0.003	≤ 0.001		
	Subadult female	≤ 0.001	≤ 0.001	≤ 0.001	
	Subadult male	0.028	0.159	≤ 0.001	≤ 0.001
SmallFloe	Adult female with older cubs	0.064			
	Solitary adult female	0.043	0.133		
	Subadult female	0.469	0.053	0.039	
	Subadult male	0.495	0.031	0.038	0.460
VastFloe	Adult female with older cubs	0.202			
	Solitary adult female	0.003	0.006		
	Subadult female	0.023	≤ 0.001	≤ 0.001	
	Subadult male	0.199	0.013	≤ 0.001	0.080
FastIce	Adult female with older cubs	0.142			
	Solitary adult female	0.500	0.304		
	Subadult female	0.178	0.456	0.299	
	Subadult male	0.500	0.092	0.500	0.149
DistLand	Adult female with older cubs	≤ 0.001			
	Solitary adult female	≤ 0.001	0.041		
	Subadult female	≤ 0.001	≤ 0.001	0.148	
	Subadult male	≤ 0.001	0.179	0.089	≤ 0.001

Table B.7: The top three Resource Selection Function models for habitat selection by subadult and adult polar bears in the Southern Beaufort Sea from winter 2007-2011 and the associated AIC (Akaike Information Criterion), ΔAIC (difference in AIC between each model and the top model), and *w* (Akaike weight). Model number corresponds to Table 3.1.

Subadult					Adult				
Model	Covariates	AIC	ΔAIC	*w*	Model	Covariates	AIC	ΔAIC	*w*
24	*Ice* + Ice^2 + *FirstYear* + *VastFloe* + *FastIce* + *DistLand*	2817.4	0	0.37	14	*Ice* + Ice^2 + *FastIce* + *DistLand*	6307.4	0	0.35
14	*Ice* + Ice^2 + *FastIce* + *DistLand*	2817.6	0.2	0.33	18	*Ice* + Ice^2 + *VastFloe* + *FastIce* + *DistLand*	6307.4	0	0.35
15	*Ice* + Ice^2 + *FirstYear* + *FastIce* + *DistLand*	2817.8	0.4	0.30	16	*Ice* + Ice^2 + *OldIce* + *FastIce* + *DistLand*	6307.7	0.3	0.30

Table B.8: The top three Resource Selection Function models for habitat selection by subadult and adult polar bears in the Southern Beaufort Sea from spring 2007-2011 and the associated AIC (Akaike Information Criterion), ΔAIC (difference in AIC between each model and the top model), and *w* (Akaike weight). Model number corresponds to Table 3.1.

Subadult					Adult				
Model	Covariates	AIC	ΔAIC	*w*	Model	Covariates	AIC	ΔAIC	*w*
16	*Ice* + Ice^2 + *OldIce* + *FastIce* + *DistLand*	3617.8	0	0.48	33	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	7757.1	0	0.59
25	*Ice* + Ice^2 + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	3618.3	0.5	0.38	25	*Ice* + Ice^2 + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	7759.2	2.1	0.21
33	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	3620.3	2.5	0.14	31	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	7759.2	2.1	0.21

Table B.9: The top three Resource Selection Function models for habitat selection by subadult and adult polar bears in the Southern Beaufort Sea from summer 2007-2011 and the associated AIC (Akaike Information Criterion), ΔAIC (difference in AIC between each model and the top model), and *w* (Akaike weight). Model number corresponds to Table 3.1.

Subadult					Adult				
Model	Covariates	AIC	ΔAIC	*w*	Model	Covariates	AIC	ΔAIC	*w*
33	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	3989.6	0	0.34	9	*Ice* + *Ice*^{2} + *IceEdge* + *DistLand*	9395.0	0	0.66
31	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	3989.7	0.1	0.33	27	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *SmallFloe* + *DistLand*	9397.5	2.5	0.19
34	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *VastFloe* + *FastIce* + *DistLand*	3989.7	0.1	0.33	29	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *SmallFloe* + *DistLand*	9397.9	2.9	0.15

Table B.10: The top three Resource Selection Function models for habitat selection by subadult and adult polar bears in the Southern Beaufort Sea from autumn 2007-2011 and the associated AIC (Akaike Information Criterion), ΔAIC (difference in AIC between each model and the top model), and *w* (Akaike weight). Model number corresponds to Table 3.1.

Subadult					Adult				
Model	Covariates	AIC	ΔAIC	*w*	Model	Covariates	AIC	ΔAIC	*w*
9	*Ice* + *Ice*^{2} + *IceEdge* + *DistLand*	3600.5	0	0.43	29	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *SmallFloe* + *DistLand*	7452.3	0	0.55
27	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *SmallFloe* + *DistLand*	3601.0	0.5	0.34	33	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	7453.9	1.6	0.25
29	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *SmallFloe* + *DistLand*	3601.8	1.3	0.23	27	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *SmallFloe* + *DistLand*	7454.3	2.0	0.20

Table B.11: Akaike Information Criterion (AIC) for each resource selection function model in winter. The top ranked model for each class is indicated in bold. Model number corresponds to Table 3.1.

Model	Model structure	Subadult AIC	Adult AIC
1	*Ice* + Ice^2	3026.9	6432.3
2	*Ice* + Ice^2 + *IceEdge*	3027.9	6433.1
3	*Ice* + Ice^2 + *FirstYear*	3018.3	6433.4
4	*Ice* + Ice^2 + *OldIce*	3002.8	6398.4
5	*Ice* + Ice^2 + *SmallFloe*	3016.2	6428.8
6	*Ice* + Ice^2 + *VastFloe*	3027.8	6425.6
7	*Ice* + Ice^2 + *FastIce*	3023.4	6429.2
8	*Ice* + Ice^2 + *DistLand*	2891.0	6336.7
9	*Ice* + Ice^2 + *IceEdge* + *DistLand*	2889.9	6336.5
10	*Ice* + Ice^2 + *FirstYear* + *DistLand*	2875.8	6336.4
11	*Ice* + Ice^2 + *OldIce* + *DistLand*	2890.6	6336.0
12	*Ice* + Ice^2 + *SmallFloe* + *DistLand*	2884.5	6336.7
13	*Ice* + Ice^2 + *VastFloe* + *DistLand*	2885.2	6338.3
14	*Ice* + Ice^2 + *FastIce* + *DistLand*	2817.6	**6307.4**
15	*Ice* + Ice^2 + *FirstYear* + *FastIce* + *DistLand*	2817.8	6309.2
16	*Ice* + Ice^2 + *OldIce* + *FastIce* + *DistLand*	2818.2	6307.7
17	*Ice* + Ice^2 + *SmallFloe* + *FastIce* + *DistLand*	2819.4	6309.3
18	*Ice* + Ice^2 + *VastFloe* + *FastIce* + *DistLand*	2818.5	6307.4
19	*Ice* + Ice^2 + *FirstYear* + *SmallFloe* + *DistLand*	2877.4	6337.7
20	*Ice* + Ice^2 + *FirstYear* + *VastFloe* + *DistLand*	2864.0	6338.4
21	*Ice* + Ice^2 + *OldIce* + *SmallFloe* + *DistLand*	2884.7	6336.3
22	*Ice* + Ice^2 + *OldIce* + *VastFloe* + *DistLand*	2884.8	6337.8
23	*Ice* + Ice^2 + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	2819.8	6311.2
24	*Ice* + Ice^2 + *FirstYear* + *VastFloe* + *FastIce* + *DistLand*	**2817.4**	6309.4
25	*Ice* + Ice^2 + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	2820.0	6309.7
26	*Ice* + Ice^2 + *OldIce* + *VastFloe* + *FastIce* + *DistLand*	2819.0	6308.1
27	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *SmallFloe* + *DistLand*	2878.4	6338.2
28	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *VastFloe* + *DistLand*	2863.5	6339.1
29	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *SmallFloe* + *DistLand*	2884.3	6336.4
30	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *VastFloe* + *DistLand*	2881.3	6337.9
31	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	2821.3	6312.3
32	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *VastFloe* + *FastIce* + *DistLand*	2818.3	6310.9
33	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	2821.2	6310.6
34	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *VastFloe* + *FastIce* + *DistLand*	2819.4	6309.6

Table B.12: Akaike Information Criterion (AIC) for each resource selection function model in spring. The top ranked model for each class is indicated in bold. Model number corresponds to Table 3.1.

Model	Model structure	Subadult AIC	Adult AIC
1	*Ice* + *Ice*^{2}	3783.7	7917.7
2	*Ice* + *Ice*^{2} + *IceEdge*	3785.7	7919.5
3	*Ice* + *Ice*^{2} + *FirstYear*	3771.1	7915.3
4	*Ice* + *Ice*^{2} + *OldIce*	3719.1	7873.6
5	*Ice* + *Ice*^{2} + *SmallFloe*	3785.5	7906.0
6	*Ice* + *Ice*^{2} + *VastFloe*	3785.5	7917.0
7	*Ice* + *Ice*^{2} + *FastIce*	3785.7	7909.7
8	*Ice* + *Ice*^{2} + *DistLand*	3679.1	7838.9
9	*Ice* + *Ice*^{2} + *IceEdge* + *DistLand*	3681.0	7838.8
10	*Ice* + *Ice*^{2} + *FirstYear* + *DistLand*	3680.8	7838.1
11	*Ice* + *Ice*^{2} + *OldIce* + *DistLand*	3663.8	7835.0
12	*Ice* + *Ice*^{2} + *SmallFloe* + *DistLand*	3681.1	7828.3
13	*Ice* + *Ice*^{2} + *VastFloe* + *DistLand*	3641.7	7814.5
14	*Ice* + *Ice*^{2} + *FastIce* + *DistLand*	3628.8	7762.0
15	*Ice* + *Ice*^{2} + *FirstYear* + *FastIce* + *DistLand*	3627.1	7763.7
16	*Ice* + *Ice*^{2} + *OldIce* + *FastIce* + *DistLand*	**3617.8**	7761.6
17	*Ice* + *Ice*^{2} + *SmallFloe* + *FastIce* + *DistLand*	3628.9	7759.9
18	*Ice* + *Ice*^{2} + *VastFloe* + *FastIce* + *DistLand*	3628.0	7760.9
19	*Ice* + *Ice*^{2} + *FirstYear* + *SmallFloe* + *DistLand*	3682.8	7830.1
20	*Ice* + *Ice*^{2} + *FirstYear* + *VastFloe* + *DistLand*	3642.0	7805.7
21	*Ice* + *Ice*^{2} + *OldIce* + *SmallFloe* + *DistLand*	3665.8	7824.2
22	*Ice* + *Ice*^{2} + *OldIce* + *VastFloe* + *DistLand*	3634.3	7815.0
23	*Ice* + *Ice*^{2} + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	3628.6	7761.9
24	*Ice* + *Ice*^{2} + *FirstYear* + *VastFloe* + *FastIce* + *DistLand*	3628.7	7762.6
25	*Ice* + *Ice*^{2} + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	3618.3	7759.2
26	*Ice* + *Ice*^{2} + *OldIce* + *VastFloe* + *FastIce* + *DistLand*	3618.7	7758.7
27	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *SmallFloe* + *DistLand*	3684.7	7828.8
28	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *VastFloe* + *DistLand*	3644.0	7805.2
29	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *SmallFloe* + *DistLand*	3667.8	7823.6
30	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *VastFloe* + *DistLand*	3636.3	7814.8
31	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	3630.4	7759.2
32	*Ice* + *Ice*^{2} + *IceEdge* + *FirstYear* + *VastFloe* + *FastIce* + *DistLand*	3630.5	7760.8
33	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	3620.3	**7757.1**
34	*Ice* + *Ice*^{2} + *IceEdge* + *OldIce* + *VastFloe* + *FastIce* + *DistLand*	3620.6	7757.5

Table B.13: Akaike Information Criterion (AIC) for each resource selection function model in summer. The top ranked model for each class is indicated in bold. Model number corresponds to Table 3.1.

Model	Model structure	Subadult AIC	Adult AIC
1	$Ice + Ice^2$	4076.0	9564.0
2	$Ice + Ice^2 + IceEdge$	4013.8	9429.4
3	$Ice + Ice^2 + FirstYear$	4072.0	9548.2
4	$Ice + Ice^2 + OldIce$	4068.7	9546.6
5	$Ice + Ice^2 + SmallFloe$	4075.8	9563.9
6	$Ice + Ice^2 + VastFloe$	4073.0	9560.6
7	$Ice + Ice^2 + FastIce$	4078.0	9549.4
8	$Ice + Ice^2 + DistLand$	4033.0	9445.3
9	$Ice + Ice^2 + IceEdge + DistLand$	3994.7	**9395.0**
10	$Ice + Ice^2 + FirstYear + DistLand$	4033.5	9447.2
11	$Ice + Ice^2 + OldIce + DistLand$	4033.7	9447.3
12	$Ice + Ice^2 + SmallFloe + DistLand$	4034.0	9445.5
13	$Ice + Ice^2 + VastFloe + DistLand$	4033.8	9446.8
14	$Ice + Ice^2 + FastIce + DistLand$	4027.0	9447.2
15	$Ice + Ice^2 + FirstYear + FastIce + DistLand$	4028.3	9449.1
16	$Ice + Ice^2 + OldIce + FastIce + DistLand$	4027.7	9449.2
17	$Ice + Ice^2 + SmallFloe + FastIce + DistLand$	4027.9	9447.5
18	$Ice + Ice^2 + VastFloe + FastIce + DistLand$	4025.3	9448.6
19	$Ice + Ice^2 + FirstYear + SmallFloe + DistLand$	4034.4	9447.4
20	$Ice + Ice^2 + FirstYear + VastFloe + DistLand$	4034.5	9448.7
21	$Ice + Ice^2 + OldIce + SmallFloe + DistLand$	4034.9	9447.5
22	$Ice + Ice^2 + OldIce + VastFloe + DistLand$	4033.8	9448.8
23	$Ice + Ice^2 + FirstYear + SmallFloe + FastIce + DistLand$	4029.1	9449.4
24	$Ice + Ice^2 + FirstYear + VastFloe + FastIce + DistLand$	4027.0	9450.4
25	$Ice + Ice^2 + OldIce + SmallFloe + FastIce + DistLand$	4028.7	9449.5
26	$Ice + Ice^2 + OldIce + VastFloe + FastIce + DistLand$	4024.7	9450.6
27	$Ice + Ice^2 + IceEdge + FirstYear + SmallFloe + DistLand$	3996.9	9397.5
28	$Ice + Ice^2 + IceEdge + FirstYear + VastFloe + DistLand$	3998.6	9398.5
29	$Ice + Ice^2 + IceEdge + OldIce + SmallFloe + DistLand$	3996.6	9397.9
30	$Ice + Ice^2 + IceEdge + OldIce + VastFloe + DistLand$	3998.1	9398.9
31	$Ice + Ice^2 + IceEdge + FirstYear + SmallFloe + FastIce + DistLand$	3989.7	9399.5
32	$Ice + Ice^2 + IceEdge + FirstYear + VastFloe + FastIce + DistLand$	3990.3	9400.4
33	$Ice + Ice^2 + IceEdge + OldIce + SmallFloe + FastIce + DistLand$	**3989.6**	9399.9
34	$Ice + Ice^2 + IceEdge + OldIce + VastFloe + FastIce + DistLand$	3989.7	9400.9

Table B.14: Akaike Information Criterion (AIC) for each resource selection function model in autumn. The top ranked model for each class is indicated in bold. Model number corresponds to Table 3.1.

Model	Model structure	Subadult AIC	Adult AIC
1	*Ice* + Ice^2	3659.7	7562.0
2	*Ice* + Ice^2 + *IceEdge*	3650.9	7556.8
3	*Ice* + Ice^2 + *FirstYear*	3654.0	7558.4
4	*Ice* + Ice^2 + *OldIce*	3652.9	7559.1
5	*Ice* + Ice^2 + *SmallFloe*	3653.5	7541.6
6	*Ice* + Ice^2 + *VastFloe*	3660.0	7553.1
7	*Ice* + Ice^2 + *FastIce*	3661.4	7564.0
8	*Ice* + Ice^2 + *DistLand*	3617.6	7468.5
9	*Ice* + Ice^2 + *IceEdge* + *DistLand*	**3600.5**	7462.1
10	*Ice* + Ice^2 + *FirstYear* + *DistLand*	3612.5	7469.0
11	*Ice* + Ice^2 + *OldIce* + *DistLand*	3619.5	7469.7
12	*Ice* + Ice^2 + *SmallFloe* + *DistLand*	3618.3	7462.7
13	*Ice* + Ice^2 + *VastFloe* + *DistLand*	3619.4	7469.8
14	*Ice* + Ice^2 + *FastIce* + *DistLand*	3618.0	7469.2
15	*Ice* + Ice^2 + *FirstYear* + *FastIce* + *DistLand*	3613.8	7470.3
16	*Ice* + Ice^2 + *OldIce* + *FastIce* + *DistLand*	3619.8	7470.4
17	*Ice* + Ice^2 + *SmallFloe* + *FastIce* + *DistLand*	3619.0	7464.0
18	*Ice* + Ice^2 + *VastFloe* + *FastIce* + *DistLand*	3619.8	7470.4
19	*Ice* + Ice^2 + *FirstYear* + *SmallFloe* + *DistLand*	3613.7	7463.4
20	*Ice* + Ice^2 + *FirstYear* + *VastFloe* + *DistLand*	3613.8	7470.3
21	*Ice* + Ice^2 + *OldIce* + *SmallFloe* + *DistLand*	3620.3	7461.5
22	*Ice* + Ice^2 + *OldIce* + *VastFloe* + *DistLand*	3620.8	7468.3
23	*Ice* + Ice^2 + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	3615.2	7465.0
24	*Ice* + Ice^2 + *FirstYear* + *VastFloe* + *FastIce* + *DistLand*	3615.1	7471.5
25	*Ice* + Ice^2 + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	3621.0	7463.0
26	*Ice* + Ice^2 + *OldIce* + *VastFloe* + *FastIce* + *DistLand*	3621.2	7468.9
27	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *SmallFloe* + *DistLand*	3601.0	7454.3
28	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *VastFloe* + *DistLand*	3603.1	7464.1
29	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *SmallFloe* + *DistLand*	3601.8	**7452.3**
30	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *VastFloe* + *DistLand*	3603.4	7461.2
31	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *SmallFloe* + *FastIce* + *DistLand*	3602.5	7455.8
32	*Ice* + Ice^2 + *IceEdge* + *FirstYear* + *VastFloe* + *FastIce* + *DistLand*	3604.3	7464.9
33	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *SmallFloe* + *FastIce* + *DistLand*	3602.9	7453.9
34	*Ice* + Ice^2 + *IceEdge* + *OldIce* + *VastFloe* + *FastIce* + *DistLand*	3604.3	7461.9

Chapter 4

4 Long-distance movement of a female polar bear from Canada to Russia

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4.1 Introduction

Site fidelity, migration, and long-distance movements are all important for understanding the ecology and dynamics of a population. Movement of animals can result in gene flow and may influence population fluctuations (Slatkin 1987, Ranta et al. 1997). Movement of individuals within the context of meta-population structure (Hanski and Gilpin 1997) is important for species conservation (Esler 2000, Webster et al. 2002). For highly mobile species, understanding spatial connectivity between populations is particularly relevant.

Polar bears (*Ursus maritimus*) are distributed across the circumpolar Arctic in 19 populations in close association with the distribution of sea ice over the continental shelf where they forage for their main prey, the ringed seal (*Pusa hispida*) (Stirling and Archibald 1977, Durner et al. 2009, Stirling and Derocher 2012). Because of the importance of sea ice for polar bear movements and foraging success, climate change-induced sea ice loss is negatively affecting the survival, reproduction, and abundance of some populations, such as the Southern Beaufort Sea population (SB) (Derocher et al. 2004, Wiig et al. 2008, Hunter et al. 2010, Regehr et al. 2010, Stirling and Derocher 2012). Climate projections estimate that sea ice loss will continue, which may affect polar bear movements, influence distributions of the species, and threaten the persistence of populations (Durner et al. 2009, Hunter et al. 2010, Molnár et al. 2010, 2014, Castro de la Guardia et al. 2013, Hamilton et al. 2014).

Long-distance movements by polar bears from their population are rarely documented, and populations are considered relatively discrete (Durner and Amstrup 1995, Amstrup et al. 2000). Polar bear movements are associated with seasonal sea ice changes because the bears rely on the ice as a platform for foraging, traveling, and mating (Ferguson et al. 1998, Durner et al. 2009, Molnár et al. 2010, 2014). In the SB, which is shared between Canada and Alaska, some polar bears move onto land when the ice melts in the summer, whereas other bears travel north to multi-year sea ice (Amstrup et al. 2000, Stirling 2002, Schliebe et al. 2008, Pongracz and Derocher 2017). Pregnant female polar bears in the Beaufort Sea make maternity dens in the winter on land or sea ice (Lentfer 1975, Fischbach et al. 2007), and females show strong site fidelity to denning regions and at-sea feeding areas (Derocher and Stirling 1990, Ramsay and Stirling 1990, Mauritzen et al. 2001).

As part of a multi-year study to monitor the movements of the SB population, female polar bears were collared and tracked by satellite telemetry. Here, we describe the exceptionally long-distance movement of one female and compare her movements to those of other females collared as part of the same study and to the previously observed long-distance movement of another adult female from Alaska to Greenland (Durner and Amstrup 1995). These comparisons provide insights into this rarely documented behaviour that have implications for gene flow between polar bear populations.

4.2 Methods

Polar bear location data were collected from females in the Canadian region of the southern Beaufort Sea from 2009 to 2011 (Fig. 4.1). Bears were immobilized with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Laboratoires Virbac, Carros, France) using standard methods (Stirling et al. 1989). Body condition (subjective measure of body fat on a scale of 1 to 5; Stirling et al. 1989, 2008) and age (based on tooth section cementum annuli counts; Stirling et al. 1977) were recorded at capture for each bear. Adult (≥ 4 years old) female bears were fitted with GPS (global positioning system) collars that had a programmable release (CR2a; Telonics, Mesa, Arizona) timed to open in 2.2 years. The GPS collars were linked to the Argos satellite system (CLS America Inc., Lanham, Maryland) and programmed to provide location data every four hours and transmit these data to a satellite once a day. GPS locations that were erroneous (i.e., not biologically possible) were omitted from analysis. Additionally, the first three days of location data after capture were omitted from movement analyses because it takes approximately three days for the movement rates of polar bears to recover from the effects of chemical immobilization during capture (Thiemann et al. 2013). All capture and handling protocols for polar bears were conducted in accordance with the guidelines of the Canadian Council on Animal Care (http://www.ccac.ca/en_/standards/guidelines) and approved by the University of Alberta BioSciences Animal Care and Use Committee.

The movements of the female polar bear of interest (hereafter referred to as “Bear A”) were analyzed and compared to the movements of four adult females from the same study that were captured in spring 2009 and had collars transmitting data in the same period as Bear A (spring 2009 to 2011). Movement analyses included the distance traveled in the first year (first 365 days post-capture) and the movement rate in the first 79 days. The distances traveled were compared for the first year to ensure that movements were compared for the same length of time, while the movement rates were calculated for the first 79 days to allow for comparison with Durner and Amstrup (1995). Movement metrics were calculated using ArcGIS (ArcGIS version 10.3.1, Environmental Systems Research Institute, Redlands, California). Additionally, the swim speed for a long-distance swimming event by Bear A was calculated as 0.75 km/h. We then used a correction factor of 1.4× to account for locations that the collar failed to transmit while Bear A was swimming (Pilfold et al. 2017), which resulted in an adjusted swim speed of 1.05 km/h.

In addition, the annual home range in the first year was calculated for each bear using two methods. First, we created minimum convex polygons (MCPs) using ArcGIS to estimate the home range, which allowed comparison with previous home range estimates for polar bears (e.g., Parks et al. 2006, McCall et al. 2015). For Bear A, an annual MCP home range for her second year of tracking (last 365 days of tracking) was also calculated to compare her initial movements with her later movements. MCPs are a common method, but they can produce biased home range estimates, e.g., by overestimating home range size (Burgman and Fox 2003). Therefore, Brownian bridge movement models (BBMMs) were also used to estimate the home ranges. This method is based on the movement path and models an animal's utilization distribution, therefore incorporating the intensity of use of different areas by the animal (Horne et al. 2007, Kranstauber et al. 2012). BBMMs were calculated in R (R Core Team 2015) using the adehabitatHR package (Calenge 2006), and the variance of the Brownian motion (σ^2_m) was estimated using the maximum likelihood technique (Horne et al. 2007) with a telemetry error (δ^2) of 30 m, which is a reasonable estimate for GPS collar data (Tomkiewicz et al. 2010, Kranstauber et al. 2012).

4.3 Results

Polar bear research has been conducted in the southern Beaufort Sea for the past 40 years, but Bear A had not previously been handled by scientists. Bear A was a four-year-old nulliparous female who was captured on 20 April 2009 in average body condition. The GPS collar on Bear A transmitted data for 798 days, from 24 April 2009 to 30 June 2011, before the collar released as programmed. Bear A traveled west from Yukon, Canada, across northern Alaska to Wrangel Island in Russia, then moved south along the coast of Russia before crossing to the west coast of Alaska and returning north to Wrangel Island (total distance traveled = 11 686 km; Fig. 4.1). The four other female bears included for comparison (ages 5, 7, 13, and 15 years at capture) were also captured in spring 2009 in average body condition and had combined location data from 24 April 2009 to 13 November 2011. Two of these bears were captured for the first time, and the other two had been handled previously. These four bears had localized travel in the Beaufort Sea region and mainly remained near the coast of Alaska and Canada, with some northward movement before returning to the coast (Fig. 4.1). Compared to the mean movements of the four other females, Bear A traveled 1.3 times as far in the first year and moved 1.4 times as fast in the first 79 days (Table 4.1).

When calculated using the MCP method, Bear A's first-year home range area was 5.4 times the size of the mean home range of the other four females, while her second-year home range area was only 0.11 the size of the others' mean home range (Table 4.1). When calculated using the BBMM method, Bear A's first-year home range was 1.8 times as large as that of the other females. Comparing the results from the two home range methods, Bear A's first-year MCP home range was 23.7 times as large as her first-year BBMM home range (Table 4.1, Fig. 4.2).

4.4 Discussion

Long-distance movement by polar bears is rarely documented (Durner and Amstrup 1995), and most bears in the Beaufort Sea move between different habitats within a year and show fidelity to large geographic regions (Amstrup et al. 2000, Stirling 2002). Bear A in this study was unusual because her movements took her from the SB in Canada to the Chukchi Sea population (CS) in Russia over the first two months of collar deployment. Ice drift is variable across seasons and locations, making it difficult to determine whether this bear was moving with or against the sea ice circulation as she moved from the SB to the CS. Bear A traveled both farther and faster than the other adult female bears in this study and also had the most western and southern locations of the bears examined (Fig. 4.1). The female polar bear documented by Durner and Amstrup (1995) had a larger annual home range and traveled at about the same speed but covered a shorter overall distance than Bear A. However, the distance reported by Durner and Amstrup (1995) was underestimated because collars in use at that time recorded location data less frequently than current GPS collars (Table 4.1; Andersen et al. 2008). These bears were similar in that they both displayed more extensive travel than bears from other populations (e.g., Ferguson et al. 1999, McCall et al. 2015). Both individuals showed directed long-distance travel away from the populations where they were captured: the bear monitored by Durner and Amstrup (1995) eventually resided off the northern Greenland coast, and Bear A in our study traveled out of the SB and into the CS.

Even though polar bear home ranges are variable and differ between individuals and populations (Ferguson et al. 1999, McCall et al. 2015), Bear A's first-year MCP home range of 952 813 km^2 was considerably larger than those of the other females in this study. Her first-year MCP home range was also larger than the mean and maximum for adult females in the SB from

1985 to 1995 (mean = 166 694 km^2; maximum = 616 800 km^2) recorded by Amstrup et al. (2000). Similarly, her MCP home range in the first year was larger than the mean and maximum for adult females from populations in Arctic Canada and Greenland (mean = 125 500 km^2; maximum = 540 700 km^2) from 1989 to 1997 (Ferguson et al. 1999). Furthermore, Bear A's first-year MCP home range was also larger than the mean and maximum for adult females in the Western Hudson Bay population from 1992 to 1998 (mean = 106 613 km^2; maximum = 311 646 km^2) (Parks et al. 2006) and from 2004 to 2012 (mean = 353 557 km^2; maximum < 500 000 km^2) (McCall et al. 2015). Her large home range in the first year resulted from her initial movement from Yukon to Wrangel Island in the first two months and her subsequent travel along the coasts of Russia and Alaska before returning to Wrangel Island. The conclusions of our study (i.e., that Bear A had a larger first-year home range than the other four females) remained the same when the home ranges were calculated using the BBMM method; however, the MCP method overestimated the home range sizes, while the BBMM method produced less biased estimates (Table 4.1, Fig. 4.2). BBMMs take into account both the order of GPS locations and the time between them while modeling the animal's movement path (Horne et al. 2007, Kranstauber et al. 2012), and this method therefore has advantages over traditional MCP home range estimates.

After the long-distance movements in her first year, Bear A traveled locally close to Wrangel Island, and her second-year MCP home range was smaller than that of the other females in this study and those of most other females in previous studies. Wrangel Island is the major polar bear maternity denning location in the Chukchi Sea and is a common summering area for all age/sex classes (Belikov 1980, Uspenski and Belikov 1980, Garner et al. 1994). The fact that Bear A spent 26 days (28 December 2009 to 23 January 2010) in approximately the same location on Wrangel Island suggests that she made a temporary den, which some bears use for shelter under unfavourable conditions such as poor food or bad weather (Schweinsburg 1979, Ramsay and Stirling 1990, Ferguson et al. 2001). This temporary den use appeared to follow a long-distance swimming event (54 km over three days) with an adjusted swim speed of 1.05 km/h, which is within the adjusted swim speed range (0.5 to 3.7 km/h) noted by Pilfold et al. (2017). Such long-distance swims, which can be energetically expensive, are increasing in frequency in the Beaufort Sea as a result of changing sea ice conditions (Pilfold et al. 2017). The following year, Bear A spent 125 days (8 December 2010 to 11 April 2011) in approximately the same location on Wrangel Island, which contributed to her smaller home range in the second year. Polar bears overwinter in maternity dens and emerge from dens on Wrangel Island from February to April (Uspenski and Kistchinski 1972). Given the nulliparous state of Bear A at capture, it is likely that this was her first maternity den. After den emergence, Bear A traveled close to shore, which is common for females with small cubs because cubs are at risk of infanticide or hypothermia (Derocher and Stirling 1990, Durner and Amstrup 1995, Pilfold et al. 2014).

The original population of Bear A is unknown, as it was for the female polar bear described by Durner and Amstrup (1995). It is possible that Bear A was from the SB and traveled to the CS, or that she made a long-distance movement from the CS to the SB (where she was captured) before returning to the CS. Either way, the long-distance movement of this bear supports the potential for gene flow between these two populations. Bear A’s movements are noteworthy because long-distance movements among polar bear populations are rarely documented (Durner and Amstrup 1995), as is demonstrated in this study, which tracked 65 bears as part of the multi-year monitoring program in the SB from 2007 to 2012 and found only one bear that moved such a long distance. Female polar bears often return to the region where their mother denned and display fidelity to these denning areas (Derocher and Stirling 1990, Zeyl et al. 2010); therefore, they may not be major contributors to gene flow. However, genetic analyses of the SB and CS indicate a region of overlap, small genetic differences, and both females and males contributing to gene flow between populations (Paetkau et al. 1999, Cronin et al. 2006), and Bear A's movements support these findings. Analyses of telemetry data in this region indicate population overlap, but movements far into adjacent populations are uncommon (Amstrup et al. 2004).

While the long-distance movement by Bear A occurred in a period of changing environmental conditions, Durner and Amstrup (1995) found that their bear traveled from Alaska to Greenland in a period when sea ice melt was not extensive. It is therefore possible that long-distance movements by polar bears may be influenced by a variety of factors, such as exploration, dispersal, or habitat conditions, but the reasons for this behaviour are not well understood. The SB has experienced major changes in sea ice habitat (Parkinson 2014), which have resulted in associated declines in survival and reproduction (Hunter et al. 2010, Regehr et al. 2010). Climate change is therefore already affecting the dynamics of the population, while future changes to population boundaries may influence conservation and management. Long-distance movements by polar bears may become more common as climate change causes sea ice to decline (Derocher et al. 2004, McKeon et al. 2016). It is important to understand this possibility, because these long-distance movements could increase gene flow and therefore alter population boundaries.

Table 4.1: Movement metrics for Bear A and a subset of four adult females from the Southern Beaufort Sea population. The long-distance movement of another adult female previously described by Durner and Amstrup (1995) is included for comparison. SE = standard error.

	Bear A (2009-2011)	Subset of four bears (2009-2011)	Previous long-distance movement (1992-1993)
Distance travelled in first year (km)	7546	Mean = 6035 SE = 569.4 Range = 4677 to 7444	5256
Rate of travel in first 79 days (km/hour)	Mean = 1.46 SE = 0.06 Range = 0 to 5.40	Mean = 1.02 SE = 0.02 Range = 0 to 6.02	Mean = 1.4 Range = 0.2 to 3.7
Minimum Convex Polygon first-year home range size (km^2)	952 813[1]	Mean = 175 622 SE = 28 096 Range = 115 967 to 251 426	1 902 108 (US Geological Survey, unpublished data)
Brownian Bridge movement model first-year home range size (km^2)	40 282	Mean = 22 164 SE = 3598 Range = 15 563 to 28 643	N/A
Total duration of collar deployment (days)	798	Mean = 543 SE = 127.4 Range = 391 to 924	576
Number of locations in first year	1867	Mean = 1617 SE = 152.8 Range = 1161 to 1799	115 (US Geological Survey, unpublished data)

[1] In the second year, Bear A's home range size was 20 486 km^2.

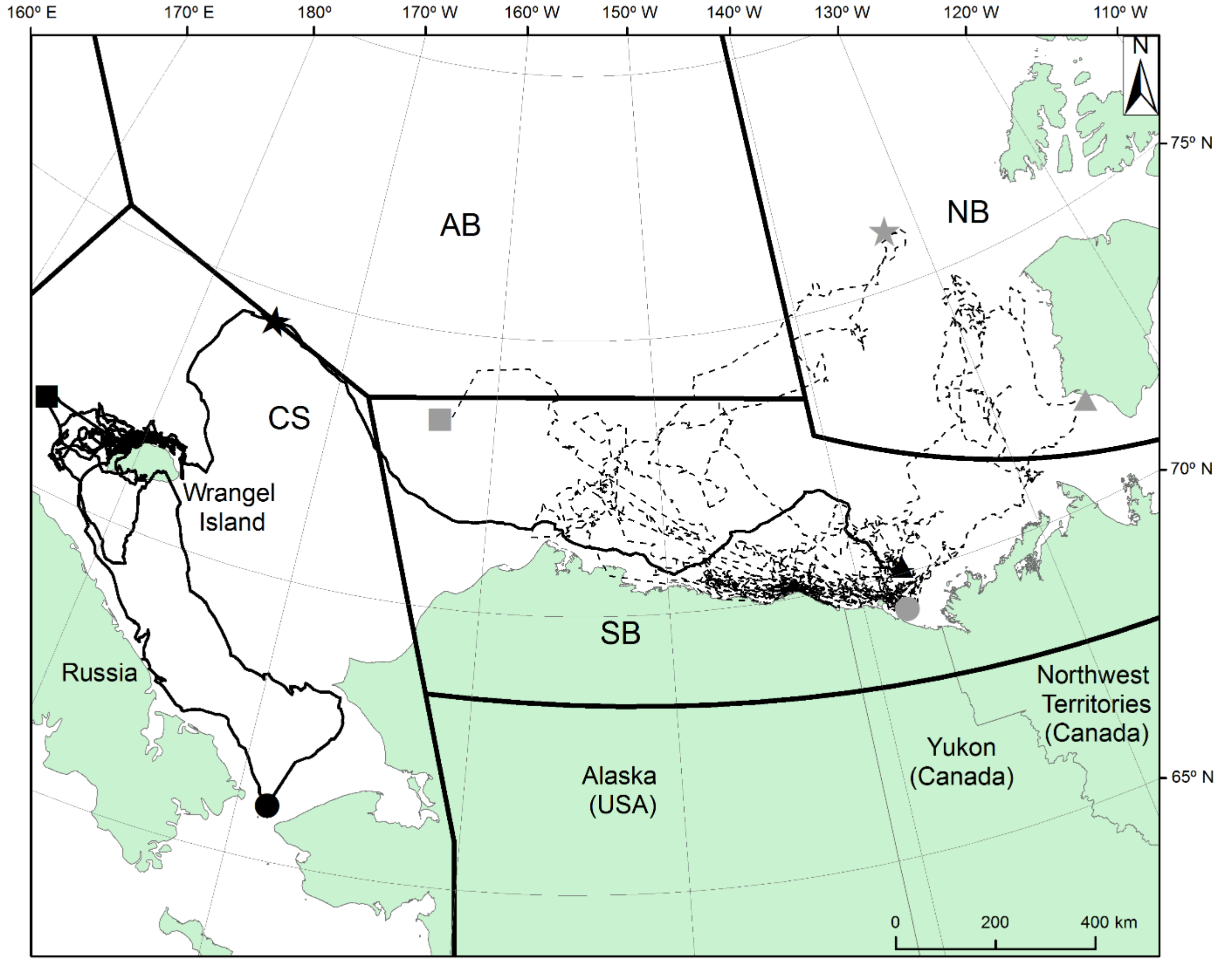

Figure 4.1: Map showing the long-distance movement of Bear A (solid black line) and those of a subset of four other adult female polar bears (dashed black lines) in 2009–11. The symbols indicate the farthest extent of travel in each direction (star = N, triangle = E, square = W, and circle = S) for Bear A (black) and the subset of four bears (grey). The thicker black lines indicate approximate boundaries of four polar bear populations - Southern Beaufort Sea (SB), Northern Beaufort Sea (NB), Chukchi Sea (CS), and Arctic Basin (AB) - as identified by the Polar Bear Specialist Group of the Species Survival Commission, International Union for Conservation of Nature (Obbard et al. 2010).

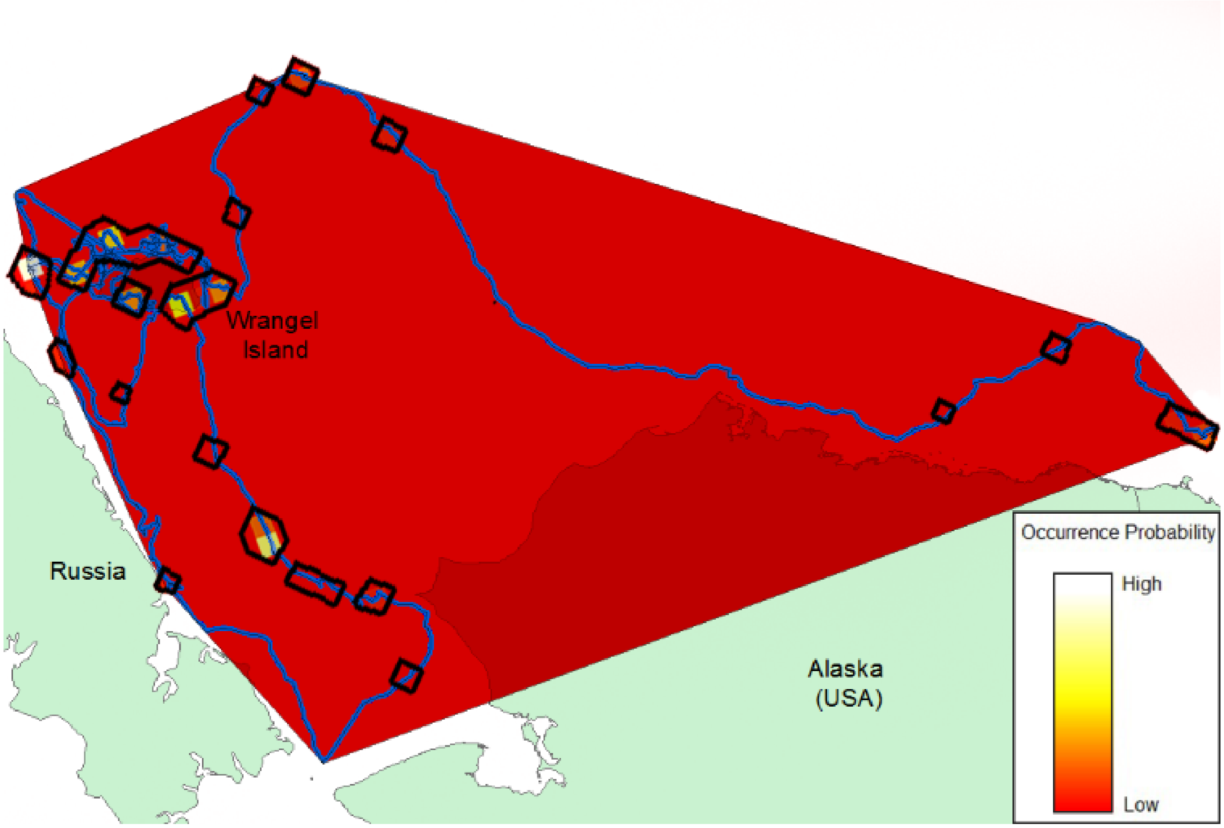

Figure 4.2: A comparison of the first-year home range estimates for Bear A calculated by two methods: Minimum convex polygon (MCP) and Brownian Bridge movement model (BBMM). The MCP home range, shown as the large red polygon, overestimates the home range size. The BBMM home range is shown as the smaller polygons outlined in black along Bear A's movement track (thin blue line). Within these polygons, white and yellow indicate the highest probability of occurrence. The BBMM method produces a less biased estimate because it incorporates the animal's movement path, the order of GPS locations, and the time between them.

Chapter 5

5 Influence of sea ice dynamics on population energetics of Western Hudson Bay polar bears

The work presented in this chapter has been submitted as: Johnson AC, Reimer JR, Lunn NJ, Stirling I, McGeachy D, Derocher, AE (2020). Influence of sea ice dynamics on population energetics of Western Hudson Bay polar bears. *Functional Ecology*.

5.1 Introduction

Population and ecosystem dynamics are key ecological processes to monitor as ecosystems undergo anthropogenic alterations due to habitat fragmentation and loss (Fahrig 2003, Mantyka-Pringle et al. 2012) and climate warming (Parmesan and Yohe 2003, Scheffers et al. 2016). Species have responded to their changing environments through changes in ecological processes including shifts in phenology (Parmesan and Yohe 2003, Visser and Both 2005), changes to foraging behaviour (Mahan and Yahner 1999), altered habitat use/distribution (Mantyka-Pringle et al. 2012, Kortsch et al. 2015), and reduced reproductive and survival rates, with resulting declines in population abundance (Fahrig 2003, Scheffers et al. 2016). These changes in species' abundances and distributions can lead to altered community structure and trophic interactions (Rall et al. 2010, Molinos et al. 2015, Scheffers et al. 2016) as well as regime shifts (Petchey et al. 1999, Kortsch et al. 2014), with implications for ecosystem function and stability (de Ruiter et al. 1995, Neutel et al. 2002, Rall et al. 2010). Changes in community structure are especially critical to ecosystems where higher trophic levels are vulnerable to anthropogenic change because altered top predator population dynamics can cause cascading effects (Shackell et al. 2010).

Examining energy dynamics over time can provide insights into ecological responses to both natural and anthropogenic change. Bioenergetics has been studied at individual/species levels using ingestion and assimilation rates (Bailey and Mukerji 1977, Cressa and Lewis 1986), prey consumption estimates (Lantry and Stewart 1993), and metabolism (Lam et al. 1991). Furthermore, broader-scale energetics studies have documented patterns in population energetic requirements (Markussen and Øritsland 1991, Ryg and Øritsland 1991, Ernest et al. 2003) and ecosystem energetic dynamics across trophic levels (Sakshaug et al. 1994). Bioenergetics research at various scales is useful for monitoring ecological patterns given that alterations in individual energetic balances may lead to changes in population dynamics (Yodzis and Innes 1992, Humphries et al. 2004). Thus, understanding temporal dynamics in energetics and relationships to environmental conditions can provide insights into the mechanisms influencing population dynamics and improve our ability to predict how populations respond to future stressors.

The Arctic marine ecosystem has experienced rapid and extensive changes in sea ice in response to climate warming (Comiso 2002, Stirling and Parkinson 2006, Stroeve and Notz 2018, IPCC 2019). Reduced sea ice extent and earlier sea ice breakup are major factors that affect many Arctic marine species (Comiso 2002, Stirling and Parkinson 2006, Meier et al. 2014), especially sea ice-dependent marine mammals including polar bears (*Ursus maritimus*) (Laidre et al. 2008, Post et al. 2009, Wassmann et al. 2011). Due to their reliance on sea ice for movement, reproduction, and as a platform from which to hunt their main prey, ice-associated seals (Stirling and Archibald 1977, Smith 1980), polar bears are particularly vulnerable to sea ice decline (Stirling et al. 1999, Stirling and Derocher 2012). As both a top predator and a species sensitive to sea ice conditions, polar bears are useful for monitoring changing Arctic marine ecosystem dynamics. Long-term research of the Western Hudson Bay (WH) polar bear population, where individuals have been captured and measured over three decades, provides a unique opportunity to examine energetic dynamics relative to sea ice habitat. Declines in WH polar bear body condition (Sciullo et al. 2016), reproductive rates (Stirling et al. 1999), survival (Regehr et al. 2007), and abundance (Lunn et al. 2016) have all been associated with climate warming. Such changes to population dynamics are influenced by individual condition and energy balances (Yodzis and Innes 1992, Humphries et al. 2004), which in turn are driven by alterations in energy intake and expenditure (Pagano et al. 2018). For Hudson Bay, the open-water period, during which polar bears fast on land, has lengthened (Stern and Laidre 2016) and an increase to a 180 day fasting period is predicted to result in increased starvation and mortality rates (Molnár et al. 2010, 2014, Pilfold et al. 2016). It is therefore important to examine energetic dynamics at various levels and long-term studies can provide important insights into top predator bioenergetic responses to climate warming and implications for ecosystem dynamics.

Energetics has been examined in polar bear populations using a fat condition index (Stirling et al. 2008b), metabolic rates (Pagano et al. 2018), body condition metrics and fasting (Atkinson and Ramsay 1995, Robbins et al. 2012, Rode et al. 2018), and lipid content (Sciullo et al. 2016). Additionally, the use of body measurements to estimate individual energetic stores can provide insights into energetic dynamics. For example, storage energy and energy density have been used to quantify energy budgets for individual polar bears (Molnár et al. 2009, 2010, Sciullo et al. 2016). Storage energy represents the energy that is available for maintenance, reproduction, and growth, and is influenced by energy intake and expenditure (Molnár et al.

2009, 2010, Sciullo et al. 2016). However, because not all energy is available for use when individuals are fasting (due to somatic maintenance), energy density is another useful metric as it accounts for the energy content per unit mass (Molnár et al. 2009, 2010, Sciullo et al. 2016). These measures are both informative for understanding changes in individual energy balances, as well as predicting changes in population dynamics in response to future conditions.

We used data on population abundance, age/sex structure, and morphometrics collected from WH polar bears to estimate the population energy density and storage energy from 1985 to 2018. Our objectives were to: 1) examine temporal dynamics of energy in the WH population, 2) assess the influence of environmental conditions on population energy, and 3) explore lagged effects of environmental variables. In addition, we analyzed energy dynamics within the population to provide insights into intra-population variation and examine the vulnerability of different age/sex classes based on energy. This research increases our understanding of the temporal and intra-population energetic patterns of a top predator experiencing habitat loss due to climate warming, as well as potential implications for Arctic marine ecosystem dynamics.

5.2 Methods

5.2.1 Field sampling

Hudson Bay is an inland sea that is seasonally ice covered (autumn to spring) and ice-free in summer (Hochheim et al. 2010; Fig. 5.1). When sea ice retreats in summer, WH polar bears come ashore along the western coast of the Bay in northeastern Manitoba, Canada and remain on land until sea ice freeze-up (Stirling et al. 1999, Lunn et al. 2016). Polar bears were captured in the core summering area of the WH population (Fig. 5.1) in late August to early October from

1985 to 2018 following standard methods (Stirling et al. 1989). Bears were measured (straight-line body length and axillary girth), marked with uniquely numbered ear-tags and tattoos, and released. Age was determined from an extracted vestigial premolar (Calvert and Ramsay 1998) or tooth eruption patterns for dependent offspring. Bears were categorized into seven age, sex, and reproductive classes: adult male (≥ 5 years), solitary adult female (≥ 5 years), adult female (≥ 5 years) with offspring, subadult male (2-4 years), subadult female (2-4 years), yearling (ca. 20-22 months, dependent and independent), and cub (ca. 8-10 months). Most solitary adult females should be pregnant during the autumn (Derocher et al. 1992). All capture and handling techniques were in accordance with the Canadian Council on Animal Care (www.ccac.ca) guidelines and approved by Environment and Climate Change Canada's Western and Northern Animal Care Committee. Research was conducted under wildlife research permits issued by the Government of Manitoba and the Parks Canada Agency.

5.2.2 Environmental data

Annual dates of sea ice breakup and freeze-up for the WH management zone were extracted from 323 grid cells with 25 x 25 km resolution passive microwave satellite raster imagery from the National Snow and Ice Data Center (Cavalieri et al. 1996). The first ordinal date in spring when sea ice concentration was ≤ 50% for three consecutive days was used as the date of sea ice breakup, while the first ordinal date in autumn when sea ice was ≥ 10% for three consecutive days was used as the date of freeze-up (Etkin 1991, Stirling et al. 1999, Lunn et al. 2016). The length of the open-water period (i.e., when bears are on land) was calculated as the date of freeze-up minus the date of breakup, then further subtracting 25 days due to the bears arriving onshore approximately 21 to 28 days after breakup (Stirling et al. 1999, Castro de la

Guardia et al. 2017, Johnson et al. 2019). In addition, the Arctic Oscillation winter index (AOw) and the North Atlantic Oscillation winter index (NAOw) were extracted for each year to examine broad climate variability. The AO affects sea ice distribution (Stroeve et al., 2011) and is related to polar bear reproduction rates and diet (Derocher 2005, McKinney et al. 2017), while NAO influences sea ice extent and has been linked to polar bear stress hormones (Bechshøft et al. 2013). AOw was calculated as the mean of January to March AO in each year (National Ocean and Atmospheric Administration; https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml). NAOw was calculated as the winter index (December to March) from the National Centre for Atmospheric Research (Hurrell 2012). To account for the influence of environmental conditions of the previous year, we also calculated lagged environmental variables in each year.

5.2.3 Age/sex class energy patterns

Individual body measurements collected at capture were used to estimate energetic metrics for each bear. Straight-line body length and axillary girth were used to estimate body mass using regression equations in Table 2 from Thiemann et al. (2011b) and then energy density (MJ kg^{-1}) and storage energy (MJ) were calculated using equations 18 A-E from Molnár et al. (2009).

Energy density and storage energy trends over time for each demographic class were analyzed using linear regression models. In addition, multiple linear regression models (Table C.1) were defined *a priori* based on ecological hypotheses and were used to assess the relationship between energy density or storage energy for each class and the environmental variables (sea ice breakup, length of the open-water period, AOw, NAOw, and lagged effects).

Environmental variables were assessed for collinearity and variables that were correlated ($r > |0.6|$) were not included in the same model (Table C.2). Model selection was determined using Akaike's Information Criterion (AIC).

As the energy density and storage energy values were non-normally distributed (Shapiro-Wilk test, $p \leq 0.05$) and standard transformations did not improve normality, we used Kruskal-Wallis ANOVA and Dunn's non-parametric tests to examine differences among age/sex classes.

5.2.4 *Estimating population energy density and storage energy*

Total population energy density and storage energy were calculated based on population structure, abundance estimates, and individual body measurements. Capture records from 1985 to 2018 were used to estimate population structure; however, variation in yearly sample sizes (e.g., low numbers of bears caught from certain age classes in certain years) necessitated the use of bootstrapping over a five-year moving window to estimate yearly percentages of each age/sex class. Therefore, step one of the population energy estimation process involved calculating the mean percentage of each class in the five-year window around the year of interest from 2000 bootstrap iterations (sampling with replacement from the percentage of bears in each class in each year from the five-year period) using the *boot* package in R (Canty and Ripley 2019) to represent yearly population structure.

Abundance estimates were calculated in the program MARK using the POPAN formulation (Schwarz and Arnason 1996; Appendix C.3). To account for uncertainty in MARK estimates, step two involved drawing a random value from a normal distribution (based on the MARK values) to estimate the annual abundance. The numbers of bears of each class were then calculated in step three by multiplying the bootstrapped age/sex class structure by the estimated annual abundance.

In step four, the yearly mean energy density and storage energy of an individual bear in each class were calculated from 2000 bootstrap iterations (sampling with replacement from the energy values of bears in that class in the year of interest) using the *boot* package in R (Canty and Ripley 2019). Step five involved calculating the yearly total energy density and storage energy for each class by multiplying the number of bears in that class by the mean energy of that class.

In step six, the yearly total population energy density and storage energy were calculated by summing the energy values across classes. To account for uncertainty in this process, steps 1-6 were conducted 10,000 times and the resulting mean and standard error of the mean (SE) were used as the total population energy density and storage energy estimates in further analyses.

5.2.5 Temporal dynamics of population energy and environmental analyses

We examined temporal trends (1985-2018) in total population energy density, storage energy, and temporal dynamics of sea ice variables using linear regression models. We used multiple linear regression analysis to examine the relationship between total population energy values and environmental variables (Table C.1). Model selection was conducted using AIC and the top model was used to make predictions about population energy given potential future environmental conditions (i.e., 180 day fasting period; Molnár et al. 2010, 2014, Pilfold et al. 2016). Statistical analyses were conducted in R v.3.6.1 (R Core Team 2019).

5.3 Results

There were 4346 captures from 1985 - 2018 of 2533 individual bears, with a mean of 128 bears (SE = 11) captured/year (Table C.3). There were 1159 adult male, 540 solitary adult female, 807 adult female with dependent offspring, 296 subadult male, 331 subadult female, 393 yearling, and 820 cub captures (Table C.4).

5.3.1 Age/sex class energy patterns

Energy density declined significantly over time for solitary adult females (mean 1.4 MJ kg^{-1}/decade) (linear regression, $p = 0.015$), while energy density did not change significantly over time for adult males, adult females with offspring, subadult males, subadult females, yearlings, or cubs (linear regression, $p = 0.860, 0.430, 0.500, 0.226, 0.577, 0.438$, respectively; Fig. 5.2). Storage energy declined significantly over time for solitary adult females (mean 225 MJ/decade) and yearlings (mean 74 MJ/decade) (linear regression, $p = 0.001, 0.041$, respectively), but was not significant for adult males, adult females with offspring, subadult males, subadult females, or cubs (linear regression, $p = 0.313, 0.977, 0.052, 0.121, 0.358$, respectively; Fig. 5.3).

Energy density of adult males and subadult females was significantly lower when sea ice breakup dates were earlier (mean 0.067 MJ kg^{-1}/day and 0.074 MJ kg^{-1}/day, respectively; multiple linear regression, $p = 0.020, 0.034$, respectively; Fig. C.1; Tables C.5, C.6), but there was no significant relationship between energy density and breakup date for solitary adult females, adult females with offspring, subadult males, yearlings, or cubs (multiple linear regression, $p = 0.199, 0.331, 0.073, 0.335, 0.056$, respectively; Fig. C.1; Table C.6). Storage energy levels were significantly lower for adult males, subadult males, subadult females, and cubs with earlier sea ice breakup dates (mean 14.90 MJ/day, 16.18 MJ/day, 9.50 MJ/day, 4.10 MJ/day, respectively; multiple linear regression, $p = 0.004, 0.014, 0.012, 0.029$, respectively; Fig C.2; Tables C.7, C.8), but non-significant for solitary adult females, adult females with offspring, or yearlings (multiple linear regression, $p = 0.128, 0.184, 0.134$, respectively; Fig. C.2; Table C.8). A longer lagged open water period was associated with significantly reduced storage energy for solitary adult females (mean 9.88 MJ/day), while there was no significant relationship with energy density (multiple linear regression, $p = 0.028, 0.074$, respectively; Figs. C.3, C.4; Tables C.6, C.8).

Energy density was significantly different among classes (Kruskal-Wallis, $\chi^2 = 958.3$, df $= 6$, $p < 0.001$). Solitary adult females had significantly higher energy density than all other classes (Dunn's test, $p \leq 0.05$; Tables C.4, C.9). Cubs and adult females with offspring had significantly lower energy density than all other classes, while adult males, subadult males/females, and yearlings had intermediate energy density. Storage energy was also significantly different among classes (Kruskal-Wallis, $\chi^2 = 3398.2$, df $= 6$, $p < 0.001$). Adult males had significantly higher storage energy than all other classes, followed by solitary adult females (Dunn's test, $p \leq 0.05$; Tables C.4, C.10). Subadult males/females and adult females with offspring had intermediate storage energy. Cubs and yearlings had significantly lower storage energy than all other classes. Furthermore, there was a decline in the contribution of subadult males (mean 1.3%/decade) and subadult females (mean 1.0%/decade) to total population storage energy over time (linear regression, $p = 0.015, 0.071$, respectively), while adult males increased (mean 3.2%/decade) in their contribution to total population storage energy over time (linear regression, $p = 0.022$) (Fig. C.5).

5.3.2 Temporal dynamics of population energy

From 1985 to 2018, the total population energy density declined by 53% (mean 3668 MJ kg^{-1}/decade) and total population storage energy declined by 56% (mean 435900 MJ/decade) (linear regression, $p < 0.001$, 0.001, respectively; Fig. 5.4). There was a significant positive correlation between yearly population abundance estimates and both population energy density and storage energy (Spearman's correlation, coefficient = 0.69 and 0.68, respectively).

5.3.3 Population energy and the environment

Sea ice breakup varied from 17 May (2015) to 10 July (1992) and occurred significantly earlier from 1985 to 2018, with mean breakup occurring 5.5 days/decade earlier (linear regression, $p \leq 0.05$; Fig. C.6). Sea ice freeze-up varied from 4 November (1993) to 7 December (2016) and occurred significantly later over time, with mean freeze-up occurring 4.3 days/decade later (linear regression, $p \leq 0.001$; Fig. C.6). The length of the open water period varied from 102 days (1992) to 166 days (2015) and significantly lengthened over time, with a mean increase of 9.9 days/decade (linear regression, $p \leq 0.001$; Fig. C.6).

The top ranked models for population energy density and storage energy included sea ice breakup and the lagged open water period, while AOw, NAOw, and their lagged effects were not included in the top models (Table C.11-C.13). Total population energy density was significantly lower when sea ice breakup occurred earlier and the lagged open water period was longer (multiple linear regression, $p < 0.001$, $p = 0.001$, respectively; Fig. 5.5, Table 5.1). The top multiple linear regression model predicted that at the earliest observed breakup (ordinal date 137) and 180 day lagged open water period, total population energy density would be 8303 MJ

kg^{-1} (58% lower than the mean energy density value that was calculated in our study, 19945 MJ kg^{-1}).

Similarly, total population storage energy was significantly lower when sea ice breakup occurred earlier and the lagged open water period was longer (multiple linear regression, $p <$ 0.001, 0.001, respectively; Fig. 5.5, Table 5.1). At the earliest breakup (ordinal date 137) and 180 day lagged open water period, population storage energy was predicted to be 838781 MJ (63% lower than our mean estimated storage energy, 2270218 MJ).

5.4 Discussion

We examined intra-population variation in energy density and storage energy, temporal dynamics in energetics, and the influence of sea ice dynamics on WH polar bear population energetics from 1985 to 2018. We found temporal variation in energetic dynamics among age/sex classes. Solitary adult females showed decreases in energy density over time while solitary adult females and yearlings declined in storage energy over time. Energy density is determined as the ratio of storage energy to body mass (Molnár et al. 2009) and was less variable than storage energy. In contrast, storage energy indicates the total amount of energy in an individual (Molnár et al. 2009) and is therefore more sensitive to changes in body condition given that the amount of storage energy is lower at smaller body sizes. Decreases in storage energy indicate that bears had less energy available for maintenance, growth, and survival (Molnár et al. 2009, Sciullo et al. 2016). These results are similar to Sciullo et al. (2016) where WH polar bear storage energy declined from 2004-2013 across classes. Due to the relationship between energy reserves, body condition, and fitness (Jakob et al. 1996, Sciullo et al. 2016), the observed reductions in available energy will influence survival and reproduction, with consequences for individual fitness. The significant reductions in energy density and storage energy for solitary adult females and storage energy for yearlings indicates the vulnerability of these classes to future environmental changes. Furthermore, adult males contributed a larger percentage to the total population storage energy over time, while the contributions of subadults declined. The small body size, dietary constraints, energetic demands of growth, and inexperienced hunting skills of younger bears make them more vulnerable to reductions in sea ice and thus prey availability (Rode et al. 2010, Thiemann et al. 2011a, Pilfold et al. 2016, Johnson et al. 2019, Laidre et al. 2020). In contrast, adult males can best buffer against sub-optimal conditions given their larger body size, broader diets, more effective hunting skills, and kleptoparasitism of smaller bears (Stirling 1974, Regehr et al. 2007, Thiemann et al. 2011a, Pilfold et al. 2016, Johnson et al. 2019). These patterns highlight the importance of continued monitoring of the condition of young bears.

The reproductive status of adult female polar bears in WH influenced their energy patterns. Solitary adult females had higher energy density and storage energy than adult females with offspring, but solitary females experienced significant declines in both energy metrics over time whereas females with offspring had lower but relatively stable energy values. These results are consistent with observations that solitary adult females have higher body condition due to their accumulation of body fat in preparation for the energetic requirements of gestation and lactation (Atkinson and Ramsay 1995, Thiemann et al. 2006, Sciullo et al. 2016). The maternity denning period in WH involves up to eight months of fasting (Ramsay and Stirling 1988) and the amount of energy a solitary adult female accumulates before denning determines the likelihood of successfully producing cubs, as well as subsequent cub survival (Derocher and Stirling 1994, 1996, 1998, Atkinson and Ramsay 1995) and litter size (Laidre et al. 2020). Decreases in solitary adult female condition can therefore translate into a decline in cub production, cub survival, and reproductive success, which have already been documented in WH (Derocher and Stirling 1995, Stirling et al. 1999). The observed declines in solitary adult female energy may reflect increased difficulty over time in accumulating sufficient resources. In contrast, females with offspring have lower energy reserves due to ongoing lactational energetic demands that make the accumulation and storage of energy more difficult (Derocher et al. 1993, Arnould and Ramsay 1994, Atkinson and Ramsay 1995). There is likely a threshold of energetic reserves that is required to successfully reproduce (Molnár et al. 2010, Reimer et al. 2019). For instance, Derocher et al. (1992) found that the lowest weight of an adult female known to have successfully reproduced was 189 kg, Robbins et al. (2012) indicated that females require 20% body fat when entering a den to be able to successfully produce cubs, and Reimer et al. (2019) suggested a reproductive threshold for energy density of ~14 MJ kg^{-1}. Similarly, our results indicated that adult females with offspring had relatively stable energy density (median: 19.8 MJ kg^{-1}; Fig. 5.2) and storage energy (median: 2241 MJ; Fig. 5.3), suggesting energetic thresholds for reproduction. In agreement with Robbins et al. (2012), our results highlight the vulnerability of females with offspring to nutritional stress due to their low energetic reserves, as well as the sensitivity of solitary adult females that need sufficient energy to reproduce.

Our study also demonstrated the association between age/sex class energetic patterns and environmental conditions. Reduced energy density and storage energy were associated with earlier sea ice breakup and this relationship was significant for adult males, subadult males/females, and cubs. These results are consistent with the relationship between earlier breakup and reduced body condition in WH (Stirling et al. 1999, Sciullo et al. 2016). Our finding that the lagged open-water period was an important predictor for solitary adult female storage energy suggests that the previous year's sea ice conditions influenced the ability of solitary females to accumulate energy reserves in preparation for reproduction. Similarly, Derocher & Stirling (1994) found that an adult female's condition in the previous year was a strong determining factor for reproductive success in WH. In other polar bear populations, lower body condition has been associated with time lags in breakup date and the duration of the ice-free period (Galicia et al. 2019, Laidre et al. 2020). The observed decline in solitary adult female energy and the relationship with the lagged open-water period suggests that females may not be able to recover from declines in stored energy that have occurred in previous years, which may accumulate over time and affect lifetime reproductive success. As cub survival has declined in relation to earlier breakup (Regehr et al. 2007), a factor potentially contributing to the decline in energy metrics for solitary adult females is the addition of non-pregnant females in poor condition that lost cubs to this class. A limitation of our study is an inability to distinguish between pregnant and non-pregnant solitary females, as well as differences in the probability of detecting each during the on-land period. Overall, our results indicate that polar bear energetic balances are negatively affected by sea ice declines and that vulnerable demographic groups include younger bears and adult females.

WH total population energy density and storage energy declined significantly over the 34 year study. The WH population declined from approximately 1185 to 806 bears from 1987 to 2011 (Lunn et al. 2016); furthermore, WH body condition has also declined over time (Derocher and Stirling 1995, Stirling et al. 1999, Sciullo et al. 2016). Reduced population abundance in addition to declining body condition of individuals both contribute to the observed decline in the total energy stored in this population. Declines in individual energy balances and subsequent consequences for survival and reproduction illustrate the mechanism linking climate change and population dynamics (Yodzis and Innes 1992, Humphries et al. 2004, Molnár et al. 2009, 2010, Pagano et al. 2018). Understanding the ecological mechanisms behind demographic change is important for wildlife management and can improve our predictions about how populations may respond to future climate warming (Cherry et al. 2009, Pagano et al. 2018, Reimer et al. 2019).

We found that western Hudson Bay experienced significant long-term change in sea ice dynamics, with a lengthening of the open-water period by approximately 9.9 days/decade. WH polar bear population energy density and storage energy were both significantly reduced when sea ice breakup was earlier and the lagged open-water period was longer, demonstrating a linkage between declining sea ice and reduced energetic balances. Sea ice is probably the most important single factor influencing polar bear demographic responses in the changing Arctic marine ecosystem. Our results are consistent with the association between earlier breakup/later freeze-up and declining body condition (Stirling et al. 1999, Obbard et al. 2016, Sciullo et al. 2016, Laidre et al. 2020), altered foraging ecology (McKinney et al. 2009, Johnson et al. 2019), and reduced reproduction/survival rates and abundance (Regehr et al. 2007, Rode et al. 2010, Lunn et al. 2016, Obbard et al. 2018) in various polar bear populations. Changes to energetic intake and expenditure in response to sea ice dynamics have consequences for energetic balances (Pagano et al. 2018). Polar bear energetic intake is reduced when breakup occurs earlier and freeze-up occurs later because the spring hunting period is shortened and bears are forced to fast on land for longer periods in poorer condition (Cherry et al. 2009, 2013, Rode et al. 2014, 2018). Meanwhile, energetic expenditure increases due to declines in optimal habitat (Durner et al. 2009, Stern and Laidre 2016), increasingly fragmentated and drifting sea ice (Mauritzen et al. 2003, Sahanatien and Derocher 2012, Auger-Méthé et al. 2016, Durner et al. 2017) and long-distance swims as a result of more open water (Durner et al. 2011, Pagano et al. 2012, Pilfold et al. 2017). We found that the open-water period increased from 105 days in 1985 to 145 days in 2018, with a maximum of 166 days in 2015. An increase in the fasting period from 120 days to 165 days was predicted to lead to higher starvation rates for adult male polar bears in WH (Robbins et al. 2012), while fasts >180 days were predicted to lead to additional increases in starvation-related mortality (Molnár et al. 2010, 2014, Pilfold et al. 2016). Similarly, our predictions indicated that at 180 day previous fasting period, population energy density and storage energy would be 58% and 63% lower than the mean estimated values, respectively. Decreases in the length of the spring foraging period are predicted to lead to declines in female polar bear expected fitness (Reimer et al. 2019) and higher fasting rates have occurred concurrently with reductions in survival and abundance (Cherry et al. 2009, Rode et al. 2014, 2018). Our predicted declines in WH population energy at longer fasting periods have implications for individual fitness and population vital rates. Moreover, the importance of the lagged open-water period suggests that there are cumulative effects of prior conditions that affect the ability of bears to recover from nutritional stress. Hudson Bay is expected to undergo continued sea ice loss in the future and WH polar bears are therefore at risk of further declines to energetic balances leading to reduced survival rates for young bears and decreased reproductive success, which may ultimately result in a functionally extinct population (Castro de la Guardia et al. 2013, Pilfold et al. 2016).

While the Arctic marine ecosystem has already experienced various alterations due to climate warming (Wassmann et al. 2011), our observed decline in population energy of a top predator has implications for ecosystem dynamics. Altered top predator population dynamics may cascade through ecosystems and influence trophic interactions and food web dynamics (Pace et al. 1999, Schmitz et al. 2000, Frank et al. 2005). For example, reduced body size of top predators has been associated with a weakening of predation pressure on lower trophic levels (Shackell et al. 2010). A potential consequence of reduced WH polar bear energetic balances is therefore altered trophic interactions with their primary prey species, ringed seals (*Pusa hispida*). However, Hudson Bay ringed seals have similarly shown population declines over time (Young et al. 2015, Ferguson et al. 2017); thus, our limited understanding of changing predator-prey interactions in the Arctic would benefit from long-term monitoring of ecological parameters across multiple trophic levels (Yurkowski et al. 2020). As the Arctic continues to warm, polar bears can act as an indicator species to improve our understanding of changing ecosystem dynamics (Rode et al. 2018). Our research reinforces the importance of long-term monitoring of individual physiological condition and broad population patterns.

Table 5.1: The top multiple regression models for total population energy density and storage energy with the environmental covariates for Western Hudson Bay polar bears from 1985 to 2018. The model F-statistic, R^2, β coefficients (β), standard error (SE), and *p*-values (*p*) are included. Model number corresponds to Table C.1. * indicates significant $p \leq 0.05$.

Response	Model no.	Covariates	F	R^2	Intercept β	β	SE	*p*
Energy density	7	Breakup	18.42	0.543	5186.56	176.60	45.82	< 0.001*
		OpenWater_Lag				-117.10	33.59	0.001*
Storage energy	7	Breakup	21.18	0.578	392250	21970	5261	< 0.001*
		OpenWater_Lag				-14241	3857	< 0.001*

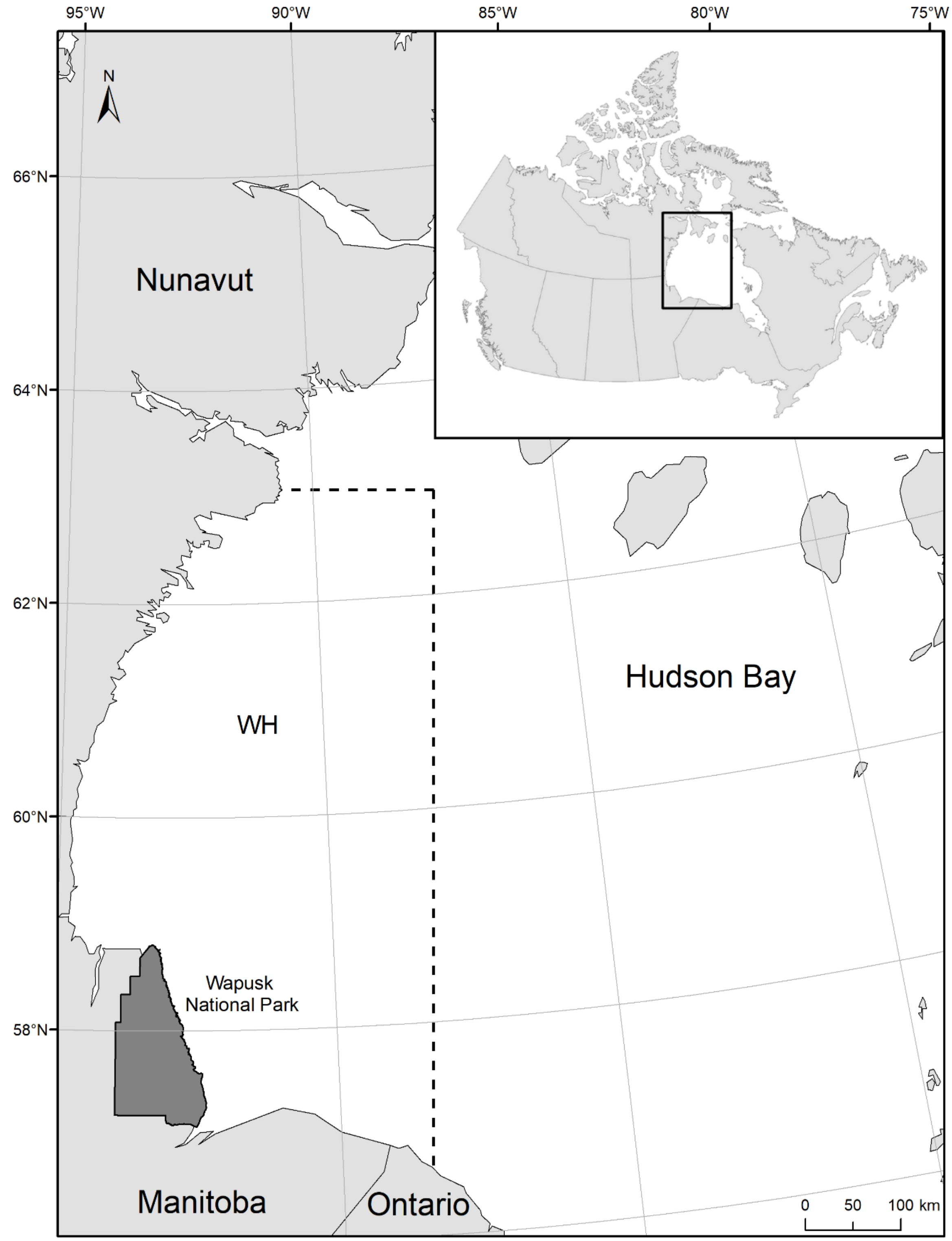

Figure 5.1: Western Hudson Bay, Canada, where polar bears were captured near the core summering area, including Wapusk National Park, from 1985-2018. The management boundary of the Western Hudson Bay (WH) population is indicated by the dashed line.

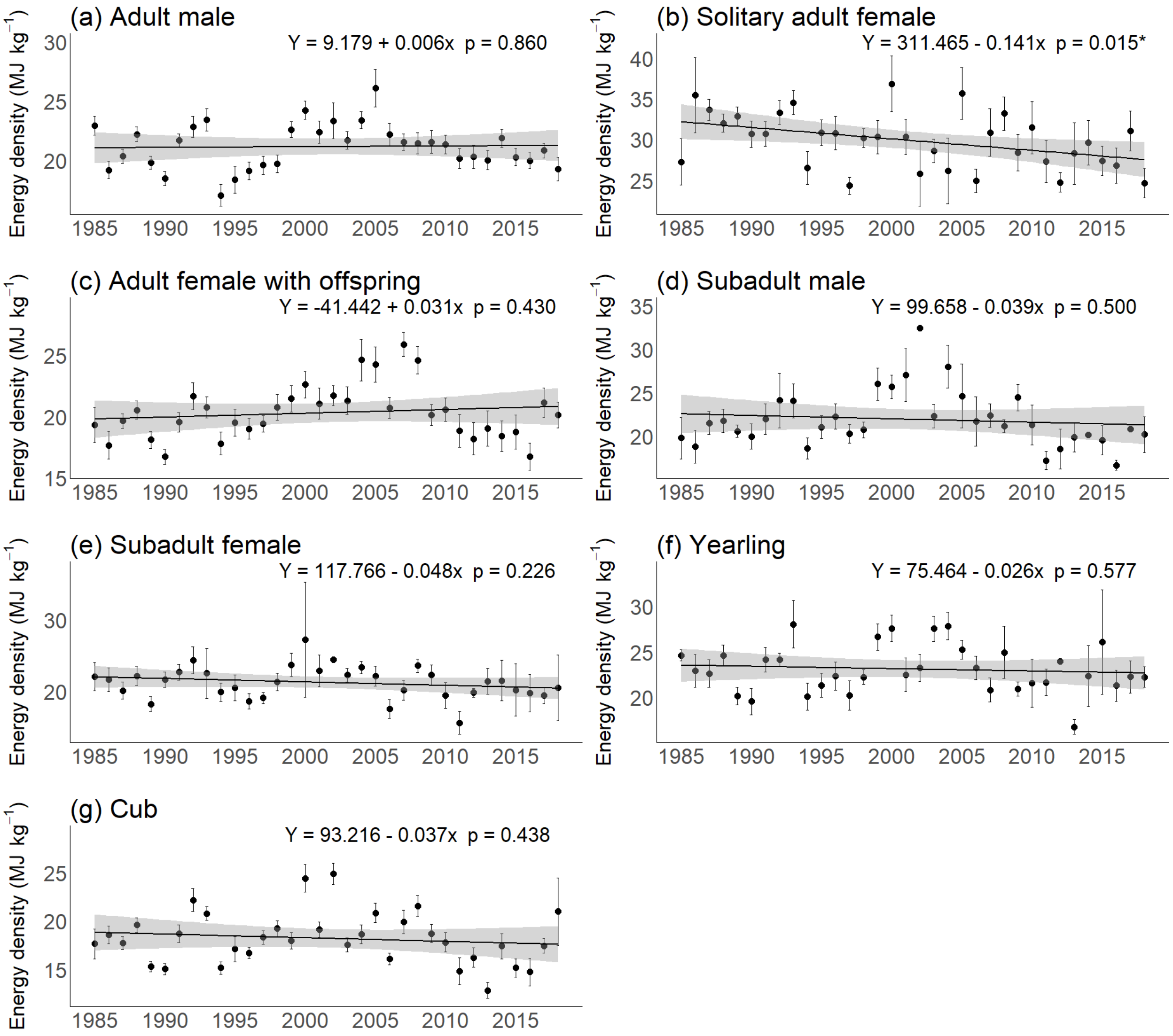

Figure 5.2: Mean energy density over time for each age/sex class of Western Hudson Bay polar bears.

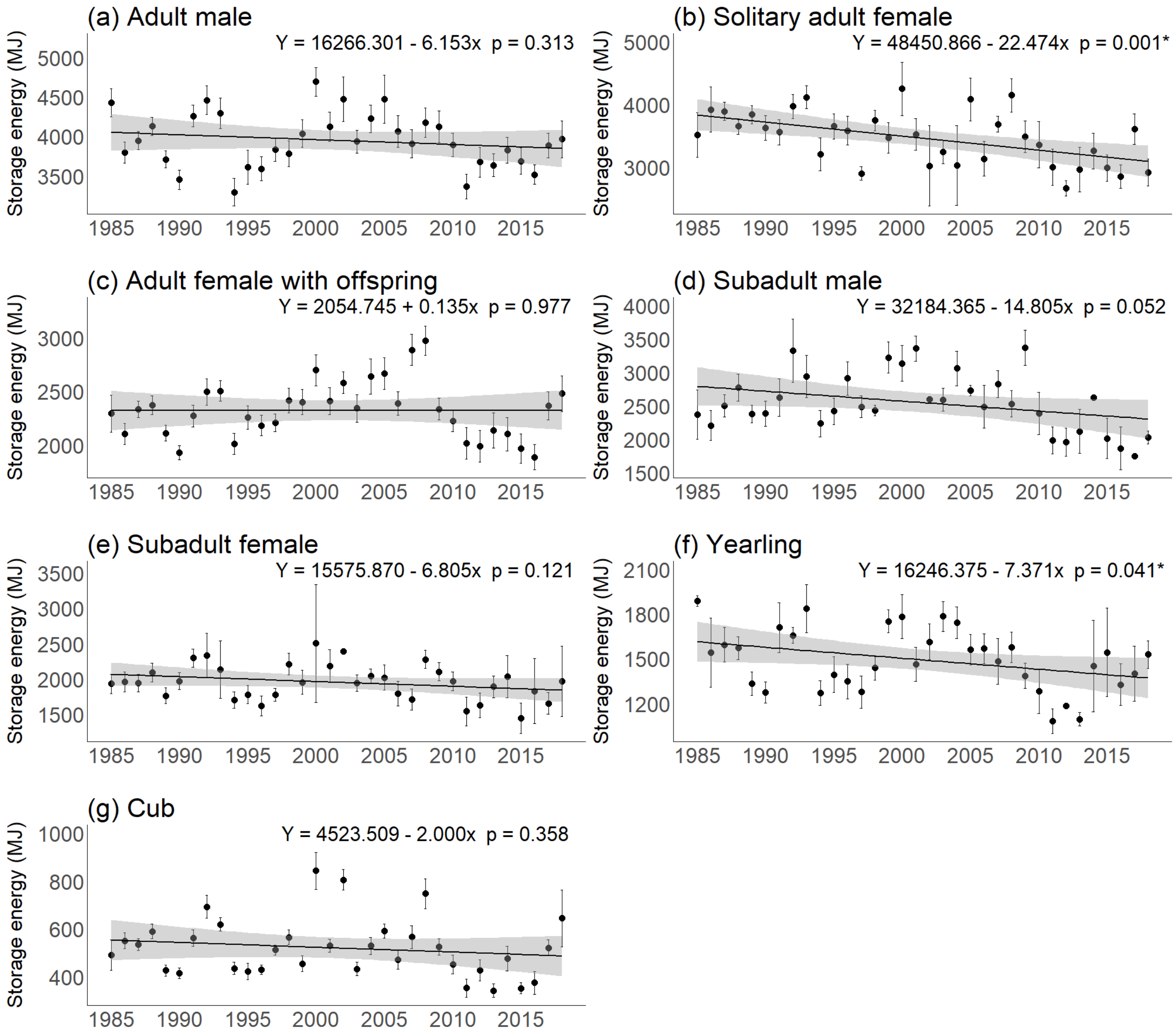

Figure 5.3: Mean storage energy over time for each age/sex class of Western Hudson Bay polar bears.

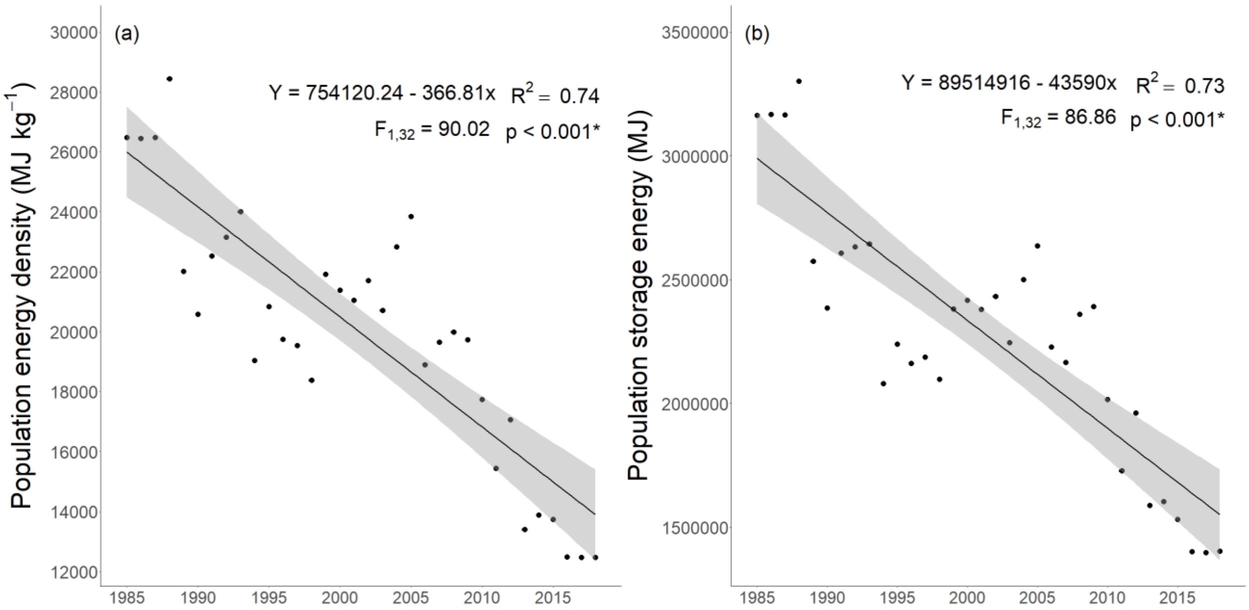

Figure 5.4: Estimated total population energy density (a) and population storage energy (b) for Western Hudson Bay polar bears from 1985 to 2018.

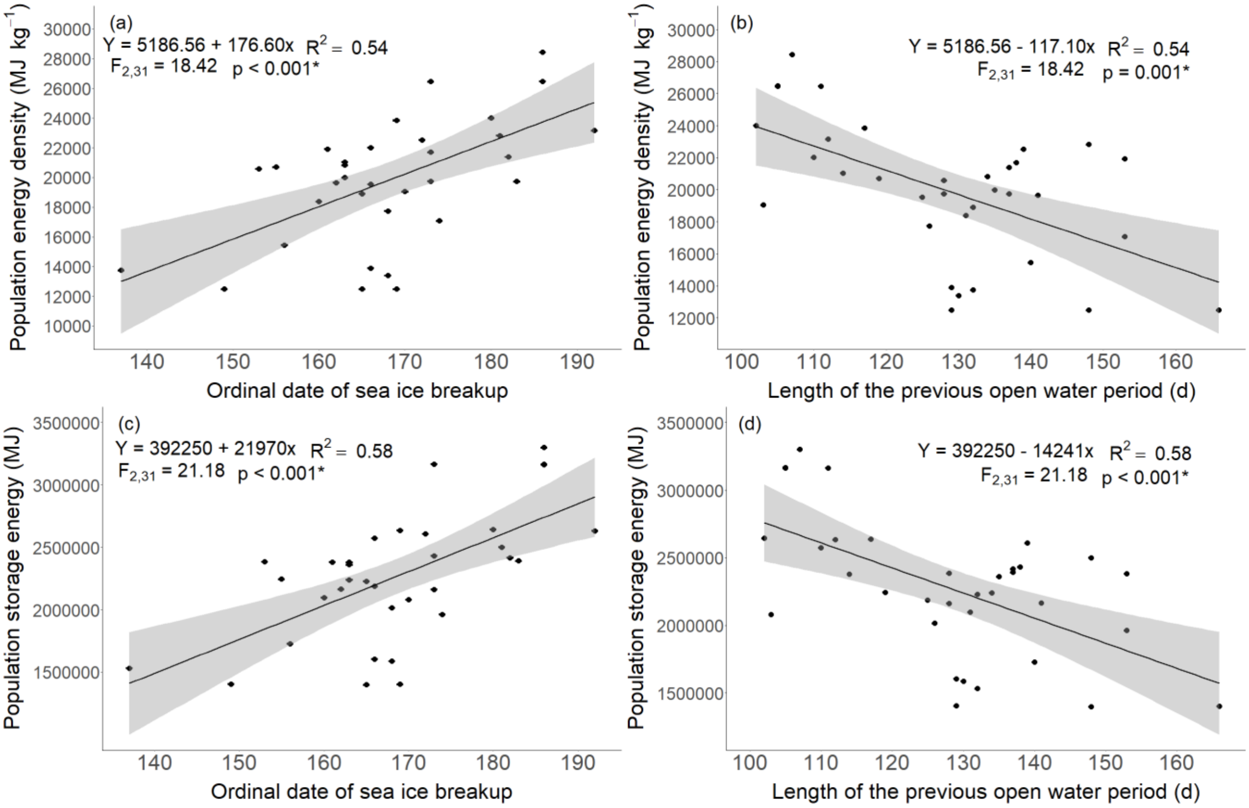

Figure 5.5: Estimated total population energy density (a, b) and storage energy (c, d) with sea ice breakup and the length of the previous open-water period (lagged by one year) for Western Hudson Bay polar bears from 1985 to 2018.

Appendices

C.1 Additional tables

Table C.1: List of *a priori* multiple linear regression models. The response variable was either energy density or storage energy of polar bears in the Western Hudson Bay population. Explanatory covariates included combinations of large scale atmospheric indices and local sea ice conditions (and lagged effects): Breakup (date of sea ice breakup), NAOw (winter North Atlantic Oscillation), AOw (winter Arctic Oscillation), OpenWater_Lag (length of the previous open water period), NAOw_Lag (previous winter North Atlantic Oscillation), and AOw_Lag (previous winter Arctic Oscillation).

Model no.	No. covariates	Model structure
1	4	Breakup + NAOw + OpenWater_Lag + NAOw_Lag
2	3	Breakup + NAOw + OpenWater_Lag
3	3	Breakup + NAOw + NAOw_Lag
4	3	Breakup + OpenWater_Lag + NAOw_Lag
5	3	NAOw + OpenWater_Lag + NAOw_Lag
6	2	Breakup + NAOw
7	2	Breakup + OpenWater_Lag
8	2	Breakup + NAOw_Lag
9	2	NAOw + OpenWater_Lag
10	2	NAOw + NAOw_Lag
11	2	OpenWater_Lag + NAOw_Lag
12	1	Breakup
13	1	NAOw
14	1	OpenWater_Lag
15	1	NAOw_Lag
16	4	Breakup + AOw + OpenWater_Lag + AOw_Lag
17	3	Breakup + AOw + OpenWater_Lag
18	3	Breakup + AOw + AOw_Lag
19	3	Breakup + OpenWater_Lag + AOw_Lag
20	3	AOw + OpenWater_Lag + AOw_Lag
21	2	Breakup + AOw
22	2	Breakup + AOw_Lag
23	2	AOw + OpenWater_Lag
24	2	AOw + AOw_Lag
25	2	OpenWater_Lag + AOw_Lag
26	1	AOw
27	1	AOw_Lag

Table C.2: Pearson correlation matrix to test for collinearity of environmental variables. Variables that were correlated ($r > |0.6|$) are in bold and indicated with an asterisk (*) and were not included in the same multiple linear regression model. See Table C.1 for descriptions of covariates. Correlated variables included: OpenWater and Breakup/Freeze-up, OpenWater_Lag and Breakup_Lag /Freeze-up_Lag, NAOw and AOw, and NAOw_Lag and AOw_Lag.

	Freeze-up	OpenWater	AOw	NAOw	Breakup_Lag	Freeze-up_Lag	OpenWater_Lag	AOw_Lag	NAOw_Lag
Breakup	-0.26	**-0.88***	-0.24	-0.12	0.15	-0.32	-0.27	-0.15	-0.05
Freeze-up		**0.69***	-0.27	-0.27	-0.36	0.31	0.41	0.009	-0.17
OpenWater			0.05	-0.05	-0.29	0.39	0.41	0.12	-0.05
AOw				**0.78***	-0.02	-0.005	0.01	0.10	0.06
NAOw					-0.09	-0.07	0.02	0.14	0.14
Breakup_Lag						-0.33	**-0.88***	-0.29	-0.13
Freeze-up_Lag							**0.74***	-0.24	-0.28
OpenWater_Lag								0.08	-0.05
AOw_Lag									**0.77***

Table C.3: Sample sizes of captures (n), mean ± SE energy density, and mean ± SE storage energy for polar bears captured in western Hudson Bay, Canada from 1985 to 2018.

Year	n	Energy density (MJ kg^{-1})	Storage energy (MJ)
1985	53	21.5 ± 0.7	2640 ± 205
1986	117	20.5 ± 0.6	2572 ± 125
1987	309	21.9 ± 0.4	2464 ± 85
1988	306	23.3 ± 0.4	2679 ± 83
1989	299	21.0 ± 0.4	2489 ± 82
1990	178	19.9 ± 0.5	2309 ± 105
1991	158	22.0 ± 0.5	2634 ± 121
1992	158	24.5 ± 0.6	2828 ± 127
1993	139	24.9 ± 0.7	2554 ± 129
1994	114	18.3 ± 0.5	2021 ± 119
1995	111	20.9 ± 0.6	2242 ± 127
1996	150	20.4 ± 0.5	2275 ± 112
1997	187	19.8 ± 0.3	2136 ± 93
1998	177	21.7 ± 0.4	2472 ± 99
1999	130	23.0 ± 0.6	2570 ± 133
2000	90	25.8 ± 0.7	3051 ± 172
2001	117	22.5 ± 0.6	2375 ± 139
2002	87	23.5 ± 0.6	2588 ± 174
2003	153	21.8 ± 0.5	2452 ± 117
2004	116	23.6 ± 0.6	2826 ± 144
2005	91	25.0 ± 0.7	2481 ± 161
2006	105	20.9 ± 0.5	2467 ± 143
2007	80	22.3 ± 0.5	2628 ± 158
2008	86	23.9 ± 0.6	2748 ± 151
2009	111	21.3 ± 0.5	2414 ± 140
2010	102	21.3 ± 0.6	2460 ± 145
2011	99	19.9 ± 0.7	2280 ± 133
2012	64	19.5 ± 0.6	2337 ± 173
2013	68	19.9 ± 0.9	2437 ± 166
2014	81	21.6 ± 0.8	2412 ± 157
2015	68	19.8 ± 0.7	2124 ± 168
2016	74	19.6 ± 0.7	2215 ± 141
2017	89	21.3 ± 0.6	2532 ± 156
2018	79	21.4 ± 0.7	2595 ± 144

Table C.4: Sample sizes (n) and the median energy density and storage energy (range) for each age/sex class of Western Hudson Bay polar bears from 1985 to 2018.

Class	n	Energy density (MJ kg^{-1})	Storage energy (MJ)
Adult male	1159	20.8 (5.6, 44.6)	3895 (1156, 8206)
Solitary adult female	540	30.3 (9.9, 57.1)	3525 (1016, 6590)
Adult female with offspring	807	19.8 (7.9, 44.1)	2241 (916, 4736)
Subadult male	296	21.3 (10.7, 57.0)	2533 (948, 5541)
Subadult female	331	20.6 (7.9, 45.6)	1885 (794, 3857)
Yearling	393	22.8 (6.8, 50.0)	1457 (457, 3116)
Cub	820	17.6 (4.7, 41.2)	490 (79, 1694)
Total	4346	20.8 (4.7, 57.1)	2370 (79, 8206)

Table C.5: The top ranked multiple regression models for energy density and the environmental covariates for each polar bear age/sex class in Western Hudson Bay from 1985 to 2018. The model F-statistic, R^2, β coefficients (β), standard error (SE), and p-values (*p*) are included. Bold and * indicates significant ($p \leq 0.05$). Model number corresponds to Table C.1.

Class	Model no.	Covariates	F	R^2	Intercept β	β	SE	*p*
Adult male	22	**Breakup**	4.271	0.216	11.752	**0.056**	**0.026**	**0.040***
		AOw_Lag				-0.448	0.275	0.114
Solitary adult female	14	**OpenWater_Lag**	5.101	0.138	40.010	**-0.079**	**0.035**	**0.031***
Adult female with offspring	30	AOw_Lag	1.313	0.039	20.334	-0.395	0.344	0.260
Subadult male	12	Breakup	3.119	0.089	8.040	0.082	0.047	0.087
Subadult female	3	**Breakup**	3.698	0.270	7.512	**0.079**	**0.030**	**0.014***
		NAOw				0.239	0.159	0.144
		NAOw_Lag				0.250	0.158	0.125
Yearling	12	Breakup	0.939	0.029	16.730	0.038	0.039	0.340
Cub	12	**Breakup**	4.423	0.121	4.620	**0.081**	**0.038**	**0.043***

Table C.6: Multiple regression model results for energy density with sea ice breakup and previous open-water period for each polar bear age/sex class in Western Hudson Bay from 1985 to 2018. The model F-statistic, R^2, β coefficients (β), standard error (SE), and p-values (*p*) are included. Bold and * indicates significant ($p \leq 0.05$). Model number corresponds to Table C.1.

Class	Model no.	Covariates	F	R^2	Intercept β	β	SE	*p*
Adult male	7	**Breakup**	2.986	0.162	8.019	**0.067**	**0.028**	**0.020***
		OpenWater_Lag				0.014	0.020	0.503
Solitary adult female	7	Breakup	3.467	0.183	27.585	0.064	0.049	0.199
		OpenWater_Lag				-0.066	0.036	0.074
Adult female with offspring	7	Breakup	0.719	0.044	11.648	0.034	0.034	0.331
		OpenWater_Lag				0.023	0.025	0.365
Subadult male	7	Breakup	1.736	0.101	3.681	0.091	0.049	0.073
		OpenWater_Lag				0.023	0.036	0.527
Subadult female	**7**	**Breakup**	2.502	0.139	7.792	**0.074**	**0.033**	**0.034***
		OpenWater_Lag				0.008	0.024	0.750
Yearling	7	Breakup	0.481	0.030	15.445	0.040	0.041	0.335
		OpenWater_Lag				0.007	0.030	0.824
Cub	7	Breakup	2.143	0.122	4.863	0.080	0.040	0.056
		OpenWater_Lag				-0.001	0.030	0.966

Table C.7: The top ranked multiple regression models for storage energy and the environmental covariates for each polar bear age/sex class in Western Hudson Bay from 1985 to 2018. The model F-statistic, R^2, β coefficients (β), standard error (SE), and p-values (*p*) are included. Bold and * indicates significant ($p \leq 0.05$). Model number corresponds to Table C.1.

Class	Model no.	Covariates	F	R^2	Intercept β	β	SE	*p*
Adult male	12	**Breakup**	11.13	0.258	1434.598	**14.918**	**4.471**	**0.002***
Solitary adult female	1	Breakup	4.177	0.366	2796.362	10.695	5.617	0.067
		NAOw				43.655	28.503	0.1365
		OpenWater_Lag				**-9.437**	**4.093**	**0.029***
		NAOw_Lag				41.621	28.383	0.153
Adult female with offspring	12	Breakup	1.751	0.052	1458.604	5.131	3.878	0.195
Subadult male	12	**Breakup**	8.052	0.201	-278.688	**16.783**	**5.915**	**0.008***
Subadult female	23	**Breakup**	5.098	0.248	212.406	**10.324**	**3.373**	**0.005***
		AOw_Lag				48.973	35.675	0.180
Yearling	12	Breakup	3.355	0.095	569.217	5.479	2.991	0.076
Cub	21	**Breakup**	4.095	0.209	-279.393	**4.735**	**1.723**	**0.010***
		AOw				26.213	18.272	0.161

Table C.8: Multiple regression model results for storage energy with sea ice breakup and previous open-water period for each polar bear age/sex class in Western Hudson Bay from 1985 to 2018. The model F-statistic, R^2, β coefficients (β), standard error (SE), and p-values (*p*) are included. Bold and * indicates significant ($p \leq 0.05$). Model number corresponds to Table C.1.

Class	Model no.	Covariates	F	R^2	Intercept β	β	SE	*p*
Adult male	7	**Breakup**	5.393	0.258	1445.311	**14.897**	**4.715**	**0.004***
		OpenWater_Lag				-0.056	3.456	0.987
Solitary adult female	7	Breakup	5.213	0.252	3193.620	9.149	5.852	0.128
		OpenWater_Lag				**-9.881**	**4.290**	**0.028***
Adult female with offspring	7	Breakup	0.922	0.056	1246.197	5.540	4.080	0.184
		OpenWater_Lag				1.118	2.991	0.711
Subadult male	7	**Breakup**	3.983	0.204	36.702	**16.177**	**6.224**	**0.014***
		OpenWater_Lag				-1.660	4.563	0.719
Subadult female	7	**Breakup**	3.925	0.202	390.028	**9.502**	**3.562**	**0.012***
		OpenWater_Lag				-0.288	2.611	0.913
Yearling	7	Breakup	1.984	0.114	919.803	4.805	3.122	0.134
		OpenWater_Lag				-1.845	2.289	0.426
Cub	7	**Breakup**	2.879	0.157	-157.586	**4.101**	**1.792**	**0.029***
		OpenWater_Lag				-0.105	1.314	0.937

Table C.9: Dunn's test comparing energy density among age/sex classes of western Hudson Bay polar bears from 1985 to 2018. Significant differences are indicated by asterisks (* indicates $p \leq 0.05$; ** indicates $p \leq 0.001$).

	Adult male (1159)	Solitary adult female (540)	Adult female with offspring (807)	Subadult male (296)	Subadult female (331)	Yearling (393)	Cub (820)
Adult male		< 0.001**	< 0.001**	0.073	0.431	< 0.001**	< 0.001**
Solitary adult female			< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**
Adult female with offspring				< 0.001**	0.012*	< 0.001**	< 0.001**
Subadult male					0.094	0.002*	< 0.001**
Subadult female						< 0.001**	< 0.001**
Yearling							< 0.001**

Table C.10: Dunn's test comparing storage energy among age/sex classes of western Hudson Bay polar bears from 1985 to 2018. Significant differences are indicated by asterisks (* indicates $p \leq 0.05$; ** indicates $p \leq 0.001$).

	Adult male (1159)	Solitary adult female (540)	Adult female with offspring (807)	Subadult male (296)	Subadult female (331)	Yearling (393)	Cub (820)
Adult male		< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**
Solitary adult female			< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**
Adult female with offspring				0.002*	< 0.001**	< 0.001**	< 0.001**
Subadult male					< 0.001**	< 0.001**	< 0.001**
Subadult female						< 0.001**	< 0.001**
Yearling							< 0.001**

Table C.11: Model selection for total population energy density and storage energy for Western Hudson Bay polar bears from 1985 to 2018. The top four models for each energy variable are shown with the associated Akaike Information Criterion (AIC), ΔAIC (AIC difference between each model and the top ranked model), and Akaike weight (w_i). The top ranked model is indicated in bold. Model number corresponds to Table C.1.

Response	Model no.	Covariates	AIC	ΔAIC	w_i
Energy density	**7**	**Breakup + OpenWater_Lag**	**645.007**	**0**	**0.43**
Energy density	2	Breakup + NAOw + OpenWater_Lag	646.453	1.446	0.21
Energy density	17	Breakup + AOw + OpenWater_Lag	646.569	1.562	0.20
Energy density	19	Breakup + OpenWater_Lag + AOw_Lag	646.965	1.958	0.16
Storage energy	**7**	**Breakup + OpenWater_Lag**	**967.551**	**0**	**0.45**
Storage energy	2	Breakup + NAOw + OpenWater_Lag	969.175	1.624	0.20
Storage energy	17	Breakup + AOw + OpenWater_Lag	969.276	1.725	0.19
Storage energy	19	Breakup + OpenWater_Lag + AOw_Lag	969.488	1.937	0.17

Table C.12: Akaike Information Criterion (AIC) for each model for total population energy density. The top ranked model is indicated in bold. Model number corresponds to Table C.1.

Model no.	Covariates	AIC
1	Breakup + NAOw + OpenWater_Lag + NAOw_Lag	648.384
2	Breakup + NAOw + OpenWater_Lag	646.453
3	Breakup + NAOw + NAOw_Lag	657.820
4	Breakup + OpenWater_Lag + NAOw_Lag	646.982
5	NAOw + OpenWater_Lag + NAOw_Lag	660.130
6	Breakup + NAOw	655.820
7	**Breakup + OpenWater_Lag**	**645.007**
8	Breakup + NAOw_Lag	656.246
9	NAOw + OpenWater_Lag	658.270
10	NAOw + NAOw_Lag	671.610
11	OpenWater_Lag + NAOw_Lag	658.201
12	Breakup	654.250
13	NAOw	669.626
14	OpenWater_Lag	656.316
15	NAOw_Lag	669.622
16	Breakup + AOw + OpenWater_Lag + AOw_Lag	648.507
17	Breakup + AOw + OpenWater_Lag	646.569
18	Breakup + AOw + AOw_Lag	657.574
19	Breakup + OpenWater_Lag + AOw_Lag	646.965
20	AOw + OpenWater_Lag + AOw_Lag	659.869
21	Breakup + AOw	655.705
22	Breakup + AOw_Lag	656.154
23	AOw + OpenWater_Lag	658.228
24	AOw + AOw_Lag	670.966
25	OpenWater_Lag + AOw_Lag	657.924
26	AOw	669.557
27	AOw_Lag	669.008

Table C.13: Akaike Information Criterion (AIC) for each model for total population storage energy. The top ranked model is indicated in bold. Model number corresponds to Table C.1.

Model no.	Covariates	AIC
1	Breakup + NAOw + OpenWater_Lag + NAOw_Lag	971.117
2	Breakup + NAOw + OpenWater_Lag	969.175
3	Breakup + NAOw + NAOw_Lag	981.654
4	Breakup + OpenWater_Lag + NAOw_Lag	969.527
5	NAOw + OpenWater_Lag + NAOw_Lag	984.591
6	Breakup + NAOw	979.654
7	**Breakup + OpenWater_Lag**	**967.551**
8	Breakup + NAOw_Lag	979.937
9	NAOw + OpenWater_Lag	982.720
10	NAOw + NAOw_Lag	996.831
11	OpenWater_Lag + NAOw_Lag	982.606
12	Breakup	977.943
13	NAOw	994.843
14	OpenWater_Lag	980.725
15	NAOw_Lag	994.831
16	Breakup + AOw + OpenWater_Lag + AOw_Lag	971.192
17	Breakup + AOw + OpenWater_Lag	969.276
18	Breakup + AOw + AOw_Lag	981.399
19	Breakup + OpenWater_Lag + AOw_Lag	969.488
20	AOw + OpenWater_Lag + AOw_Lag	984.099
21	Breakup + AOw	979.556
22	Breakup + AOw_Lag	979.819
23	AOw + OpenWater_Lag	982.514
24	AOw + AOw_Lag	996.026
25	OpenWater_Lag + AOw_Lag	982.257
26	AOw	994.674
27	AOw_Lag	994.136

C.2 Additional figures

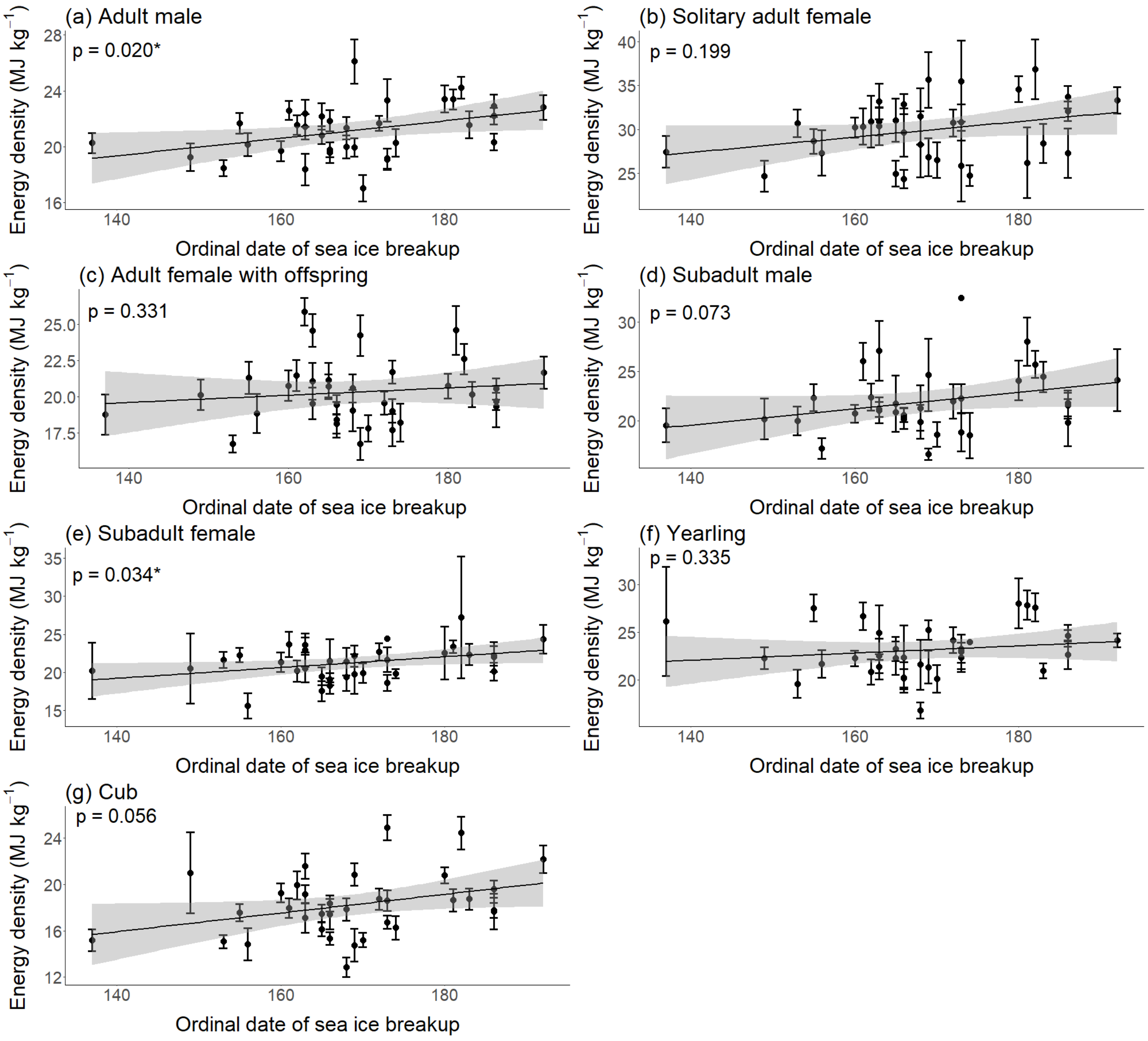

Figure C.1: Energy density with the date of sea ice breakup for each age/sex class of Western Hudson Bay polar bears. See Table C.6 for model coefficients.

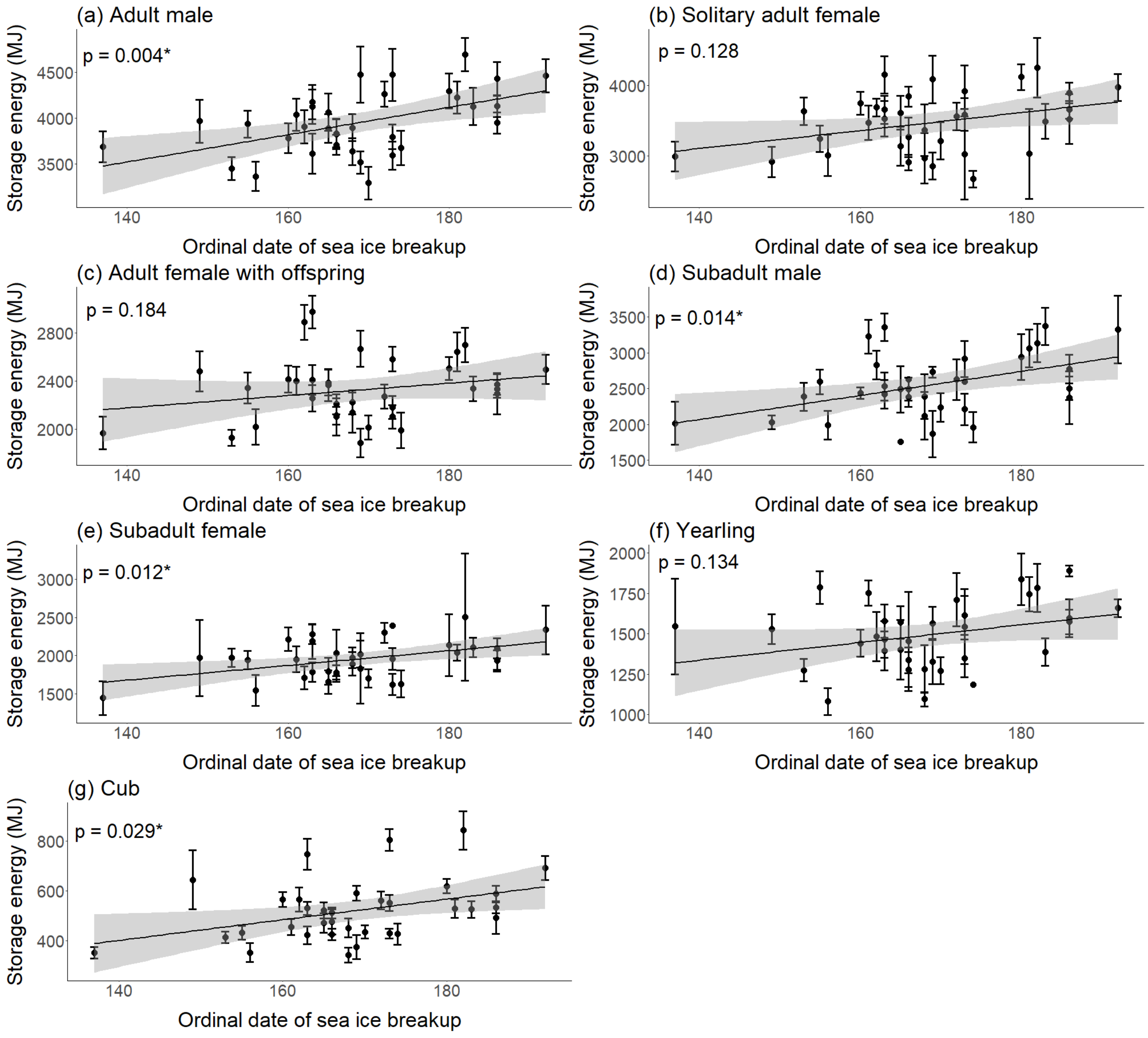

Figure C.2: Storage energy with the date of sea ice breakup for each age/sex class of Western Hudson Bay polar bears. See Table C.8 for model coefficients.

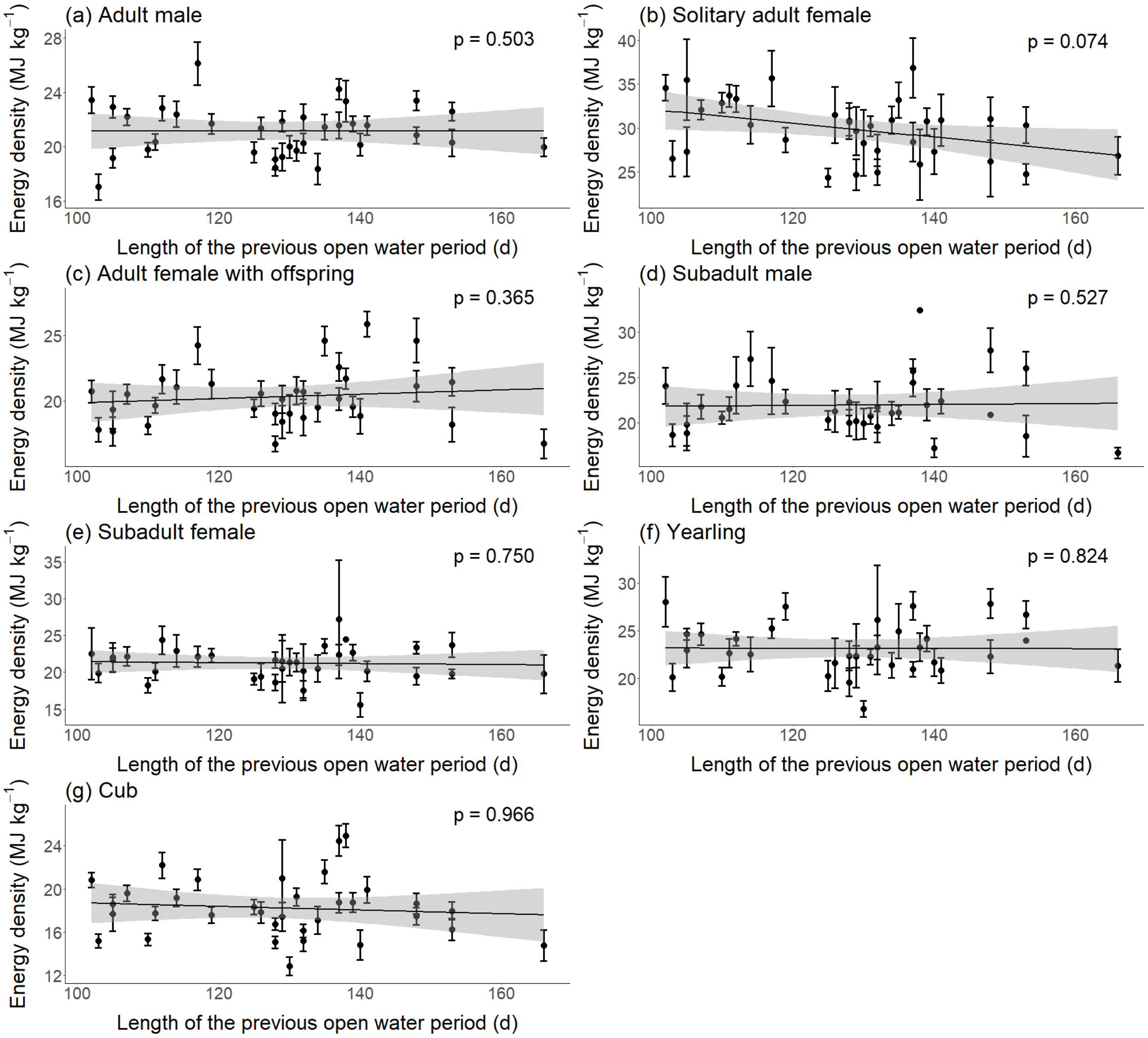

Figure C.3: Energy density with the length of the previous open-water period for each age/sex class of Western Hudson Bay polar bears. See Table C.6 for model coefficients.

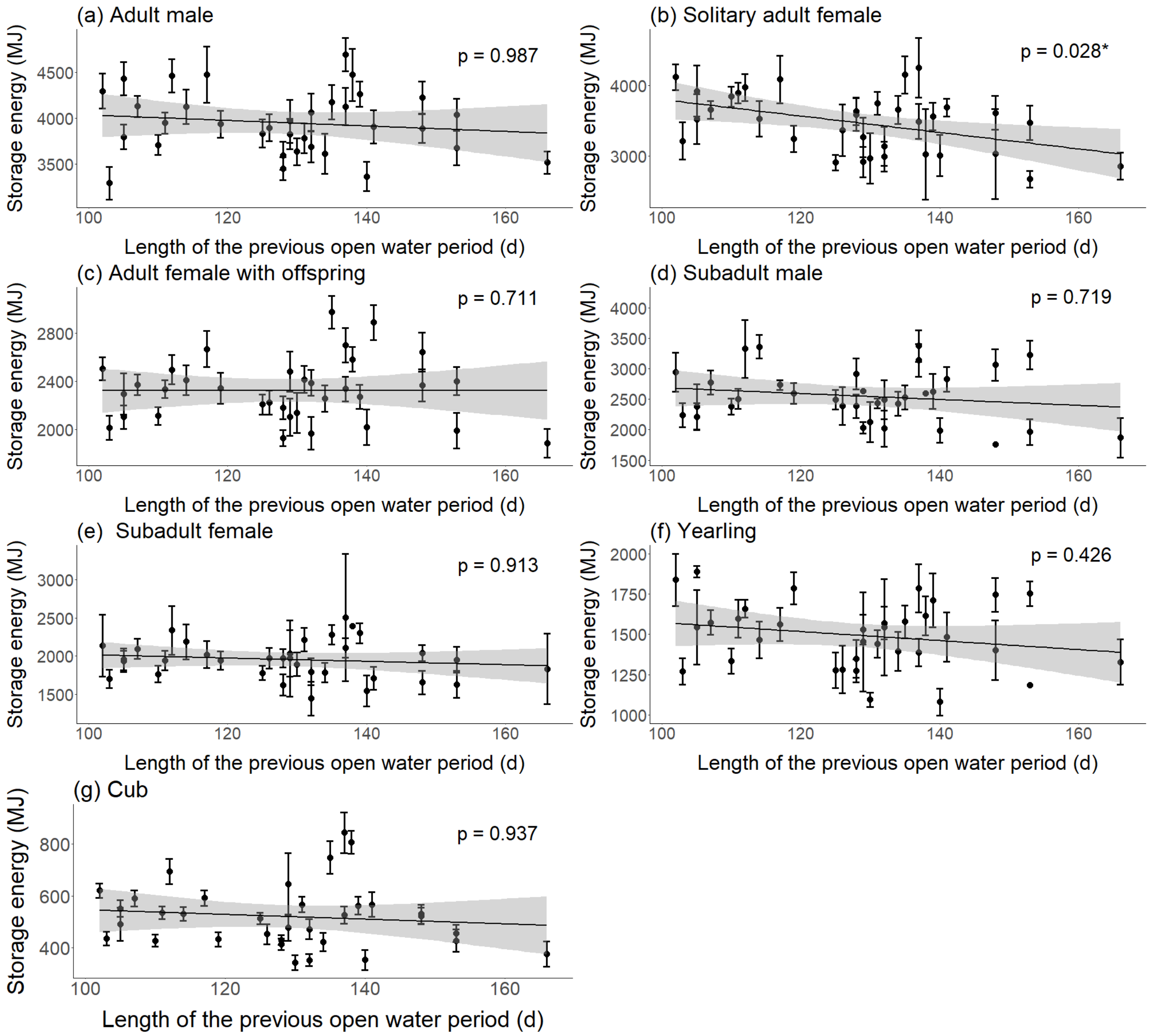

Figure C.4: Storage energy with the length of the previous open-water period for each age/sex class of Western Hudson Bay polar bears. See Table C.8 for model coefficients.

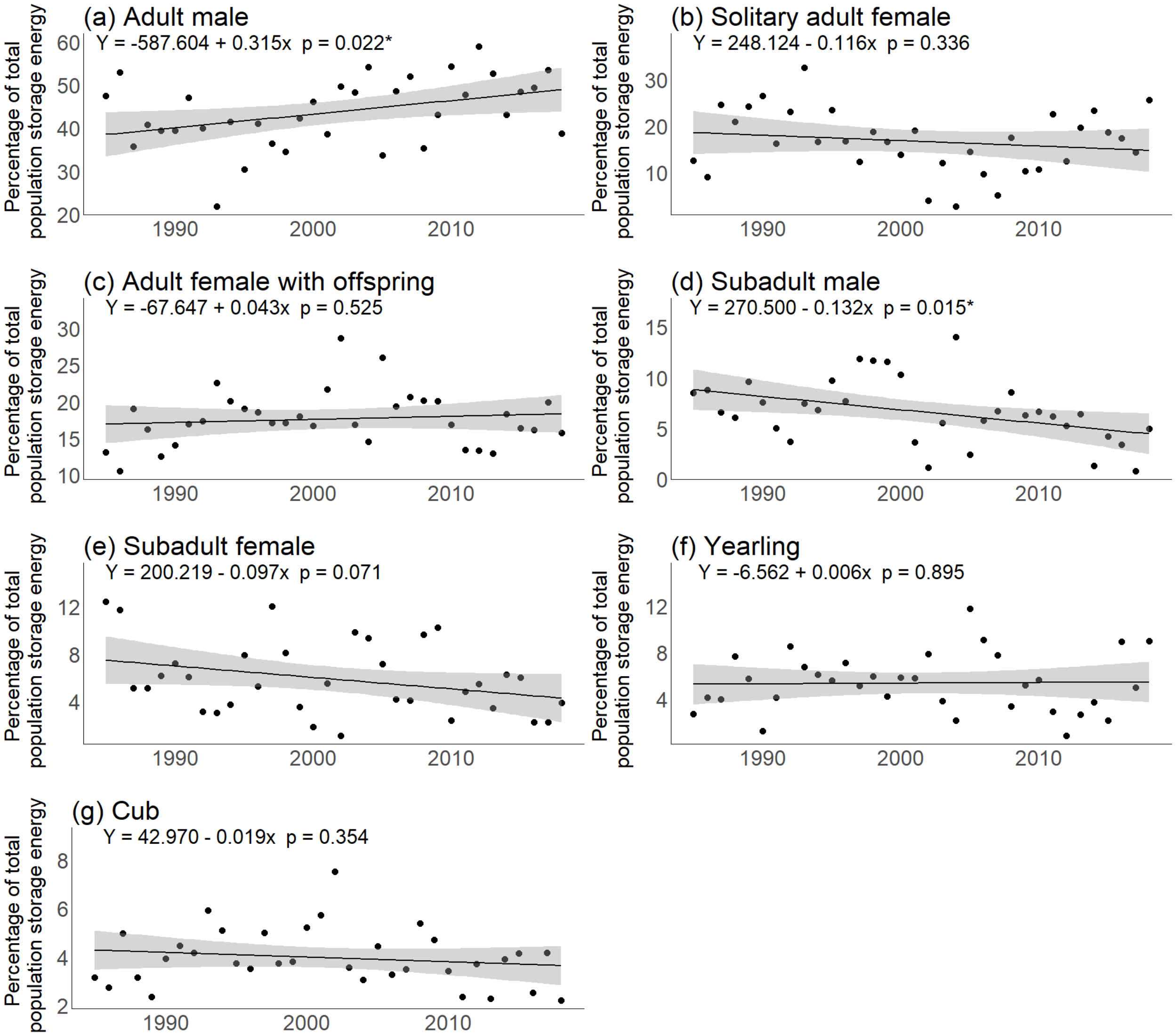

Figure C.5: Percentage of the total population storage energy contributed by each age/sex class over time for Western Hudson Bay polar bears.

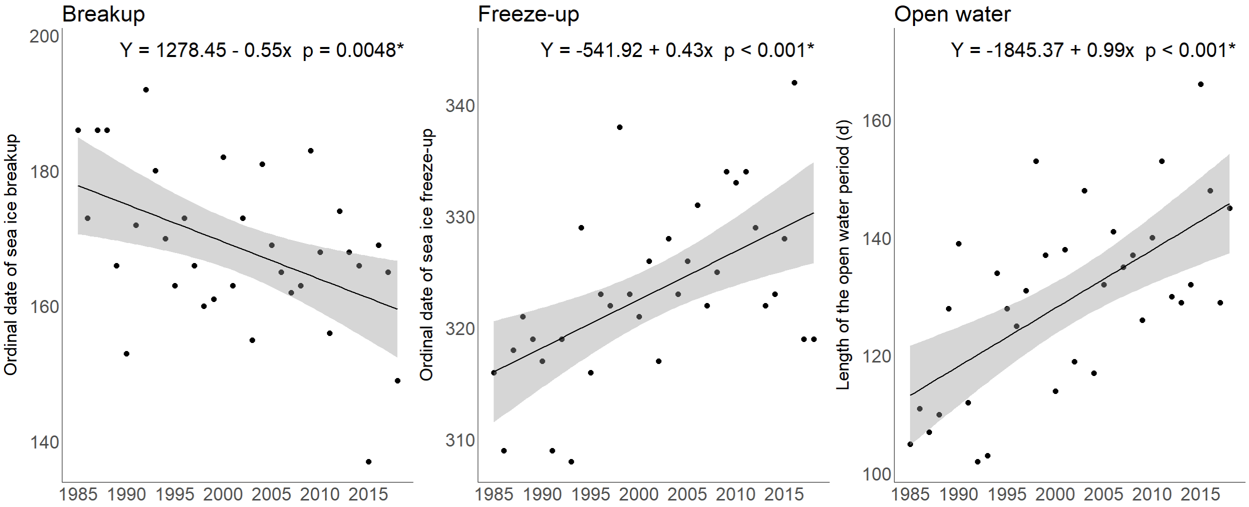

Figure C.6: Temporal dynamics of sea ice breakup, freeze-up, and the length of the open-water period in western Hudson Bay from 1985 to 2018.

C.3 Supplementary methods

Estimating population energy density and storage energy

The program MARK

Abundance estimates were calculated in the program MARK using the POPAN formulation (Schwarz and Arnason 1996). This method uses apparent survival, probability of detection, and the Probability of Entrance (PENTS) to estimate the super-population (N) for which subsequent abundance estimates N_I are derived parameters where the standard error is calculated using the Delta method. Captures were grouped by sex, bears greater or equal to one year of age were used, and estimates of COYs were included following methods by Lunn et al. (1997). *A priori* models consisted of a full time dependent model, both ϕ and p time-invariant, a ϕ time-invariant and p time-invariant model, and a ϕ time-invariant for males/time-variant for females with p time-variant. Model fit was assessed using median $\hat{c}$ estimated from the chi square of Test 2 + Test 3 from program release divided by the degrees of freedom. The estimate of $\hat{c}$ was > than 1 and to account for lack of fit, model adjustments were made and $\hat{c}$ was adjusted to 1.68. We used QAICc to select the top model. The top model carried 100% of the model weight and included constant survival and time varying probability of detection. There was a significant correlation between these abundance estimates and the abundance estimates from Lunn et al. (2016) (Pearson correlation, coefficient = 0.79, $p < 0.001$).

Chapter 6

6 Discussion

The Arctic is warming at twice the global rate and the Arctic marine ecosystem has experienced rapid alterations in sea ice extent, distribution, and period of ice cover (Comiso 2002, Stirling and Parkinson 2006, Stroeve and Notz 2018, IPCC 2019). As an apex predator whose ecology is related to sea ice conditions, polar bears (*Ursus maritimus*) are a key indicator species by which to monitor population responses to climate warming and Arctic marine ecosystem dynamics. In this dissertation, I examined various polar bear ecological processes at different spatiotemporal scales in two declining populations to provide insights into the factors driving population change. The primary outcome of this dissertation is an increased understanding of the ecological mechanisms that help drive polar bear population responses to climate warming.

6.1 Contributions to polar bear ecology

Food web dynamics and trophic relationships are key ecological aspects to monitor as ecosystems respond to climate warming (de Ruiter et al. 1995, Neutel et al. 2002, Rall et al. 2010). In Chapter 2, I examined intrapopulation and temporal foraging ecology patterns in the Western Hudson Bay (WH) polar bear population. I found variation in isotopic niche size and diet within the population, adult females and subadults had narrower diets and isotopic niches, reinforcing the vulnerability of these groups to changes in sea ice habitat and thus prey availability (Rode et al. 2010, Thiemann et al. 2011a, Laidre et al. 2020). In contrast, adult males had broader diets and isotopic niches, suggesting an ability to adjust foraging behaviour in response to alterations in prey availability (Thiemann et al. 2011a). Furthermore, I documented changes in WH population isotopic values over time, indicating interannual variation in foraging ecology (Sciullo et al. 2017) and/or alterations to the Hudson Bay ecosystem food web (Gaston et al. 2003, Yurkowski et al. 2016, Lowther et al. 2017). In this chapter, I demonstrated that $\delta^{13}C$ values were associated with the length of the open-water period, providing support for the association between polar bear foraging ecology and changing sea ice dynamics (McKinney et al. 2009, Sciullo et al. 2017, Boucher et al. 2019a). This research improves our understanding of the mechanisms behind changes in WH population dynamics as well as potential ecosystem shifts in response to climate warming.

Habitat loss and degradation are primary factors influencing biodiversity (Brook et al. 2008, Mantyka-Pringle et al. 2012), especially in the Arctic where climate warming has led to extensive declines in sea ice habitat (Comiso 2002, Stroeve and Notz 2018, IPCC 2019). In Chapter 3, I analyzed the spatial ecology of subadult and adult polar bears in the Southern Beaufort Sea (SB) population. I identified broad population habitat preferences such as a strong association with intermediate to high sea ice concentration over the continental shelf (Durner et al. 2009, Laidre et al. 2018, Lone et al. 2018b) and seasonal movements in response to sea ice formation and breakup (Amstrup et al. 2000, Pongracz and Derocher 2017), highlighting the vulnerability of SB polar bears to further declines in optimal sea ice habitat. Furthermore, this research documented variation in habitat preferences within the population. Adult females with cubs-of-the-year and subadult males used stable landfast ice, while adult females with older cubs and solitary adult females used higher-quality active ice habitat, and subadult females used both zones. Adult females with cubs-of-the-year likely use landfast ice to protect dependent young from adult males (Stirling et al. 1993, Freitas et al. 2012, Pilfold et al. 2014), while subadult males may use this habitat in an attempt to reduce intra-specific competition and/or kleptoparasitism (Egbert and Stokes 1976, Mattson et al. 1987). This chapter provided novel insights into the spatial ecology of subadults, which are particularly vulnerable to sea ice decline (Rode et al. 2010, Thiemann et al. 2011a, Laidre et al. 2020) and are experiencing reduced survival in the SB (Bromaghin et al. 2015). Examining population habitat use patterns can identify the vulnerability of certain demographic classes to future habitat loss as well as monitor changes in population spatial ecology over time.

While polar bear populations are relatively discrete and individuals display a high degree of fidelity (Derocher and Stirling 1990, Amstrup et al. 2000), individual movements have implications for gene flow and spatial connectivity (Slatkin 1987, Ranta et al. 1997). In Chapter 4, I examined the movements of an individual bear that travelled from the SB population to the Chukchi Sea population. This chapter compared this individual's movements to those of other bears and documented a long-distance swimming event, which is energetically expensive and may occur more often as the open-water period lengthens (Durner et al. 2011, Pagano et al. 2012, 2020, Pilfold et al. 2017). I also showed that Brownian bridge movement models are less biased for home range analyses than minimum convex polygons (Burgman and Fox 2003, Kranstauber et al. 2012). This study provided additional evidence for the potential for gene flow between these populations and highlights the importance of monitoring spatial ecology. As sea ice declines, long-distance movements (Derocher et al. 2004, McKeon et al. 2016) and riskier behaviour (Reimer et al. 2019) may become more common, with implications for individual fitness and population boundaries (McCall et al. 2015).

Lastly, long-term bioenergetics research is a useful method for identifying vulnerable demographic classes and examining the factors affecting population vital rates (Yodzis and Innes 1992, Humphries et al. 2004). In Chapter 5, I examined intra-population variation in WH energetics, temporal dynamics from 1985-2018, and the relationship between population energetics and sea ice dynamics. Here, I presented a novel approach for estimating population energetic balances using abundance, age/sex structure, and body condition. This study found that energy values declined over time and supported the vulnerability of adult females and younger bears to nutritional stress (Atkinson and Ramsay 1995, Rode et al. 2010, Thiemann et al. 2011a, Laidre et al. 2020). Furthermore, population energy values declined over time in relation to earlier breakup and longer lagged open-water periods, suggesting multi-year, cumulative effects of sea ice decline and corroborating the linkage between reduced polar bear body condition and sea ice dynamics (Stirling et al. 1999, Sciullo et al. 2016). This chapter contributes to our understanding of the ecological factors underlying population responses to Arctic warming as well as provides evidence for the utility of long-term bioenergetics research.

6.2 Conservation and management

A primary finding of this dissertation is the importance of monitoring intra-population variation to identify vulnerable groups and provide insights into the factors affecting population dynamics. Chapter 4 indicated the importance of monitoring individual movements, while adult females and subadults were demonstrated to have smaller isotopic niches/constrained diets (Chapter 2), use sub-optimal habitat (Chapter 3), and have reduced energy values associated with sea ice decline (Chapter 5). These results reinforce the importance of monitoring demographic classes that are more sensitive to habitat loss and declining prey availability. Additionally, this dissertation reinforced the utility of long-term monitoring programs, which provide the ability to conduct longitudinal and cross-sectional studies to examine temporal dynamics of population ecological processes. Examining ecological dynamics over multidecadal periods documented interannual variation in foraging (Chapter 2) and energetics (Chapter 5), providing insights into the factors underlying population responses to climate warming. As the Arctic marine ecosystem continues to change, long-term monitoring of wildlife populations will be useful for defining baseline ecological parameters, monitoring changes over time, separating annual variation from long-term trends, identifying mechanisms behind population change, and predicting future population dynamics.

Furthermore, this dissertation reinforced the importance of examining the relationship between polar bear life history, ecology, and sea ice dynamics. Earlier breakup and longer open-water periods were related to changes in WH foraging ecology (Chapter 2) and reduced WH population energy (Chapter 5), while sea ice features were key in SB habitat selection (Chapter 3). Declines in optimal sea ice habitat contribute to reduced access to prey and longer fasting periods (Cherry et al. 2009, Durner et al. 2009, Rode et al. 2018) and sea ice is predicted to continue to decline (IPCC 2019, Hwang et al. 2020). Therefore, researching the relationship between polar bear ecology and environmental change will help inform predictions of ecological responses to climate warming. As WH and SB are two of the most well-studied polar bear populations, the results from this dissertation outline the utility of long-term research programs that facilitate studies of polar bear life history and ecology in a changing environment that can be used to form the basis for management strategies in understudied populations.

6.3 Future research

This dissertation provided insights into multiple aspects of polar bear ecology in the changing Arctic, while highlighting improvements that can benefit future research. Chapter 2 illustrated the difficulty in identifying the dominant driver of variation in isotopic values. Further development of techniques to differentiate baseline isotope changes (Lowther et al. 2017, de la Vega et al. 2019, Haywood et al. 2019), changes in diet in response to altered prey availability (Sciullo et al. 2017, Florko et al. 2018), and changes in fasting (Hobson et al. 1993, Newsome et al. 2010) would improve food web analyses. Future work would benefit from documenting/updating prey isotope values for a wide range of species, age/sex classes, tissue types, and regions (especially as species expand their ranges into the Arctic [Kortsch et al. 2015, Huntington et al. 2020]), controlled feeding experiments to inform isotopic discrimination between predator and prey (Rode et al. 2016, Barton et al. 2019), and identifying contributions of dietary sources to metabolic pathways (Newsome et al. 2010, Cherry et al. 2011, Haywood et al. 2019). Furthermore, the integration of multiple isotopes (hydrogen and oxygen: Koehler et al. 2019, mercury: Yurkowski et al. 2020) and fatty acid analysis (Belicka et al. 2012, O'Donovan et al. 2018, Haywood et al. 2019) would provide a more comprehensive understanding of niche dynamics and foraging patterns. Lastly, applying these techniques through time would provide insights into changing predator-prey interactions and shifts in food web dynamics.

Chapter 3 examined variation in SB habitat use while highlighting the knowledge gap regarding adult male spatial ecology. Limited research has involved observational surveys (Stirling et al. 1993) and implanted tags (Amstrup et al. 2001); however, the use of novel smaller tags (Laidre et al. 2013) over longer periods would improve our understanding of adult male movement patterns and inform predictions about their responses to future habitat loss, as well as potential consequences for other classes. In addition, Chapter 3 documented the importance of considering multiple sea ice features (age, type, thickness, concentration) when analyzing habitat selection. Incorporating additional environmental features in future research (e.g., sea ice drift [Mauritzen et al. 2003, Auger-Méthé et al. 2016, Durner et al. 2017] and wind [Togunov et al. 2017]) at a range of scales (e.g., higher temporal resolution tags and more localized environmental data [Turner et al. 1995, Cherry et al. 2013, Suraci et al. 2019]) can provide a more in-depth understanding of the factors affecting fine-scale movements. A variety of movement ecology techniques such as state-space modelling (Patterson et al. 2008, Auger-Méthé et al. 2020) and dynamic occupancy models (Mackenzie et al. 2003, Piédallu et al. 2019; e.g., from aerial surveys [Obbard et al. 2018]) can provide new insights into spatial ecology. Moreover, the integration of polar bear telemetry with prey kill sites (Pilfold et al. 2014) and/or prey telemetry (Hamilton et al. 2017) would improve our understanding of predator-prey interactions, resource availability, and habitat quality. Furthermore, while resource selection functions are commonly created over multi-year periods (Durner et al. 2009, Pilfold et al. 2014, Laidre et al. 2018), future research would also benefit from annual habitat models to examine temporal trends (e.g., shifts in distribution or changes in habitat quality) as polar bears experience declines in optimal habitat (Durner et al. 2009, Stern and Laidre 2016). Future research can also focus on adaptive management to monitor interannual trends in population distributions and assess agreement with population boundaries (McCall et al. 2015) as sea ice conditions change.

In Chapter 5, I documented interannual changes in WH polar bear energetics in relation to sea ice dynamics; however, this research lacks context for changes in prey availability. Future research would benefit from improvements to prey population estimates (Young et al. 2015, Ferguson et al. 2017) combined with prey physiological condition (Harwood et al. 2000, 2012) to contextualize changes in polar bear energetic stores in response to energy intake. In addition, the incorporation of energetics research with other physiological stressors, such as contaminants (Liu et al. 2018, Boisvert et al. 2019, Routti et al. 2019), would provide insights into the synergistic factors influencing polar bear health and fitness. Furthermore, the incorporation of physiological biomarkers (i.e., serum urea and creatinine; Cherry et al. 2009, Rode et al. 2014, 2018) would improve the ability to confirm increased fasting in the WH population concurrently with changes in isotopic dynamics (Chapter 2) and energetic declines (Chapter 5), with implications for mortality risk (Molnár et al. 2010, 2014, Pilfold et al. 2016).

Lastly, the simultaneous integration of foraging, spatial, and energetics ecology would provide novel insights and a more comprehensive understanding of polar bear ecological dynamics in response to climate warming. This could include the combination of isotope analysis and spatial ecology (Rubenstein and Hobson 2004, Boucher et al. 2019b), satellite collars with accelerometers to examine spatial ecology and energetics (Suraci et al. 2019, Pagano et al. 2020), and monitoring recaptured individuals over time to examine the interactions between these ecological processes, environmental change, and lifetime fitness.

6.4 Conclusions

This dissertation examined multiple ecological processes of an apex predator in a rapidly changing ecosystem, providing insights into the mechanisms underlying population dynamics and potential responses to future environmental change. The Arctic marine ecosystem has experienced rapid climate warming and changing ecological dynamics can be influenced by lower trophic level trends (Brown et al. 2018, Waga et al. 2019) as well as altered top predator dynamics (Pace et al. 1999, Schmitz et al. 2000, Frank et al. 2005, Huntington et al. 2020). As future sea ice declines threaten Arctic wildlife populations (Post et al. 2019, Hwang et al. 2020), examining trends in various aspects of apex predator ecology at multiple scales can be a useful tool for monitoring changing ecological dynamics.

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