### Polar Bear (Ursus maritimus) Distribution in the Southern Beaufort Sea

by

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#### Abstract

Polar bears (*Ursus maritimus*) are an apex predator of the Arctic marine food web and vulnerable to changes in sea ice because various aspects of their existence depend on this dynamic platform. Arctic sea ice extent and thickness have declined, and been particularly low since the first record low in 2007. I examined polar bear distribution using satellite telemetry in 2007-2011 including years of record low sea ice extent using kernel density methods to evaluate how recent changes to sea ice conditions may be affecting their distribution. I examine use of land and relate polar bear distributions to bathymetry. My research suggests that polar bear movement patterns and distribution are changing in response to sea ice conditions. Bears are forced to travel greater distances and remain over deeper waters longer as they maintain a presence at the edge of the pack that varies annually. Bears also used land areas in Alaska greater than previously documented. I explore the consequences of these changes and examine summer refugia.

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#### **Chapter 1 - General Introduction**

The distribution of species is closely linked to resources available within the surrounding environment (Brown and Orians 1970, Altmann 1979). Behaviour, sex, age, weight, and season may also affect spacing patterns (Burt 1943, Brown and Orians 1970, Harestad and Bunnel 1979); and metabolic needs, diet and bioenergetics furthermore play a role in the size of areas used (McNab 1963, Gittleman and Harvey 1982). It has been long recognized that animals relocate if local resources are depleted or there are superior resources at other locations (MacArthur and Pianka 1966, Pyke 1983). Hence, organisms adapt to predictable seasonal changes in their environment (habitat) and respond to successional changes in their food resources (Ramenofsky and Wingfield 2007). One mechanism by which species adapt to resources that fluctuate in space, time, and location is migration, seasonal movements between locations where environments are alternately favourable (Dingle and Drake 2007). Migration is most commonly driven by effort to remain within habitats that offer food, shelter, and mates, resources obligatory for persistence and procreation (Dingle and Drake 2007). A key component to survive in habitats that vary spatiotemporally is to preemptively abandon a habitat before it deteriorates beyond a threshold quality (Dingle and Drake 2007). As climate change alters environmental conditions there is potential for a mismatch in phenology to occur between species and the resources they exploit (Visser and Both 2005), potentially resulting in population declines (Both et al. 2006), and reduced reproductive success (Post and Forchhammer 2008).

The study of space use and movement patterns is pivotal to the management and conservation of species. Information regarding species' space use and movement patterns over time can provide an understanding of how animals are affected by and adapt to both natural variation in climate and directional climate change. Studying space use and movement patterns can furthermore be used to identify critical habitat and mitigate anthropogenic impacts, important factors in the context of climate change that may facilitate the expansion of anthropogenic development into regions previously unoccupied.

Polar bears (Ursus maritimus) evolved from brown/grizzly bears (U. arctos) somewhere between 150,000 to millions of years ago (Lindqvist et al. 2010, Miller et al. 2012, Welch et al. 2014) to exploit the sea ice niche and evolved to survive on this highly seasonal habitat (Stirling and Derocher 1993). Polar bears are a circumpolar species dispersed among 19 populations found in the United States, Canada, Russia, Greenland, and Norway (Aars et al. 2006). The estimated global population of polar bears is 20,000 - 25,000 (Aars et al. 2006). They are designated as a species of Special Concern in Canada (Canada 2011), Threatened in the United States (U.S Fish and Wildlife Service 2008), and Vulnerable internationally (Obbard et al. 2010). These designations are based on projected declines in sea ice and their predicted negative impact on polar bear physical condition, abundance, and distribution. Historically, the principal threat to polar bears was unsustainable harvest (Prestrud and Stirling 1994), however they now face the greater threat of climate change, which is rapidly altering the sea ice habitat polar bears depend on. If there are no actions taken to mitigate greenhouse gas emissions, the driver of climate change, researchers predict there will be significant declines in polar bear populations by the end of the 21<sup>st</sup> century (Stirling and Derocher 1993, Derocher et al. 2004, Amstrup et al. 2010, Hunter et al. 2010, Regehr et al. 2010)

Polar bears are entirely dependent on sea ice from which they hunt, travel, mate (Smith 1980, Stirling and Derocher 1993), and in some areas, den on (Amstrup and Gardner 1994). Polar bear distribution is largely dictated by the distribution of sea ice and prey species (Derocher and Stirling 1998). Primary prey for polar bears are ringed seals (*Pusa hispida*) and to a lesser degree, bearded seals (*Erignathus barbatus*) (Ramsay and Stirling 1986). Polar bears are able to hunt all ages of seals, however, young of the year have been identified as an important component of their diet (Stirling 2002, Pilfold et al. 2012).

Seal distribution, and therefore polar bear distribution, is strongly influenced by shore leads, polynyas, areas of annual and multi-year sea ice, and patterns of freeze-up and break-up (Stirling 2002). Furthermore, the survival and successful reproduction of ringed seals are intimately related to sea ice type, condition, extent, and duration (Stirling 2002, Laidre et al. 2008, Harwood et al. 2012). Polar bears focus their hunting efforts on ringed seals during spring, commencing in mid-April and coinciding with ringed seal breeding (Stirling and McEwan 1975, Ramsay and Stirling 1988, Hammill and Smith 1991, Stirling and Øritsland 1995, Pilfold et al. 2012).

Polar bears are physiologically adapted to environmental stochasticity, and store large quantities of adipose tissue as reserves to survive periods with no food (Ramsay and Stirling 1988). Their survival and reproduction is critically dependent on the acquisition of sufficient adipose reserves in spring and early summer (Stirling and Lunn 1997, Stirling et al. 2008). Predation is focused at seal birth lairs and along narrow open or refrozen leads (Stirling and Derocher 1990, Stirling et al. 2008), although pups are often killed they are sometimes not consumed if too lean and have low energy content (Stirling and McEwan 1975), however ringed seal pups are important prey for females with cubs-of-the-year (COYs). Upon emergence from the den, females select ringed seal pupping habitat to replenish depleted fat reserves (Stirling and Lunn 1997), such habitat has been identified as lower quality but is likely sought by family groups to protect cubs from infanticidal males (Pilfold et al. 2013).

Polar bear reproductive-related activities also occur on the sea ice substrate. April and May is the peak mating period, in which males sequester females to isolate them from other males that could be encountered along feeding areas or travel routes (Ramsay and Stirling 1986). It is presumed that females distribute themselves according to favourable hunting areas and males distribute themselves in response to females (Ramsay and Stirling 1986). In some populations, polar bears also depend on sea ice from late autumn through spring as a substrate for denning (Amstrup and Gardner 1994).

Climate change is decreasing the extent (defined as the area of the ocean with >15% fractional ice cover/concentration) and thickness of sea ice in the Arctic. Monthly average sea ice extent has declined from 1979 through 2006 (Serreze et al. 2007). The minimum sea ice extent in 2012 was  $3.4 \text{ million km}^2$ , 55% less than the minimum sea ice extent in 1980 when observations commenced (Jeffries et al. 2013), a reduction that is occurring at a rate of 12.4% per decade (Stroeve et al. 2012). The lowest ice extents on record occurred from 2007 through 2012 (Jeffries et al. 2013). Multiyear sea ice extent has also drastically declined, as a result only 10% of the remaining multiyear ice is greater then five years old (Maslanik et al. 2011). In 2012, sea ice was younger and thinner with the majority (58%) less than a year old, characteristics that make it more susceptible to melting and retreat (Jeffries et al. 2013). In summary, there has been an increase in the rate of sea ice loss in last decade (Comiso et al. 2008, Stroeve et al. 2012) and scientists predict that sea ice will continue to thin during winter and summer over the next 30 years (Wang and Overland 2009). Projections suggest that September (summer) may be ice free as early as the late 2020s (Wang and Overland 2009).

The impact of climate change on ice conditions varies between geographic regions and it is uncertain how predicted patterns of seasonal ice declines and loss will affect the different polar bear populations or their distribution and movements (Derocher et al. 2004, Stirling and Parkinson 2006). Climate change induced variation in the distribution, abundance, and characteristics of sea ice have

affected polar bear reproduction and survival in some populations (Stirling et al. 2008, Regehr et al. 2010).

An intricate understanding of a species in the context of its environment (e.g. habitat requirements, phenology, range, species interactions) is required to examine the potential impact of climate change and explore how a species may adapt to its altered environment (Davis et al. 1998, Walther et al. 2002, Parmesan and Yohe 2003). Most simplistically, climate change will impact sea ice and thus the distribution and abundance of resources available to polar bears (food, mates, and a substrate for locomotion/denning/hunting) (Stirling and Derocher 1993, Derocher et al. 2004). Climate change may lead to a shift in availability of polar bear prey species and consequent shift in polar bear diet (Derocher et al. 2004, Thiemann et al. 2008, McKinney et al. 2009, McKinney et al. 2013). Furthermore, an alteration in climate may affect migration and movement patterns, increase fasting period, influence the ability of polar bears to find mates, and increase the threat of disease and anthropogenic conflict (Stirling and Derocher 1993, Derocher et al. 2004, Miller et al. 2006, Molnár et al. 2010, Cherry et al. 2013).

Both ringed seals and bearded seals are strongly associated with sea ice throughout the year; in some areas moving north and south with retreating and advancing sea ice (Burns 1970, Simpkins et al. 2003, Kovacs and Lydersen 2008, Cameron and Boveng 2009). They are vulnerable to changes in the sea ice regime because they depend on it for resting, pupping, molting, and access to foraging areas (Tynan and DeMaster 1997, Ferguson et al. 2005, Learmonth et al. 2006, Kovacs and Lydersen 2008). For ringed seals, successful breeding is dependent on specific snow and ice characteristics suitable for construction and maintenance of birth lairs in regions where food is available (Kovacs and Lydersen 2008); lower snow depths, rain and warm temperatures during spring, as well as premature break up of landfast ice may result in lair deterioration and low neonate survival (Harwood et al. 2000, Ferguson et al. 2005, Kovacs and Lydersen 2008). Furthermore, recent lack of sea ice in some regions has resulted in some ringed seal breeding areas being vacant in multiple years, indicative of either a change in ringed seal breeding distribution or failed reproduction (Kovacs and Lydersen 2008). For breeding, bearded seals are dependent upon the presence of small ice floes in close proximity to water over regions suitable for foraging (Kovacs et al. 1996); their overall range is generally restricted to areas of open ice cover over shallow waters, and they prefer to use small and medium sized floes, rarely basking/resting more than a meter from open water (Stirling et al. 1977, Kingsley et al. 1985, Simpkins et al. 2003). A trend towards warmer spring temperatures, earlier break up, and overall less ice over shallow continental shelf waters will unquestionably affect the distribution and abundance of these ice-dependent seals and have a cascading affect on polar bears. Furthermore, snow cover on sea ice during spring, an essential feature in ringed seal breeding habitat (Smith and Stirling 1978, Smith and Lydersen 1991), is projected to decline in depth (Hezel et al. 2012). Climatic alterations and how they influence seals may vary

geographically, thus leading to differing responses by polar bears (Rode et al. 2014).

In addition to forming a platform for Arctic marine mammals, sea ice also provides habitat to an array of sea ice biota (including bacteria, algae, protozoans, and metazoans) (Horner 1985). Ice algae compose approximately 57% of the primary production (including those contained in the water column) in the central Arctic (Gosselin et al. 1997). It is essential to consider how primary producers at the base of the Arctic food chain will be affected by climate change as their impacts will cascade through the food web of which polar bears are at the apex. Difference in ice cover, ocean depth, and hydrography result in differences in primary production between the deeper Arctic Ocean and surrounding shelf regions (Bluhm and Gradinger 2008). A reduction of ice in seasonally covered regions is anticipated to increase primary production by extending the growing season, however, this is dependent on regional conditions including upwelling, wind driven vertical mixing, and freshwater supply (Carmack et al. 2004, Loeng et al. 2005, McLaughlin and Carmack 2010). The dynamics related to primary production in the pack ice over deeper Arctic waters are somewhat more complicated and there are differing theories regarding future trends in these regions. Loeng et al. (2005) suggest that primary production in areas currently covered in multiyear sea ice are light limited, therefore, melting of ice in these regions would remove this limitation and lead to a two to five fold increase in primary production assuming sufficient nutrient supply would be produced by wind mixing. In contrast, McLaughlin and Carmack (2010) suggest sea ice retreat

may affect the structure of the upper ocean and increase stratification (+25%) below the seasonal mixed layer, and will reduce primary production assuming freshwater continues to be stored in the Beaufort Gyre and the Arctic Oscillation remains anticyclonic. Taken as a whole, total net primary production over the entire Arctic Ocean increased by 20% between 1998 – 2009 (Arrigo and van Dijken 2011), primarily as a result of an increase in the extent and duration of open water (Arrigo et al. 2008, Arrigo and van Dijken 2011). Noteworthy, however, the distribution of increase in primary productivity differed geographically, with the greatest increases in the eastern Arctic (Arrigo and van Dijken 2011). Differences in primary productivity have been related to polar bear prey species condition and reproduction, and used to explain differing response to reduced ice conditions in two adjacent polar bear populations (Rode et al. 2014).

Changing environmental conditions instigated by climate change may not only alter biological productivity, but also change dynamics within the food web shifting the relative abundance of differing species, and potentially allowing for species range expansion, yielding 'new' Arctic species. Predictions that polar bear diets will shift in response to climate-related changes in the abundance and distribution of Arctic marine mammals (Stirling and Parkinson 2006) may already exist in some areas (Derocher et al. 2004, Thiemann et al. 2008, McKinney et al. 2009, McKinney et al. 2013). East Greenland polar bear have demonstrated a shift in consumption from nearshore/benthic/ice-associated prey to offshore/pelagic/open-water-associated prey, with the shift most prominently

associated to years with warmer temperatures and lower sea ice cover (McKinney et al. 2013).

Polar bear space use and movement patterns are also anticipated to change in response to the alteration of resource distribution and abundance. As duration and extent of sea ice continues to decline, polar bears will be forced to move greater distances from preferred habitat over the continental shelf regions (Durner et al. 2009) to remain in contact with sea ice as it retreats, or alternatively remain on land for a longer duration risking the threat of conflict with humans.

The Southern Beaufort (SB) population inhabits an area stretching from Pearce Point, Northwest Territories in Canada to Icy Cape, Alaska in the United States (Amstrup et al 1986). The Beaufort Sea is fed by cool unproductive waters of the Polar Basin via the Beaufort Gyre, and by more productive waters of Amundsen Gulf. Sea ice remains on the Beaufort Sea year round with multi-year pack ice over the polar basin covering the deeper ocean waters, and annual ice over the continental shelf. The annual ice melts by late July and freeze-up starts in early to mid-October (Carmack and Macdonald 2002).

The SB population is important to monitor because it is at the south extent of the species' range and anticipated to be among the first populations to demonstrate the impacts of climate change (Vongraven et al. 2012). The primary concern is that pack ice now retreats beyond the continental shelf where prey species occur in high densities (Frost et al. 2004), and biological productivity is higher than over the deeper basin waters (Sakshaug 2004), thus limiting polar bears access to prey. The most recent mark recapture analysis indicates that the population is estimated to consist of 1526 (95% Confidence Interval: 1211-1841) bears, and is likely declining (Regehr et al. 2006). Ongoing analyses suggest a much lower population abundance (A.E. Derocher, pers. comm.). Primary concerns for this population include: climate warming, oil and gas development in near-shore habitat, increase of contaminants to the region by atmospheric and oceanic transport, overharvest, and cumulative effects (Aars et al. 2006).

An examination of changing sea ice conditions on a regional scale reveal that the bulk of multiyear sea ice extent reductions are occurring in the Beaufort and Canadian Basin, with remaining multiyear sea ice concentrated along the side of the Arctic Islands (Maslanik et al. 2011). The Canada Basin has also experienced an increase of up to 25% in upper ocean heat content when compared to the 1970s; furthermore, fresh water accumulation in the Beaufort Gyre has increased by 25% since 1970, and lead to a deepening of the halocline, which may be limiting primary production (Jeffries et al. 2013), likely an indication of why this region has not yielded any statistically significant increases in net primary productivity (Arrigo and van Dijken 2011). Multiyear sea ice loss coupled with increasing heat absorption in open waters, and accelerated ice motion suggests a 'regional tipping point' may have occurred (Maslanik et al. 2011).

In response to annual fluctuations in sea ice, SB bears move north to remain on multi-year pack ice when the annual ice melts and return south when it refreezes (Stirling and Lunn 1997, Stirling 2002). Most SB bears rarely move ashore (Amstrup et al. 2000, Schliebe et al. 2008). Recently, there has been a trend of later sea ice freeze-up and earlier sea ice break-up (Gearheard et al. 2006), which results in bears remaining for a longer duration over the deeper unproductive waters or on land where food is limited (Amstrup et al. 2006). To date, changes in sea ice extent and condition in the outhern Beaufort Sea have been associated with declines in survival rates, instances of unusual hunting behaviour, cannibalism, drowning, and starvation (Amstrup et al. 2006, Monnett and Gleason 2006, Regehr et al. 2007, Stirling et al. 2008, Regehr et al. 2010). Furthermore, a longer open water season and favourable economic conditions have renewed interest in oil and gas exploration in the Beaufort Sea. As climate warms increased shipping and anthropogenic development, concurrent with changing habitat will pose additional stress on this apex predator.

Climate change is already impacting a diverse array of species, resulting in directional shifts polar ward or up in elevation (Root et al. 2003). The objective of my thesis is to better understand how climate change, evident through changing sea ice conditions, may have affected polar bear space use and movement patterns in the SB population. In this thesis I use satellite telemetry data to explore polar bear movement and distribution patterns throughout the year as they relate to features of their environment, thus providing information that can be used by managers for the conservation of the SB polar bears.

In the second chapter, I examine polar bear annual distribution in a seasonal context that is biologically relevant to polar bears. I explore inter-annual

differences in seasonal distributions and evaluate potential causes for the variation observed. I evaluate use beyond currently delimited population boundaries, and discuss how polar bear space use and movement patterns relate to resources, how space use has changed with changing sea ice conditions, and what the potential ecological impacts on polar bears are. Lastly, I highlight the relevance of knowledge regarding polar bear distribution during different times of the year during a period with sea ice conditions resembling what the future may hold for the purpose of mitigating anthropogenic development that is anticipated to increase with warming climates.

The third chapter exclusively examines summer polar bear distribution by month, and identifies refuge areas in the context of climate change. The open water season, which occurs in summer, is thought to impact polar bears the greatest, and examination of distribution and habitat use for this season over years of minimal sea ice extent provides an indication of how bears are responding within this vulnerable season. I examine distributions as they relate to sea ice extent, and bathymetry, and discuss space use as it relates to resources. Lastly, I examine use of land.

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# Chapter 2 - Seasonal and Interannual Variation in Polar Bear (Ursus maritimus) Distribution in the Southern Beaufort Sea

#### 2.1 Introduction

How animals use space and move through their environment are closely linked to availability of resources (Brown and Orians 1970, Altmann 1979, Ballance 1992, Kelly et al. 2010, Laidre et al. 2010, Sheppard et al. 2010, Barnett et al. 2011). Animals that occupy habitats that predictably change often use space in predictable patterns; habitats that change seasonally commonly elicit responses that involve alternating space use between localized areas that contain resources and making large movements (Dingle 1996). Seasonal site fidelity is one way species obtain shelter and food resources, and avoid predators (Alerstam and Enckell 1979). Spatiotemporal variation in habitats is particularly prevalent in the marine environment. High seasonal site fidelity is observed in many marine vertebrates (ringed seals (Pusa hispida) (Kelly et al. 2010), polar bears (Ursus maritimus) (Stirling et al. 1980, Derocher and Stirling 1990, Wiig 1995, Mauritzen et al. 2001), bottlenose dolphin (Tursiops truncatus) (Ballance 1992), broadnose sevengill sharks (Notorynchus cepedianus) (Barnett et al. 2011)), and has been closely linked to food resources (Ballance 1992, Kelly et al. 2010, Barnett et al. 2011). As food resources within a habitat change, animals move to exploit more favourable conditions. Because movements are so closely tied to resources, the timing of migration and availability of resources may become mismatched as climate changes (Visser and Both 2005), potentially negatively affecting populations (Both et al. 2006, Cherry et al. 2013).

The Arctic climate is changing and shifts in temperature, winds, and precipitation will all affect the species that live there (Hezel et al. 2012, Post et al. 2013). The lowest sea ice extents on record occurred between 2007-2012, with the minimum sea ice extent in September 2012 having less than half the cover than in 1980 (Jeffries et al. 2013). Multiyear sea ice in March has also decreased in extent from 75% in mid 1980s to 45% in 2011; furthermore, only 10% of the remaining multiyear ice is greater then five years old (Maslanik et al. 2011). The resulting younger sea ice is thinner and more prone to melting and retreat during summer (Jeffries et al. 2013). As a result sea ice duration is expected to be 10 days shorter by 2020 and 20-30 days shorter by 2080 (Loeng et al. 2005).

Arctic species have evolved to live in the north, adapting over hundreds of thousands or millions of years to exploit the harsh environmental conditions. Many Arctic marine mammals (e.g., ringed seals, bearded seals (*Erignathus barbatus*), walrus (*Odobenus rosmarus*), polar bears, beluga (*Delphinapterus leucas*)) have become highly specialized to exist with sea ice and their life histories, behaviours, and feeding require the use of the sea ice substrate (Lydersen and Kovacs 1999, Harington 2008, Laidre et al. 2008). The ability of ice dependent Arctic marine mammals to adapt to dramatic changes in sea ice in a limited time frame is questionable as many are currently being negatively affected by climate change (Laidre et al. 2008).

Polar bears diverged from brown bears (*U. arctos*) up to 4-5 million years ago (Miller et al. 2012) to exploit the dynamic yet predictable sea ice niche and evolved to survive on this highly seasonal habitat (Stirling and Derocher 1993). They depend on sea ice for all critical aspects of life; sea ice is used as the platform to hunt for food (Stirling 1974, Smith 1980), travel on to encounter and secure mates (Ramsay and Stirling 1986), and in some areas, den on to produce their young (Amstrup and Gardner 1994), or to avoid inclement conditions (Ferguson et al. 2000b). Further, their main prey, seals, rely on the presence of sea ice. Bathymetry is also an important factor for polar bear prey species, and consequently polar bears. The highest densities of seals occur at relatively shallow depths (Burns 1970, Stirling et al. 1982, Frost et al. 2004) where productivity is greater than the deeper waters beyond the continental shelf (Pabi et al. 2008).

Sea ice as a habitat is dynamic in the sense that formation and ablation occurs differently each year in terms of timing and sea ice characteristics. It is predictable in that every spring a flaw lead forms over the continental shelf (Carmack and Macdonald 2002). Surrounding this lead, and in the pack ice are ringed seals and bearded seals which polar bears prey on (Stirling and Derocher 1993, Frost et al. 2004); landward of this lead is the landfast ice which provides the primary habitat for breeding ringed seals and their young, a food source that adult females with young cubs-of-the-year rely on to replenish reserves depleted during winter denning (Stirling and Lunn 1997). During summer, the sea ice retreats; polar bears have adapted to the circannual sea ice patterns and the seasonality of prey distribution and availability through their ability to undergo prolonged periods of fasting (Ramsay and Stirling 1988), delay implantation (Lønø 1970) and through high seasonal site fidelity (Stirling et al. 1975, Derocher and Stirling 1990, Amstrup et al. 2000, Mauritzen et al. 2001).

Sea ice timing, extent of retreat, and formation differ between years and have been changing over time (Stroeve et al. 2008, Maslanik et al. 2011, Stroeve et al. 2011, Jeffries et al. 2013). Polar bears can persist under dynamic yet predictable sea ice conditions, however, the extent to which they can respond to extreme climatic changes remains unknown. The resilience of polar bears to the affects of climate change is somewhat obscured because it varies between populations (Stirling et al. 2011, Rode et al. 2014), and can be dependent on several factors including the ecology of the region (Rode et al. 2014), potential refuge habitats, resilience to increased energetic demands, and effects of population density (Rode et al. 2012). The Southern Beaufort (SB) polar bear population is showing negative effects potentially linked to climate including: drownings (Monnett and Gleason 2006), unusual predation attempts, starved polar bears, observations of intraspecific predation and cannibalism (Amstrup et al. 2006, Stirling et al. 2008), long distance swim events (Durner et al. 2011) that appear to be increasing (Pagano et al. 2012), and reduced stature and survival (Regehr et al. 2010, Rode et al. 2010).

From an ecological perspective, knowledge of a species' distribution provides information regarding conditions suitable for survival and reproduction. How a species' distribution changes over time with changing environmental conditions is central for understanding population demographics and trend. In this study I examine polar bear distribution between June 2007 and May 2011, a period with record breaking years of low sea ice extent (Stroeve et al. 2012, Jeffries et al. 2013). Seasonal and monthly patterns of SB polar bear distribution provide insight on responses to rapidly declining sea ice extent, though most apparent during summer months (Chapter 3), also affect polar bear distribution during other times of the year. I document seasonal distributions of SB polar bears using utilization distributions to examine how their distribution may have changed in response changing sea ice conditions. I also examine bathymetry of seasonal habitats, and explore metrics related to monthly utilization distributions in a seasonal context in an attempt to identify and understand annual variation in space use. Lastly, the utility of the existing population boundary used to delineate the population is explored.

#### 2.2 Materials and Methods

#### 2.2.1 Study Area

The study area includes the Beaufort Sea and the northern portion of the Chukchi Sea (Fig. 2-1). The distribution of sea ice, leads, and gyres in the region are influenced by an influx of cold polar water, ocean currents, wind patterns, and temperature (Carmack and Macdonald 2002, Proshutinsky et al. 2002). A shore lead extends along the southern mainland coast and merges with the Cape Bathurst polynya but extensive ice-free areas may extend several hundred kilometres off shore during late summer (Carmack and Macdonald 2002). Within the Beaufort Sea, the Beaufort Gyre moves sea ice and surface water in a clockwise direction (Coachman and Aagaard 1974), with waters beneath reversing to form the Beaufort Undercurrent (Aagaard 1984). The Undercurrent moves nutrient rich waters that have arrived via the Bering Straight onto the Canadian Shelf (Carmack et al. 2004).

East of the Mackenzie Delta the landfast ice extends 25-30 km offshore from the mainland to the 20 m contour with its maximum extent in April (Cooper 1974, Aagaard 1984), at which time it is approximately 2 m thick (Carmack and Macdonald 2002). West of the Mackenzie Delta to Shingle Point there is a thinner strip of landfast ice and west of Shingle Point to the Alaskan border there is no stable growth of ice and open water can extend to shore even in February (Cooper 1974). At the edge of the landfast ice is a rubble field or *stamukhi* that extends to the ocean floor and is created by ice convergence. Beyond the *stamukhi* is the shore lead, followed by the drifting pack ice (Carmack and Macdonald 2002). The shore lead can be > 1 km wide in spring with either side having several smaller open and refrozen leads parallel to the floe edge (Stirling et al. 1993).

Break-up begins in late April at the headwaters of the Mackenzie River and melts northward along the continental shelf from the shore lead (Carmack and Macdonald 2002). Pack ice persists thought the summer typically moving in a clockwise direction under the influence of the Beaufort Gyre. Reductions in sea ice extent and thickness have resulted in a sea ice cover vulnerable to summer and autumn storms (Parkinson and Comiso 2012).

Freeze-up normally begins in early to mid-October (Carmack and Macdonald

2002). Ice growth commences with a thin layer of ice forming on the surfacing, growing south from the pack ice and spreading north from the coast.

#### 2.2.2 Capture and collaring

Bears were located by helicopter during mid-April to mid-May in 2007 to 2010 on the Canadian side of the Beaufort Sea (Fig. 2-1). Bears were immobilized with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil® Laboratoires Virbac, Carros, France) following standard procedures (Stirling et al. 1989). Adult female and subadult bears were fit with global positioning system (GPS) Argos® satellite-linked collars (Telonics Gen III GPS collars and Telonics Gen IV GPS collars; Telonics, Mesa, AZ). All collars were equipped with a programmed release mechanism (CR2a, Telonics, Mesa, AZ): 1 year for subadults and 2 years for adults. Subadult collars were also linked with corrodible hardware that would erode after 1 year. Adult males were not collared as the diameter of their necks exceeds the diameter of their heads and thus collars slip off. Bears tracked were considered representative of the adult female and subadult portion of the SB population and were not analyzed by age, sex, or reproductive status. GEN III collars have 95% of fixes accurate to 13-36 m and GEN IV collars are accurate to 2-10 m. Locations and paths of bears tracked were visually scrutinized, and erroneous locations were removed. Location data from collars thought to be dropped on ice were excluded from analysis; suspect collars were identified from high similarity to sea ice movement rate and patterns compared to known bear movements and seasonal activities. Locations occurring within the
initial 48 hours post immobilization were excluded from analysis because movement rates within this period are lower as animals recover (Thiemann et al. 2013). Adult female polar bears were excluded from analysis during the months they were in dens to avoiding high probability values for single den sites, and to evade the bias that their inclusion would have introduced to the examination of seasonal and interannual comparisons. Capture and handling methods were approved by the University of Alberta BioSciences Animal Care and Use Committee and in agreement with guidelines from the Canadian Council on Animal Care.

## 2.2.3 Data analyses

Four seasons were identified based on bear biology, regional bear movement patterns and sea ice phenology. During spring (March – May) bears hunt seals (Stirling and Archibald 1977, Smith 1980, Stirling 2002) to accumulate reserves for survival and reproduction (Ramsay and Stirling 1988, Stirling 2002), and mate (Ramsay and Stirling 1986). During summer (June – September) SB bear movement rates increase as bears respond to sea ice retreat, with net monthly movement northward (Amstrup et al. 2000), a portion of the population also moves shoreward during this period congregating around areas where subsistenceharvested bowhead whale (*Balaena mysticetus*) remains are located (Schliebe et al. 2008). Correspondingly, during autumn net monthly movement is south (Amstrup et al. 2000) as bears that remain on pack ice during the open water period follow ice growth south during freeze-up; monthly movement rates peak in November (Amstrup et al. 2000). Presumably, bears on land may take advantage of hunting opportunity on landfast ice as it forms (Schliebe et al. 2008), thus moving northward.

I examined polar bear space use using kernel densities, which provide an estimated probability density function corresponding to an individual animal's utilization distribution (UD) or space use (Van Winkle 1975, Worton 1987, Kernohan et al. 2001). UDs measure the intensity or probability of use over an animal's home range (Van Winkle 1975, Kernohan et al. 2001).

The kernel estimator can be visualized as the sum of bumps placed over each bear location, where the height of the bumps is determined by the probability density function that describes the relative likelihood of use given a location and the width of the bumps is determined by the smoothing parameter or bandwidth selected (Silverman 1986). The probability density at a given location is the sum of all kernels at that location. The kernel density approach is nonparametric. Autocorrelation of location data likely causes home range estimate bias (Swihart and Slade 1985). However, when the study period is fixed, autocorrelation is less important than the representative sample and subsampling decreases home range estimation (Otis and White 1999, Fieberg 2007). Therefore, I used all available locations.

Kernel density is sensitive to the bandwidth and over-smoothing (too large of a bandwidth) will extend a home range beyond realistic boundaries and a bandwidth too small will produce a fragmented distribution resulting in inadequate connection of space within a home range (Blundell et al. 2001, Kernohan et al. 2001, Gitzen et al. 2006). Bandwidth should be selected based on data characteristics because no bandwidth method is superior in all situations (Gitzen et al. 2006). I used the plug-in bandwidth calculation method which performs as well as or better than least squares cross validation (LSCV) (Gitzen et al. 2006), which has a tendency to cause data to fragment (Kie et al. 1996, Blundell et al. 2001, Kernohan et al. 2001) and can fail if many points have the same, or close to the same, value (Silverman 1986). Furthermore, the plug-in method performs best with partially-clumped data, and is recommended when examining species that range widely (Gitzen et al. 2006). The plug-in method was chosen a priori because 1) polar bears move widely across their home ranges, and 2) location data tend to be clumped at differing time scales (seasonally and on a smaller scale due to foraging activities). Bandwidth was constant for each density estimate (fixed kernel), resulting in a bandwidth that may have been unique for each bear for each month. The two stage plug-in approach to estimate bandwidth calculates a preliminary bandwidth based on the covariance matrix. This initial bandwidth is plugged into a function estimating the first stage bandwidth, and the resultant bandwidth is plugged into a lower-derivative function; this second stage bandwidth is then used to estimate the final bandwidth (Wand and Jones 1994, Gitzen et al. 2006). Bandwidth was calculated in R (R Foundation for Statistical Computing, Vienna, Austria) using package 'ks' (Duong 2007). The plug-in approach used the asymptotic integrated mean squared error approach (Duong and Hazelton 2003), the bandwidth matrix was diagonal (constrained to smooth in

directions parallel to the co-ordinate axes), and the data were pre-scaled. To accommodate kernel density analysis, the study area was overlaid with a grid of 2.5 km<sup>2</sup> cells with a modified Albers projection with a central meridian of 138.3° W and standard parallels of 67.9° and 75.7° N latitude.

I first used UDs to measure space use on an individual level, and then pooled UDs to measure joint space use of multiple animals to represent seasonal patterns. Collars provided between 0 and 6 locations per bear per day. A monthly kernel density was estimated for each bear with  $\geq$ 47 locations in  $\geq$ 20 days. Kernel estimates of home range size are influenced by sample size; however, a sample of  $\geq$  50 reduces bias to asymptotic levels (Seaman et al. 1999). In consideration of the small number of bears tracked during March of 2008 that met this requirement (n=2), a kernel density was estimated for one bear with 47 locations over  $\geq$ 20 days in analysis.

I examined the correlation between number of locations used to create kernel densities and the resulting area of use to ensure volume contours were not influenced by sample size. To examine the joint space use of multiple animals, I calculated monthly kernel densities weighted by the number of monthly locations contributed by each bear. Seasonal kernel densities were calculated by summing months within the season, where each month was weighted equally. I used the 'kde' function in Geospatial Modeling Environment Version 0.4.0 Beta (Beyer, H.L., available at www.spatialecology.com/gme) to calculate kernel densities, and Hawth's Analysis Tools for ArcGIS Version 3.27 (Beyer, H.L., available at www.spatialecology.com/htools) to identify percent volume contours with 10, 50, and 95% probability of use.

To examine area of use I computed the area of 95% probability of use contours for each bear month. Probability of use contours could not be generated for 4 bear months due to small use areas (few pixels), so I calculated 95% minimum convex polygons (MCP) using Hawth's Analysis Tools for ArcGIS Version 3.27 (Beyer, H.L., available at http://www.spatialecology.com/htools) and determined their area. These 4 bears had ≥100 locations per month, which is within the requirement of accurate analysis of MCP home range sizes (Bekoff and Mech 1984).

To further explore metrics related to polar bear distributions, I calculated the centroid of 95% probability of use contours/MCPs and determined the distance from centroid points to the 200 m isobath (i.e., the continental shelf edge), whereby centroids deeper than the 200 m isobath were negative and those shallower than the 200 m isobath were positive. Centroids were calculated using Geospatial Modeling Environment Version 0.7.2 RC2 (Beyer, H.L., available at www.spatialecology.com/gme).

To examine differences in distributions between months, I compared area of use, and distance from centroid to the 200 m isobath using Kruskal-Wallis and median tests followed by *post hoc* tests to determine significance of pairwise comparisons. Because the number of individuals tracked per month varied, and there were statistically significant differences between months, it was not possible to make direct statistical comparisons between seasons.

To examine differences in distributions between months across years, I square root transformed area of use in an attempt to normalize the data. For months in which transformed data were normally distributed, I used one-way ANOVA tests followed by Tukey HSD tests to examine differences in mean monthly area of use between years. When data could not be normalized, I used Kruskal-Wallis and median tests to compare mean monthly area of use for a given month between years, followed by *post hoc* tests to determine significance of pairwise comparisons.

To assess habitat used by collared bears I focussed on bathymetry. I characterized substrates used by bears using bathymetry data with a 2.5 km<sup>2</sup> resolution (Jakobsson et al. 2008). Firstly, I calculated the mean bathymetry of 95% probability of use contours/MCPs for each bear-month using Geospatial Modeling Environment Version 0.7.2 RC2 (Beyer, H.L., available at www.spatialecology.com/gme). I tested the correlation between mean bathymetry of probability of use contours to distance of centroids to 200 m isobath using a nonparametric Spearman's rho test. Secondly, I reclassified bathymetry data as land, by 100 m increments to 3500 m, and pooled for > 3500 m, and then determined the volume of kernel density in each of the values above for each seasonal UD in each year. Statistical analysis was completed with SPSS version 21, IBM Corp., Armonk, NY. To assess how much SB polar bears used areas outside the current SB boundaries, I calculated the number of locations by month, season, and year that were outside the SB population boundary as identified by the IUCN/SSC Polar Bear Specialist Group (Derocher et al. 1998).

I calculated the proportion of the study region that was covered in open water and mean sea ice concentration for each month in each year to characterize sea ice dynamics. Mean monthly sea ice concentrations were created using daily 6.25 km grid resolution ASI Algorithm AMSR-E sea ice concentration obtained from the Integrated Climate Date Center (ICDC, http://icdc.zmaw,de/), University of Hamburg, Hamburg, Germany. I determined the monthly proportion of open water (proportion of pixels that contained  $\leq 15\%$  sea ice concentration), and estimated the monthly sea ice concentration by calculating the mean sea ice concentration of pixels that contained  $\geq 15\%$  sea ice concentration. All habitat extractions were made using ArcGIS 9.3, Environmental Systems Research Institute, Redlands, CA, unless otherwise noted.

## 2.3 Results

Collars were deployed on 17 solitary adult females, 5 females with cubs-ofthe-year, 15 females with yearlings, 4 females with two-year-olds, and 23 on subadults ( $\leq$ 4 years old) (12 females, 11 males) for a total of 60 different bears (4 bears were recollared) (Appendix 2-1). One adult bear emigrated from the study area and was excluded from analyses.

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Individual bear monthly kernel densities (n=558) were calculated from 74,370 bear locations obtained from June 2007 through May 2011 (Table 2-1). Mean number of locations per month per bear for kernel densities was 133 (SD=31, range 47-186). There was not a strong relationship between number of locations used to create use areas and the resulting area of use (Spearman's rho  $r_s = -0.14$ , p<0.001).

Seasonal kernel densities calculated to measure the joint space use of multiple animals indicated that during summer the highest probability of use was along Barter Island and the Barrier Islands from Kaktovik to Prudhoe Bay in Alaska and in the near shore regions to east and west (Fig. 2-2). Probability of use along the continental shelf north of Alaska was largely between the 200 m isobath and the coastline. There were areas of higher probability of use west of Banks Island, and along the edge of the polar pack ice. During most summers, the probability of use contours revealed a gap between use near shore and use on pack ice with a continuum located north of Kaktovik that connected the two regions. There were subtle interannual differences in summer distributions. In comparison to the other summers, summer 2008 displayed more concentrated probability of use near shore along the Alaskan coast, and a more prominent gap between near shore and areas of higher probability of use west of Banks Island, and along the edge of the polar pack ice. During summer 2009, the 95% probability of use area did not extend as far north as previous summers, and during summer 2010 there was low probability of use over the continental shelf of mainland Northwest

Territories compared to other summers. For a more detailed examination of polar bear summer distribution see Chapter 3.

Autumn kernel densities indicated the highest probability of use was along the continental shelf between Kaktovik and Barrow. There was also notable use along the continental shelf of Northwest Territories in all autumns except 2007. 95% probability of use contours extended in a north-south direction over the deeper basin waters of the Beaufort Sea in 2007 and 2008; similar contours oriented north-south were apparent in 2009 and 2010, however, occurred in closer proximity to Banks Island. There was high probability of use west of Banks Island in most years with 2008 being the exception. In 2009 and 2010, the gap between near shore and pack-ice regions was evident but more distinct in the western Beaufort than in the eastern Beaufort.

Winter kernel densities indicated use was concentrated along the continental shelf north of Tuktoyaktuk Peninsula to Kaktovik. In all years examined except 2010, bears also used regions along the continental shelf west of Kaktovik to Barrow. In 2007, winter distributions extended westward into the neighbouring Chukchi Sea population.

In all springs, two high use areas were identified: 1) the middle of the continental shelf north of Tuktoyaktuk Peninsula, and 2) the region near shore from Shingle Point to Kaktovik. There was some annual variation; few bears were tracked in spring 2008 (n=3) yielding relatively fragmented probability of use contours with an outlier to this region occurring in the Chukchi Sea northwest

of Barrow. All springs except spring 2008 revealed use of Amundsen Gulf. Spring 2010 displayed some use around Barrow and more use beyond the continental shelf than other years examined.

95% minimum convex polygons were calculated for 4 bear months due to the small area used during the month relative to the grid cell size (2.5 km<sup>2</sup>). The resulting areas were small (5 km<sup>2</sup>, 5 km<sup>2</sup>, 8 km<sup>2</sup>, 1km<sup>2</sup>) and derived from 145, 107, 113, and 124 locations per month, respectively. In all situations the locations occurred in September/October in a restricted area around Kaktovik, Alaska. The determination of area of home range for these 4 bear months through alternate means was unlikely to affect further analysis because the confined distribution of locations and large sample sizes likely minimized the bias of area estimates.

Analyses revealed differences in the distribution (Kruskal-Wallis, H=132.88, df=11, p<0.001) and median of area of use (median test,  $\chi^2 = 112.77$ , df=11, p<0.001) between months. In summary, distribution of area of use during winter and spring was different than that of summer and autumn, and the distribution of area of use during early summer (June) was different than that of late summer (August and September). Similarly, medians of area of use during winter and spring were lower than those of summer and autumn, and the median of area of use during June was significantly greater than that of August and September (Table 2-2 and Fig. 2-3).

The distribution and median of centroid distance to 200 m isobath differed significantly between months (Kruskal-Wallis, H=156.43, df=11, p<0.001),

(median test,  $\chi^2$ =115.11, df=11, p<0.001). Distribution of centroid distance to 200 m isobath during all months of winter and spring was significantly different than that during all months of summer and the first half of autumn (October). Distribution of centroid distance to 200 m isobath during November was significantly different than that during all months of summer (June-September). The median of centroid distance to 200 m isobath during all months of winter and spring was significantly higher than that during all months of summer. The median of centroid distance to 200 m isobath during December through April was significantly higher than that during October. Lastly, the median of centroid distance to 200 m isobath during November was significantly higher than the medians in June, July, and September (Table 2-3 and Fig. 2-4).

There was a strong correlation between distance from centroid to 200 m isobath and mean bathymetry of 95% probability of use contours/MCPs (Spearman's rho,  $r_s$ =0.93, p≤0.001) therefore, I only analyzed distance from centroid to 200 m isobath.

For comparisons of annual differences between months I report only significant results. The only months that tested normal (after transformation) across all years were February, August, and September, therefore, I used one-way ANOVA tests to compare means of these months across years. ANOVA results indicated area of use differed across years only during February (F=3.36, df=3, p=0.033). February area of use during 2008 was greater than 2010 (Tukey HSD,

mean difference= 52.24, p=0.047) and 2011 (Tukey HSD, mean difference=62.69, p=0.021).

The remainder of monthly comparisons across years were made with nonparametric tests. Distribution of area of use during January was significantly different between years (Kruskal-Wallis, H=9.80, df=3, p=0.020); *post hoc* analysis indicated that that distribution of area of use ranked significantly higher in 2008 than 2009 (rank difference=16.67,  $p_{adj}$ =0.029). Median area of use during January differed significantly between years (median test,  $\chi^2$ =8.84, df=3, p=0.032), however, *post hoc* tests were insignificant with adjusted p-values.

Distribution of area of use during May was significantly different between years (Kruskal-Wallis, H=13.36, df=3, p=0.004). *Post hoc* tests indicated that the distribution of area of use ranked significantly lower in 2009 than 2010 (rank difference=-21.00,  $p_{adj}$ =0.002). Median of area of use during May differed significantly between years (median test,  $\chi^2$ =17.13, df=3, p=0.001), *post hoc* tests indicated the median of area of use during May was significantly less in 2009 than 2010 (difference=14.81,  $p_{adj}$ =0.001).

The distribution of area of use during November differed significantly between years (Kruskal-Wallis, H=13.15, df=3, p=0.004). *Post hoc* tests revealed that the distribution of November area of use ranked significantly higher in 2007 than 2009 (rank difference=18.41, p<0.001,  $p_{adj}$ =0.002). Further, median of area of use during November was significantly different between years (median test,  $\chi^2$ =12.76, df=3, p=0.005), *post hoc* tests indicated the median area of use during

November was significantly greater during 2007 than 2008 ( $\chi^2$ =8.24, p=0.004, p<sub>adj</sub>=0.025), and 2009 ( $\chi^2$ =12.76, p=<0.001, p<sub>adj</sub>=0.002). See Fig. 2-3 for monthly area of use comparisons between years.

I tested the normality of centroid distance to 200 m isobath for comparisons across years by month. February and May were normally distributed across all years, therefore I used a one-way ANOVA to compare means of these months across years. The remainder of comparisons were made using nonparametric Kruskal-Wallis and median tests. Mean centroid distance to 200 m isobath was significantly different between years during May (ANOVA, F=7.41, df=3, p<0.001). Mean centroid distance from 200 m isobath during May 2009 was greater than during May 2010 (Tukey HSD, difference=70.8 km, p<0.001), and May 2011 (Tukey HSD, difference 56.1 km, p=0.030). Median centroid distance to 200 m isobath differed between years during June (median test,  $\chi^2 = 9.33$ , df=3, p=0.025). Post-hoc tests indicated the median of centroid distance to the 200 m isobath during June was greater in 2007 than 2008 ( $\chi^2 = 9.26$ , p=0.002,  $p_{adj}=0.014$ ), and greater in 2009 than 2008 ( $\chi^2 = 8.34$ , p=0.004,  $p_{adj}=0.023$ ). Comparisons of centroid distance to 200 m isobath between years during January, February, March, April, July, August, September, October, November and December were made with nonparametric tests and all results were nonsignificant. See Fig. 2-4 for monthly comparisons of distance from centroids to 200 m isobath between years.

In general, use was more variable and over deeper waters during summer and autumn than winter and spring (Fig. 2-5). There was high use of shallow depths (1-99 m) in all seasons in all years (Fig. 2-6). During winter and spring, bears used shallow depths the greatest, and made little to no use of depths >600 m. During summer and autumn the distribution of depths used was bimodal, with relatively high use of shallow depths (1-500 m), minimal if any use of depths 600-1600 m, and evenly distributed use of depths >1600 m. Land was used in autumn every year, however, land was not used consistently in other seasons.

The proportion of bear locations outside the SB population boundary was greatest in summer and autumn and lowest in winter and spring in all years examined (Table 2-4). The pattern of use outside the current SB population boundary was consistent across years; use outside the SB population boundary increased throughout summer, peaked in September, decreased in autumn, and remained low during winter and spring (Fig. 2-7). The proportion of locations outside the SB varied minimally between months across years (Fig. 2-7, Table 2-4). The annual pattern of proportion of open water followed that of polar bear use outside the current SB population boundary. Open water increased throughout summer, peaked in September, then decreased and remained low through winter and spring (Fig. 2-8).

Sea ice concentration decreased during summer reaching a low in August, increased through autumn, was greatest in winter and early to mid-spring, and commenced decreasing again in May (Fig. 2-9). Annual patterns of proportion of open water and sea ice concentration demonstrated interannual variation during summer, autumn, and May, with little variation from December through April.

## 2.4 Discussion

Polar bears were concentrated over the shallower waters of the continental shelf in spring and as the ice melted, they moved to three areas: near shore along the Alaskan coast, offshore over the deeper waters of the Beaufort Sea, and west of Banks Island. In autumn, their distribution shifted southward to shallower waters over the continental shelf as permitted by sea ice extent, and remained there during winter then gradually shifted to regions used in spring.

Kernel density estimates identified areas of seasonal importance where polar bears spent more time within each season. Though these areas of seasonal importance were similar in most years, there was variation among seasonal use between years that was likely attributable to sea ice conditions and distribution, as well as individual variation and number of individuals tracked.

Polar bear distribution during spring and winter was nearly exclusively concentrated over the shallow waters of the continental shelf, as described historically (Stirling et al. 1975, Stirling 2002), and was likely driven by the distribution of ringed seals. In the Canadian Beaufort Sea, shallow depths (50-100 m) coincide with the highest ringed seal densities, which occur at depths of 50-75 m and decline over deeper waters (Stirling et al. 1982). In the Alaskan Beaufort Sea ringed seal densities during spring and early summer are highest in shallow waters between 5 and 35 m deep (Frost et al. 2004). The discrepancy in depths between regions may be a result of differences in coastlines and thus landfast ice; north of Alaska water depths increase as one moves north and landfast ice forms a linear band; whereas in the eastern Beaufort Sea fast ice is more extensive extending over deeper water as a result of protection from land (Frost et al. 2004). High use of the shallow depths in spring also coincided with the floe edge. The edge of the landfast ice and areas of open water and active ice are important habitats where the most successful predation by polar bears occurs (Stirling et al. 1975); adult and subadult males, lone adult females, and adult females with two-year-olds prefer floe edge habitat in spring (Stirling et al. 1993). Floe edge habitat has the highest densities of ringed seals and bearded seals (Frost et al. 2004), and non-breeding ringed seals and bearded seals of all ages are also abundant in moving ice habitat found near the floe edge (Stirling et al. 1993). The floe edge may furthermore be sought for high potential to encounter mates during the spring breeding season (Ramsay and Stirling 1986, Stirling et al. 1993). In the eastern Beaufort Sea males and reproductive females (single females and females with two-year-olds) concentrate along the floe edge, with females presumably distributing themselves to take advantage of food resources, and males distributing themselves in response to females (Ramsay and Stirling 1986).

Polar bears may also congregate over the continental shelf to hunt at ringed seal birth lairs (Stirling et al. 2008). During late March to early April ringed seals give birth to their pups and nurse them in subnivean liars above their breathing holes (Smith and Stirling 1975). Subnivean liars are located in drifting snow accumulated along cracks and pressure ridges where breathing holes may be present (Stirling and Archibald 1977), habitat that is commonly found in stable fast ice with pressure ridges (Stirling et al. 1993), but may also extend into the pack ice (Pilfold et al. 2014). In the study region, such habitat occurs landward of the moving ice near the shore lead from Cape Bathurst west to Shingle Point (Stirling et al. 1993). Ringed seal pups are a vital food source for females with cubs-of-the-year in particular; upon emergence from the den, females immediately select ringed seal pupping habitat to replenish depleted fat reserves (Stirling and Lunn 1997). Females with cubs-of-the-year are the only age group to preferentially select such habitat, likely because it avoids exposing their young to the potential hazards of open water and the risk of encountering infanticidal adult males (Stirling et al. 1993, Pilfold et al. 2013), and in addition provides a stable environment not requiring cubs-of-the-year to swim, thus avoiding hypothermia (Blix and Lentfer 1979, Pilfold et al. 2013).

Furthermore, it should be acknowledged that bear distributions in spring were concentrated in the region collars were deployed for two reasons, firstly, many bears tracked in May were recently collared, and secondly, bears have been noted to display a high degree of seasonal fidelity (Stirling et al. 1975, Derocher and Stirling 1990, Amstrup et al. 2000, Mauritzen et al. 2001).

Summer and autumn kernel densities were consistent with previously described strategies of response to annual patterns of sea ice ablation and growth in the region. SB polar bears either followed the southern edge of the pack ice as it retreated north (Stirling et al. 1975, Amstrup et al. 2000), spent the summer off the west coast of Banks Island (Stirling 2002); or alternatively moved from sea ice to mainland when the landfast ice melted (Stirling et al. 1975, Durner et al. 2011, Pagano et al. 2012). The bimodal pattern in which high use of shallow depths and deeper waters occurs with minimal use in between, and wide distribution of area of use during summer and autumn were a result these strategies (bears that remained on pack ice covered large areas over deeper waters, whereas bears that remained near shore or on land covered much smaller areas and inhabited shallower depths). Further discussion on summer use is presented in the subsequent chapter.

Mean area of use dropped slightly through the summer and increased in autumn, a pattern reflective of bear movements south as advancing sea ice during October and November facilitates their return to shallower depths. The northsouth lines in autumn kernel densities were indicative of these movements. Although these lines were apparent in most years, they were prominent in autumn of 2007 and 2008 when sea ice retreated further to the north and central than other years.

Distributions and movement patterns examined are representative of adult females and their dependent cubs, subadult females, and subadult males of the SB population. Results presented are limited in that they are not representative of adult male bears, a subset of the population that remains difficult to track. Attempts have been made to track adult male polar bears through transmitters surgically implanted, glued on, and fixed to their ears, however, the duration of transmission has been limited to a few months (Mulcahy and Garner 1999, Laidre et al. 2014, USFWS 2014). Results presented furthermore exclude adult female polar bears during the months they were in dens, however, there is an abundance of both scientific and traditional knowledge regarding the spatial location and chronology of denning in the SB population (Amstrup and Gardner 1994, Durner et al. 2003, Durner et al. 2010, Joint Secretariat 2014). Research regarding maternity denning remains important in the context of resource extraction and associated mitigation (Amstrup 1993, Durner et al. 2001, Amstrup et al. 2004, Durner et al. 2006, Durner et al. 2013) and climate change (Stirling and Derocher 1993, Fischbach et al. 2007).

My research suggests the distribution of SB polar bears is changing. Summer and autumn of all years examined had an unprecedented proportion of bear locations outside the SB population boundary. Sea ice extent is projected to continue declining resulting in an open water season that is more extensive with a longer duration (Serreze et al. 2007, Jeffries et al. 2013). My study suggests that in response, polar bears will spend increasingly more time beyond currently delineated population boundaries and away from optimal habitat, an outcome that may have energetic consequences. As proportion of open water increases, bears will be forced to move further beyond delineated subpopulation boundaries to remain on the edge of the pack ice as it retreats north. As the open water period lengthens, the duration of sea ice over the productive continental shelf shortens, and time bears spend in this optimal habitat will be limited. The anticipated changes in the Arctic sea ice will likely increase Arctic marine travel (Hovelsrud et al. 2008, Prowse et al. 2009), and combined with favourable economic conditions have renewed interest in oil and gas exploration in the Beaufort Sea (Fidler and Noble 2013). It is anticipated that large ship traffic will increase, particularly in the Beaufort Sea and Hudson Bay regions, the former of which could facilitate shipping from offshore hydrocarbon developments through the Bering Strait (Prowse et al. 2009). Furthermore, Arctic tourism particularly through the Northwest Passage has increased and is anticipated to continue (Hovelsrud et al. 2008, Headland 2010).

Sound management depends on accurate and current information regarding population abundance and distribution. This study provides current seasonal distribution information, applicable for mitigating affects on polar bears from shipping and oil and gas exploration. Managers in the Beaufort region must acknowledge and utilize information regarding changing polar bear distributions and how they are influenced by sea ice distribution and dynamics. Furthermore, although polar bear summer and autumn distributions appear to have shifted, winter and spring distributions have seemingly remained within the SB boundary for the most part. This is also valuable information for wildlife managers as the harvest primarily occurs in spring and to a lesser extent winter (M. Branigan, Government of the Northwest Territories, pers. comm.).

In subpopulations where bears are forced ashore for the duration of the open water season due to complete melting of sea ice, they fast (Derocher et al. 1993, Ferguson et al. 1997, Ferguson et al. 2000a). One consequence of a longer icefree period is a longer fasting period, which may affect reproduction and survival if excessively long (Molnár et al. 2010, Molnár et al. 2011). Satellite collar information indicated that the majority of polar bears in the SB population remained on ice throughout the year (Amstrup et al. 2000, Schliebe et al. 2008), although the proportion of bears moving to land during the summer has been increasing (Gleason and Rode 2009, also see Herreman and Peacock 2013). As the open water period increases, these bears will likely experience increased duration of fasting and potentially increased threat of conflict with humans as has been observed in other areas (see Towns et al. 2009). Availability of preferred habitat over the continental shelf has declined (Durner et al. 2009), and long distance swim events that come with risks (Durner et al. 2011) may be increasing (Pagano et al. 2012). Furthermore, recent changes to ice conditions have resulted in a denning shift landward and eastward, and a decline in the proportion of dens on pack ice (Fischbach et al. 2007).

With increasing changes in sea ice distribution the SB/Northern Beaufort population boundary may become obscured as SB bears shift to occupy Northern Beaufort regions where apparent conditions are more favourable. During 2004, bears captured west of Banks Island were in significantly better condition in spring than those captured in the eastern portion of the Alaskan Beaufort Sea, with 47% of independent (not with mother) bears captured east of 150° west considered lean (body condition 1 or 2), and only 26% of bears captured west of Banks Island in similarly poor condition (Amstrup et al. 2006). To an extent this already may be occurring, and should not be a surprise as Derocher et al. (2004) predicted climate change and associated shifts in sea ice distribution would alter bear movement patterns, weakening boundries as bears shift northward or to common refuge areas; they furthermore predicted that SB will merge with NB.

## 2.5 References

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**Figure 2-1.** Study area encompassing estimates of polar bear utilization distributions in the Beaufort Sea, 2007-2011; polar bear collar deployment locations indicated by year. Solid line indicates the Southern Beaufort population boundary as identified by the IUCN/SSC Polar Bear Specialist Group (Derocher et al. 1998).



Figure 2-2. Polar bear seasonal 10% (red) 50% (yellow) and 95% (blue) volume contours for kernel densities, 2007-2011.



**Figure 2-3.** Box plot of the area of polar bear monthly use (includes 95% probability of use contours (n=554) and 95% minimum convex polygons (n=4).



**Figure 2-4.** Distance between centroids of polar bear 95% probability of use contours/minimum convex polygons (n=558) to 200 m isobath (km) by month, 2007/08 (white), 2008/09 (off white), 2009/10 (light grey), 2010/11 (dark grey). Negative values indicate centroid is deeper than the 200 m isobath; positive values indicate centroid is shallower than the 200 m isobath. Vertical bars indicate 95% CI. Note that centroid outliers located south of the 200 m isobath during winter used the region southwest of Barrow in the shallow waters of the Chukchi Sea.



**Figure 2-5.** Mean bathymetry of polar bear 95% probability of use contours/minimum convex polygons (n=558) by month, 2007/08 (white), 2008/09 (off white), 2009/10 (light grey), 2010/11 (dark grey). Vertical bars indicate 95% CI.


**Figure 2-6.** Volume of kernel densities pooled by land/ocean depth (m) for polar bears in the southern Beaufort Sea by season 2007-2011.



**Figure 2-7.** Proportion of locations from polar bears tracked by satellite telemetry in the Beaufort Sea that were outside the SB population boundary 2007-2011.



**Figure 2-8.** Proportion of open water in the Beaufort Sea study area 2007/08 (dotted), 2008/09 (dot-dashed), 2009/10 (dashed), 2010/11 (solid).



**Figure 2-9.** Sea ice concentration (%) in the Beaufort Sea study area 2007/08 (dotted), 2008/09 (dot-dashed), 2009/10 (dashed), 2010/11 (solid).

**Table 2-1.** Number of polar bears tracked by satellite telemetry in the Beaufort Sea used to estimate monthly kernel densities for June to May, 2007-2011.

	Summer			Autumn			Winter			Spring			
Year	June	July	August	September	October	November	December	January	February	March	April	May	Total
2007/08	17	15	12	11	12	11	8	6	3	3	2	11	111
2008/09	10	9	9	9	8	6	7	6	6	5	4	25	104
2009/10	25	22	18	15	14	15	12	13	14	14	15	21	199
2010/11	19	17	15	11	14	12	10	10	8	9	10	10	145
Total	71	63	54	46	48	44	37	35	31	31	31	67	558

**Table 2-2.** Results from Kruskal-Wallis tests (above - left side of table) examining area of use between months (top month - left month). Results of median test (above - right side of table) examining area of use between months. Adjusted p-values indicated (below); significant results noted in bold.

	January	February	March	April	May	June	July	August	September	October	November	December
January		1.52	1.52	0.55	3.52	22.66	16.04	10.05	7.95	10.50	21.68	6.73
Januar y		1.000	1.000	1.000	1.000	<0.001	0.004	0.101	0.318	0.079	<0.001	0.627
February	53.11		0.07	1.61	17.03	33.78	21.23	17.64	18.68	18.39	28.06	17.13
February	1.00		1.000	1.000	0.002	<0.001	<0.001	0.002	0.001	0.001	<0.001	0.002
Manah	39.79	-13.32		1.61	7.97	28.96	25.46	17.64	11.51	18.39	33.25	10.02
March	1.000	1.000		1.000	0.313	<0.001	<0.001	0.002	0.046	0.001	<0.001	0.102
A	24.76	-28.36	-15.03		3.82	33.78	21.23	10.88	8.57	14.65	28.06	2.91
April	1.000	1.000	1.000		1.000	<0.001	<0.001	0.064	0.225	0.009	<0.001	1.000
N	-63.24	-116.35	-103.03	<b>-</b> 8.00		18.13	2.50	0.66	0.21	2.53	15.67	0.04
May	1.000	0.070	0.254	0.934		0.001	1.000	1.000	1.000	1.000	0.005	1.000
Trees	-210.02	-263.14	-249.81	-234.78	-146.78		2.43	12.49	13.77	0.45	2.14	11.88
June	<0.001	< 0.001	<0.001	<0.001	<0.001		1.000	0.027	0.014	1.000	1.000	0.037
Table	-137.61	-190.73	-177.40	-162.37	-74.37	72.41		1.06	1.17	0.22	0.75	1.07
July	0.004	< 0.001	<0.001	<0.001	0.669	0.738		1.000	1.000	1.000	1.000	1.000
	-99.89	-153.00	-139.68	-124.65	-36.65	110.14	37.73		0.00	1.42	4.13	0.96
August	0.336	0.002	0.009	0.047	1.000	0.012	1.000		1.000	1.000	1.000	1.000
Garritanakan	-77.85	-130.96	-117.64	-102.60	-14.61	132.18	59.77	22.04		2.73	4.45	0.32
September	1.000	0.037	0.132	0.481	1.000	0.001	1.000	1.000		1.000	1.000	1.000
	-117.50	-170.62	-157.29	-142.26	-54.26	92.52	20.11	-17.62	-39.66		0.00	1.00
October	0.081	< 0.001	0.002	0.010	1.000	0.166	1.000	1.000	1.000		1.000	1.000
Name	-178.10	-231.31	-217.99	-202.96	-114.96	31.83	-40.55	-78.31	-100.35	-60.69		3.63
November	<0.001	< 0.001	<0.001	<0.001	0.019	1.000	1.000	1.000	0.247	1.000		1.000
	-83.98	-137.09	-123.77	-108.74	-20.74	126.04	53.63	15.91	-6.13	33.52	94.22	
December	1.000	0.037	0.126	0.437	1.000	0.009	1.000	1.000	1.000	1.000	0.686	

**Table 2-3.** Results from Kruskal-Wallis tests (above - left side of table) examining distance from centroid of 95% probability of use contours/minimum convex polygons to 200 m isobath between months (top month – left month). Results of median test (above - right side of table) examining distance from centroid of 95% probability of use contours/minimum convex polygons to 200 m isobath between months. Adjusted p-values indicated (below); significant results noted in bold.

	January	February	March	April	May	June	July	August	September	October	November	December
January		0.06	0.06	0.55	7.35	26.66	32.40	25.77	27.63	18.64	4.57	0.50
		1.00	1.00	1.00	0.44	<0.001	<0.001	<0.001	<0.001	0.001	1.00	1.00
February	14.94		0.07	0.58	3.82	20.44	21.23	19.04	24.74	19.97	1.61	0.06
	1.00		1.00	1.00	1.00	<0.001	<0.001	0.001	<0.001	0.001	1.00	1.00
March	1.30	-13.65		0.58	7.97	20.44	21.23	19.04	24.74	<b>19.9</b> 7	3.02	0.53
	1.00	1.00		1.00	0.31	<0.001	<0.001	0.001	<0.001	0.001	1.00	1.00
April	-14.57	-29.52	-15.87		7.97	24.52	25.46	27.72	29.58	19.97	4.87	1.48
	1.00	1.00	1.00		0.31	<0.001	<0.001	<0.001	<0.001	0.001	1.00	1.00
May	66.36	51.42	65.07	80.94		15.35	22.45	15.54	20.41	8.68	0.22	3.40
	1.00	1.00	1.00	1.00		0.006	<0.001	0.005	<0.001	0.21	1.00	1.00
June	191.59	176.65	190.30	206.17	125.23		3.63	1.87	1.13	0.09	12.44	18.13
	<0.001	<0.001	<0.001	<0.001	<0.001		1.00	1.00	1.00	1.00	0.028	0.001
July	203.15	188.21	201.86	217.73	136.79	11.56		0.01	0.09	1.52	16.08	22.69
	<0.001	<0.001	<0.001	<0.001	<0.001	1.00		1.00	1.00	1.00	0.004	<0.001
August	194.55	179.61	193.26	209.13	128.19	2.96	-8.60		0.00	1.42	10.56	20.87
	<0.001	<0.001	<0.001	<0.001	0.001	1.00	1.00		1.00	1.00	0.08	<0.001
September	215.44	200.50	214.14	230.01	149.08	23.85	12.29	20.89		1.53	21.52	22.43
	<0.001	<0.001	<0.001	<0.001	<0.001	1.00	1.00	1.00		1.00	<0.001	<0.001
October	172.26	157.32	<b>170.9</b> 7	186.84	105.90	-19.33	-30.89	-22.29	-43.18		8.54	11.40
	<0.001	0.002	<0.001	<0.001	0.034	1.00	1.00	1.00	1.000		0.230	0.048
November	76.86	61.917	75.56	91.43	10.50	-114.74	-126.29	-117.69	-138.58	-95.40		1.48
	1.00	1.00	1.00	1.00	1.00	0.014	0.004	0.021	0.003	0.32		1.00
December	28.01	13.069	26.71	42.59	-38.35	-163.59	-175.14	-166.54	-187.43	-144.25	-48.85	
	1.00	1.00	1.000	1.00	1.00	<0.001	<0.001	<0.001	<0.001	0.003	1.00	

	Number of locations outside SB	Number of locations	% of locations outside SB
2007/08	3,339	12,258	27%
Summer	2,167	6,035	36%
Autumn	836	2,572	33%
Winter	232	1,881	12%
Spring	104	1,770	6%
2008/09	3,859	13,359	29%
Summer	2,264	4,152	55%
Autumn	695	1,821	38%
Winter	263	2,225	12%
Spring	637	5,161	12%
2009/10	9,063	28,064	32%
Summer	4,641	10,890	43%
Autumn	1,900	4,303	44%
Winter	1,099	5,622	20%
Spring	1,423	7,249	20%
2010/11	7,661	20,532	37%
Summer	3,904	7,893	49%
Autumn	1,810	3,775	48%
Winter	718	4,182	17%
Spring	1,229	4,682	26%
Total	23,922	74,370	32%

**Table 2-4.** Number of locations from polar bears tracked by satellite telemetry in the Beaufort Sea that were outside the IUCN/SSC Polar Bear Specialist Group SB population boundary by season, 2007-2011.

# Appendix 2-1

Bear ID	Collaring Date	Sex	Age Class	Offspring	Days Tracked	Collar Type
A20163	14-May-07	F	adult	no	415	Gen III
A20434	6-May-07	F	adult	yearling (1)	274	Gen III
A20716	6-May-07	F	subadult	no	206	Gen III
A20760	2-May-07	F	adult	yearling (1)	216	Gen III
X32253	15-May-07	F	subadult	no	254	Gen III
X32373	6-May-07	F	subadult	no	51	Gen III
X32381	13-May-07	F	subadult	no	312	Gen III
X32606	14-May-07	F	adult	no	357	Gen III
X32608	2-May-07	Μ	subadult	no	331	Gen III
X32620	15-May-07	F	subadult	no	157	Gen III
X32628	28-Apr-07	F	adult	yearling (1)	198	Gen III
X32650	22-Apr-07	F	subadult	no	140	Gen III
X32651	22-Apr-07	F	adult	yearling (1)	337	Gen III
X32654	22-Apr-07	Μ	subadult	no	77	Gen III
X32655	23-Apr-07	F	adult	yearling (2)	477	Gen III
X32658	28-Apr-07	F	adult	yearling (1)	235	Gen III
X32660	2-May-07	F	adult	no	233	Gen III
X32665	17-May-07	F	subadult	no	328	Gen III
A20521	7-May-08	F	adult	no	290	Gen III
X32606*	7-May-08	F	adult	cub-of-the-year (1)	361	Gen III
X32611	19-Apr-08	Μ	subadult	no	375	Gen III
X32665*	23-Apr-08	F	subadult	no	371	Gen III
X32670	19-Apr-08	F	adult	no	410	Gen III
X32671	22-Apr-08	М	subadult	no	350	Gen III
X32672	23-Apr-08	F	adult	yearling (2)	31	Gen III
X32675	25-Apr-08	F	subadult	no	305	Gen III
X32677	7 <b>-</b> May-08	Μ	subadult	no	41	Gen III
X32680	17-May-08	Μ	subadult	no	547	Gen III
X32685	17-May-08	F	adult	cub-of-the-year (1)	869	Gen IV
A20415	30-Apr-09	F	adult	no	759	Gen IV
A20522	25-Apr-09	F	adult	no	174	Gen IV
A20667	23-Apr-09	F	adult	yearling (1)	446	Gen IV
A20854	17-Apr-09	Μ	subadult	no	674	Gen IV
A20961	20-Apr-09	F	adult	no	415	Gen IV
X19450	29-Apr-09	F	adult	no	173	Gen IV
X32268	27-Apr-09	F	adult	two-year-old (2)	74	Gen IV
X32606	5-May-09	F	adult	yearling (1)	492	Gen IV
X32611*	1-May-09	М	subadult	no	413	Gen IV

Details of bears collared in the southern Beaufort Sea, 2007 – 2010.

		_				
X32643	25-Apr-09	F	subadult	no	449	Gen IV
X32644	19-Apr-09	F	adult	yearling (1)	678	Gen IV
X32647	25-Apr-09	F	subadult	no	87	Gen III
X32672*	25-Apr-09	F	adult	two-year-old (2)	445	Gen IV
X32673	25-Apr-09	F	subadult	no	375	Gen III
X32681	18-Apr-09	Μ	subadult	no	343	Gen III
X32682	18-Apr-09	F	adult	cub-of-the-year (2)	771	Gen IV
X32687	19-Apr-09	F	adult	yearling (1)	365	Gen IV
X32690	20-Apr-09	F	Adult	No	771	Gen IV
X32692	25-Apr-09	Μ	subadult	no	691	Gen IV
X32693	27-Apr-09	F	adult	yearling (1)	570	Gen IV
X32698	30-Apr-09	F	adult	cub-of-the-year (1)	760	Gen IV
X32700	1-May-09	F	adult	no	758	Gen IV
X32701	1-May-09	F	adult	cub-of-the-year (1)	759	Gen IV
X32703	1-May-09	F	adult	no	392	Gen IV
X32704	5-May-09	Μ	subadult	no	57	Gen IV
X32613	20-Apr-10	F	adult	no	397	Gen IV
X32614	21-Apr-10	F	adult	two-year-old (2)	397	Gen IV
X32617	22-Apr-10	F	adult	two-year-old (1)	397	Gen IV
X32645	25-Apr-10	F	adult	yearling (2)	269	Gen IV
X32649	27-Apr-10	F	adult	no	396	Gen IV
X32707	27-Apr-10	F	adult	no	156	Gen IV
X32711	25-Apr-10	F	adult	yearling (2)	226	Gen IV
X32803	22-Apr-10	F	adult	no	55	Gen IV
X32804	24-Apr-10	F	adult	yearling (1)	397	Gen IV
X32808	25-Apr-10	F	adult	no	335	Gen IV

\* indicates bears that were relocated and recollared

# Chapter 3 – Summer Refugia of Polar Bears (*Ursus maritimus*) in the Southern Beaufort Sea

#### 3.1 Introduction

Species' presence, abundance, distribution, and diversity can be linked to characteristics of their environments (MacArthur et al. 1966, Brown 1984). Habitat used by a given species is an area that provides the resources and conditions needed to survive and reproduce (Hall et al. 1997). Selection of habitat varies between locations and across time (Rosenzweig 1991) making spatial and temporal patterns of resource abundance and availability of utmost importance when examining habitat use (Southwood 1977). In a temporal context, resource requirements often differ depending on aspects of life history, or stages within a season (Block and Brennan 1993). Furthermore, differences in a species' habitat use between years is connected to the distribution of available resources and how they have been modified by abiotic and biotic factors (Block and Brennan 1993).

There is growing evidence of ecological responses to climate change, with regional changes having the greatest relevance (Walther et al. 2002, Parmesan et al. 2013). Habitats are changing in response to climate change and in effect altering the distribution of species (Peterson et al. 2001, Konvicka et al. 2003, Perry et al. 2005, Grebmeier et al. 2006, Hitch and Leberg 2007, Kelly and Goulden 2008). The term refugia has historically been used in a biogeographic context, and is now applicable to biodiversity under climate change in the context that it refers to habitats that retain conditions, once widespread, and provide home for components of biodiversity to persist under changing environmental conditions (Keppel et al. 2012). The identification of refugia is of increasing conservation importance in the rapidly changing Arctic.

Changes in the distribution and phenology of plants and animals have been linked to local or regional climate change; with species that have a restricted range occurring in polar or mountain top regions to be the most vulnerable (Parmesan and Yohe 2003, Parmesan 2006). One habitat that is showing rapid change is the sea ice of the circumpolar Arctic. The Arctic has been warming at an unprecedented speed; sea ice extent (defined as the area of the ocean with a fractional ice cover/concentration  $\geq 15\%$ ) has declined from 1979 through 2006 when analyzed by month (Serreze et al. 2007). The first record breaking sea ice minimum in the modern satellite record occurred in 2005, and was broken in September 2007 (Stroeve et al. 2008), and again in 2012 (Parkinson and Comiso 2012). The six years between 2007-2012 have the lowest recorded sea ice extents since recording commenced (Jeffries et al. 2013). The bulk of multiyear sea ice extent reductions are occurring in the Beaufort Sea and the Canadian Basin, with most remaining multivear sea ice in this region concentrated in the east along side the Arctic islands (Maslanik et al. 2011). Species living in sea ice habitat are being affected; changes in sea ice and snow cover due to climate change are predicted to affect ice algal production (Arrigo et al. 2008, Li et al. 2009, McLaughlin and Carmack 2010, Zhang et al. 2010), which plays a pivotal role in sustaining secondary production through their effect on the phytoplankton bloom near the ice edge. Changing sea ice conditions are also projected to decouple phytoplankton and copepod grazers with potential for cascading effects through

the food web (Hansen et al. 2003) with significant implications for fish (Johannessen and Miles 2011), birds (Gaston et al. 2009), and marine mammals including ice-associated pinnipeds and cetaceans inhabiting Arctic waters (Laidre et al. 2008, Ragen et al. 2008, Kovacs et al. 2011). Polar bears (*Ursus maritimus*) that inhabit this region have been identified as particularly vulnerable to climate warming (Stirling and Derocher 1993, Tynan and DeMaster 1997, Regehr et al. 2007, Laidre et al. 2008).

Polar bears are dependent on sea ice from which they hunt, travel, mate (Smith 1980, Stirling and Derocher 1993, Durner et al. 2009), and in some cases use as a substrate for maternity dens (Amstrup and Gardner 1994). They are an obligate predator of seals, and their survival and reproduction are dependent on the acquisition of sufficient adipose reserves obtained during late spring and early summer (Ramsay and Stirling 1988, Stirling et al. 2008). Ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) are the primary prey of polar bears (Stirling and Archibald 1977, Smith 1980, Thiemann et al. 2008). Seal distribution, and therefore polar bear distribution, is strongly influenced by shore leads, polynyas, areas of annual and multi-year sea ice, and patterns of freeze-up and break-up (Stirling 2002). Annual ice overlaying the continental shelf is the most biologically productive polar bear habitat, yielding greater seal density than deeper waters of the polar basin (Derocher et al. 2004, Frost et al. 2004, Durner et al. 2009).

Climate change induced loss of sea ice will affect the 19 polar bear populations that range across the circumpolar north (Regehr et al. 2010, Derocher et al. 2013).

One population that has been identified at risk of extirpation is the Southern Beaufort Sea polar bear population (SB) (Hunter et al. 2010, Regehr et al. 2010), which inhabits the area from Pearce Point, Northwest Territories to Barrow, Alaska (Fig. 2-1). In overview, annual sea ice covers the near shore areas, with multiyear ice found further offshore over the deeper water. This region, however, is experiencing notable declines in sea ice extent (Comiso and Parkinson 2004) and multiyear ice (Rothrock and Zhang 2005, Stroeve et al. 2007, Maslanik et al. 2011). Until recently, SB bears responded to seasonal changes in sea ice by moving north to multiyear ice when the annual ice melted, and returned south when it froze (Stirling et al. 1975, Stirling and Lunn 1997, Stirling 2002). The recent trend of later sea ice freeze-up and earlier sea ice break-up is forcing SB bears to either spend the summer on sea ice over deep water where productivity is low or on land where food is limited (Amstrup et al. 2006, Schliebe et al. 2008). Further, changes were noted in the distribution of maternity denning. Over recent decades, polar bears in the Beaufort Sea have shifted from denning on sea ice to denning on land and this shift was attributed to a decline in suitable sea ice substrate for denning (Fischbach et al. 2007). Changes in sea ice extent and condition in the Beaufort Sea have been associated with declines in cub survival, instances of bears clawing through ice in an attempt to catch seals, cannibalism, drowning, and starvation (Amstrup et al. 2006, Monnett and Gleason 2006, Stirling et al. 2008, Hunter et al. 2010, Regehr et al. 2010, Rode et al. 2010, Durner et al. 2011).

Polar bears respond to seasonal and interannual variation in sea ice distribution (Stirling and Derocher 1993, Mauritzen et al. 2003, Durner et al. 2009), yet quantification of temporal variation in polar bear distribution largely remains unstudied. How bears cope with reduced sea ice habitat provides insight to how bears may respond to ongoing climatic change. In this study I examine polar bear distribution between June through September, covering the period of rapidly declining sea ice and the month of the sea ice minimums, in 2007 – 2010, a period with record breaking years of low sea ice extent (Stroeve et al. 2012, Jeffries et al. 2013). I evaluate the response of polar bears to reduced sea ice habitat during summer using utilization distributions to examine their distribution over time and how their distribution changes in response to sea ice cover. I also examine use of terrestrial areas and sea ice as summer refugia when nearshore sea ice melts. To characterize refugia habitat, I examine the bathymetry of summer habitats.

#### 3.2 Materials and Methods

#### 3.2.1 Study Area

The study area encompasses the Beaufort Sea and northern region of the Chukchi Sea (Fig. 2-1). Regional sea ice dynamics are influenced by the clockwise Beaufort Gyre (Coachman and Aagaard 1974), an influx of cold polar water, as well as currents, wind patterns, and temperature. Maximum sea ice extent occurs during spring, in which landfast ice east of the Mackenzie Delta extends 25-30 km offshore (Cooper 1974, Aagaard 1984). A thinner strip of landfast ice occurs from the Mackenzie Delta west to Shingle Point and west of this open water can prevail even in February (Cooper 1974). The shore lead

exists at the edge of the landfast ice, beyond which is the drifting pack ice (Carmack and Macdonald 2002).

During break-up, which commences in April, the shore lead widens and ice begins breaking up and melting originating at the headwaters of the Mackenzie River and progressing northward along the continental shelf (Carmack and Macdonald 2002). Beyond the shore lead, pack ice persists throughout the summer but may be several hundred kilometres from shore, and typically follows the movement of the Beaufort Gyre. Freeze-up normally commence in mid-October and grows from the pack ice south, and from the coastline north (Carmack and Macdonald 2002).

## 3.2.2 Capture and collaring

Polar bears were located using a helicopter and immobilized with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil® Laboratoires Virbac, Carros, France) in accordance with standard procedures (Stirling et al. 1989). Adult and subadult bears were the focus due to their ability to be fit with collars for 1-2 years. All collars had a programmable release (CR2a; Telonics, Mesa, Arizona) and collars on subadults were attached with corrodible links that would erode after 1 year.

Location data were obtained with global positioning system (GPS) Argos® satellite-linked collars (Telonics Gen III GPS collars and Telonics Gen IV GPS collars; Telonics, Mesa, Arizona) deployed on the Canadian side of the Beaufort Sea (Fig. 2-1). Collars were deployed between mid-April and mid-May in 2007 to 2010, and programmed to acquire GPS locations every 4 hours. Erroneous locations and data from suspect dropped collars were excluded from analysis. Methods to capture and handle polar bears were in accordance with the Canadian Council on Animal Care guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee.

### 3.2.3 Data analyses

I examined the space use of polar bears using kernel densities following rationale and details outlined in Chapter 2. Number of locations per bear per day varied between 0 and 6. I estimated a kernel density for each month in which a bear had >50 locations in  $\geq 20$  days. I examined the correlation between the number of locations used to create monthly kernel densities and the corresponding area of 95% volume contours. Monthly kernel densities were calculated to measure the joint space use of multiple animals. Because bear locations per month varied, monthly bear kernel densities were weighted by the number of monthly locations per bear. Hence, grouped monthly kernel densities were determined by multiplying each bear density by the proportion of data contributed during that month and summing all resulting kernel densities. Kernel densities were calculated using the 'kde' function in Geospatial Modeling Environment Version 0.7.2 RC2 (Beyer, H.L., available at www.spatialecology.com/gme); and were depicted using percent contours with 50 and 95% probability of use calculated using Hawth's Analysis Tools for ArcGIS Version 3.27 (Beyer, H.L., available at http://www.spatialecology.com/htools).

To quantitatively examine area of use I calculated the area of 95% probability of use contours for each bear month when possible and for 3 bears with very small use areas (a few pixels or less), I calculated 95% minimum convex polygons using Hawth's Analysis Tools for ArcGIS Version 3.27 (Beyer, H.L., available at http://www.spatialecology.com/htools). The effect of sample size and estimator used must be considered when comparing home range sizes because sample size bias differs between estimators of home range (Boulanger and White 1990). Minimum convex polygons increase in size as sample size increases; accurate analysis of home range size by this estimator requires between 100 – 200 locations (Bekoff and Mech 1984).

Variation in area of use was analyzed in a nested ANOVA to determine the relative contribution of individual, monthly, and annual variation. Area of use was compared temporally among months and years, with months nested within years. Bear ID was included to account for individual variability. Probability of use contour area was square root transformed to conform to assumptions of normality and equal heterogeneity of variances between months and across years. I used a Tukey's HSD test to examine differences in area of use between months. Statistical analysis was completed with SPSS version 21, IBM Corp., Armonk, NY.

To assess substrates used by collared bears, I quantified the number of individuals tracked throughout the summer (June – September) 2007-2010 that used land areas in Alaska relative to those that did not, and identified bears that used land outside Alaska. I determined the volume of monthly kernel densities in

each category of land/bathymetry following procedures outlined in chapter 2. Sea ice extent and concentration were examined following procedures summarized in Chapter 2.

#### 3.3 Results

A total of 64 collars were deployed on 60 different bears with 17 on solitary adult females, 5 on females with cubs-of-the-year, 15 on females with yearlings, 4 on females with two-year-olds, and 23 on subadults ( $\leq$ 4 years old) (12 females, 11 males) (Appendix 2-1). Four bears were recollared. The number of bears tracked varied over time due to collar design, deployment, and both planned and unplanned collar retention. One adult female collared in April 2009 emigrated to the Chukchi Sea near Wrangel Island, Russia and was excluded from analyses.

Individual bear monthly kernel densities (n=234) were calculated for June through September between 2007 and 2010 (Table 3-1). Mean number of locations per month per bear for kernel densities was 124 (SD=28, range 61-186) (see Appendix 3-1). Number of locations per month was not related to area of use (Spearman's rho,  $r_s$ =-0.005, p=0.936). Monthly kernel densities calculated to measure the joint space use of multiple animals indicated the highest probability of use during summer in all years was concentrated in two regions: along the Alaskan coast and along the southern edge of the pack ice (Fig. 3-1). Use along the Alaskan coast was concentrated at Barter Island and along the nearshore islands between Kaktovik and Prudhoe Bay. The spatial location of kernel density concentrations along the pack ice varied annually with melt patterns (Fig. 3-1).

The three individual bear monthly 95% probability distributions that failed all occurred in September around Kaktovik, Alaska with MCPs of  $5 \text{ km}^2$ ,  $5 \text{ km}^2$ , and  $8 \text{ km}^2$ , and derived from 145, 107, and 113 locations, respectively. The MCPs used to determine home range area for three bear months was unlikely to affect analyses due to the confined distribution of locations and large sample sizes that minimized the bias of area estimates.

There was a high level of individual variability of bear monthly area of use (F=2.00, df=54, p<0.001). The mean area of monthly use varied between months (F=13.27, df=3, p<0.001) (Table 3-2, Fig. 3-2). Mean area of use decreased from June to September in 2008 and 2010, but peaked in July of 2009, and increased between August and September in 2007 (Fig. 3-2). Variation in monthly area of use between years was not significant (F=1.14, df=12, p=0.33). Results from Tukey's HSD tests comparing monthly area of use suggested area of use in June was significantly different that July, August, and September; and area of use in July was significantly different than September (Table 3-3). Distributions of monthly probability of use contours appeared to be the tightest in August and September of 2009 and 2010, and the widest in September 2007 (Fig. 3-3).

Of the bears tracked throughout the summer, 29% (19/66) used land areas in Alaska: 33% (5/15) in 2007, 22% (2/9) in 2008, 26% (6/23) in 2009, and 32% (6/19) in 2010. Further, 53% of bears on land areas in Alaska were near Kaktovik: 5/5 (100%) in 2007, 1/2 (50%) in 2008, 4/6 (67%) in 2009, and 0/6 (0%) in 2010. Three bears tracked (5%) used land outside Alaska: one near the coast east of Sachs Harbour (3 locations), a second on Herschel Island (13 locations), and the third on Prince Patrick Island (17 locations) (Appendix 3-2).

Bears on sea ice made high use of shallow water (1-99 m) in all months in all years (Fig. 3-4). In 2010 there was notably high use of shallow depths (1-99 m) during July and August. A peak in use over waters 300-399 m deep was most prominent in August and September of all years and coincided with the edge of the continental shelf (Fig. 3-4). Beyond this depth, volume of kernel density decreased (Fig. 3-4). There was high use of depths ≥3500 m during August and September in 2007 (Fig. 3-4).

Proportion of open water increased through the summer in each year; and was greatest in 2008 in all months except June (Fig. 3-5). Sea ice concentration was greatest in June and lowest in August in all years (Fig. 3-6). Ice concentration was lower in 2008 than other years in all month examined.

# 3.4 Discussion

The distributions and analysis presented are unique in that they include not only locations from adult females but also those from subadult males and females. Until now, information regarding movements and distribution of subadults has been limited. Although researchers have been tracking female polar bears for decades (Larsen et al. 1983), tracking adult male bears remains a challenge. Several attempts to track male bears through various means have been made (Mulcahy and Garner 1999, Amstrup et al. 2001, Laidre et al. 2014, USFWS 2014), however, resulting locations and insights gained have been, by enlarge, limited to the spring season (Amstrup et al. 2001, Laidre et al. 2014).

Summer kernel densities suggested bears employed two strategies in response to the retraction of sea ice. As documented historically, I observed some SB polar bears to follow the southern edge of the pack ice as it retreated north (Stirling et al. 1975, Amstrup et al. 2000), and spend the summer off the coast of Banks Island (Stirling 2002). Other bears either moved between mainland and the pack ice as long as the sea ice was in close proximity to the coast (Stirling et al. 1975, Durner et al. 2011, Pagano et al. 2012), or moved to land. In 2000 to 2005, it was estimated that an average of 3.7% (maximum of 8%) of bears from the SB population were on land during autumn (Schliebe et al. 2008). In contrast, I found an average of 29% (maximum 32%) of bears made use of land along the Alaskan coast during summer; giving strength to the premise that bears have increased their use of land as sea ice has reduced in extent, and open water increased (Fischbach et al. 2007, Schliebe et al. 2008, Gleason and Rode 2009). My results suggest that the majority of the SB population still remains on sea ice during summer and autumn; furthermore, in years when sea ice retreats further off shore, bears are forced to make larger movements and make greater use of less productive deeper ocean depths as seen in September 2007. Kernel densities viewed in conjunction with sea ice concentrations during the same period, revealed that bears that remained on the pack ice made use of the edge of the pack ice most notably in the region west of Banks Island. Bears may choose to remain near the edge of the pack ice because the pack ice edge is nearest to the shallow

waters of the continental shelf, which when overlain by annual ice, house the most biologically productive polar bear habitat (Derocher et al. 2004). Alternatively, bears near the pack ice edge minimize the amount of energy required to travel back towards shallower depths when the ice begins to form again. The ability of polar bears to access food from sea ice over the deeper waters of the ocean basin remains largely unknown.

Some polar bears likely move to land to scavenge bowhead whales (*Balaena mysticetus*) harvested as part of a subsistence hunt (Miller et al. 2006) and terrestrial kernel densities were concentrated around such regions. Many polar bears observed during bowhead whale and aerial surveys were associated with harvested whales (Rode and Gleason 2009), particularly at Barter Island (Schliebe et al. 2008). Bowhead whales have been documented to compose a variable proportion of polar bear diets that differ between individuals and across years (Bentzen et al. 2007). In 2003, whales composed between 11-26% of polar bear diets sampled along the Alaskan Beaufort Sea but was only 0-14% in 2004 (Bentzen et al. 2007).

Higher bear densities at Barter Island may be in part attributable to its frequent feature as the shortest distance from land to pack ice (Schliebe et al. 2008). Bears observed making long distance swims have been concentrated in this region (Monnett and Gleason 2006). Most bears observed feeding at the whale carcasses arrived and departed by swimming (Miller et al. 2006). It may be a viable strategy for bears to move between pack-ice and bone piles at Barter Island and surrounding areas to meet nutritional needs during autumn, however, swimming between pack ice and land may come at a cost. As sea ice continues to recede further from the coast each year and storms increase as is predicted (Serreze et al. 2000), polar bears will be forced to swim further distances through rougher waters between pack ice and land and risk drowning (Monnett and Gleason 2006) or substantial loss of body mass, and offspring (Durner et al. 2011). Long distance swims may have the greatest affect on younger bears because they are more vulnerable to the affects of expending increased energy due to sea ice movement and requirements to move greater distances/swim to maintain contact with preferred habitats (Derocher et al. 2004).

The current study found the highest volume of kernel densities to be located over shallow depths (1-99 m) that coincide with the highest ringed seal densities (Stirling et al. 1982, Frost et al. 2004). Ringed seals have been observed to comprise the majority (53-100%) of SB polar bear diet (Bentzen et al. 2007, Cherry 2011). Seals may also attract bears to the near shore regions. The bears along the coast may select these areas so they have access to seals over the continental shelf on any remaining ice or to remain close to good hunting habitat once the Beaufort Sea begins to freeze again (Schliebe et al. 2008).

My results support the premise that polar bears take advantage of the sea ice to hunt from when it is available (Schliebe et al. 2008, Gleason and Rode 2009). None of the bears observed on land along the Alaskan coast in 2010 visited Kaktovik. Instead of being concentrated around Barter Island, as in previous years, use during summer 2010 was concentrated just offshore and along the Barrier Islands. MODIS images of sea ice (NASA 2011) reveal there was a large amount of broken sea ice in the near shore region throughout the summer and autumn of 2010. Bears were likely taking advantage of hunting off the available sea ice during this time, rather than using anthropogenic-derived food sources as in previous years. High volume of kernel density over shallow depths during 2010 reflect this use.

I observed a large degree of individual variation in area of use in SB polar bears. I hypothesize that the variation observed in the current study likely originates from differing habitat use strategies that stem from the initial choice of whether to remain on landfast ice, moving to land when it melts, or retreat north with the sea ice. A large degree of variation in home range size has been documented in several polar bear populations (Wiig 1995, Ferguson et al. 1999, Amstrup et al. 2000, Mauritzen et al. 2001), and has been related to choice to move to land during ice free period (Mauritzen et al. 2001). Variation in home range size has been attributed, in part, to seasonal variation in sea ice, with bears inhabiting areas with many islands (i.e., Arctic Archipelago) documented to have smaller seasonal home ranges than bears living in environments accustom to annual ablation of ice during late summer (Ferguson et al. 1999).

A visual examination of monthly kernel densities across years highlights interannual variability in the spatial location of areas used, however, the size of areas used was not found to differ significantly between years. The spatial variability observed was closely related to annual patterns and timing of sea ice formation and ablation. Interannual variability in space use by individual polar bears has been documented (Ferguson et al. 1999, Amstrup et al. 2000). Sea ice

habitat quality varies spatially and temporally (DeMaster et al. 1980, Ferguson et al. 1997, Amstrup et al. 2000, Ferguson et al. 2000a, Ferguson et al. 2000b), the resulting unpredictability of resources forces bears to continually seek suitable habitats to adapt to the dynamic sea ice environment that may prove to be more unpredictable as climate continues to change. The increase in the rate of sea ice loss in the last decade (Comiso et al. 2008, Parkinson and Comiso 2012, Stroeve et al. 2012) is expected to continue with sea ice thinning during winter and summer over the next 30 years (Wang and Overland 2009). Projections suggest that September (summer) may be ice free as early as the late 2020s (Wang and Overland 2009). Furthermore, it is expected that climate change will increase storms particularly in autumn (Carmack and Macdonald 2002). Overall, the loss of multiyear sea ice in the Beaufort Sea and Canada Basin, coupled with an increase in heat absorption in open waters and the effects of the Arctic Dipole may be evidence that a 'regional tipping point' may have occurred (Maslanik et al. 2011).

If sea ice extent continues to decrease as is predicted by climatic models (Zhang and Walsh 2006), and the distance from pack ice to land increases, bears that remain on ice will be forced to travel greater distances and remain over greater depths for long durations. For bears that move to land, the consequence would be an increase in the amount of time bears spend on land because sea ice formation starts in the north and moves south. SB polar bear survival, breeding probability, and cub litter survival have decreased with longer ice free conditions over the continental shelf, likely because bears are nutritionally stressed as a result

of having less opportunity to forage over the productive waters of the continental shelf and thus enter winter in poorer condition (Hunter et al. 2010, Regehr et al. 2010). The proportion of bears fasting in the SB has also increased from 1985-1986 to 2005-2006 (Cherry et al. 2009), and declining sea ice has been associated with reductions in body size and reproduction of SB polar bears due to nutritional limitations (Rode et al. 2010). Furthermore, reproductive output and juvenile survival has been observed to decrease after years with lower availability of favourable sea ice habitat (Rode et al. 2010). The SB polar bear population is projected to decline with less sea ice coverage, largely due reduced adult female survival and reduced breeding (Hunter et al. 2010). An eventual ice free summer will result in a loss of the offshore refuge and force bears to move to shore. The affect of such a shift will be likely be influenced by the availability of food sources on land.

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**Figure 3-1.** Polar bear monthly 50% (red) and 95% (yellow) volume contours for kernel densities, June through September, 2007-2010 displayed over monthly sea ice concentration (white - blue) and open water (dark blue).



**Figure 3-2.** The mean area of polar bear monthly use (includes 95% probability of use contours (n=231) and 95% minimum convex polygons (n=3)) for June - September, 2007 (dotted line), 2008 (dot-dashed line), 2009 (dashed line), 2010 (solid line). Vertical bars indicate 95% CI.



**Figure 3-3.** Box plot of the area of polar bear monthly use (includes 95% probability of use contours (n=231) and 95% minimum convex polygons (n=3)) for June - September, 2007-2010.



**Figure 3-4.** Volume of pooled monthly polar bear kernel densities by land/ocean depth (m) in the Beaufort Sea June to September, 2007-2010.



**Figure 3-5**. The proportion of open water in the Beaufort Sea (study area) during June to September, 2007 (dotted), 2008 (dot-dashed), 2009 (dashed), 2010 (solid).



**Figure 3-6.** Sea ice concentration in the Beaufort Sea (study area) during June to September, 2007 (dotted), 2008 (dot-dashed), 2009 (dashed), 2010 (solid).

Month	2007	2008	2009	2010	Total
June	17	10	25	19	71
July	15	9	22	17	63
August	12	9	18	15	54
September	11	9	15	11	46
Total	55	37	80	62	234

**Table 3-1.** Number of polar bears tracked by satellite telemetry in the Beaufort Sea used to estimate monthly kernel densities for June to September, 2007-2010.

**Table 3-2.** Mean area of polar bear monthly use (includes 95% probability of use contours (n=231) and 95% minimum convex polygons (n=3)) for June to September, 2007-2010. See Table 3-1 for sample sizes.

Year	Month	Area (km <sup>2</sup> )	Range
2007	June	27,564	7,615 - 60,756
	July	15,214	374 - 49,373
	August	11,183	2,027 - 26,754
	September	20,147	5 - 67,328
2008	June	33,110	6,189 - 99,622
	July	24,121	1,868 -73,626
	August	22,633	650 - 57,320
	September	15,341	5 -34,468
2009	June	18,304	7,709 -36,852
	July	21,001	4,429 -70,862
	August	12,724	465 -33,827
	September	9,547	8 -21,984
2010	June	22,821	4,035 -70,493
	July	15,370	1,411 -50,014
	August	11,757	858 -54,046
	September	9,557	469 -22,365

Month (A)	Month (B)	Mean difference
August	July	-16.12 <sup>ns</sup>
C	June	-39.23*
	September	8.43 <sup>ns</sup>
July	August	16.12 <sup>ns</sup>
	June	-23.13*
	September	24.55*
June	August	39.25*
June	July	23.13*
	September	47.68*
September	August	-8.43 <sup>ns</sup>
-	July	-24.55*
	June	-47.68*

**Table 3-3**. Results from Tukey HSD multiple comparisons test on polar bear monthly area of use (square root transformed) for June to September, 2007-2010.

\*  $P < \overline{0.01}$ ;  $n^{s} = P > 0.05$ ; Mean difference = month (A) – month (B)

## Appendix 3-1

A total of 28,970 polar bear locations were used to calculate kernel densities; 6,035 locations from 2007, 4,152 from 2008, 10,890 from 2009, and 7,893 from 2010.

Number of polar bear locations for each bear that were used to estimate monthly kernel densities for June - September 2007.

Bear ID	June	July	August	September	Total
A20163	116	123	117	105	461
A20434	105	90			195
A20716	114	85	82	115	396
A20760	124	98	98	88	408
X32253	112	97			209
X32373	88				88
X32381	119	98	103	107	427
X32606	86	94			180
X32608	131	89	79	82	381
X32620	133	129	84	145	491
X32628	118	116	101	83	418
X32650	123	122	139		384
X32651	125	139	127	113	504
X32654	112				112
X32655	131	132	135	130	528
X32660	108	130	111	97	446
X32665	112	125	86	84	407
Total	1,957	1,667	1,262	1,149	6,035

Bear ID	June	July	August	September	Total
A20163	80				80
A20521	123	130	99	98	450
X32606	116	108	132	107	463
X32611	93	81	64	110	348
X32665	91	84	96	109	380
X32670	120	113	110	129	472
X32671	107	129	131	127	494
X32675	119	107	115	74	415
X32680	123	119	103	101	446
X32685	98	172	171	163	604
Total	1,070	1,043	1,021	1,018	4,152

Number of polar bear locations for each bear that were used to estimate monthly kernel densities for June - September, 2008.

Bear ID	June	July	August	September	Total
A20415	124	100			224
A20522	125	109	105	113	452
A20667	171	175	173	162	681
A20854	135	158	143	150	586
A20961	155	139	107	97	498
X19450	107	140	116	85	448
X32268	150				150
X32606	124	69	90		283
X32611	123	69			192
X32643	92	95			187
X32644	103	86			189
X32647	113				113
X32672	154	145	69		368
X32673	121	125	138	89	473
X32681	110	116	109	122	457
X32682	166	181	181	167	695
X32685	161	156	165	119	601
X32687	171	180	183	172	706
X32692	157	175	152	139	623
X32693	142	163	141	139	585
X32698	165	138	113	148	564
X32700	134	163	140		437
X32701	156	180	182	176	694
X32703	143	141	100	149	533
X32704	151				151
Total	3,453	3,003	2,407	2,027	10,890

Number of polar bear locations for each bear that were used to estimate monthly kernel densities for June - September, 2009.

Bear ID	June	July	August	September	Total
A20415	173	160	129	95	557
A20667	86				86
A20854	105	90	106	98	399
X32613	142	116		108	366
X32614	152	113	82	77	424
X32645	135	136	94	110	475
X32649	137	124	71	98	430
X32682	157	165	171	152	645
X32685	115	134	61		310
X32692	149	166	147	103	565
X32693	105	109			214
X32698	113	101	113		327
X32700	131	144	139		414
X32701	152	152	153	150	607
X32707	109	153	80		342
X32711	131	129	91		351
X32803	82				82
X32804	161	186	176	156	679
X32808	168	169	148	135	620
Total	2,503	2,347	1,761	1,282	7,893

Number of polar bear locations for each bear that were used to estimate monthly kernel densities for June - September, 2010.

## Appendix 3-2

Bear ID	June	July	August	September
A20163	116	123	117	105
A20434	105	90	52	64
A20716	114	85	82	115
A20760* <sup>K</sup>	124	98	98(21)	88(62)
X32253* <sup>K</sup>	112	97(16)	74(27)	66(52)
X32381	119	98	103	107
X32606* <sup>K</sup>	86	94	22	17(12)
X32608* <sup>K</sup>	131(8)	89	79(19)	82(50)
X32620* <sup>K</sup>	133	129	84(23)	145(100)
X32628	118	116	101	83
X32650	123	122	139	39
X32651	125	139	127	113
X32655	131	132	135	130
X32660	108	130	111	97
X32665	112	125	86	84

Number of locations of polar bears tracked each month between June – September 2007 (n=15); locations on land are indicated in parenthesis.

Notes: \* indicates bears that made use of land areas in Alaska <sup>K</sup> Indicates bears that used Kaktovik

Bear ID	June	July	August	September
A20521	123	130	99	98
X32606* <sup>K</sup>	116	108(17)	132(67)	107(62)
X32611*	93(3)	81	64(15)	110(33)
X32665	91	84	96	109
X32670	120	113	110	129
X32671	107	129	131	127
X32675	119	107	115	74
X32680	123	119	103	101
X32685	98	172	171	163

Number of locations of polar bears tracked each month between June - September 2008 (n=9); locations on land are indicated in parenthesis.

Notes: \* indicates bears that made use of land areas in Alaska <sup>K</sup> Indicates bears that used Kaktovik

Bear ID	June	July	August	September
A20415**	124	100	49(13)	22
A20522* <sup>K</sup>	125	109(2)	105(62)	113(92)
A20667	171	175	173	162
A20854	135	158	143	150
A20961* <sup>K</sup>	155	139	107(5)	97(46)
X19450	107	140	116	85
X32606* <sup>K</sup>	124	69(9)	90(23)	51(2)
X32611*	123	69	70(12)	55(23)
X32644	103	86	25	32
X32672	154	145	69	63
X32673	121	125	138	89
X32680	61	22	55	48
X32681	110	116	109	122
X32682***	166	181	181(3)	167
X32685	161	156	165	119
X32687	171	180	183	172
X32692	157	175	152	139
X32693	142	163	141	139
X32698* <sup>K</sup>	165	138	113(3)	148(65)
X32700*	134	163	140	87(42)
X32701	156	180	182	176
X32703	143	141	100	149

Number of locations of polar bears tracked each month between June - September 2009 (n=23); locations on land are indicated in parenthesis.

Notes: \* indicates bears that made use of land areas in Alaska <sup>K</sup> Indicates bears that used Kaktovik \*\* Indicates a bear that used Hershel Island

\*\*\*Indicates a bear that used the coast near Sachs Harbour

Bear ID	June	July	August	September
A20415*	173	160	129	95(8)
A20854	105	90	106	98
X32606*	32	37	26(2)	10
X32613	142	116	53	108
X32614*	152	113	82(9)	77
X32617	29	4	23	40
X32645	135	136	94	110
X32649	137	124	71	98
X32682	157	165	171	152
X32685	115	134	61	28
X32692	149	166	147	103
X32693	105	109	72	21
X32698*	113	101	113	49(5)
X32700*	131	144	139(5)	88(49)
X32701	152	152	153	150
X32707**	109	153	80	72(17)
X32711	131	129	91	31
X32804	161	186	176	156
X32808*	168	169	148	135(18)

Number of locations of polar bears tracked each month between June – September 2010 (n=19); locations on land are indicated in parenthesis.

Notes: \* indicates bears that used land areas in Alaska

\*\*Indicates a bear that used land on Prince Patrick Island

## **Chapter 4 - General Conclusion**

Arctic sea ice extent and thickness have declined (Serreze et al. 2007, Maslanik et al. 2011) and are projected to decline over the next three decades (Wang and Overland 2009). Sea ice extent and thickness have been particularly low since the first record low in 2007 (Jeffries et al. 2013). Several linked processes are considered responsible for the reduction in Arctic sea ice, and warming temperatures in all seasons have diminished the likelihood sea ice will recover (Stroeve et al. 2012a). In summary, low sea ice extent (extensive open water) during autumn yields first year ice the following spring that will melt faster the subsequent summer (Lindsay et al. 2009). A significant decline in the proportion of the oldest and thickest ice within the multiyear pack ice results in ice that is more susceptible to breaking up through rafting and ridging yielding open water earlier in the summer that increases solar input into the ocean and subsequently bottom melting (Maslanik et al. 2007, Perovich et al. 2011). Climate models from the most recent World Climate Research Program Coupled Model Intercomparison Project are consistent in that they indicate the Arctic will eventually be ice free as greenhouse gas concentrations increase (Stroeve et al. 2012b). As sea ice extent diminishes, summer ice cover is predicted to be more variable between years (Holland and Stroeve 2011, Stroeve et al. 2014). The accurate prediction of September sea ice extent on an annual basis remains a challenge as several environmental conditions in addition to ice thickness/age contribute to the resulting minimum sea ice cover (Stroeve et al. 2012b, Schröder et al. 2014).

Polar bears (*Ursus maritimus*) are an apex predator of the arctic food web and vulnerable to changing conditions in sea ice because their existence is dependent on this dynamic platform (Smith 1980, Stirling and Derocher 1993, Amstrup and Gardner 1994, Durner et al. 2009). Movement patterns and space use of this apex predator are anticipated to change in response to changes in their resource distribution and abundance, namely sea ice and ice affiliated prey species (Derocher et al. 2004). Although climate change will likely affect all polar bears in the long term, it is anticipated to impact populations at the southern extent of their range first (Stirling and Derocher 1993). The SB population is already showing the effects of climate induced changes in their environment evident through reduced survival, body size, and cub recruitment (Regehr et al. 2010, Rode et al. 2010a).

Examining the distribution of a species in space and time provides information about a species' habitat within the greater environment (Carey et al. 1992, Tufto et al. 1996). Environmental changes may cause a species to respond by altering movement and space use patterns (Carey et al. 1992, Trombulak and Frissell 2000, Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2006). The monitoring of resource use, space use, and movement patterns can provide information valuable in identifying critical habitat, understanding population demographics and trend, and mitigating anthropogenic impacts (Ingram and Rogan 2002, Cameron et al. 2005, Schwartz et al. 2006).

My research indicates that climate change is impacting the distribution and movements of SB polar bears. In Chapter 2 I examined the distribution of SB

bears during 2007 - 2011, years of record low sea ice extent. I observed that polar bear distribution during spring and winter was concentrated over shallow waters of the continental shelf as has been observed historically. Sea ice is at a maximum during these months and bears have not been forced to alter their space use patterns due to a lack of sea ice coverage. In contrast, my results indicate that SB bear distributions during summer and autumn are changing. The change is most evident from the unprecedented proportion of SB bear locations observed outside the SB population boundary during these seasons. During years in which sea ice retreats further from shore, bears are forced to travel further offshore and consequently cover greater distances during the summer to remain on the edge of the sea ice. Thus they also cover greater areas as they travel south following the advancing ice as it grows towards shore during autumn. Consequently, SB bear distribution covered the greatest area in autumn when bear movements reflected this behaviour. Furthermore, mean area of use during late autumn was also observed to change between years, likely due to the interannual variability in distribution and location of sea ice. As the open water period lengthens and sea ice extent continues to decline bears will be forced to travel greater distances to remain in contact with sea ice. Furthermore, as sea ice retreats further north bears will be further from the productive shallow waters of the continental shelf and remains over deeper waters (where hunting success is uncertain) for a longer period of time.

Increased movement will come with energetic consequences. Long distance swimming has been suggested as a behaviour response to climate-induced sea ice

decline (Pagano et al. 2012). Although swimming has likely occurred previously, researchers speculate that recently swim distances have changed from tens of kilometres to hundreds of kilometres (Durner et al. 2011), and may be occurring more frequently (Pagano et al. 2012). Long distance swims are energetically demanding, may compromise reproductive fitness (Durner et al. 2011), and pose the risk of drowning (Monnett and Gleason 2006). Observed downing events have been associated with stormy weather (Monnett and Gleason 2006). The predicted increase in storms during autumn (Carmack and Macdonald 2002), a period when polar bears have been observed to make long distance swims (Monnett and Gleason 2006), could increase the risk further.

Some SB bears remain near the coast during periods of the open water season. My research identified one area of use during both summer and autumn to be concentrated along the Barrier Islands of Alaska. This is of importance because an increase in the duration of open water will force bears using this region to either spend more time on land or alternatively risk the long distance swim to the pack ice.

In Chapter 3 I examined polar bear response to decreased sea ice habitat during summer (June – September) using utilization distributions to evaluate how distributions change in relation to sea ice cover. In response to annual patterns of sea ice melt, SB bears either travelled to remain along the edge of the pack ice as it retreats north or moved to land, however, there are also few bears who moved between the mainland and pack ice. Bears that remained on sea ice during the open water period utilized the edge of the pack ice, and most notably made use of the region west of Banks Island where the ice edge was nearest to the shallow waters of the continental shelf.

My research indicates the proportion of bears using land areas in Alaska are greater than previously documented, potentially indicative of increased use of land coinciding with reduced sea ice extent and increased open water. For polar bears that utilize land during the ice free period, earlier break-ups and later freezeups mean a longer time on land. Although some bears consume terrestrial foods while on land including vegetation (Derocher et al. 1993), reindeer (Rangifer tarandus) (Derocher et al. 2000), seabird nesting colonies (Donaldson et al. 1995, Iverson et al. 2014), fish (Dyck and Romberg 2007), gulls, nesting geese (Abraham et al. 1977, Madsen et al. 1989, Smith and Hill 1996, Stempniewicz 2006), and little auks (Alle alle) (Stempniewicz 1993), the ability of these foods to provide significant energy is believed to be low (Ramsay and Hobson 1991, Derocher et al. 2004, Rode et al. 2010b). There is, however, evidence that demand on terrestrial foods is increasing, and in some situations affecting predator-prey relationships (Iverson et al. 2014). The consequence of a longer period on land with limited energetic input will likely have reproductive consequences as breeding female polar bears require minimum fat stores to survive and produce viable offspring (Derocher et al. 1992). Furthermore, energetic modelling suggests a high proportion of pregnant females will fail to reproduce and mean litter size will decrease with an increasing open water period (Molnár et al. 2011).

My research indicates that polar bear use of land was concentrated at Barter Island and along the nearshore islands between Kaktovik and Prudhoe Bay. Within this region are two noted whale bonepiles, one at Barter Island (located approximately 2 km from the community of Kaktovik) and a second at Cross Island (a barrier island approx 20 km north of Prudhoe Bay). A third bone pile exists further west at Barrow, Alaska. Subsistence harvest of bowhead whales (Balaena mysticetus) during autumn has increased since the early 1990s (Bacon et al. 2010), and polar bears have learned to make use of the remains of harvested whales which are left on land. Non-invasive genetic sampling indicated an estimated 228 bears visited the Barrow bone pile alone between November 2010 – February 2011; equivalent to approximately 15% of the SB population (Herreman and Peacock 2013). Bowhead whales composed up to 26% of winter diets for SB bears (Bentzen et al. 2007). On September 13, 2012 a record 80 bears were counted in one day near Kaktovik, likely drawn in by a recent whale harvest (Anderson 2012). Although scavenging on the remains of bowhead whales may be a viable option for polar bears, it may also prove challenging in years when no whales are harvested. An abundance of food stressed bears on land and near communities have potential to increase human-bear conflicts (Miller et al. 2006, Towns et al. 2009).

Congregations of wildlife at bone piles may furthermore lead to increased transmission of disease among polar bears and other terrestrial species that utilize remains (foxes (*Vulpes* spp.), wolves (*Canis lupus*), avian species) (Miller et al. 2006). It has been hypothesized that climate change may lead to emerging

diseases in Arctic wildlife (Bradley et al. 2005). Increasing temperatures could positively affect bacteria and parasites by speeding development, and increasing survival in temperature limited species (Bradley et al. 2005). Rising temperatures may also facilitate species to expand their ranges and potentially transport pathogens to Arctic regions (i.e., ticks, mosquitoes, grizzly bears (*U. arctos*)) (Bradley et al. 2005).

Wild polar bears have few parasites and diseases but have *Trichinella* sp. (Rodgers and Rodgers 1977, Forbes 2000), rabies (Taylor et al. 1991), antibodies from Toxoplasma gondii (Jensen et al. 2010, Elmore et al. 2012), canine adenovirus and morbilliviruses (Philippa et al. 2004, Kirk et al. 2010b), and Brucella (Rah et al. 2005, O'Hara et al. 2010). Climate change will likely expose polar bears to additional pathogens (Derocher et al. 2004, Kutz et al. 2005). Increased scavenging for food while on land may furthermore expose bears to a variety of diseases; the SB population is currently being examined to assess the prevalence of Brucella spp., Coxiella burnetii, and Toxoplasma gondii due to this concern (Atwood et al. 2014). To date research suggests that *Toxoplasma gondii* in some populations has already doubled over the last decade (Jensen et al. 2010, Kirk et al. 2010a), with suggested causes related to increased survivorship of oocysts, the presence of a more diverse assortment of migratory bird species, and increased human traffic (Jensen et al. 2010), all of which are related to climate changes. The prevalence of Brucella has also increased (Rah et al. 2005, O'Hara et al. 2010) in the SB population, and the exposure appears to be from a terrestrial source (O'Hara et al. 2010). Furthermore, recent research suggests polar bears

have low genetic diversity in a major histocompatibility complex loci (part of the immune system) (Weber et al. 2013). Though likely a result of having low exposure to low levels of disease and parasites, this finding may have negative implications if bears are exposed to new pathogens (Weber et al. 2013).

Climate change may furthermore affect polar bears' ability to locate mates and find a suitable quality of sea ice to den on (Derocher et al. 2004, Fischbach et al. 2007). As pack ice becomes more fragmented and open water increases during the mating period, males may have difficulty finding contiguous tracks from which they locate mates (Derocher et al. 2004). Furthermore, modeling indicates that mating success could decline if searching success declines faster than habitat area, however, it could increase under the opposite conditions (Molnár et al. 2010), the latter of which may occur if bear density increases during the mating season (Derocher et al. 2004). There has also been a shift from denning on sea ice to denning on land in the southern Beaufort region (Amstrup and Gardner 1994, Fischbach et al. 2007). The change is believed to be in response to a decrease of stable old ice, an increase in unconsolidated ice, and a lengthening of the open water season (Fischbach et al. 2007).

The combination of a warming Arctic and increased demand for resources makes resource extraction more feasible, and will likely lead to an increase in anthropogenic development in Arctic regions inhabited by polar bears (Loeng et al. 2005). The Beaufort Sea region is expected to experience an increase in shipping as changes to sea ice cover and duration in the region facilitate the moving of extracted resources from hydrocarbon development (Prowse et al.

2009). Previously, resource development was limited to shallow waters, but is now open to the deep offshore (Fidler and Noble 2013), expanding the area of potential development and potentially increasing the risk (Boesch 2012). Although no large oils spills have occurred in the Beaufort Sea there is a concern and growing interest in understanding the potential impacts of resource development on Arctic species (Aboriginal Affairs and Northern Development Canada 2012). Oil is toxic to marine mammals (Geraci and St. Aubin 1990, NRC 2003); laboratory experiments which involved coating polar bears with crude oil caused bears to continually groom and resulted in liver and kidney damage causing mortality (Øritsland et al. 1981). Polar bears habitat preferences (along open cracks and the floe edge), hunting techniques (which involve grasping prey in water), and movement patterns suggest polar bears are particularly vulnerable to oil contamination (Stirling 1990). Presence of anthropogenic activity in Arctic regions may furthermore impact bears. Permanent offshore drill rigs may create cracks downstream, and provide open water where seals are more abundant, and thus attract polar bears to the region (Stirling 1988). Curiosity or increased hunting potential may attract bears to anthropogenic structures, leading to increased human-bear conflict that may be fatal (Stirling 1988). Furthermore, bears' curiosity may lead them to ingest dangerous substances. For example, a polar bear died on the North Slope of Alaska after ingesting dye used to mark airstrips and roads during winter (Amstrup et al. 1989).

One of the most prominent impacts of a changing Arctic climate is anticipated to present through Arctic marine travel. Sea ice duration is projected to be 10

days shorter by 2020 and up to 30 days shorter by 2080 (Loeng et al. 2005). Transit though the Northwest Passage has become more frequent and is associated with decreasing concentration and increasing variability in Arctic sea ice (Headland 2010). Summer shipping through the Northwest Passage and cruiseship traffic is expected to increase (Jeffries et al. 2013). Increased traffic in the Arctic may impact marine mammals through sound pollution, boat strikes, increased interactions with humans, and overall increased disturbance to marine mammal habitat (Burek et al. 2008, Hovelsrud et al. 2008).

An understanding of a species distribution in space and time is central to mitigating the impact of anthropogenic development. My research provides managers with insight regarding seasonal and monthly (summer) polar bear distribution during a period of low sea ice extent reflective of conditions in recent years (Stroeve et al. 2012a). Increased interest in oil and gas development in the Beaufort Sea and surrounding areas has lead to an increased interest in identifying the potential impact of oil spills and blowouts on various marine mammals including polar bears (F. Pokiak, Chair of Inuvialuit Game Council, pers. comm). Polar bear distributions from my research could assist in identifying oil spill impacts on this vulnerable species. Results from my thesis could also support the identification of critical habitat and be incorporated into discussions regarding population trends.

Research on polar bear movement patterns and space use to date has not been inclusive of subadults. My study is unique in that it provides detailed information regarding the distribution of adult females and subadults during a period of low

sea ice extent. Adult females tracked were of varying reproductive classes, thus, resulting distributions are inclusive of cubs-of-the-year, yearlings, and dependent two-year-olds. The distributions presented are, however, limited in that they do not include locations from adult males and thus do not represent this section of the population. It remains difficult to obtain detailed information regarding the movement of male polar bears. Researchers have attempted to track male bears through fixing transmitters to them in a variety of ways with limited success. A study in the Southern Beaufort tracked 7 adult male polar bears using transmitters surgically implanting on the midline of neck (Mulcahy and Garner 1999, Amstrup et al. 2001); the resulting mean duration of locations collected was 97 days (max 161 days) (Mulcahy and Garner 1999). More recently (2007-2011), ear transmitters were used to track adult male polar bears in the East Greenland and Baffin Bay populations; mean duration of transmitters varied from 49 to 115 days (Laidre et al. 2014). The most recent (2011 and 2013) attempts to track males bears have occurred in the Beaufort Sea using ear mount and glue on satellite telemetry tags, however, retention rates for transmitters deployed in 2011 were low, and ear transmitters may have furthermore caused ear damage (USFWS) 2014).

Although male polar bear distribution throughout the year remains largely unknown for all populations, there has been some identification of movement patterns and habitat use during spring and to a lesser extent summer. In the Southern Beaufort population net monthly geographic movements (distance from the first to last movement in a month), mean azimuths of net monthly movements,

and size of monthly activity area of male polar bears was comparable to that of females during April – September (Amstrup et al. 2001). In contrast, Laidre et al. (2014) found that during the breeding season adult females of both East Greenland and Baffin Bay populations had significantly more linear movements and significantly larger ranges than adult males. Laidre et al. (2014) hypothesized that female movements were reflective of searching for sparsely distributed prey, where as male movements were reflective of behaviour during the breeding season (the location of receptive females and subsequent restriction of movements during induced ovulation). Habitat use was not found to differ between sexes during May – June in either population (Laidre et al. 2014). These studies provide insight regarding how male and female polar bear movements/space use/habitat use compare during spring and early summer, however, comparability during the remainder of the year remains unknown.

Because polar bear habitat is closely associated with sea ice dynamics and characteristics, continued research regarding polar bear movement patterns and distribution will be required as sea ice conditions continue to change. Sea ice conditions vary regionally, therefore, a regional approach to analysis would be most suitable. Future research should include developing a seasonal Beaufort Sea polar bear resource selection function that incorporates habitat variables (e.g., snow, sea ice characteristics, bathymetry) to assess polar bear probability of use.

Perhaps one of the best sources of information regarding polar bear condition and habitat use comes from Traditional Ecological Knowledge (TEK) held by Inuvialuit and Inupiat who subsistence harvest SB bears. TEK gained through

extensive experience observing the environment over a long period and passed down through generations (Huntington 2000) can provide insight into species' movements, distribution, abundance, and condition, and how they have changed over time (Huntington et al. 1999, Lyver and Gunn 2004, Moller et al. 2004, Noongwook et al. 2007, Ramstad et al. 2007, Thornton and Scheer 2012, Parlee et al. 2014). Through their extensive experience on the land and observing the surrounding environment, TEK holders have the invaluable ability to observe initial signs of ecosystem change (i.e. food-web changes) before thresholds are met and detected by scientific studies (Huntington 2011). TEK may also provide insight into factors contributing to phenomenon observed (Carter and Nielsen 2011) and has the ability to identify important relationships, some of which may not be intuitive to researchers (Huntington et al. 1999, Huntington 2011, Polfus et al. 2014). As climate continues to change and species respond accordingly, harvesters will be the first to observe changes in this dynamic environment (Nichols et al. 2004). Scientists and resource managers will benefit from working with local subsistence hunters to better understand how polar bears respond to changing conditions and how to best mitigate anthropogenic impacts. The optimal approach to monitoring species should integrate both science and TEK as they are complementary; traditional knowledge provides temporal depth, where as science can identify changes outside areas of harvest (Moller et al. 2004).

The outcome of SB polar bears may in part depend on quality habitat that exists beyond the SB population boundaries. Current summer and autumn polar bear distributions are already beyond IUCN defined population boundaries. It is likely that as sea ice conditions in the southern Beaufort Sea continue to decline there will be a shift in polar bear distribution to regions such as the northern Beaufort Sea west of the Arctic Archipelago or to the Chukchi Sea where conditions appear less affected to date (Derocher et al. 2004, Stirling et al. 2011, Rode et al. 2014).

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