Polar Bear (*Ursus maritimus*) Habitat, Space Use, and Movements in a Seasonal Sea Ice Ecoregion

by

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Abstract

Polar bears (*Ursus maritimus*) are sea ice habitat specialists and climate change has affected sea ice throughout this species' circumpolar range. The annual phenological cycle of sea ice growth and decay is a strong influence on polar bear distribution and ecology. Study of the habitat selection, movements and spatial ecology of polar bears in the seasonal sea ice ecoregion has been limited but this is where the most rapid loss of ice has occurred. In this thesis, to study movements and space use, I used satellite telemetry to collect year round (2007-2011) location data of female polar bears and ice-free season location data of male polar bears, and, satellite imagery to analyze sea ice habitat. I began with an overall assessment of the state of sea ice habitat in Foxe Basin. Using microwave satellite imagery (25 x 25 km^2 resolution) sea ice concentration maps were classified into four habitat quality categories and the trends (1979-2008) in fragmentation patch metrics analyzed. I found that the amount of preferred sea ice habitat declined in autumn and spring, sea ice season length decreased, and habitat fragmentation increased. The observed trends may affect polar bear movement patterns, energetics, and ultimately population trends. When on the sea ice, female polar bears were distributed in three spatial clusters that broadly coincided with the three marine water bodies, Foxe Basin, Hudson Strait and Hudson Bay. Differences in movement metrics (home range, movement rates, time on ice) were observed between clusters that may reflect sea ice habitat conditions and ocean productivity. Annual and seasonal home range fidelity were observed and the bears used two movement patterns: on-ice range residency and annual migration. High resolution (150 x 150 m) synthetic aperture radar (SAR) was tested as an information source to examine sea ice habitat structure, as described by floes and leads that were available to female polar bears during their daily movements. I found that the fine scale ice floe and lead patch density were the most important sea ice characteristics for bears when foraging on sea ice. Standard important broad scale variables, ice concentration, bathymetry and distance to land were not in the top resource selection models. I examined the terrestrial movement patterns and behaviour of female and male polar bears during the annual period of minimum ice cover. The bears remained near the coast but were segregated by sex and reproductive status. All bears moved extensively and swimming was a regular behaviour. I propose an explanatory mechanistic model for terrestrial movement patterns and behaviours during the ice free season based on external (abiotic and biotic) and internal (sex, reproductive status) factors. My research provides new analytical approaches for monitoring sea ice habitat and study of the functional relationships between bears, their prey and the sea ice ecosystem.

Preface

This thesis is an original work by Vicki Ann Marie Sahanatien. Field methods were in accordance with the Canadian Council on Animal Care guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee (Permit #A5070-01). The polar bear location data for this thesis was collected in collaboration with the Nunavut Department of Environment as part of the Foxe Basin polar bear study.

Chapter 2 of this thesis was published as V. Sahanatien and A.E. Derocher, "Monitoring sea ice habitat fragmentation for polar bear conservation," Animal Conservation 15:397-406. I was responsible for concept and study design, accessing the data, analysis and manuscript composition. A.E. Derocher contributed to the manuscript composition. Chapter 3 of this thesis was published as V. Sahanatien, L. Peacock, and A. E. Derocher, "Population substructure and space use of Foxe Basin polar bears," Ecology and Evolution 14:2851-2864. I was responsible for concept and study design, data collection and analysis, and manuscript composition. L. Peacock and A. E. Derocher contributed to data collection and manuscript composition. J. Nagy contributed to data analysis but was unable to participate in manuscript composition due to health reasons.

To my father and grandfather.
Sorry I did not finish before you departed.

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It is wonderful to be able to thank the most important person of my academic life: a polar bear sized hug to my supervisor, Dr. Andrew E. Derocher. AED without hesitation took me on, a some-what aged and sometimes head-strong graduate student. I am extremely grateful for his patience, as I took my rather indirect path to completing my Ph.D. Looking back it is incredible how much I have learned and grown during my apprenticeship with AED. Thank-you for deploying the first set of satellite collars when I was down with pneumonia. Getting that first batch out was critical to the overall Foxe Basin study and you did it in rather difficult circumstances. I arrived at the University of Alberta with many years of Arctic field research experience under my belt and the desire to learn more about doing science. I depart as a better scientist, with greater understanding of and love for the Arctic.

A very special thanks to Elizabeth (Lily) Peacock, past Nunavut Polar Bear Biologist, who played an essential role in my collaboration with the Nunavut Department of Environment and deployed the Year 2 and 3 sets of satellite collars. Working along-side with Lily in the field was a joy and one of the most awesome learning experiences of my life. Lily also reviewed and provided insightful comments on Chapters 3 and 5.

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Chapter 1

1 Introduction

1.1 Sea Ice as Habitat

Each winter sea ice forms and covers the oceans' surfaces in the sub-Arctic, Arctic and Antarctic. At its maximum extent, in March sea ice covers up to 15,700,000 km² in the northern hemisphere and in September 18,800,000 km² in the southern hemisphere (Comiso 2003). The sea ice ecosystem dwarves most others (Arrigo 2014) except the boreal forest (16,600,000 km²). Sea ice plays a crucial role in regulating the earth's climate system by limiting heat transfer from the ocean to the lower atmosphere. The ice is also protective layer for the oceans, creating a stable marine environment by limiting heat loss in winter and reflecting back ultra-violet radiation in summer. Sea ice is not a barrier but it is porous, with gaseous and energy flux through it from the ocean to atmosphere (Vancoppenolle et al. 2013). Sunlight penetrates through sea ice, providing energy to bacteria, phytoplankton, and macroalgea for primary production.

Sea ice is replete with life, supporting unique ecosystems with specialized species (Kovacs et al. 2011, Post et al. 2013) (Fig. 1.2). Pagophilic species have evolved to use sea ice for reproduction, foraging, resting, and protection from predators (Tynan and DeMaster 1997, Gilg et al. 2012). The top surface of the ice is a platform for marine and terrestrial mammal movement, dispersal, migration, foraging, and reproduction (Laidre et al. 2008, Post et al. 2013). Within the ice are brine channels that house a diverse community of small organisms (Arrigo 2014), discontinuities created by rafting of ice (Sturm et al. 2006), and tunnels excavated by seals to the surface for breathing (Smith and Hammill 1981). The sea ice bottom is porous, reticulated, undulating and keeled; on and under this 3-dimensional surface primary productivity occurs, providing energy to zooplankton, invertebrate and vertebrate grazers, and eventually to the entire sea ice ecosystem (Bluhm and Gradinger 2008, Arrigo 2014).

Sea ice dependent species are categorized as ice obligate (some or all life history stages requires sea ice habitat) and ice associated (adapted to sea ice habitat but it is not essential for life) (Ainley et al. 2003, Bhatt et al. 2014); both categories include microorganisms, invertebrates, fish, birds and mammals. Ice obligate, upper trophic level marine mammals, birds, and fish are thought to be sentinels of the effects of climate change on sea ice habitat and ecosystems (Moore and Huntington 2008, Bhatt et al. 2014, Moore and Stabeno 2015). Sea ice habitat use and selection has been studied in a diversity of sentinel Arctic species, for example, ringed seals (*Pusa hispida*) (Crawford et al. 2012), walrus (*Odobenus rosmarus*) (Jay et al. 2014), bowhead whale (*Balaena mysticetus*) (Ferguson et al. 2010), and polar bears (*Ursus maritimus*) (Laidre et al. 2015a).

1.2 Sea Ice Habitat and Climate Change

It is possible that the Arctic will be mostly ice free during summer as early as 2020 and if not then likely by 2050 (Stroeve et al. 2007, Overland and Wang 2013). The primary cause of sea ice loss is greenhouse gas emissions that cause increased sea surface temperatures and ocean water temperatures that affect the development and retention of sea ice (Vaughn et al. 2013). More open water during spring and summer enhances the positive ice-albedo feedback; the low albedo of the dark ocean water absorbs the solar energy, and the additional heat stored in the ocean increases melting of remaining sea ice and delays the onset of freeze-up in fall (Stroeve et al. 2012).

Currently in the Arctic, at high latitudes, some ice remains throughout the summer and grows again the following winter and, is called multi-year ice. There has been rapid decline in multi-year sea ice during the past 10 years (Kwok et al. 2009, Stroeve et al. 2012, Meier et al. 2014). Ice that completely melts each year is called seasonal, annual, or first-year ice sea ice and now constitutes the dominant form of Arctic ice over winter and in spring (Stroeve et al. 2012). Climate change has effected seasonal sea ice by reducing its extent, thickness, duration of coverage, and timing of phenological events (Stroeve et al. 2012, Vaughn et al. 2013).

Changes in sea ice are accompanied by ecosystem changes that span all trophic levels. Earlier onset of the annual phytoplankton bloom has caused mismatched availability of prey for some species, increased marine productivity has increased the quality of available sea ice habitat for low and high trophic consumers, northward range expansions of subarctic and temperate species, diets change as the abundance of prey species shift, changes in species assemblages and community structure as some benthic systems become more pelagic (Gaston et al. 2005, Grebmeier et al. 2006, Higdon and Ferguson 2009, Kahru et al. 2011, Wassmann et al. 2011, Post et al. 2013, Bhatt et al. 2014, Arrigo and van Dijken 2015). Loss of sea ice habitat has already affected ice dependent species and the magnitude of effects on body condition, reproduction, abundance and distribution varies by region (Laidre et al. 2008, Gilg et al. 2012, Stirling and Derocher 2012, Post et al. 2013, Bhatt et al. 2014, Rode et al. 2014b, Crawford et al. 2015, Harwood et al. 2015). Cumulatively, such changes may result in major ecosystem reorganization that reach to the top of the food web. For example, killer whales (*Orcinus orca*) have expanded their range northward as sea ice has retreated (Higdon and Ferguson 2009, Matthews et al. 2011).

1.3 Polar Bear Sea Ice Habitat

Polar bears are sea ice specialists and their circumpolar range is broadly coincident with the winter extent of sea ice (DeMaster and Stirling 1981, Amstrup 2003). Polar bears use both multi-year and seasonal sea ice (Fig. 1.1), and are found in greater numbers on the sea ice over the continental shelves and shallow (<300 m) basins where their prey, mainly ringed seals and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980), occur in higher density compared to over the deep waters of the Arctic Basin (Burns 1970, Frost et al. 2004) Nineteen world-wide populations of polar bears have been delineated based on geographic fidelity and genetic relatedness (Obbard et al. 2010)

Four ecoregion of polar bear sea ice habitat have been identified (divergent, convergent, archipelago, and seasonal) based on ice composition, duration, ocean circulation, and how bears respond to sea ice dynamics (Amstrup et al. 2008). Much of our understanding of polar bear sea ice spatial ecology, movements and habitat selection has come from studies where there is a mixture of multi-year and annual sea ice, and polar bears have year round access to ice habitat (Schweinsburg et al. 1982, Messier et al. 1992, Ferguson et al. 1999, Amstrup et al. 2000, Mauritzen et al. 2002, Durner et al. 2009, Wilson et al. 2014, Laidre et al. 2015a). These are the divergent, convergent and archipelago ecoregions, which include 14 of the 19 polar bear populations in the circumpolar Arctic. The fourth ecoregion, seasonal ice, has received less attention and includes five populations of bears that must retreat to land each summer when sea ice melts (Ferguson et al. 2001, Parks et al. 2006, Obbard and Middel 2012, McCall et al. 2015).

Polar bears move and forage on the sea ice year round unless in a maternity den (November-April) (Ramsay and Stirling 1988) or there is no available ice. On an annual basis, female bears have been recorded to move from 574 km to 4,935 km and home range sizes vary from 185 km^2 to 596,800 km^2 (Amstrup et al. 2000, Mauritzen et al. 2001, Wiig et al. 2003, Parks et al. 2006, McCall et al. 2015). Polar bear movements and space use appears to be tied to the regional sea ice habitat types and conditions. Home range size is variable within and between populations, and is reflective of habitat availability, habitat quality, geographic features and individual movement behaviour (Ferguson et al. 1999). Two patterns have been observed: bears that prefer the near shore, fiords and fast ice that tend to have smaller home range sizes and bears that prefer the off shore, pelagic and active floe ice with larger home range (Amstrup et al. 2000, Mauritzen et al. 2001). Bears in many populations show fidelity to denning and foraging areas within their ranges (Schweinsburg and Lee 1982, Derocher and Stirling 1990a, Born et al. 1997, Amstrup et al. 2000, Zeyl et al. 2010, Lone et al. 2012, Sahanatien et al. 2015). There is little year round information about male polar bear movements because of the difficultly attaching satellite collars but there has been some success implanting transmitters and attaching ear tags (Amstrup et al. 2001, Laidre et al. 2012). Observations to date have found that male bear movements are generally similar to females except during the spring mating season (Laidre et al. 2012).

Polar bear habitat selection studies have found that sea ice concentration is the most important factor, followed by ice type (i.e., fast, pack, annual, multiyear), bathymetry, distance to ice edge, and distance to land (Arthur et al. 1996, Mauritzen et al. 2003a, Durner et al. 2009, Freitas et al. 2012, Laidre et al. 2015a). There is less understanding of how ice structure (e.g., floes, leads, surface roughness) influences polar bear movements but it has been identified as important for both bears and their primary prey, ringed seals (Smith 1980, Hammill and Smith 1989, Kingsley and Stirling 1991, Stirling et al. 1993, Stirling 1997, Durner et al. 2004, Pilfold et al. 2014a). Bears show seasonal differences in habitat use. In summer and autumn when sea ice is at its minimum bears select the highest concentration of what is available (Ferguson et al. 2000, Wilson et al. 2014). In winter and spring when sea ice is ubiquitous there is strong selection for ~ 85% ice concentration (Durner et al. 2009, Pilfold et al. 2014a) suggesting that the mix of ice and open water creates high quality habitat.

Like many species, habitat loss is the main threat to the long term survival of polar bears and the origin of the threat is global greenhouse gas emissions (Stirling and Derocher 1993, Schipper et al. 2008, Stirling and Derocher 2012). Research to collect empirical data for modeling future polar bear sea ice habitat and identifying habitat thresholds for population decline are ongoing (Durner et al. 2009, Molnár et al. 2010, Castro de la Guardia et al. 2013, Hamilton et al. 2013). These efforts are important for alerting the public and managers that mitigation and adaptation strategies are needed (Derocher et al. 2013).

1.4 Dissertation Outline

Habitat loss is recognized as the primary cause of species endangerment and fragmentation of remaining habitat can further reduce the potential for species survival (Lindenmayer and Fischer 2006). Sea ice habitat has been declining and changing throughout the polar bear's range (Stirling and Derocher 2012) but there have been few regional assessments of polar bear sea ice habitat (Stirling and Parkinson 2006). In Chapter 2, I used landscape fragmentation analysis to assess trends in available polar bear sea ice habitat and habitat fragmentation (1979-2008) in Foxe Basin, Hudson Strait and Hudson Bay, Canada. The observed trends were interpreted in relation to potential effects on polar bear movement patterns, energetics and population.

In Chapter 3, I investigated within population spatial structure and movements of polar bears and the influence of sea ice habitat on movement patterns. Population delineation is an essential step for managing the harvest of wildlife (Thomas and Kunin 1999). Polar bear management units are large in area and intra-population spatial structure has been observed that could compromise managing total allowable harvest on a population wide basis (Rode et al. 2012, Peacock et al. 2013). This was the first study to examine the spatial ecology of the Foxe Basin polar bear management unit of Nunavut, Canada. These new findings provide baseline information for harvest management.

In Chapter 4, I explored fine scale sea ice habitat selection of polar bears in Foxe Basin, Nunavut, Canada. I tested high resolution (150 m) synthetic aperture radar (SAR) satellite imagery as a base for mapping and quantifying sea ice structure. I focused down to the sea ice habitat characteristics that a polar bear would experience during its daily movements. Foxe Basin polar bears primarily use active floe ice, which moves on a daily time frame with currents, tides and wind. As such, the composition and configuration of available sea ice habitat changes as a bear moves across the sea icescape. Discrete choice habitat selection modeling (Arthur et al. 1996, McDonald et al. 2006) was used to identify the sea ice characteristics polar bears prefer. My results provide an analytical approach for research into the functional relationships between bears, their prey, and the sea ice ecosystem.

Each summer, in many parts of the Arctic, polar bears are forced on land when sea ice habitat melts and becomes unavailable (Derocher and Stirling 1990a). As the ice-free period lengthens with climate warming, changes in bear terrestrial distribution are expected (Towns et al. 2009, Vongraven et al. 2012). In Chapter 5, I examined the terrestrial movement patterns of polar bears during the ice-free season of Foxe Basin, Nunavut, Canada. I used satellite telemetry to compare female and male bear distribution, movement paths and metrics, swimming behaviour and fidelity to terrestrial range. I propose explanatory hypotheses based on external (abiotic and biotic) and internal (sex, reproductive status) factors for terrestrial movement patterns and behaviours during the ice-free season.

In Chapter 6, I consider my findings in light of newly published research on Foxe Basin polar bears, as they apply to polar bears in their circumpolar range, and discuss some information gaps and research needs for Foxe Basin region.

Figure 1.1 Polar bear on sea ice habitat, Foxe Basin, Nunavut, Canada (April 2009).

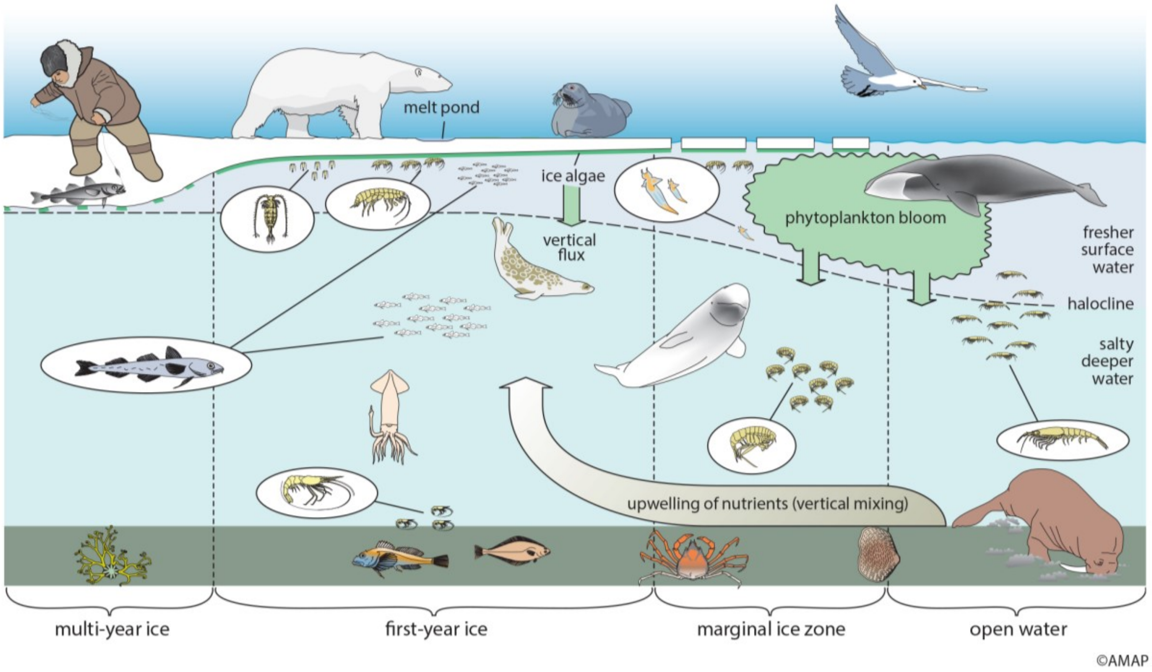

Figure 1.2 Sea ice ecosystem: biodiversity above and under the ice. (AMAP, 2012. Arctic Climate Issues 2011: Changes in Arctic Snow, Water, Ice and Permafrost. SWIPA 2011 Overview Report. Arctic Monitoring and Assessment Program (AMAP), Oslo, Norway).

Chapter 2[‡]

2 Monitoring sea ice habitat fragmentation for polar bear conservation

2.1 Introduction

Habitat loss and fragmentation have been identified as the greatest conservation threats to carnivores (Sunquist and Sunquist 2001, Crooks 2002) particularly for habitat specialists (Fischer and Lindenmayer 2007) such as the polar bear (*Ursus maritimus* Phipps, 1774). Anthropogenic land use activities such as forestry, agriculture, and urbanization have been the primary causes of habitat destruction (Schipper et al. 2008) but climate change is emerging as an equally important driver of habitat change in terrestrial and marine ecosystems (Grebmeier et al. 2006, Parmesan 2006). Sea ice provides a spatially and temporally dynamic habitat for a diversity of species and is integral to Arctic marine food webs (Bluhm and Gradinger 2008). Life history patterns of Arctic marine species are tied to sea ice phenology and structural characteristics (Gaston et al. 2005, Moore and Huntington 2008). Polar amplification of climate change in the Arctic continues to cause rapid modification and loss of sea ice (Markus et al. 2009) and is considered a threat to polar bears and their prey (Derocher et al. 2004, Laidre et al. 2008).

Polar bear demographic and habitat research has focused on the effects of changing spring sea ice break-up patterns (Stirling et al. 1999, Stirling and Parkinson 2006, Regehr et al. 2007) as well as habitat selection and loss in higher

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latitude regions (Ferguson et al. 2000, Mauritzen et al. 2003a, Durner et al. 2009). Sea ice at lower latitudes (< 70º N), however, is changing faster than higher latitudes (Markus et al. 2009) and may have greater negative effects on polar bear populations in southern regions (Amstrup et al. 2008). Climate change projections show disproportionate impacts on polar bear sea ice habitat in the seasonal ice regions of the lower latitudes (Amstrup et al. 2008), thus I anticipate increasing habitat fragmentation and declining habitat quality; changes that accompany habitat loss (Andren 1994, Lindenmayer and Fischer 2006, Mortelliti et al. 2010). Sea ice habitat fragmentation is expected to affect polar bear life history by altering movement patterns, mating ecology, and prey availability (Derocher et al. 2004, Molnár et al. 2007) yet no studies have addressed fragmentation.

Landscape and habitat fragmentation analyses have been used to monitor and quantify habitat conversion, degradation, and loss (Coops et al. 2010, Mizerek et al. 2011), to select wildlife movement corridors, species re-introduction sites, and protected areas (Hostetler et al. 2009), and to identify important regions for protecting biodiversity (Crooks et al. 2011). Fragmentation metrics describe the composition and configuration of habitat patches within a landscape (McGarigal and Marks 1995). Habitat patch quality is important in determining species occupancy and persistence (Visconti and Elkin 2009, Schooley and Branch 2011). Habitat fragmentation influences the habitat loss thresholds for species survival (Hanski and Ovaskainen 2002, Swift and Hannon 2010). Polar bear sea ice habitat is changing quickly (Stirling and Parkinson 2006) making it important to introduce rapid assessment tools for monitoring habitat change.

Polar bear conservation efforts have emphasized hunting bans and harvest management (Peacock et al. 2011). Regulated polar bear hunting is permitted in Canada, Greenland, and Alaska, with the majority of the bears being taken in Canada (Obbard et al. 2010). Canadian polar bear harvest management is based on a precautionary approach that relies on the best available information on population size and trend (Peacock et al. 2011), yet habitat monitoring is not being used in harvest management. A total allowable harvest is calculated for each population, male-biased hunting is encouraged, and the harvest is monitored by collecting biological and morphometric data on killed bears (Taylor et al. 2008). Harvest quotas do not include the influence of changing sea ice habitat conditions on polar bear populations, even though population level changes in reproduction, survival and population size related to sea ice conditions have been documented (Stirling et al. 1999, Regehr et al. 2007, Regehr et al. 2010, Rode et al. 2010a). However, region and population specific sea ice habitat monitoring is possible and habitat metrics can be included in polar bear harvest plans to augment precautionary measures associated with setting harvest levels.

In this study I quantified temporal and spatial trends in polar bear sea ice habitat in three lower latitude Arctic regions of Canada using habitat fragmentation metrics. Further I propose a new approach that uses contemporary estimates of sea ice habitat for input into harvest management.

2.2 Materials and methods

The study area covers 1,241,250 km² of ocean surface and includes three marine regions: Foxe Basin (203,750 km²), Hudson Strait (196,875 km²), and Hudson Bay (840,625 km²) (Fig. 2.1). I delineated each region using physical (coastline, bathymetry) and oceanographic (circulation, currents) characteristics. These are shallow (predominantly less than 200 metres deep), productive mid- to low-latitude Arctic seas that undergo an annual sea ice phenological cycle from ice-free to almost total ice cover. Overall duration of ice cover in the area has been declining, with delayed freeze-up and earlier break-up dates correlated with increasing surface air temperatures (Moore 2006, Stirling and Parkinson 2006, Hochheim and Barber 2010, Galbraith and Larouche 2011).

Monthly mean sea ice concentration (percent areal coverage of sea ice) data for 1979 – 2008 were obtained from the National Snow and Ice Data Center website (http://nsidc.org/). The data were collected by the Nimbus-7 Scanning Multi-channel Microwave Radiometer (SMMR) and Defense Meteorological Satellite Program (DMSP) -F8, -F11 and -F13 Special Sensor Microwave/Imager (SSM/I) and processed at a grid cell of 25 x 25 kilometres (Cavalieri et al. 1996). Each grid cell was attributed percent ice concentration between 0-100%. The temporal and spatial scales of the data are appropriate for quantifying regional trends in polar bear habitat because satellite collared polar bears can move 25 kilometres in a day and in a year traverse the extent of the study area (Amstrup et al. 2000, Parks et al. 2006).

Ice concentration data were imported into ArcMap 9.3 (ESRI, Redlands, CA, USA) as raster layers. Each monthly layer was classified into four categories reflecting a habitat type and relative quality: non-habitat (<30% ice), poor (31-60% ice or very open ice), good (61-85% ice or open ice), and best (> 85% ice or closed ice) (Fig. 2.2). Our sea ice habitat classes were adapted from known polar bear habitat selection and preferences (Ferguson et al. 2000, Mauritzen et al. 2003a, Durner et al. 2009), the sea ice habitat used by Foxe Basin polar bears, and the threshold value of 50% sea ice concentration used in population trend research (Stirling et al. 1999, Regehr et al. 2010). I acknowledge that using habitat structure as a proxy of habitat quality is not ideal (Johnson 2007) but proxies can work if there are no available species specific habitat fitness measures (e.g. survival, reproduction) (Crooks et al. 2011, Mortelliti et al. 2011), as is the case for polar bears. The classified sea ice habitat maps were exported as ASCII grid files for fragmentation analysis.

I used landscape fragmentation analysis to examine polar bear habitat trends over 30 years (1979-2008). FRAGSTATS v3.3 (McGarigal et al. 2002) was used to compute habitat patch based fragmentation metrics for each month. Patches were identified as adjacent grid cells of the same habitat class, where, the smallest patch size is one grid cell and largest patch composed of all grid cells in the region. Fragmentation metrics describe the composition and configuration of habitat patches within a landscape or in our case, a sea icescape. I used three habitat metrics to explore changes in icescape composition: PLAND, the proportional (%) area of each habitat class within each region; AREA_AM, the area weighted mean habitat patch size (km^2) to provide insight into how habitat loss is fracturing the icescape; and NP, the summed number of habitat patches as a measure of changing icescape habitat heterogeneity. Sea ice freeze-up and break-up patterns precluded use of FRAGSTATS configuration metrics such as proximity and contagion because habitat patches are spatially correlated: during freeze-up ice grows from the coastlines to the centre of each water body then reversing direction during the melt period and break-up.

The timing of sea ice phenological events was determined by binning good and best habitat PLAND into a new category called preferred habitat (i.e., ice cover >61%). Freeze-up month was identified when there was >30% PLAND of preferred habitat and break-up month when the PLAND of preferred habitat <30%, for seven years within a ten year moving window. SPSS 18 (IBM, Somers, NY, USA) was used to evaluate the fragmentation metric trends (least-squares linear regression).

2.3 Results

From 1979 to 2008, the Foxe Basin ice season declined from nine to seven months. Before 1994, break-up occurred in August as the preferred habitat PLAND in July was generally higher than our defined 30% threshold (Fig. 2.3a). After 1994, preferred habitat was usually < 30%, with a low of 6% in 2005. Freeze-up was delayed from November to December with the amount of preferred habitat in November becoming less than 30% during most years after 1994 (Fig. 2.3b). The rate of change of best and good habitat during July and November was negative, ranging from -0.5%/yr to -1.3%/yr (Table 2.1). Best habitat also declined in April - July, November and December, with the greatest loss in June (-1.2%/yr, Table 2.1). Best habitat was replaced by good habitat in April and December but in May - July and November best habitat was also replaced by poor and non-habitat (Table 2.1). Poor habitat began to appear in December as of 1998 (Fig. 2.3b).

The Hudson Strait ice season decreased from seven to five months with break-up advancing into June as of 1998 and freeze-up delayed to January after 1995 (Fig. 2.3c and 2.3d). Hudson Strait is the only region that showed loss of best habitat during the winter period, January to March, and loss of good habitat in December (Table 2.1). Best habitat also declined in April (-1.4%/yr) and May (-0.9%/yr) (Table 2.1) and was greatly reduced after 1994 in June and December (Fig. 2.3c and 2.3d). In May, best habitat was replaced by poor and non-habitat (Table 2.1). Good sea ice habitat declined at high rates in June (-1.4%/yr) and December (-1.5%/yr). Good habitat was no longer present in July after 2003 and in November after 1993 (Fig. 2.3c and 2.3d). In January, the first observation of poor habitat occurred in 2004 (Fig. 2.3d).

The Hudson Bay ice season remained at seven months with break-up in July and freeze-up occurring in December (Fig. 2.3e and 2.3f). But break-up showed signs of advancing to June with the preferred habitat break-up threshold of 30% exceeded five times in June between 1997 and 2008 (Fig. 2.3e). In addition, June preferred habitat trends were negative (best, -0.8%/yr and good, -1.0%/yr) and non-habitat increased (0.8%/yr) (Table 2.1). Hudson Bay showed high rates of best habitat loss in April (-1.0%/yr), May (-1.4%/yr) and December (-1.5%/yr) (Table 2.1). In November, good and poor habitats were replaced by non-habitat and poor habitat (Table 2.1, Fig. 2.3f).

In all regions from 1997-2008, there were generally negative trends in best habitat patch size (AREA_AM) in spring, and, positive trends in non-habitat patch size during break-up and autumn months; patch size trends were similar to the habitat loss (PLAND) trends. Foxe Basin best patch size trends were negative from April - July (-540 to -2867 km^2/yr), and in July (-1236 km^2/yr) and

November (-3112 km²/yr) good habitat patches size also declined (Table 2.2). Non-habitat patch size increased during June - August (239 to 2169 km²/yr), October (1495 km²/yr) and November (2439 km²/yr). Hudson Strait showed the most widespread declines in best habitat patch size: February - June (-1571 to 3239 km²/yr) and December (-1173 km²/yr). Good habitat patch size declined in June (-1656 km²/yr) and December (-2610 km²/yr) and increased in February - April (858 to 1978 km²/yr). Hudson Bay best patch size declined in April (-9381 km²/yr), May (-11727 km²/yr) and December (-12883 km²/yr); good patch size declined in June (-7776 km²/yr) and increased in April (5891 km²/yr), May (9626 km²/yr) and December (6615 km²/yr) (Table 2.2).

Number of patches (NP) trend from 1979 to 2008 was positive during winter and spring, negative during break-up and autumn, and Hudson Bay showed the highest rates of patch size change (Table 2.2). In all regions, most increases in number of patches occurred during months when best habitat patch size declined: in Foxe Basin from April - June (0.1 to 0.2 patch/year), in Hudson Strait from February - April (0.1 patch/year) and in Hudson Bay in April (0.2 patch/year) and May (0.3 patch/year) (Table 2.2). Increase in the number of patches is an indicator of increasing icescape heterogeneity, as large habitat patches break into smaller patches and become interspersed with other patch types. Conversely, as the number of patches decreases, the icescape becomes more homogeneous, with fewer but larger patches of a single habitat type. Negative trends in number of patches occurred when non-habitat patch size grew and increased in dominance: in Foxe Basin from June - October (-0.1 to -0.2 patch/year), in Hudson Strait in July (-0.2 patch/year) and November (-0.1 patch/year), and in Hudson Bay, with the exception of September, from June - November (-0.1 to -0.5 patch/year).

2.4 Discussion

Three sea ice habitat trends were found that may affect polar bear populations by altering movement patterns and affecting energetics: 1) changing sea ice phenology with earlier break-up and later freeze-up, 2) loss of preferred sea ice habitat in April-May (spring), and 3) increasing habitat fragmentation.

Net habitat loss, as expressed by the decline in the proportion of preferred (best and good) habitat and changes in sea ice phenology potentially reduce the on-ice foraging time and efficiency for polar bears. The spring to break-up period is critical for polar bears (Watts and Hansen 1987) because the bears are hyperphagic, feeding on vulnerable seal pups and moulting adult seals to recover the fat stores lost over-winter in preparation for the ice-free summer months and when prey is usually inaccessible (Stirling and Øritsland 1995, Derocher et al. 2004). The hyperphagic period is especially important for lactating females with high energy demands and pregnant females that need to store fat for over-winter maternal denning (Ramsay and Stirling 1988). Earlier break-up date has caused reduced caloric intake resulting in lower body condition, cub litter size, and cub survivorship in the Western Hudson Bay and Southern Beaufort Sea populations (Stirling et al. 1999, Regehr et al. 2007, Regehr et al. 2010, Rode et al. 2010a, Molnár et al. 2011). These effects have resulted in a measurable decline in the size of the Western Hudson Bay polar bear population (Regehr et al. 2007). Although a numerical response in the Southern Beaufort Sea population has not been demonstrated, changes in sea ice composition will likely produce a negative population trend (Hunter et al. 2010, Regehr et al. 2010, Rode et al. 2010a).

Regional icescape connectivity is important for polar bear populations because the bears move extensively on sea ice in search of prey and in spring during mating; female home ranges are large, up to 964,264 km² in high arctic, perennial sea ice regions (Mauritzen et al. 2002) and in our study area range from 8,470-311,646 km² (Parks et al. 2006). Female polar bears show fidelity to summer retreat and denning areas (Ramsay and Stirling 1990, Stirling et al.

1999) and to sea ice habitats (Mauritzen et al. 2001). Greater habitat fragmentation and longer ice-free seasons may disrupt their annual return and could alter population boundaries and gene flow (Derocher et al. 2004). Another more subtle affect resulting from greater habitat heterogeneity is reduced efficiency of males locating estrous females during the spring mating season resulting in reduced mating success (Molnár et al. 2007).

At the daily temporal scale, foraging energy costs for inter- and intra-habitat patch movements may add to the affects of prolonged fasting caused by shorter ice seasons. Our observations of declining best habitat patch size and rising icescape heterogeneity will increase inter-patch movements, and the frequency and distance of swimming events. Polar bears readily swim and are able to swim long distances between habitat patches but swimming has higher energetic costs than walking (Durner et al. 2011), and, can cause adult and cub mortality (Monnett and Gleason 2006, Durner et al. 2011). Cubs are particularly vulnerable to hypothermia (Blix and Lentfer 1979). Within days after den emergence, in March or April, cubs are exposed to variable sea ice habitat conditions as they begin their 2-3 year period of following their mother throughout her home range. The energy costs of intra-patch movement may increase as open ice habitats impose higher energetic costs and greater risks for polar bears than areas with higher ice concentrations (Mauritzen et al. 2003a, Mauritzen et al. 2003b). Intra-patch movements entail more and longer swimming events where lower quality habitat patches can consist of many small ice floes interspersed with open water (Fig. 2.2). Our results indicate that available habitat is composed of a greater proportion of lower quality sea ice for longer periods of each ice season since the mid-1990s.

Polar bear populations in the Canadian Arctic face the stresses of habitat loss and fragmentation as well as harvest. Sea ice habitat conditions are predicted to deteriorate throughout the range of polar bears (Durner et al. 2009, Amstrup et al. 2010) and the Canadian harvest, an integral part of arctic community culture and economy, will also continue (Peacock et al. 2011). With the habitat degradation and fragmentation that I observed in Foxe Basin, Hudson Strait and Hudson Bay, it should no longer be assumed that polar bear population parameters remain static between population inventories. I hypothesize that the polar bears of Foxe Basin and Hudson Strait regions, which are predominantly included in the Foxe Basin population, will show future reduced body condition and cub production in response to the documented changes in sea ice habitat, as have been observed in the Western Hudson Bay and Southern Hudson Bay populations (Stirling et al. 1999, Obbard et al. 2006, Regehr et al. 2007).

The polar bear is a candidate species to exhibit population lag effects and extinction debt. Highly mobile species, like polar bears, can show lag effects up to habitat loss thresholds of 70-80% (Andren 1994). Slow reproducing habitat specialists, like polar bears, are particularly prone to extinction debt (Lindenmayer and Fischer 2006). Harvest monitoring is unlikely to reveal population lag effects or extinction debt because polar bear harvest is adult- and male-biased (Derocher et al. 1997). The current polar bear population estimate interval of 15 years for most populations (Peacock et al. 2011) is inadequate to provide early detection of population decline. Habitat metric trend analyses have shown that habitat loss and fragmentation precede and are correlated with changes in species occurrence and abundance (Gu et al. 2002, Metzger et al. 2009). The effectiveness of this approach is increased if habitat fragmentation metrics are linked to biological attributes such as body condition, reproduction and prey abundance (Mortelliti et al. 2010). Trends in polar bear biological attributes have been correlated with sea ice phenology (break-up date) (Regehr et al. 2007, Rode et al. 2010a) but research is needed to link biological attributes and habitat fragmentation metrics. For our study area, this means combining the polar bear telemetry and capture datasets with sea ice habitat metrics. Ongoing monitoring of habitat loss and fragmentation can provide an early warning indicator for polar bear managers about vulnerable populations.

Microwave satellite earth observation data collection began in 1979, allowing sea ice habitat trends to be examined. Microwave imagery is available year round and its resolution is appropriate for monitoring polar bear sea ice habitat at regional or larger geographic scales. Finer scale resolution satellite imagery (e.g. AMSR-E, MODIS, SAR) is available but is limited in temporal and spatial coverage due to the timing of launch and decommission of satellites, satellite orbital path, and use of optical sensors that require sunlit, cloud-free conditions which are limited in Arctic regions. Our freeze-up and break-up trends are similar to those noted by others (Stirling and Parkinson 2006, Hochheim and Barber 2010, Galbraith and Larouche 2011) but extending the analyses to trends in habitat provides new insights into ongoing ecosystem dynamics. Our application of habitat fragmentation analysis using FRAGSTATS is robust and cost effective and has the potential to improve polar bear management and conservation.

Table 2.1 Polar bear sea ice habitat class area as proportion of icescape (PLAND) slope (%/yr) of linear regression trends over time, Foxe Basin, Hudson Strait and Hudson Bay, Canada (1979-2008).

	Foxe Basin				**Hudson Strait**				**Hudson Bay**			
	PLAND (%/yr)				PLAND (%/yr)				PLAND (%/yr)			
	[a] Non	Poor	Good	Best	Non	Poor	Good	Best	Non	Poor	Good	Best
January	~	~	nt	nt	~	nt	1.1	-1.1	~	~	nt	nt
February	~	~	nt	nt	~	nt	0.6*	-0.6*	~	~	nt	nt
March	~	~	nt	nt	~	nt	0.9*	-0.9*	~	~	nt	nt
April	~	~	0.4*	-0.4*	~	0.2*	1.2*	-1.4*	~	nt	1.0	-1.0
May	~	0.2	0.4*	-0.6*	0.4*	0.5*		-0.9		0.3	1.1	-1.4*
June	0.2	0.4*	0.5	-1.2*	2.0*		-1.4*		0.8	nt	-1.0	-0.8
July	1.1*	nt	-0.7	-0.5	1.1	-1.0		~	nt	nt	nt	~
August	0.9	-0.7	nt	~	nt	~	~	~	nt	~	~	~
September	nt	nt	~	~	nt	~	~	~	nt	~	~	~
October	0.7	-0.6		~	nt		~	~	nt	nt	~	~
November	1.0	nt	-1.3	-0.8	0.9	-0.8		~	1.2*	-0.9*	-0.3	~
December	~	nt	0.7	-1.0	1.0	1.4	-1.5*	-1.8	nt	0.5	0.8	-1.5*

* $p<0.005$ otherwise $p<0.05$; ~ habitat class not observed or trace; nt no trend

[a] Sea ice habitat classes: Non (0-30% ice cover), Poor (31-60% ice cover), Good (61-85% ice cover), Best (>85% ice cover)

Table 2.2 Polar bear sea ice habitat class area weighted mean habitat patch size (AREA_AM) slope (km^2/yr) of linear regression trends over time and region total number of habitat patches (NP) slope (patch/yr) of linear regression trends over time, Foxe Basin, Hudson Strait and Hudson Bay, Canada (1979-2008).

	Foxe Basin					**Hudson Strait**					**Hudson Bay**				
	AREA_AM (km^2/yr)				NP/yr	AREA_AM (km^2/yr)				NP/yr	AREA_AM (km^2/yr)				NP/yr
	[a] Non	Poor	Good	Best		Non	Poor	Good	Best		Non	Poor	Good	Best	
January	~	~	nt	nt	nt	~	nt	nt	nt	0.1	~	~	nt	nt	0.2
February	~	~	nt	nt	nt	~	nt	858	-1934*	0.1	~	~	nt	nt	nt
March	~	~	nt	nt	nt	~	nt	1140	-2355*	0.1	~	~	nt	nt	0.2
April	~	~	393*	-910*	0.1	~	314*	1978	-3239*	0.1	~	nt	5891	-9381	0.2*
May	~	223	455	-1314*	0.2*	562*	991*	nt	-1795	nt	nt	nt	9626	-11727*	0.3*
June	239	nt	1125	-2867*	0.2*	3522*	nt	-1656	-1571	nt	nt	nt	-7776	nt	-0.5
July	1898*	nt	-1236	-540	nt	2611	-1464	nt	~	-0.2*	nt	nt	nt	~	-0.3*
August	2169	nt	nt	~	-0.2	nt	~	~	~	~	nt	~	~	~	-0.1
September	nt	nt	~	~	-0.1	nt	~	~	~	nt	nt	~	~	~	nt
October	1495	-684	nt	~	-0.1*	nt	nt	~	~	nt	188*	nt	~	~	-0.1
November	2439*	nt	-3112	nt	nt	2002	-2670	nt	~	-0.1	3510*	-7461*	nt	~	-0.2
December	~	nt	nt	nt	nt	1921	2233	-2610	-1173*	nt	nt	4204	6615	-12883*	nt

* $p<0.005$ otherwise $p<0.05$; ~ habitat class not observed or trace; nt no trend

[a] Sea ice habitat classes: Non (0-30% ice cover), Poor (31-60% ice cover), Good (61-85% ice cover), Best (>85% ice cover)

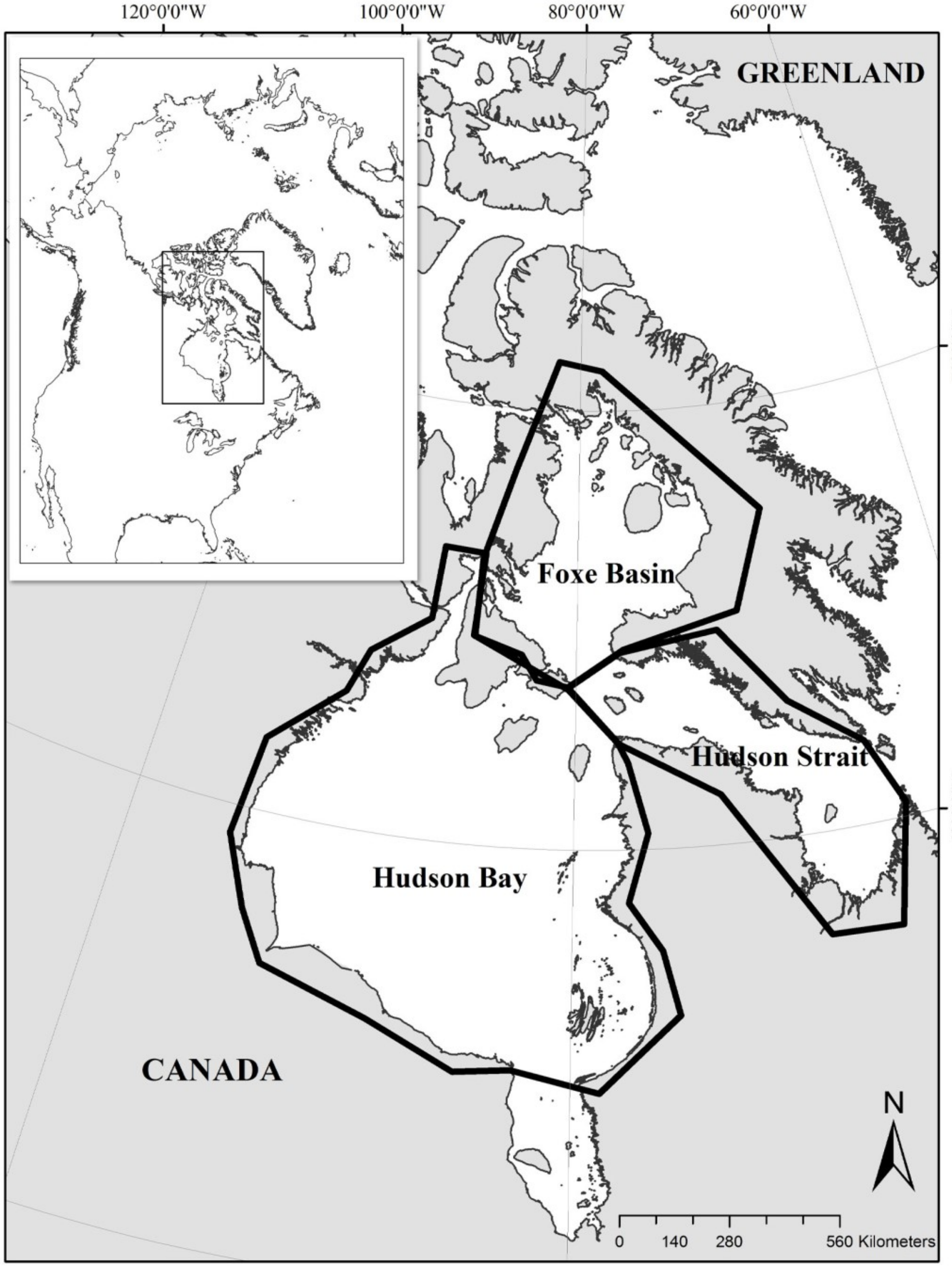

Figure 2.1 Study area map showing the marine regions of Foxe Basin, Hudson Strait and Hudson Bay, Canada.

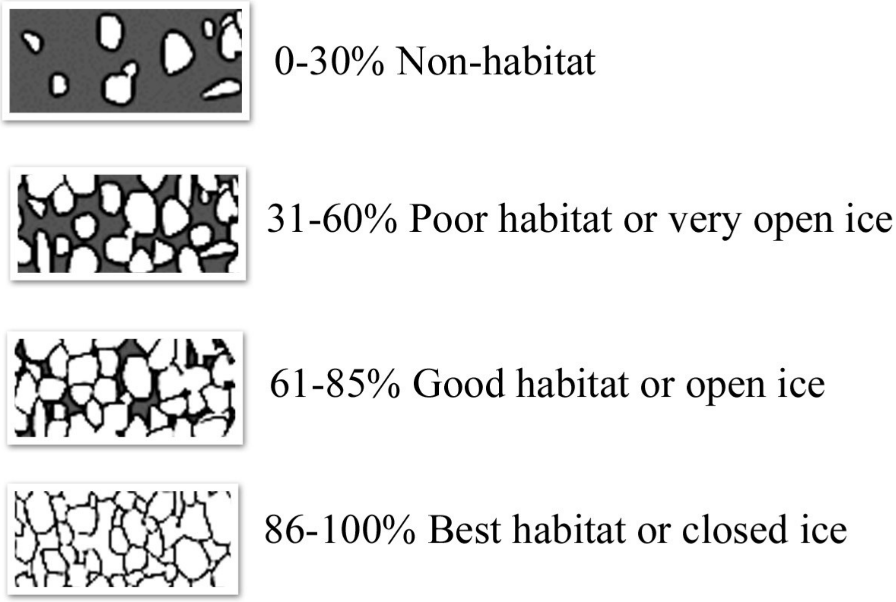

Figure 2.2 Polar bear sea ice habitat classes (adapted with permission from Canadian Ice Service).

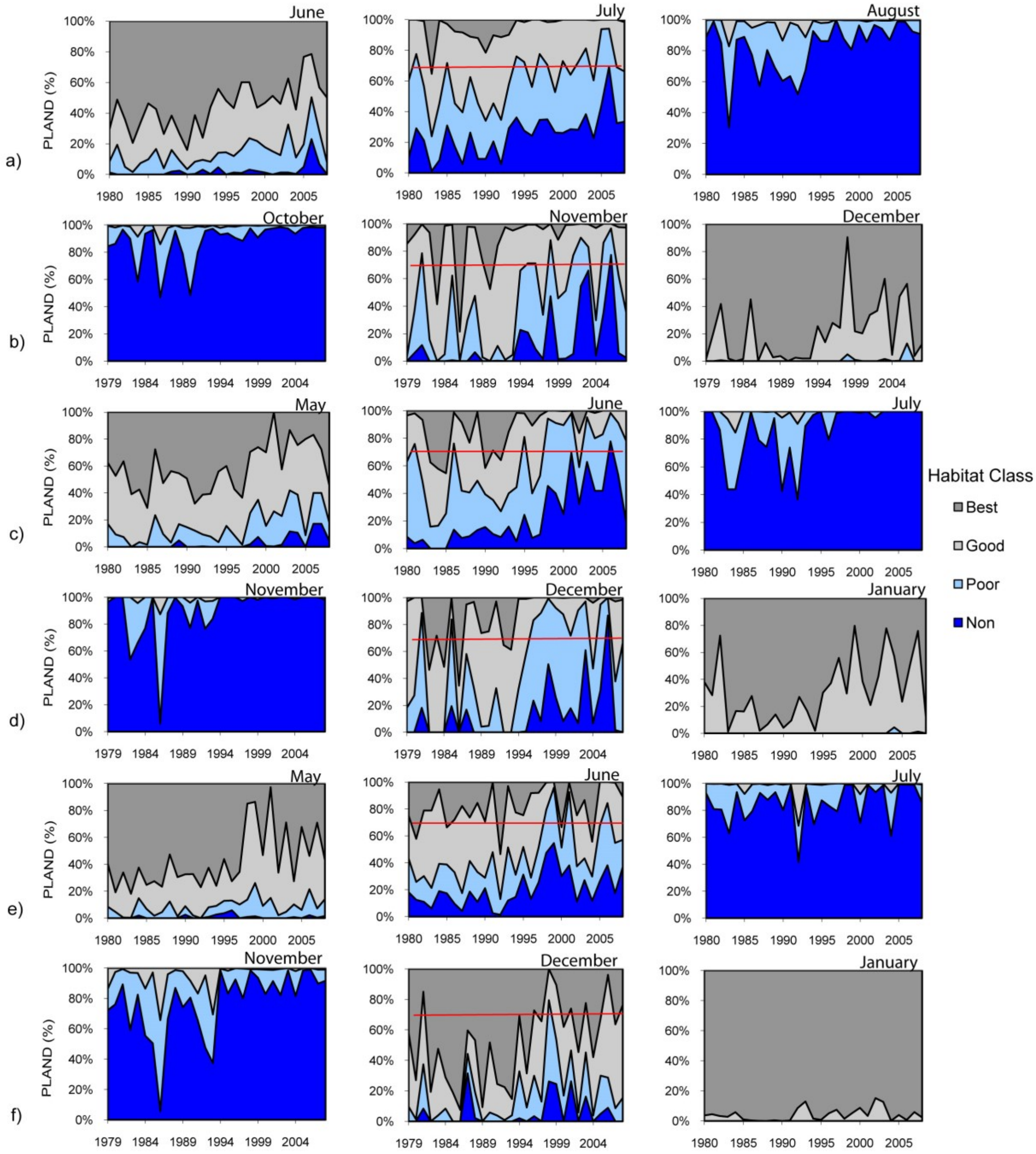

Figure 2.3 Polar bear sea ice habitat month of break-up and freeze-up (1979-2008): a) Foxe Basin break-up b) Foxe Basin freeze-up, c) Hudson Strait break-up, d) Hudson Strait freeze-up, e) Hudson Bay break-up, and f) Hudson Bay freeze-up. The horizontal red line shows the 30 % threshold of preferred (best and good) habitat that identifies break-up and freeze-up month.

Chapter 3

3 Population substructure and space use of Foxe Basin polar bears‡

3.1 Introduction

William Henry Burt was an early proponent of an integrated approach to wildlife management conservation, when he identified the need to understand a species' behaviour and spatial patterns (Burt 1943, Lima and Zollner 1996). Today, knowledge of individual movements, home range, and habitat are considered basic requirements of species conservation and management (Mueller et al. 2011b, Nagy et al. 2011). Technology now allows collection of high frequency, high resolution geographic position system (GPS) location, activity and environmental information that can be used to understand behaviour and habitat use. Such data makes it possible to study wide ranging species in remote regions, such as the Arctic, using satellites to relay next to real time information (Kie et al. 2010).

Population structure is dynamic and can be distinguished at a variety of temporal scales ranging from the movement of species in geological time to shorter times scale and ecologically important events such as dispersal and migration (Greenwood 1980, Mueller and Fagan 2008, Revilla and Wiegand 2008). Changing habitats and resource distribution can alter population size, dispersal patterns, and distribution (Parmesan and Yohe 2003, O'Corry-Crowe 2008). Climate change has been identified as a major driver of habitat change (Post et al. 2009, Wassmann et al. 2011). Within this context, Arctic habitats

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have experienced greater warming than lower latitudes (Trenberth et al. 2007, IPCC 2013). Of particular concern are species of large Arctic marine mammals that have small population sizes, slow reproductive rates, and specialized life histories that make them vulnerable to climate change (Stirling and Derocher 1993, Tynan and DeMaster 1997, Laidre et al. 2008, Gilg et al. 2012). Polar bears (*Ursus maritimus*) are one such vulnerable species, due to their high trophic level, specialized diet and reliance on the distribution of sea ice habitat for foraging (Derocher et al. 2004, Stirling and Derocher 2012).

Polar bears are distributed throughout the circumpolar Arctic in close association with the distribution of sea ice (DeMaster and Stirling 1981). Historically, their widespread distribution led Pedersen (1945) to speculate that polar bears consisted of a single large intermingling population. In the 1970s, when marked bears were recaptured or harvested, population spatial structure and regional fidelity were revealed (Lentfer 1973, Stirling et al. 1977). The first statistical assessment of polar bear spatial organization using satellite telemetry data identified the existence of geographically constrained populations (Bethke et al. 1995). As more detailed movement datasets accumulated, population delineations were revised (Taylor et al. 2001, Mauritzen et al. 2002, Amstrup et al. 2004). The IUCN/SSC Polar Bear Specialist Group has collated circumpolar input to delineate 19 populations based on a combination of telemetry data, geographic barriers, genetics, fidelity to summer ranges, and tag returns from hunters (Obbard et al. 2010); these populations serve as a basis for conservation, management, and harvest (Vongraven et al. 2012). Genetic analysis of polar bears has identified four broad groupings with subgroups of varying levels of distinction (Paetkau et al. 1999, Peacock et al. 2015). The population structure arises from spatial and temporal fidelity (Mauritzen et al. 2001, Lone et al. 2012). For example, pregnant females show fidelity to denning areas, return with their offspring and thereby may imprint travel routes and spatial information on their young (Derocher and Stirling 1990a, Ramsay and Stirling 1990). The benefits of site fidelity in a species with such prodigious abilities to move long distances (Taylor and Lee 1995, Paetkau et al. 1999) remain poorly understood.

Polar bear sea ice habitat has four broad ecoregions (divergent, convergent, archipelago, and seasonal) based on ice composition, circulation, duration, and how bears respond to sea ice dynamics (Amstrup et al. 2008). Much of our understanding of polar bear sea ice spatial ecology has come from studies in the high Arctic where there is a mixture of multi-year and annual sea ice and polar bears have access to sea ice habitat year round (Amstrup et al. 2000, Ferguson et al. 2001, Mauritzen et al. 2002). These high Arctic regions are part of the divergent, convergent, and archipelago ecoregions (Amstrup et al. 2008). The fourth zone, the seasonal ice ecoregion, includes five populations (Southern Hudson Bay, Western Hudson Bay, Foxe Basin, Davis Strait and Baffin Bay) where polar bears must retreat to land each summer when sea ice melts. Bear movements have been examined in Hudson Bay (Parks et al. 2006, Obbard and Middel 2012), Baffin Bay (Ferguson et al. 1997, Ferguson et al. 1999, Taylor et al. 2001), and Davis Strait (Taylor et al. 2001). Delayed freeze-up and earlier break-up, correlated with increasing surface air temperatures, has reduced the duration of ice cover in the seasonal ice region (Moore 2006, Stirling and Parkinson 2006, Hochheim and Barber 2010, Galbraith and Larouche 2011, Sahanatien and Derocher 2012) with negative consequences for polar bear population status and persistence (Regehr et al. 2007, Amstrup et al. 2008, Rode et al. 2012, Castro de la Guardia et al. 2013).

This is the first study to investigate the spatial ecology of female polar bears in the seasonal sea ice ecoregion of Foxe Basin in Nunavut, Canada using satellite telemetry. My objectives were to examine intra-population spatial structure, to determine movement patterns or strategies, to consider how polar bear movement behaviour may respond to changing sea ice habitat conditions, and to provide a baseline of information for management and monitoring.

3.2 Materials and Methods

Study area

Polar bears were caught and collared on land in the Foxe Basin polar bear population management unit, which includes Foxe Basin, northern Hudson Bay and western Hudson Strait in Nunavut, Canada (Fig. 3.1). The collars were distributed across the region to ensure spatial coverage for management unit delineation and characterizing intra-population spatial structure (this analysis). The polar bears of this population were historically hunted by Inuit and others (e.g., whalers); hunting continues and has been managed by a population specific quota and non-quota hunter restrictions since the early 1970s (Stirling and Smith 1974).

The study area was delineated by the locations of collared bears covering approximately 800,000 km^2 and included Foxe Basin, Hudson Strait, central and northern Hudson Bay, and eastern Gulf of Boothia (Fig. 3.1). The area extended approximately 1300 kilometres from south to north and 1400 kilometres from east to west. Hudson Bay is the largest water body (840,625 km^2), with Hudson Strait (196,875 km^2) and Foxe Basin (203,750 km^2) being similar in size. All three areas are shallow (predominantly < 200 m deep), productive seas that undergo an annual sea ice cycle from ice-free to almost total ice cover (Prinsenberg 1986b). Freeze-up begins in October and is complete in late December or January; break-up begins in May and continues into August (Saucier et al. 2004, Fequet et al. 2011). The timing of freeze-up was average in 2007-08 but in 2008-09, 2009-10 and 2010-11 above normal air temperatures slowed the growth of sea ice resulting in thinner ice (Canadian Ice Service 2008, 2009, 2010, 2011). In 2010-11, development of average winter ice concentration and extent was delayed by 4 weeks in Foxe Basin, 6 weeks in Hudson Bay and 8 weeks in Hudson Strait.

Ocean currents and coastline configuration play important roles in the development and distribution of sea ice. Foxe Basin and Hudson Bay have cyclonic circulation that results in active, centrally circulating floe ice bordered by a strip of stable landfast ice (Prinsenberg 1986a, Fequet et al. 2011). Hudson Strait also has narrow strips of landfast ice adjacent to active floe ice that moves linearly with the dominant west to east current. Hudson Strait is the outflow of Hudson Bay and Foxe Basin to the Atlantic Ocean. The coastline morphology of Hudson Bay is smooth and regular with few offshore islands, in contrast, Foxe Basin and Hudson Strait coastlines are more complex with many islands. There is a diversity of polar bear prey species including: ringed seals (*Pusa hispida*) (the main prey species), bearded seals (*Erignathus barbatus*), harbour seals (*Phoca vitulina*), harp seals (*Pagophilus groenlandicus*), walrus (*Odobenus rosmarus*), bowhead (*Balaena mysticetus*), narwhal (*Monodon monoceros*), and beluga (*Delphinapterus leucas*) (Sergeant 1986, Smith and Sjare 1990, Stewart and Lockhart 2005, Schliebe et al. 2008, Thiemann et al. 2008b).

Capture and deployment of satellite collars

Bears were immobilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol; Fort Dodge Laboratories, Fort Dodge, IA, USA) by remote injection using a dart delivered from a helicopter. All bears were caught on land, during the ice-free season, following standard capture and handling methods (Stirling et al. 1989). Animal handling protocols were approved by the University of Alberta Animal Care and Use Committee for Biosciences.

Global positioning system (GPS) satellite collars (Telonics, Inc., Mesa, AZ, USA) linked to Argos satellites (CLS America, Lanham, MD, USA) were deployed on 45 adult female polar bears with cubs-of-the-year, yearlings and 2-year olds, as well as, 2 females without offspring in August - October, 2007 – 2009.

Location data were collected at 3- or 4-hour intervals. I used GPS quality location data (accuracy < 10 m) with the exception of 2 bears whose collars provided only Doppler shift quality locations for part of the year, of which only classes 1, 2 and 3 (accurate to <1 km) were included. Daily locations at 13:00 GMT or nearest recorded values were used for the cluster analysis and overlap analyses, and all locations were used to calculate movement rates and home range size.

I defined five seasons based on sea ice dynamics, ice concentration, and ringed seal life history, similar to those used by Parks et al. (2006) and Ferguson et al. (2001). The seasons were: ice-free (minimum to no sea ice and bears were on land), freeze-up (when a bear moved onto the ice until December 31), winter (when sea ice concentration was 90-100%, 01 January – 31 March), spring (when ringed seals pup and moult, 01 April – 31 May), and break-up (when the sea ice melts and independent seal pups are available, 01 June until ice-free conditions dominate and the date that a bear returned to land).

If a bear entered a maternity or temporary den, the locations were excluded in the movement rate calculations but were included in the home range and cluster analyses. Denning was identified when a bear stopped moving for several weeks or months, and renewed movement was not attributed to sea ice movement. All suspected dens were on land.

Spatial structure of movements

I used hierarchical cluster analysis (Bethke et al. 1995, Schaefer et al. 2001, Nagy et al. 2011) to investigate if there was spatial structure and regional affinities in the movements of the Foxe Basin polar bear population using location data from the on-ice period. This data subset focuses on movement responses to the sea ice habitat where polar bears obtain most of their annual energy stores while foraging and includes their distribution during the spring mating season. Weekly median locations (latitude, longitude) were calculated for 27 bears for October – March, representing 35 ice years of movement information. The median location values were converted to metric x, y coordinates using Hawth's Tools (Beyer 2004). SPSS v19 (IBM, Somers, NY, USA) was used for the agglomerative hierarchical cluster analysis, using Ward's linkage (Bethke et al. 1995) which minimizes the within cluster variance versus the between cluster variance (Ludwig and Reynolds 1988). I used STATA 10 (STATCORP, College Station, TX, USA) to calculate the post-hierarchical clustering Duda-Hart pseudo t-test (Rabe-Hesketh and Everett 2007) to identify the optimum number of distinct groups. FUZME v3.5 (Minasny and McBratney 2002) was used to apply fuzzy c-means clustering as a third analytical approach to examine the optimum number of clusters and the assignment of bears to each cluster following Nagy et al. (2011) and Schaefer et al (2001). I used a relatively low level of fuzziness or "hard' classification (m=1.5) and the diagonal metric given the dimensions of the study area. FUZME has been applied to determine caribou (*Rangifer tarandus*) herd membership (Schaefer et al. 2001, Nagy et al. 2011, Schaefer and Mahoney 2013). To test for independent or coordinated movements within the Foxe Basin collared bears I calculated the fuzziness performance index (FPI) and modified partition entropy index (MPE) using FUZME. The clusters were mapped using kernel density distributions calculated using Home Range Tools for ArcGIS® v1.1 (Rodgers et al. 2007).

Spatial and movement metrics

To allow comparison with previous studies, I calculated minimum (100%) convex polygon (MCP) home ranges. Annual and seasonal MCPs were calculated using Hawth's Tools (Beyer 2004) in ArcMap v9.3.1 for bears with > 9 months of location data using all available locations. Most bears were collared in September and October, thus nine months of data included most of the on-ice period and did not influence individual annual MCP area but break-up season MCPs were not calculated for bears with truncated location data.

Movement rates and Euclidean distances between locations were calculated using Hawth's Tools in ArcMap v9.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). All available locations were used to calculate monthly movement rates and for each month a bear had to have ≥15 days of location data to be included. The total on-ice time (days) was calculated for each bear as the date on ice at freeze-up to the date on land the following year.

To compare differences between the movement metrics I used a one-way ANOVA and Tukey's HSD post hoc test for pair-wise comparisons. ANOVA was used to test for significant trends in monthly and seasonal movement metrics. All statistical tests and comparisons used $\alpha = 0.05$ and were performed using SPSS. Means are presented with ± 1SE.

Home range fidelity

Home range fidelity was measured by calculating individual inter-annual seasonal and annual home range overlap. Nine females from Foxe Basin and Hudson Strait had sufficient data over 2 consecutive years to be included in the overlap calculations. I used both static and dynamic overlap (Powell 2000), which were calculated using Ranges8 v2.8 (Anatrack Ltd., Wareham, UK). Static overlap describes the spatial overlap of home ranges and was used to quantify the overall repeated use of available habitat. Static overlap (0-100%) was calculated by measuring the percentage of home range overlap of Year1 on Year2 and Year2 on Year1. Dynamic overlap, also called interactive overlap, incorporates time and space by analyzing the relationship between pairs of locations (Powell 2000). In my study, paired daily locations of individual bears recorded one year apart were used to assess spatio-temporal home range fidelity. I calculated Jacobs' Index in Ranges8 to measure dynamic overlap between years for each bear. The observed and possible distances (1000 random locations) between paired locations were compared to calculate Jacobs' Index, which ranges from -1 (avoidance and no fidelity in this analysis) to +1 (attraction and complete fidelity in time and space), with 0 indicating independence of locations (Kenward et al. 2008). Jacobs' Index has been used to measure dynamic overlap and sociality between individuals, sexes, and species (Zalewski and Jedrzejewka 2006, Schmidt et al. 2009, Mattisson et al. 2011).

3.3 Results

Spatial structure of movements

Three spatial clusters were identified within the Foxe Basin population that broadly coincided with the main water bodies: Foxe Basin (FB), Hudson Strait (HS), and Hudson Bay (HB) (Fig. 3.1 and 3.2). The agglomerative hierarchical cluster analysis separated out the HB cluster at the first order level and the FB and HS clusters at the second order level (Fig. 3.3). A fourth cluster may be present based on the inflection point of the Duda-Hart pseudo t-squared test (Fig. 3.4). The fuzzy cluster results showed 2 to 4 possible geographic clusters (see Appendix A). At the third order, the hierarchical cluster analyses results split the FB cluster but the fuzzy cluster analysis (see Appendix A) split the HB cluster. Because there was disagreement on membership of bears in a fourth cluster, but agreement between three analytical approaches on the composition of the three clusters, I based subsequent comparisons on three clusters. The plotted fuzziness performance (FPI) and modified partition entropy (MPE) indices reached minima at zero for most values of the fuzziness weighting exponent (m), showing that each bear was spatially independent (see Appendix A).

Spatial and movement metrics

The mean annual MCP home range area was 115,918 ± 15,382 km^2 and varied from 19,633 km^2 to 401,351 km^2. The mean annual home range sizes differed between clusters within the Foxe Basin population ($F_{2, 26} = 6.15$, P=0.006, Table 3.1). The FB cluster mean annual home range was smaller than in HB (Tukey's HSD, P=0.006). There were also differences in the seasonal home range sizes. The freeze-up home ranges differed among clusters ($F_{2, 29}$ = 9.35, P=0.001), with those in FB and HS smaller than in HB (Tukey's HSD, P=0.001; Tukey's HSD, P=0.003). Winter home ranges also differed among clusters ($F_{2, 31}$ =3.24, P=0.05), with FB being smaller than HS and HB (Tukey's HSD, P=0.05).

Mean seasonal movement rates ranged from 0.9 km/h during freeze-up and winter to 1.8 km/h during break-up (Table 3.2). Regional movement rates significantly differed only during spring ($F_{2, 26}$=3.57, P=0.04) when HB (0.8 km/h) bears moved slower than HS (1.3 km/h) and FB (1.2 km/h) bears. Mean monthly on-ice movement rates from December to July declined in HB ($F_{1, 6}$ =10.16, P=0.02), increased in HS ($F_{1, 6}$ =41.09, P<0.001), and there was no trend in FB ($F_{1, 6}$ =2.92, P=0.14) (Fig. 3.5).

The mean number of days on the sea ice differed among the regions ($F_{2, 12}$ =8.83, P=0.004). FB bears were on the ice 31 days longer (Tukey's HSD, P=0.03) than bears in HS, and 56 days longer (Tukey's HSD, P=0.007) than bears in HB (Table 3.3). The mean date that bears moved on to the sea ice differed among regions ($F_{2, 51}$ =15.62, P<0.001). Polar bears moved onto the sea ice in FB the earliest (Tukey's HSD, P=<0.001), and HS the latest (Tukey's HSD, P=0.001). The mean date that bears left the sea ice for land also differed among regions ($F_{2, 14}$ =13.98, P<0.001) and FB bears left the ice for land latest (Tukey's HSD, P≤0.001) and HB bears earliest (Tukey's HSD, P=0.003).

Home range fidelity

Female polar bears demonstrated annual and seasonal home range fidelity in FB and HS. It was not possible to calculate HB bears' annual home range fidelity due to lack of data. There was a high level of annual and seasonal static overlap of individual polar bear home ranges (n = 9). The mean annual static overlap was 72 ± 6% (range 24-92%). The mean seasonal static home range overlap ranged from 36 ± 10% during the ice-free season to 60 ± 7%

during freeze-up (Fig. 3.6). Over the year, the individual seasonal overlap values ranged from 0 - 99%.

Annual home range dynamic (temporal and spatial) overlap was positive with mean Jacobs' index of 0.3 ± 0.06 (range 0.2 – 0.6) (Fig. 3.6). A positive Jacob's index means that individual bears are near the same geographic locations at the same times of year. Seasonal home range dynamic overlap was variable but generally positive, with individual bear Jacobs' index values ranging from -0.2 – 0.7. Bears had higher mean seasonal Jacob's indices during freeze-up, break-up and ice-free seasons. The pattern of static and dynamic home range overlap was similar except during winter and spring.

3.4 Discussion

Within the Foxe Basin population, female polar bear locations on the seasonal sea ice were distributed in three clusters and each cluster generally corresponded with the main marine regions. There were differences in the movement metrics between clusters. At the individual level, the bears showed annual and seasonal fidelity to their home ranges and moved independently of each other on the sea ice.

Intra-population spatial structure has been observed in other polar bear populations. Cluster analyses in the Barents Sea and Kara Sea populations found that the spatial clusters were related to sea ice habitat use: one cluster used seasonal fast ice in the near shore and the other used multi-year drift ice off shore (Mauritzen et al. 2002). In Davis Strait, population and genetic cluster analyses indicated two geographic groups: northern and southern Davis Strait that corresponded to the main coastal summer ice-free retreat areas (Taylor et al. 2001, Peacock et al. 2015). The genetic clusters also differed in prey (Iverson et al. 2006), birth rates, and survival rates (Peacock et al. 2013). In the Beaufort Sea, utilization distribution analysis revealed that "homebody" bears, those with small annual ranges, formed intra-population clusters (Amstrup et al. 2004). In southern Hudson Bay, seasonal utilization distributions revealed that polar bears were distributed in two spatial groups: James Bay and southern Hudson Bay (Obbard and Middel 2012), which was supported by genetic analysis (Peacock et al. 2015), suggesting breeding-season substructure.

In the 1980s, based on marks returned by Inuit hunters, it was hypothesized that there were two geographic units of bears in Foxe Basin (Stirling and Ramsay 1986): one group in the north (Foxe Basin and Hudson Strait) and the other in the south (northern Hudson Bay). My findings, however, provide empirical evidence based on the distribution and movements of polar bears. Hierarchical cluster analysis of animal movement data can be challenging to interpret as different approaches can yield varying or conflicting results (Bethke et al. 1995, Mauritzen et al. 2002, Schaefer and Wilson 2002, Amstrup et al. 2004, Nagy et al. 2011). Determining the number of clusters can be particularly difficult in species with a continuous distribution and individual movement patterns. By taking a parsimonious approach, applying knowledge of behaviour and ecological needs, and considering the movement metrics associated with the clusters it is reasonable to conclude that the Foxe Basin population is comprised of three spatial clusters.

Because the sea ice habitat is similar throughout the study area, seasonal ice with active pack ice and a small fraction of landfast ice (http://iceweb1.cis.ec.gc.ca/), the clusters were likely unrelated to differential use of sea ice habitats. Further, there were no apparent barriers (e.g. mountain ranges, vast open water) to polar bear movement and both prey and denning habitat were widely available over the region. Polar bears were capable of moving across the entire study area but they did not, instead they exhibited regional clusters that adhered to marine regions of Foxe Basin, Hudson Strait, and Hudson Bay. The clusters arose from individual home range fidelity and may be a product of learned behaviour that develops in a predictable and resource rich environment (Mueller and Fagan 2008). The clusters were also affected by ecological differences created by sea ice dynamics.

Dynamic sea ice habitats were thought to have unpredictable resource distributions that influenced polar bears' movements and thus, discrete home ranges were unexpected and female distribution assumed to vary over time (Ramsay and Stirling 1986, 1988). I agree that polar bear movements are coupled with sea ice structure and distribution but the labile ice may not be as unpredictable as previously thought. With the advantage of modern satellite imagery and ice maps, I observed that sea ice is dynamic but broadly predictable at larger spatial and longer temporal scales in Foxe Basin. This predictability makes it possible for polar bears to have home ranges in the traditional sense, where bears move repeatedly through a definable space over months and years (Powell 2000), as demonstrated by the population overlap metrics. If sea ice was an unpredictable habitat it would be conducive to nomadism (Mueller and Fagan 2008) which polar bears do not show.

Home range fidelity provides familiarity with the distribution of resources (Zalewski and Jedrzejewka 2006, Wolf et al. 2009, Spencer 2012) and may be necessary for the highly seasonal feeding behaviour of polar bears. The on land fasting period in Foxe Basin is 2.4 - 4 months long and similar to other seasonal ice populations (Parks et al. 2006, Cherry et al. 2013). The existence of fidelity to summer retreat areas, spring feeding and breeding areas in Foxe Basin was questioned because ice persists there longer than in Hudson Bay (Stirling and Ramsay 1986). While my sample size was small and included only two consecutive years, I provide evidence that Foxe Basin bears had fidelity to retreat and spring feeding areas, and likely breeding areas. This fidelity is concordant with the accumulating observations of repeated use of sites and area fidelity on annual and seasonal time frames in seasonal and multi-year ice ecoregions (Schweinsburg et al. 1982, Derocher and Stirling 1990a, Born et al. 1997, Amstrup et al. 2000, Mauritzen et al. 2001, Wiig et al. 2003, Lone et al. 2012).

Differences in polar bear space use metrics (e.g., home range size, movement rate) have been related to foraging strategies and ultimately with the structure and quality of sea ice habitat. In the Canadian Arctic and Barents Sea, female polar bears using pelagic or active pack ice habitat had larger annual ranges than the near-shore or landfast ice bears (Ferguson et al. 1999, Mauritzen et al. 2001). Ferguson et al. (1999) proposed that home range size reflected the predictability of the environment and prey; in pelagic or active pack ice, prey distribution may be less predictable than on landfast ice, and require more effort to find. Home range size can be influenced by habitat productivity or food availability with high productivity yielding smaller home range size (McLoughlin and Ferguson 2000, Moyer et al. 2007, Edwards et al. 2013). Such findings are predicted by the resource dispersion hypothesis for territorial and social carnivores (Macdonald 1983, Newsome et al. 2013). The cluster level differences in movement metrics of the Foxe Basin population may reflect the habitat conditions experienced by the bears. Like most movement studies of polar bears, I did not have quantitative information on prey distribution and density to evaluate habitat quality. Nonetheless, my results on home range size coupled with days on-ice suggest that habitat quality in Hudson Bay is lower than in Foxe Basin and Hudson Strait. The HB cluster of bears had the largest home range size, fewest days on-ice, and earliest off-ice date. The bears in FB had the smallest home ranges, greatest number of days on-ice and latest off-ice date. Based on Ferguson et al. (1999), I would have expected the movement rate to be highest in the HB cluster but it was the lowest, suggesting that prey availability is at a level such that conserving energy may be a factor. Hudson Bay has lower phytoplankton production and biomass (Ferland et al. 2011, Cyr and Larouche 2014) and lower zooplankton biomass than Hudson Strait and Foxe Basin (Estrada et al. 2012) to support polar bears and their prey (Hobson and Welch 1992, Bluhm and Gradinger 2008).

Resource distribution and landscape structure are major drivers of individual movement behaviour and mechanisms (spatial memory, oriented, and non-oriented) that results in emergent population level patterns and strategies (range residency, migration, and nomadism) (Mueller and Fagan 2008). Mueller and Fagan’s conceptual framework of temporal and spatial resources gradients with levels of heterogeneity and predictability in dynamic environments can be extended to the sea icescapes used by polar bears. In Foxe Basin, female polar bears during the sea ice season would be considered range residency strategists as I observed home range fidelity, which reflects spatial memory, annual and seasonal temporal predictability of sea ice habitat, and the predominant active floe ice that creates fine scale heterogeneity in the distribution of prey habitat. Similar to the polar bears of the adjacent Western Hudson Bay, Foxe Basin bears must move from sea ice to land for the ice-free season and the movement on shore has been described as migratory (Cherry et al. 2013). My observations suggest that Foxe Basin polar bears use both seasonal on-ice range residency and annual migration; use of dual movement patterns has been described in other species (Mueller and Fagan 2008, Mueller et al. 2011b). The switch between strategies is likely caused by fine-scale changes in the physical environment experienced by the bears. When sea ice drops below a threshold concentration, the bears move to land (Cherry et al. 2013).

Within the context of climate change, understanding polar bear movement patterns are important as a means to anticipate their potential behavioural plasticity for responding to changes in sea ice habitat phenology, distribution, and loss. Research (Ferguson et al. 2000, Mauritzen et al. 2001) suggests that polar bears have behavioural plasticity on short temporal scales (day to day, week to week, even month to month) and can exploit most sea ice habitat types (multi-year, annual, fast and drifting pack ice) but I do not know how flexible they are on annual and decadal time scales. Can individual bears switch movement strategies as environment changes? Ferguson et al. (1999) thought that polar bears could switch from a pelagic to a fast ice strategy, which implies less reliance on home range fidelity. In contrast, Mauritzen et al. (2001) proposed that polar bears had a single strategy and stayed with it over their lifetime and concluded that dynamic sea ice is a predictable habitat at relevant spatial and temporal scales. In Foxe Basin, ice seasons are changing and there has been increasing fragmentation of sea ice habitat (Stirling and Parkinson

2006, Sahanatien and Derocher 2012). If the spatial and temporal predictability of resources and sea ice habitat declines, I predict home range fidelity may decline.

Polar bear populations can be affected by the dual stresses of habitat change and hunting (Lentfer 1983, Peacock et al. 2011). Both factors will continue to influence polar bear populations, particularly in seasonal sea ice regions. The Foxe Basin polar bear population allowable harvest is set for the entire management unit but the existence of three clusters suggests that management should consider population substructure. Changing ice conditions and the differences in the ice-free period suggests that the demographics of the population may vary geographically. To date, demographic analyses have been conducted on a population basis but in areas with complex habitat structure it is important to consider regional demographics (Peacock et al. 2013). The analytical tools (e.g., GIS, resource selection analysis, movement models) and information sources (e.g., satellite imagery, sea ice charts, polar bear location data) are available to refine polar bear harvest management and a precautionary approach that includes bear behaviour, movement strategies, and sea ice habitat conditions would aid in conservation efforts.

Table 3.1 Mean annual and seasonal home range (minimum convex polygon) sizes (km²) of GPS satellite collared female polar bears in Foxe Basin (FB), Hudson Strait (HS), and Hudson Bay (HB), Canada (2007-2011). Bolded values are significantly different (one-way ANOVA, $p<0.05$).

Region	**Annual**	**SE**	**n**	**Freeze-up**	**SE**	**n**	**Winter**	**SE**	**n**	**Spring**	**SE**	**n**	**Break-up**	**SE**	**n**
FB	**59137**	9093	11	**21187**	4223	13	**13465**	2758	14	11863	2995	13	18055	4393	10
HS	**132760**	25493	8	**21415**	8008	9	**27767**	8407	10	22995	5811	8	28588	6734	6
HB	**164904**	30714	10	**53371**	6305	10	**37139**	9745	10	24235	8541	8	50791	22515	3

Table 3.2 Mean seasonal movement rates (km/h) of GPS satellite collared female polar bears in Foxe Basin (FB), Hudson Strait (HS), and Hudson Bay (HB), Canada (2007-2011). Bolded values are significantly different (one-way ANOVA, $p<0.05$).

Region	**Freeze-up**	**SE**	**n**	**Winter**	**SE**	**n**	**Spring**	**SE**	**n**	**Break-up**	**SE**	**n**
FB	1.3	0.1	17	1.1	0.1	16	**1.2**	0.1	11	1.5	0.1	10
HS	0.9	0.1	12	1.1	0.1	13	**1.3**	0.1	8	1.8	0.3	5
HB	1.2	0.1	16	0.9	0.1	13	**0.8**	0.1	10	1.1	0.1	4

Table 3.3 Time spent on the sea ice by female polar bears in Foxe Basin (FB), Hudson Strait (HS), and Hudson Bay (HB), Canada (2007-2011). Bolded values are significantly different (one-way ANOVA, $p<0.05$).

Region	**Mean days on-ice**	**SE**	**n**	**Mean ordinal date on-ice**	**SE**	**n**	**Mean ordinal date off-ice**	**SE**	**n**
FB	**294**	6	7	**306 (Nov 01)**	3	33	**238 (Aug 25)**	3	8
HS	**263**	10	6	**336 (Dec 01)**	6	15	**227 (Aug 14)**	6	7
HB	**238**	4	2	**313 (Nov 08)**	2	16	**187 (July 05)**	1	2

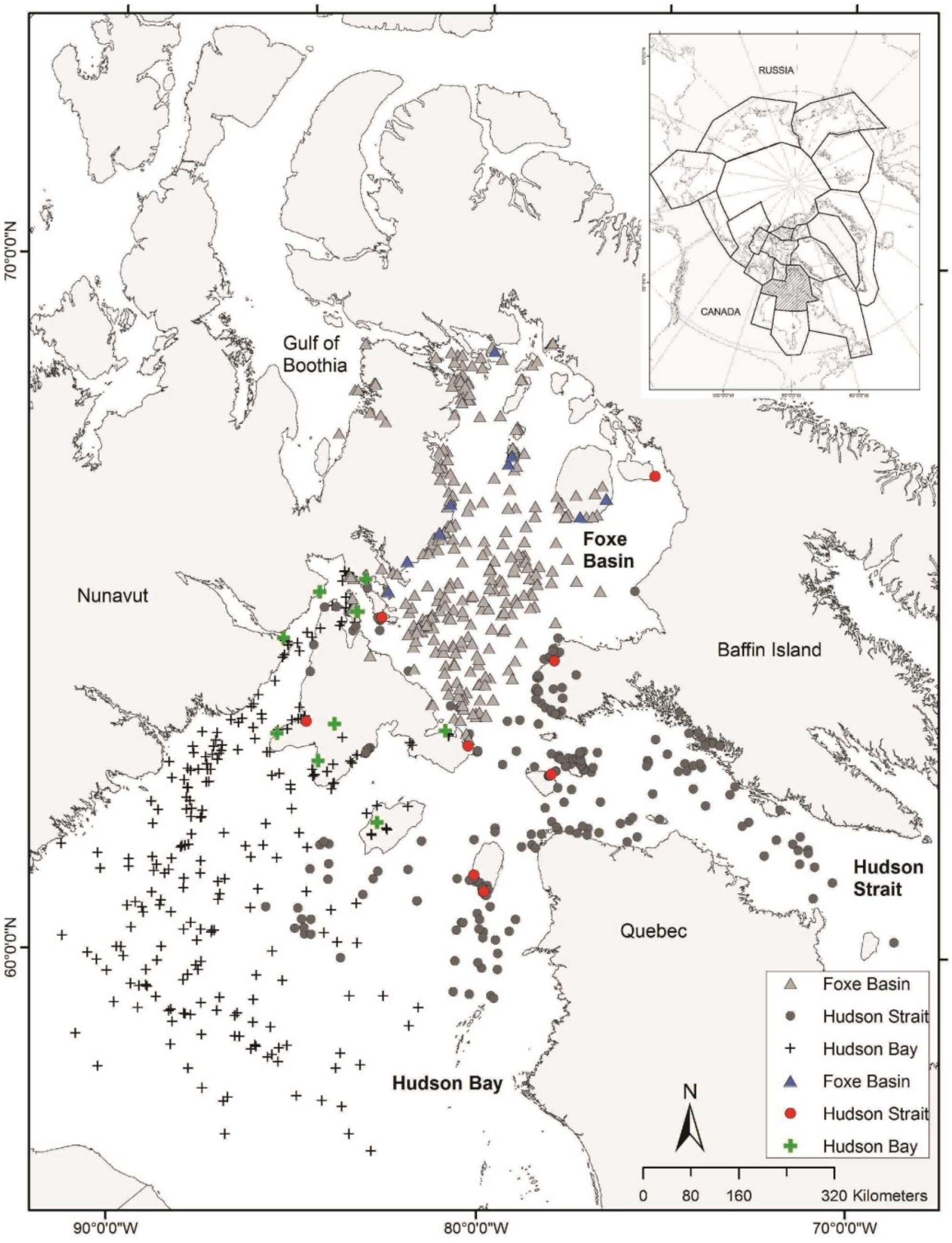


Figure 3.1 Study area, with female polar bear GPS satellite telemetry movement locations (black symbols) and capture locations (colour symbols) coded according to subpopulation cluster assignment, Foxe Basin, Nunavut, Canada, October – March, 2007-2011.

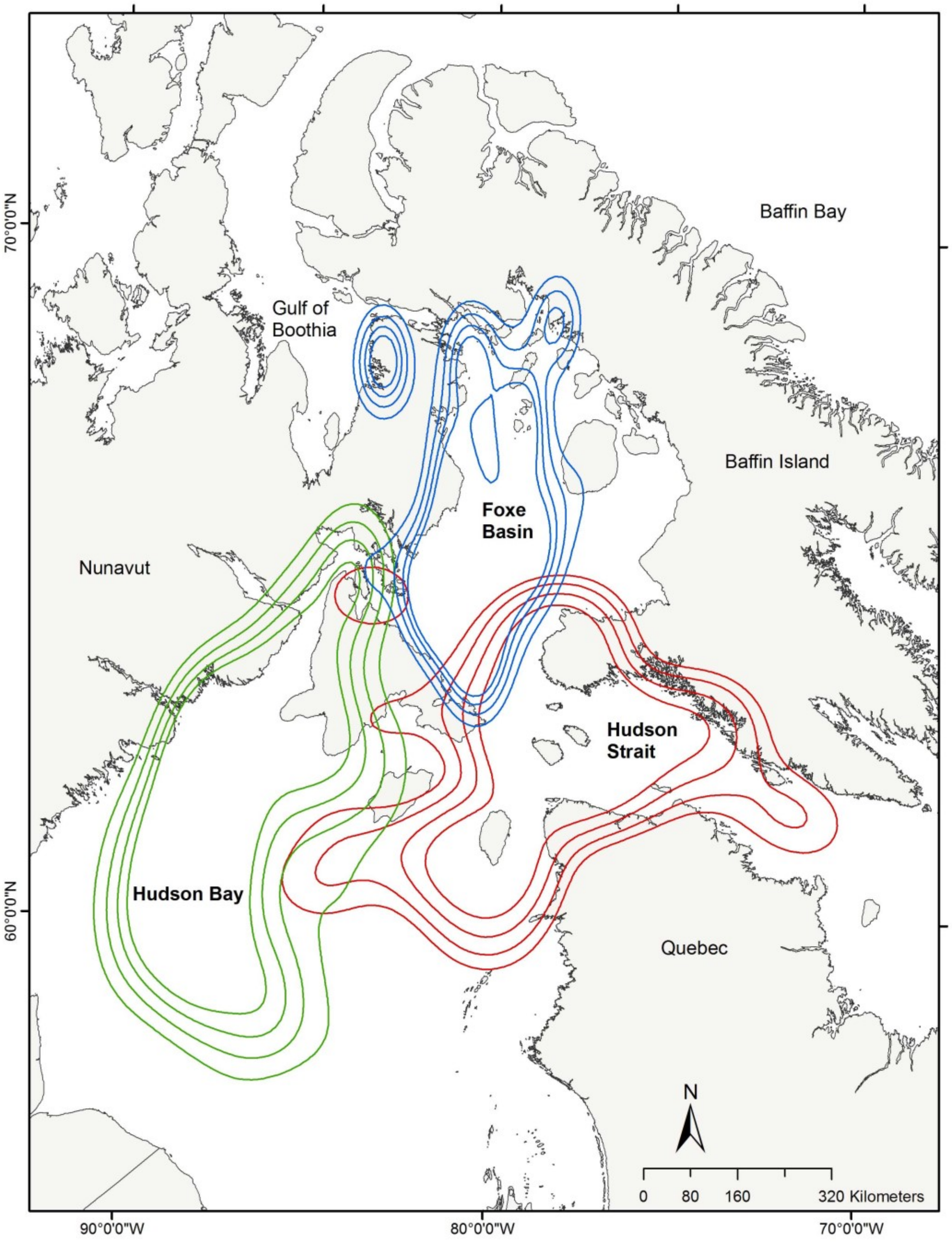


Figure 3.2 Kernel distribution (50, 60, 70, and 80%) contours of Foxe Basin (blue), Hudson Strait (red) and Hudson Bay (green) subpopulation clusters in Foxe Basin, Nunavut, Canada, October-March, 2007-2011.

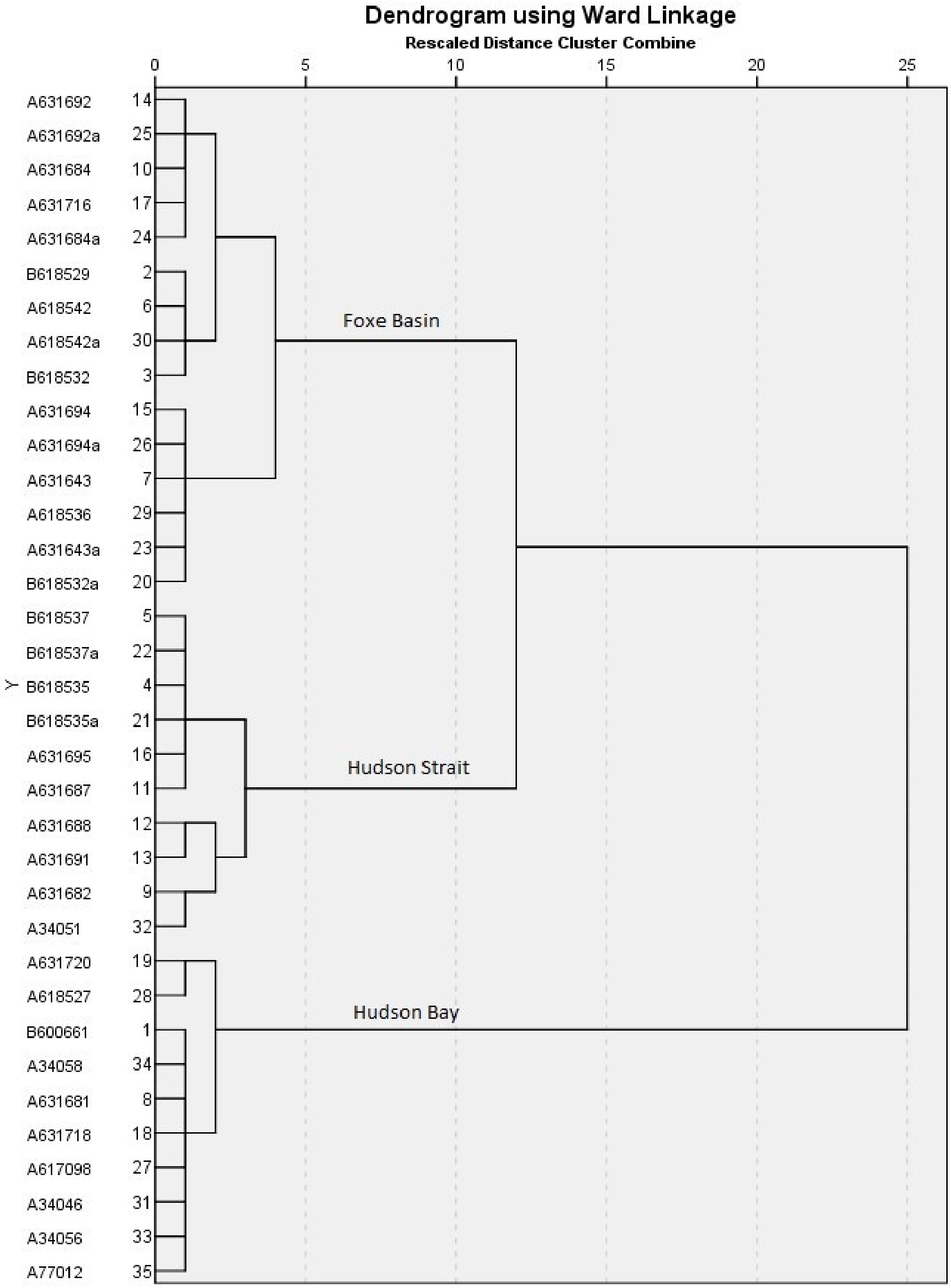


Figure 3.3 Dendrogram showing three geographic clusters of Foxe Basin female polar bears (n = 35) using GPS satellite telemetry median weekly locations for the on-ice period, October – March, 2007-2011.

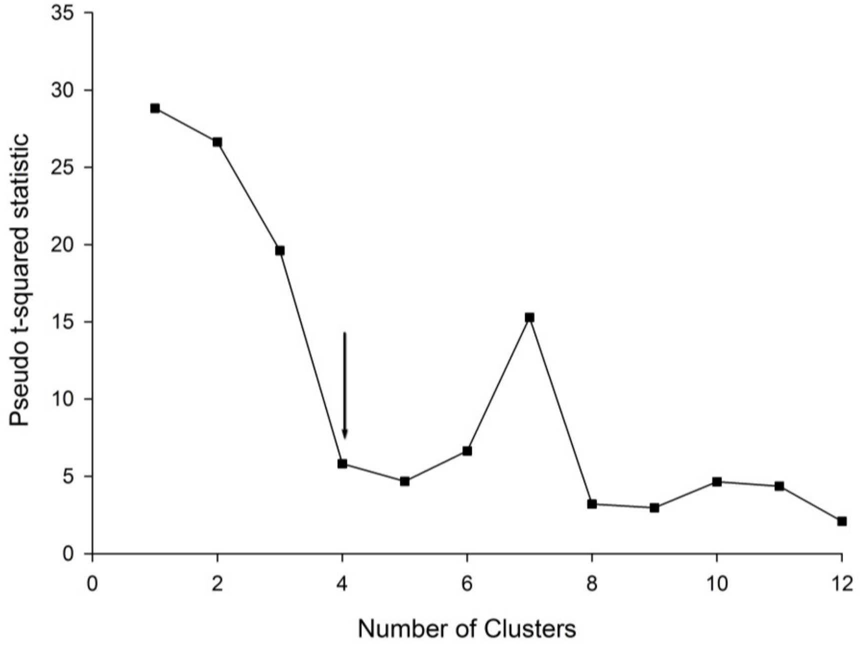


Figure 3.4 Duda-Hart pseudo t-squared test statistic graphed with the inflection point (arrow) indicating the potential optimum number of spatial clusters of female polar bears (n = 35) in the Foxe Basin population using median weekly on-ice GPS satellite telemetry locations (October – March, 2007-2011).

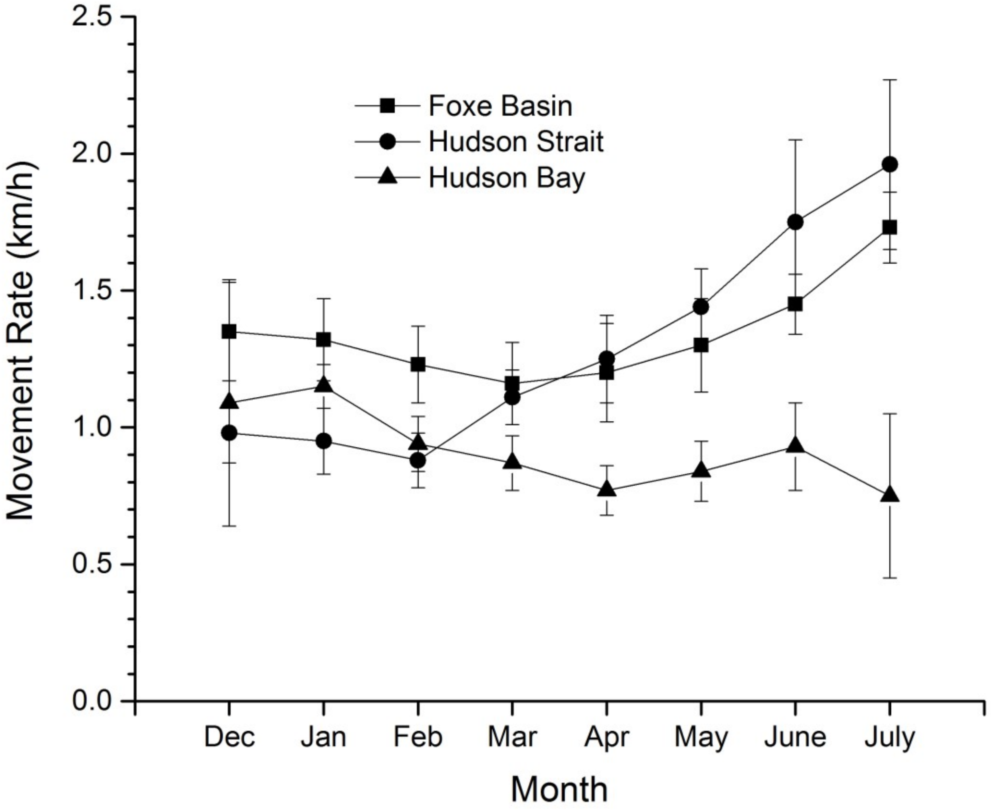


Figure 3.5 Mean monthly on-ice movement rates (km/h) of GPS satellite collared female polar bears in Foxe Basin, Hudson Strait and Hudson Bay, Canada (2007-2011).

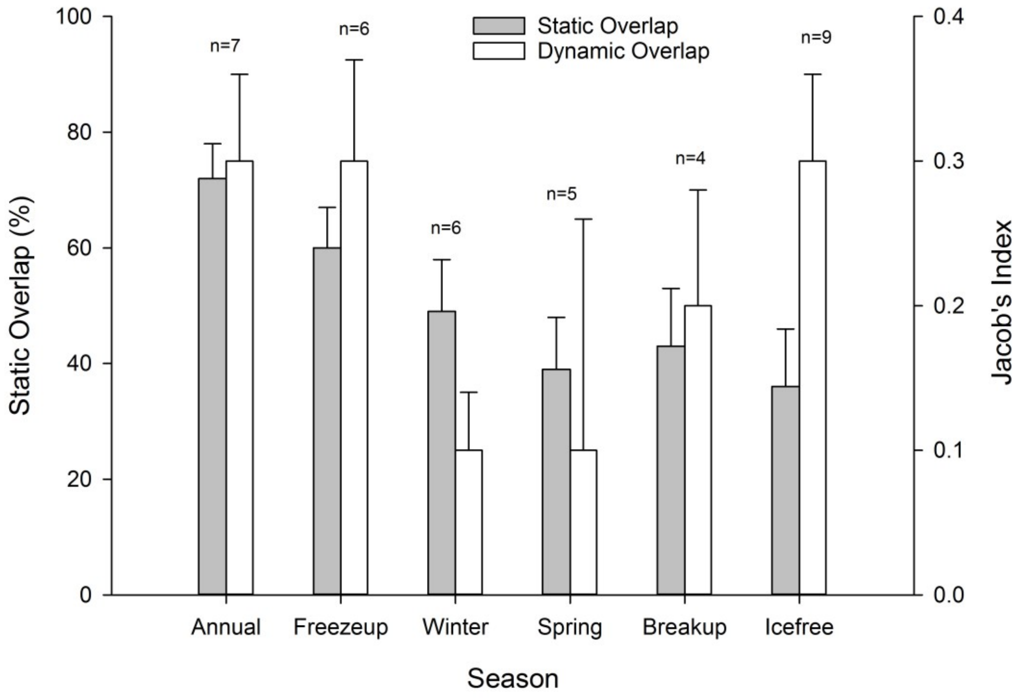


Figure 3.6 Seasonal and annual static (MCP) overlap and dynamic home range overlap of female polar bears in Foxe Basin, Hudson Strait, and Hudson Bay, Canada (2007-2011).

Chapter 4

4 Sea ice structure and polar bear habitat selection using high resolution SAR satellite imagery

4.1 Introduction

Satellite imagery and remote sensing are increasingly important means of mapping habitat and monitoring biodiversity (Pettorelli et al. 2014, Scales et al. 2014). The resolution of data available for resource selection studies affects the predictor covariates that can be used and thus, affects the scale of analyses (Boyce 2006). Ecologists now have access to imagery of varying resolution and from a variety of sensors that can be used to evaluate trends in the state, quality, quantity, and distribution of terrestrial, aquatic and marine habitats (McDermid et al. 2010, Rose et al. 2015). Satellite imagery is particularly useful for studying remote, vast regions like the oceans, Antarctica, and the Arctic. Insights into the effects of climate change on sea ice at global and regional scales have only been possible through the use of satellite imagery (Comiso 2003, Stroeve et al. 2014b).

Sea ice is mapped using a variety of satellite sensors but microwave is commonly used because images can be obtained day or night, which is important for polar regions with 24 hours of darkness in winter (Comiso 2003, 2010). Synthetic aperture radar (SAR) satellite imagery is a primary information source for sea ice mapping and research because the sensor is active, using microwaves that penetrate clouds and fog (MANICE 2005, Johannessen et al. 2007, Comiso 2010). SAR satellites cover the polar regions with high resolution (3-1000 metres) and each orbit has wide area coverage (swath widths 20-500 km). SAR identifies open water, sea ice, sea ice type (age and thickness) and ice surface roughness or topography. Ice is broadly classified as annual, which forms and melts each year, or multi-year, which survives the melt season and regrows for one or more years (World Meterological Organization 1970). Multi-year sea ice is mostly found in the Arctic Ocean and Canadian Arctic Archipelago due to ice drift dynamics and climatology. Annual ice is found throughout the Arctic, sub-Arctic, and adjacent to the Antarctic continent. Annual and multi-year ice is further characterized by its structure: extent, percent coverage, land fast, active floe or pack, relative age (e.g., new, nilas, young, grey, white), thickness (e.g. thin, medium, thick), floe size (i.e., small <2m to giant >10km), and the open water components (e.g., leads, polynya) (World Meterological Organization 1970, MANICE 2005).

Sea ice is a unique ecosystem and critical habitat for marine mammals and birds (Tynan and DeMaster 1997, Ainley et al. 2003, Laidre et al. 2008, Post et al. 2013). Pagophilic species have evolved to use sea ice for reproduction, foraging, resting, migration, and protection from predators (Moore and Huntington 2008). Sea ice habitat use and selection has been studied in a diversity of Arctic species including ringed seals (*Pusa hispida*) (Crawford et al. 2012), walrus (*Odobenus rosmarus*) (Jay et al. 2014), bowhead whale (*Balaena mysticetus*) (Ferguson et al. 2010), seabirds (Santora 2014), and polar bears (*Ursus maritimus*) (Laidre et al. 2015a). Low resolution (SSM/I-SSMIS 25 km resolution, AMSR-E 6.25 km resolution) satellite imagery has been used for modeling regional and circumpolar scale sea ice habitat (Arthur et al. 1996, Mauritzen et al. 2003b, Durner et al. 2009, Laidre et al. 2012, Wilson et al. 2014). Integrated sea ice charts created from medium (AVHRR 1 - 3 km resolution, MODIS 0.25-1 km resolution) and high (SAR 100-150 m resolution) resolution imagery have provided insights into ice habitat at regional scales (Ferguson et al. 2000, Durner et al. 2004, Ferguson et al. 2010, Wilson et al. 2014). More recently, high resolution imagery have been used to describe ice structure at the local scale of individuals and groups of animals (Bump and Lovvorn 2004, Jay et al. 2010, Melentyev and Chernook 2010, Ray et al. 2010, Laidre and Heide-Jorgensen 2011, Freitas et al. 2012, Santora 2014).

The sea icescape is composed of a dynamic mosaic of habitat patches that organisms respond to on different temporal and spatial scales (Wiens 1976, McGarigal and Marks 1995, Gustafson 1998). Studies of polar bear annual and multi-year sea ice habitat selection at the home range, population, and regional spatial and seasonal scales have found that sea ice concentration was the most important factor, followed by ice type (i.e., fast, pack, annual, multiyear), bathymetry, distance to ice edge, and distance to land (Arthur et al. 1996, Mauritzen et al. 2003a, Durner et al. 2009, Freitas et al. 2012, Laidre et al. 2015a). There is less understanding of how ice structure or microhabitat features, such as floe and lead characteristics, influence polar bear habitat selection. However, there is some understanding of the importance of floe size. For example, bears in the Arctic Archipelago selected large (>2000 m) floes in spring, summer, and autumn and in Baffin Bay, large floes in winter, spring, and summer (Ferguson et al. 2000), and, in the Beaufort Sea vast floes (2-10 km) were selected during spring and winter (Durner et al. 2004). More recently, a study of polar bear seal kills found that pack ice with floe size from 20-2000 m and thickness 10-30 cm was higher quality habitat (Pilfold et al. 2014a), and during the spring foraging season, there is strong selection for sea ice with about 85% ice cover (Durner et al. 2009, Pilfold et al. 2014a) suggesting that the mix of ice and open water creates high quality habitat. These studies used low resolution sea ice charts that did not allow exploration of micro-habitat structure. For example, leads vary in width from a few meters to tens of kilometers and are thought to be important polar bear habitat components (Kingsley and Stirling 1991, Stirling et al. 1993, Stirling 1997). Despite the importance of leads in polar bear habitat selection, quantification of such preference is limited because the imagery (SSM/I, AMSR-E) and maps (ice charts) used to describe ice habitat are only able to detect wide (>6.25- 25 km) flaw leads.

The objective of this paper is to use SAR imagery to study fine scale habitat selection of satellite collared female polar bears in the Foxe Basin population in Nunavut, Canada. We focus on the local spatial and 24 hour temporal scale (Mayor et al. 2009) or 3rd order of habitat selection (Johnson 1980, Meyer and Thuiller 2006). We examine how bears daily movements are influenced by sea icescape structure, as described by ice floes and open water leads (Fig. 1).

4.2 Methods

The study area included the sea ice of Foxe Basin, Hudson Strait and Hudson Bay, Canada (Fig. 2). These marine areas are shallow (predominantly <200 metres), productive seas that undergo an annual sea ice phenological cycle from ice-free to almost total ice cover (Prinsenberg 1986b, Fequet et al. 2011). All sea ice in the study area is annual and mainly comprised of active pack ice with a narrow band of fast ice adjacent the coastline and islands. In Foxe Basin and Hudson Bay the active pack ice circulates counter-clock wise with gyres, and in Hudson Strait it moves west to east with the dominant current (Prinsenberg 1986a). By March, the sea ice concentration is 80-100% comprised of a mix of medium (70-120 cm) and thick (>120 cm) first year ice, with floe sizes from 20-10,000 metres (http://iceweb1.cis.ec.gc.ca/Archive20). There are two large polynyas, Roes Welcome Sound and northern Foxe Basin, many small polynyas between islands and at the mouth of some bays, and recurring shore leads that parallel some of the coastlines (Stirling 1997). Climate change is affecting the sea ice, with later freeze-up date, earlier break-up and changes in the characteristics of the sea ice habitat (Saucier et al. 2004, Sahanatien and Derocher 2012, Hochheim and Barber 2014).

The study period was November – April in 2008-2010. These months have the coldest temperatures (mean monthly temperature range -16 to -33 C; http://climate.weather.gc.ca/), with little chance of water accumulation on the ice from melt or rain to complicate interpreting SAR satellite imagery. These months include the dark, often cloudy, and stormy winter period when optical satellite imagery is limited or unavailable but SAR imagery remains effective. Foxe Basin polar bears were active throughout winter, moving in the pack ice (Sahanatien et al. 2015). There are approximately 2,598 bears in the Foxe Basin population (Stapleton et al. 2015). The main polar bear prey species, the ringed seal, is abundant. Bearded seals (*Erignathus barbatus*), walrus, and other marine mammals (harp seals (*Pagophilus groenlandica*), harbour seals (*Phoca vitulina*), bowhead whales, narwhal *Monodon monoceros*), and beluga (*Delphinapterus leucas*)) are also present depending on sea ice conditions (Sergeant 1986, Stewart and Lockhart 2005, Thiemann et al. 2008b, Ferguson et al. 2010, Pilfold et al. 2012).

Polar Bear Locations

Location data from 27 adult female polar bears were obtained by global positioning system (GPS) satellite collars (Telonics Inc., Mesa, AZ, USA) linked to Argos satellites (CLS America, Lanham, MD, USA) deployed in August-October, 2008 and 2009. Standard capture and handling protocols were used (Stirling et al. 1989) and were approved by the University of Alberta Animal Care and Use Committee for Biosciences. The GPS location accuracy was <10 metres, well within the resolution of the SAR satellite imagery. The reproductive status of the female bears used in this study was: 11 with cubs-of-the-year, 15 with yearlings and 1 with no cubs. The SAR archives were searched for images within the study area and were collected within 48 hours of bear locations. Bear locations were used in sequential pairs separated by 24 hours: a location at time 1 (T_1) was used to establish availability (choice sets, see below) and a second location 24 hours later (T_2) was used as an observation of selected habitat. Considering the availability of SAR images, a total of 131 pairs (November n=15, December n=22, January n=20, February n=24, March n=24, April n=26) generated by 27 bears were used in the analysis. All bear location pairs were in Foxe Basin, Hudson Strait and Hudson Bay (Fig. 2).

Sea ice Conditions 2008-2009

Freeze-up, ice thickness, concentration and extent were near average in 2008-09 except in Hudson Strait during December when ice thickness was less than average, with predominantly grey white (15-30 cm) rather than first year ice (≥ 30 cm) (Canadian Ice Service 2009). By the end of January 2009, ice conditions were near average. In 2009-10, ice growth was slower than average but by the end of December ice concentrations were average but ice thickness remained lower than average in Hudson Strait (thin first year ice 30-70 cm) (Canadian Ice Service 2010). Because SAR image classification describes the sea ice surface conditions, variation in ice thickness should not have affected the results.

Satellite Imagery & Sea Ice Habitat Classification

SAR imagery was used to map sea ice habitat structure. We used SAR (C-band, HH polarization, ascending and descending node) imagery from three satellites: ENVISAT, RADARSAT-1 and RADARSAT-2. ENVISAT ASAR wide swath images https://earth.esa.int/ (pixel size 75 metres with nominal resolution of 150 m and swath width 500 km) were acquired from the European Space Agency background archive (Project A0E.500, Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Canada). The RADARSAT-1 and RADARSAT-2 ScanSAR wide images http://www.asc-csa.gc.ca/eng/satellites/radarsat/ (pixel size 50 metres with nominal resolution 100 metres and swath 500 km wide,) were obtained from the Canadian Space Agency archive through a collaborative research agreement with Parks Canada.

Each SAR image was imported, geo-referenced and projected using ENVI© software v4.7 (Boulder, CO, USA). All original images were resized to approximately 60 x 60 km regions of interest (ROI) to reduce processing time (smaller file size) and to reduce backscatter variation due to satellite slant range, thus permitting consistent ice structure classification. ROI dimensions were calculated using the mean monthly on-ice movement rate of satellite collared female polar bears in Foxe Basin (mean ± standard error = 1.1 ± 0.03 km/h). Each ROI was centred on an initial polar bear location (i.e., a location at T_1 of a pair) and if a bear moved beyond the ROI in 24 hours, the ROI was adjusted accordingly.

Sea ice habitat structure was described by mapping ice floes and open water lead features or patches. To map the features we used ENVI-EX© software (Boulder, CO, USA) to classify and create a separate floe and lead layer for each ROI (Fig. 3). Floes were classified using the feature (object based) extraction work flow (ITTVIS 2009) and shape (round) based rules, with texture and spectral fuzzy classification tolerances. Floe ice, which is relatively smooth and level produced low backscatter and was contrasted with the higher backscatter values of ridged ice that delineates floe edges (Fig. 1) (Johannessen et al. 2007). Leads were classified using the supervised classification work flow, where training areas were manually selected on each ROI to identify lead backscatter values; smoothing and aggregation was permitted to reduce the number of isolated lead pixels. Leads were distinguished by their linear form with low backscatter values that are dark on the imagery (Johannessen et al. 2007). Land was masked out in all ROIs. MODIS images (http://modis.gsfc.nasa.gov/), when available, were used to visually verify the accuracy of the lead classifications. We did not ground validate the satellite images because this study was developed after the images were collected but we observed the sea ice types, structure, and distribution during an April 2009 helicopter aerial survey for polar bears in the study area which assisted in accurate image classification.

Each floe and lead classified ROI was imported into ArcGIS v9.3.1 (ESRI, Redlands, CA, USA), re-projected (Polar Stereographic, central meridian -79.00° W and parallel of 66.50° N) because the projection was lost during processing in ENVI-EX, and exported as an ASCII file. The ROI ASCII files and bear location files were imported into R software (R Development Core Team 2010) to calculate the patch configuration metrics. The metrics described the presence, amount, and spatial distribution of floe and lead patches (Table 1, Appendix B) at each used and available bear location. Patch metrics were computed by calling custom Fortran routines from within R to mimic the functionality of FRAGSTATS (McGarigal et al. 2002). While unavailable at the time, similar functionality is now available in R package 'SDMTools' (https://cran.r-progject.org/web/packages/SDMTools/).

Each pair of polar bear locations was intersected with its time coincident floe and lead ROIs, as well as broad scale variables. A circular large buffer with radius 26.4 km, the mean distance that a study bear moved in 24 h, was delineated on each ROI with the bear location T_1 at its centre (Fig. 3). The large buffer represented the habitat available to a bear for the following 24 h (Arthur et al. 1996, Durner et al. 2009). The second bear location (T_2) was considered a selected habitat, or used point. A smaller buffer of radius 4.4 km was constructed around the used point to delineate the icescape that a polar bear potentially experienced in the 4 h preceding the T_2 GPS location. Other locations that could have been selected by the bear were represented by a systematic (grid) sample of 20 points, and their associated 4.4 km radius buffer, drawn from the large circular buffer centred on the location at T_1. Ice floe and open water lead characteristics were summarized within all 21 4.4 km buffers, in each ROI.

In addition to ice floes and open water lead features, three broad scale variables, distance to land (km), bathymetry (m) and ice concentration (%) were measured in ArcGIS to allow comparison with other polar bear habitat analyses. Bathymetry was determined using the General Bathymetric Chart of the Oceans (www.gebco.net). Sea ice concentrations were gathered from daily Special

Sensor Microwave/Imager (SSM/I) passive microwave data, with 25 km resolution (Cavalieri et al. 1996).

Sea Ice Habitat Modelling

We used discrete choice resource selection functions (RSFs) (McDonald et al. 2006) to evaluate habitat selection. Before modelling, we examined all continuous variables for nonlinearity using natural log and quadratic transformations, as well as potential covariate interactions. Pairwise correlations were evaluated using Pearson's correlation matrix (Conover 1980) and variables with a correlation coefficient $|r| > 0.6$ were excluded from the same model (Appendix B). We compared the suite of sea ice characteristics including floe, lead, distance to land, bathymetry, and ice concentration (Table 1) of the used and available locations by estimating the discrete choice habitat model and performing variable selection. Discrete choice models are commonly employed for polar bear RSFs (Arthur et al. 1996, Durner et al. 2004, Durner et al. 2009) because they allow individual used points to be matched temporally to available points within a defined buffer; these models have been shown to perform equivalent to or better than alternative techniques (Baascha et al. 2010). Here, each of the $n = 131$ choice sets had 1 used point (at T_2) matched to the 20 available points selected by the systematic sample. Our sample size was limited by the spatial and temporal availability of SAR imagery that coincided with the distribution of polar bear locations.

We used a fixed effects model design and evaluated 39 *a priori* models using Akaike's Information Criterion for small sample sizes (AIC_C; (Burnham and Anderson 2002)) (Appendix B). Covariates were ranked by importance using the sum Akaike weights (w_i). Scaled response curves for the covariates in the top model were generated for the range of values observed, excluding outliers.

4.3 Results

The polar bear locations (n=131) and SAR imagery were distributed throughout the study area (Fig. 4.2). All bears were located in active pack ice. Used locations had mean ice concentration of 88 ± 1% (range 27-100%), mean distance to land of 52 ± 4 km (range 0-242 km), and mean ocean depth of 153 ± 9 m (range 1-468 m). These broad scale covariates were not significant in the top set of resource selection models (Appendix B).

One lead and three floe patch metrics were included in highest ranked (Δ $AIC_c \leq 2$) habitat selection models (Table 4.2). The top model had two metrics of sea ice structure: floe patch density and lead patch density. The top model was slight improvement over the single covariate models but not significantly (Table 4.3). Polar bears had positive selection for lead patch density and negative selection for flow patch density (Table 4.4, Fig. 4.4). Floe patch configuration may have greater influence on bear sea ice habitat selection as two additional floe metrics were in model 3 and 5: the number of floe patches and density (km/km^2) of floe patch edge.

4.4 Discussion

We documented female polar bears' response to sea ice habitat structure at the local spatial and daily temporal scale. This is a fine scale or grain of habitat selection (Kotliar and Wiens 1990) and the highest resolution described for this species. Standard broad scale variables, ice concentration, bathymetry and distance to land (Mauritzen et al. 2003a, Durner et al. 2009, Pilfold et al. 2014a, Wilson et al. 2014), were not in the top models. Instead the fine scale characteristics of sea ice, floe and lead patch density were found to be important to bears when foraging on the annual sea ice of Foxe Basin-Hudson Bay-Hudson Strait. We recognize the results are based on a small sample size (n=131), which affected the strength of the beta estimates, but we demonstrate that fine scale research is needed to reveal the functional relationships between bears, their prey and the sea ice ecosystem.

Polar bears capture most of their prey on or from the sea ice (Stirling 1974, Stirling and Latour 1978). When the Foxe Basin bears return to the sea ice at freeze-up they end a 3-4 month fast in terrestrial habitat (Sahanatien et al. 2015). Thus during the study period, the satellite collared female bears were foraging to recover mass lost during the annual ice-free season and to feed their cubs (Derocher and Stirling 1990a). A second important behavioural driver is the peak of the mating season, from March-May (Ramsay and Stirling 1986). During mating season female bear habitat selection can be influenced by male bears when females with cubs avoid males (Pilfold et al. 2014a) or when receptive females (solitary or females with 2.5 year old cubs) are courted and their movements restricted by males (Ramsay and Stirling 1986, Derocher et al. 2010). But in either instance, during the mating season, females will continue to forage (Laidre et al. 2012) as this is also the beginning of the hyperphagic feeding period (Stirling and Øritsland 1995), when seals and walrus are vulnerable because they are giving birth or have dependent young.

Floe patch density described the complexity and roughness of sea ice. High floe patch density means the icescape is composed of many, smaller ice floes. Smaller floes result from high energy environments, with strong winds, currents and/or tides that move, deform and fracture sea ice (Johannessen et al. 2007, Comiso 2010). Lower energy environments result in larger, smoother surfaced ice floes. Our observation that female polar bears have negative selection for floe patch density, thus select for larger floe size, supports habitat selection studies that included a floe structure covariate (Ferguson et al. 2000, Durner et al. 2004, Pilfold et al. 2014a). Ringed seals also prefer sea ice with lower degrees of deformation (Hammill and Smith 1989, Moulton et al. 2002, Frost et al. 2004, Bengtson et al. 2005) but not so smooth to preclude snow accumulation for building haul-out and birth lairs (Stirling et al. 1993). Lairs are a focus for polar bear foraging in winter and spring (Smith and Stirling

1975, Gjertz and Lydersen 1986, Hammill and Smith 1991, Furgal et al. 1996, Pilfold et al. 2014b). Too little ice structure, in the form of ridges and pressure ice, can also reduce the diversity and abundance of lower trophic species that support seals (Gradinger et al. 2010).

Lead patch density described the amount of detectable open water in the icescape and bears selected for this characteristic. Leads are areas of active ocean-atmospheric energy exchange, where heat escapes to the surface during winter and year round gaseous exchange occurs (Smith et al. 1990, Miles and Barry 1998, Marcq and Weiss 2012, Moore et al. 2014). Higher sea surface temperature during winter at and near leads may provide thermoregulation benefits to wildlife that use the sea ice surface (Santora 2014). Leads also allow the penetration of sunlight into the ocean which increases local under and within ice productivity (Garćia-Martín et al. 2014), producing greater biodiversity and biomass along the pack ice edges (Gradinger and Bluhm 2004). Productivity in winter is reduced but it continues even during the 24 hour dark period in the high arctic (Darnis et al. 2012). In northern Foxe Basin sunlight is lost from December 1st – January 9th but by mid-January there are 3 hours of sunlight and in the southern part of the study area at the winter solstice there are 4 hours of sunlight to provide energy to power the sea ice ecosystem.

Low lead patch density means the pack ice is consolidated or closed, with restricted access to the surface for marine mammals to breath and to enter the water from the ice surface for foraging or escape from predatory polar bears (Stirling 1997, Heide-Jorgensen et al. 2012). Ringed seals are primarily found in stable fast ice and consolidated pack ice where they maintain breathing holes (Smith and Stirling 1975). Breeding ringed seals maintain territories over winter in fast ice (Kelly et al. 2010) which would affect the density of available prey in this habitat. Higher lead patch density or open pack ice has higher biodiversity and potentially better foraging as bearded seals, harp seals and walrus preferentially inhabit open pack ice. Marine mammals are vulnerable at leads because bears still-hunt at the ice edge waiting for surfacing prey and can be killed while hauled-out on the ice next to a lead by a bear stalking from the water or the ice surface (Stirling 1974, 2011, Pilfold et al. 2015).

It is difficult to interpret our lead density results without additional empirical information. Stirling et al (1993) hypothesized that high lead density would make movement across the icescape physically difficult thus energetically expensive for polar bears and there would be greater opportunities for prey to escape into the water. While winter observations of polar bears and Arctic seals are limited, biologists and Inuit hunters have observed that polar bears commonly follow leads for many kilometers, apparently searching for foraging opportunities (Stirling 2011, Derocher 2012) and Pilfold et al. (2014a) found that bears had a preference for hunting in active pack ice. Adult and subadult ringed seals use pack ice habitat throughout the ice season and will breed there if the ice is sufficiently stable to support pups in lairs for 5-6 week nursing period (Finley et al. 1983, Hammill and Smith 1991, Wiig et al. 1999, Bengtson et al. 2005). Spring aerial surveys during peak haul-out time (May-June) found that ringed seals preferred land fast ice and consolidated pack ice (Frost et al. 2004, Bengtson et al. 2005, Chambellant et al. 2012a). Frost et al. (2004) also found that seal density was highest near the fast ice edge, where open water and leads are found. During spring and early summer, ringed seals and bearded seals make extensive use of leads (Kingsley and Stirling 1991). Little was known about ringed seal ecology in the pack ice due to the logistical challenges (Smith 1980, Hammill and Smith 1991) until satellite telemetry showed that subadult seals move preferentially to the pack ice in winter (Krafft et al. 2007, Crawford et al. 2012). In western Hudson Bay, ringed seals pup from mid-February – May (Chambellant et al. 2012b) so it is possible that juvenile seals were available in birth lairs on the pack ice in Foxe Basin during the study period as observed in other regions (Pilfold et al. 2014b).

The satellite-collared Foxe Basin bears moved almost exclusively in the active pack ice from freeze-up to break-up. Polar bears in other regions also make extensive use of active pack ice (Stirling et al. 1975, Smith 1980, Ferguson et al. 2001, Mauritzen et al. 2003b, Laidre et al. 2015a). All four primary prey species (ringed, bearded and harp seals and walrus) are present in the pack ice of our study area but data are unavailable on the distribution and abundance of prey species on the sea ice. Based on these observation it follows that prey are either more abundant or have greater vulnerability to predation on the pack ice than land fast.

While ringed seals are the primary prey of polar bears it is important to consider the distribution of other prey in relation to pack ice. Bearded seals preferentially use pack ice and the fast ice floe edge throughout the year (Bengtson et al. 2005, Ray et al. 2010) and can maintain breathing holes in winter (Stirling and Archibald 1977). They give birth and rear their pups on stable pack ice but do not build subnivian lairs (Kovacs et al. 1996, Lydersen and Kovacs 1999). Harp seals, an important prey species for the adjacent Davis Strait polar bears (Iverson et al. 2006, Peacock et al. 2013), in late winter may become an important prey species in Hudson Strait where the pack ice is more open and climate change is reducing sea ice. Walrus also prefer open pack ice from which they forage and birth (Ray et al. 2010, Jay et al. 2014), and this species is observed throughout our study area (Stewart et al. 2013).

Application of SAR imagery to sea ice habitat analyses

The SAR imagery captured the detailed structure (floes and leads) of the pack ice. We used landscape configuration metrics to control for the dynamic nature of pack ice, where leads open, close, change size and shape on a daily basis.

The two main challenges we identified were processing time and potential imagery costs. Separate images had to be manipulated for each bear location but the benefits of high resolution imagery and dark season availability offset the processing time. Automated classification techniques for SAR imagery continue to improve (Ochilov 2012, Zakhvatkina et al. 2013, Liu et al. 2014) and the recent integration of ENVI with ArcGIS may increase the efficiency of using SAR for fine scale sea ice habitat research. SAR spatial and temporal coverage can be a challenge unless a mission is planned in advance. Otherwise it is necessary to rely on the coverage provided through other research and monitoring efforts. In this study, we relied upon the SAR images collected for the production of the weekly and monthly sea ice charts and the additional images that were collected for other projects in the region. SAR imagery can be expensive (gs.mdacorporation.com/SatelliteData/Radarsat2/Radarsat2.aspx) to acquire *de novo,* but there are new SAR equipped satellite missions planned like the European Space Agency's Sentinel mission (https://sentinel.esa.int/web/sentinel/home) which will provide SAR imagery for free.

SAR and other high resolution imagery have potential for describing and quantifying fine scale polar bear sea ice habitat, particularly in the high Arctic where darkness dominates for 6 months each year. There are many avenues for remote sensing research, a few examples are: model a regional seal habitat suitability index (Iacozza and Ferguson 2014), create a continuous surface metric (e.g., texture) layers (McGarigal et al. 2009), and develop a floe stability index based on ice thickness.

Research to date has provided broad scale perspectives of polar bear sea ice habitat selection and is probably not detecting important information. Only one other study used high resolution SAR imagery and it revealed that an important habitat, the thin strip of fast ice adjacent land and glacier fronts, had been overlooked because it could not be detected by lower resolution imagery that is commonly used in polar bear habitat studies (Freitas et al. 2012). Our study demonstrates that by using high-resolution imagery to study ice floe and lead structural characteristics we can more closely link this top predator with the sea ice ecosystem and begin to consider the influence of bottom-up processes on bears. The second contribution we make is to bring attention to pack ice and its value as polar bear habitat. Pack ice has received superficial attention considering it is the dominant sea ice habitat of many polar bear populations. Pack ice may have been overlooked due to logistical challenges of working in this harsh environment for humans and aircraft; resulting lower levels of direct experience, observations, and insights about the active pack ice. This deficiency can be overcome by use of ice-breaker ship based field research, high resolution temporal resolution GPS satellite collar movement data from polar bears and their prey species, and increased use of high resolution satellite imagery.

Table 4.1 Covariates used to model the fine scale sea ice habitat resource selection function of satellite collared female polar bears, Foxe Basin, Nunavut, Canada (November-April, 2008-2010).

Habitat Covariate	**Definition**
Floe.patch.number	Number of floe patches in small buffer[1]
Floe.patch.area	Area (km²) of all floe pixels in small buffer[1]
Floe.patch.density	Density (patch/km²) of floe patches in small buffer[1]
Floe.edge.density	Length of floe patch edge per small buffer (km/km²)[1]
Floe.centre.value	Value (0=not in floe, 1=in floe) of pixel at the used or available location[1]
Distance.to.floe	Distance from centre of small buffer to nearest floe patch[1]
Lead.patch.density	Density (patch/km²) of lead patches in small buffer[1]
Lead.mean.patch.size	Mean size (km²) of lead patches in small buffer[1]
Lead.SD.patch.size	Standard deviation of the mean lead patch size in small buffer[1]
Lead.centre.value	Value (0=not in lead, 1=in lead) of pixel at the used or available location[1]
Distance.to.lead	Distance from centre of small buffer to nearest lead patch[1]
Distance.to.Land	Distance from used or available location to land
Depth	Depth of ocean at used or available location[2]
Ice.Concentration	Ice concentration (%) at used or available location[3]

[1] Source: SAR satellite imagery, [2] Source: GEBCO bathymetric chart, [3] Source: SSM/I satellite imagery

Table 4.2 Model selection results for satellite collared female polar bear fine scale sea ice habitat resource selection with Akaike Information Criterion scores corrected for small sample sizes (AIC_c), delta AIC_c (ΔAIC_c), model weight (*w*) and number of parameters retained (*k*), Foxe Basin, Nunavut, Canada (November-April, 2008-2010).

Model	***k***	**AIC_c**	**ΔAIC_c**	***wi***
Floe.patch.density + Lead.patch.density	2	794.5	0	0.19
Floe,patch.density	1	795.5	1.02	0.12
Floe.patch.number + Floe.patch.density + Lead.patch.density	3	795.6	1.12	0.11
Lead.patch.density	1	795.9	1.44	0.09
Floe.patch.density + Floe.edge.density + Lead.patch.density	3	796.2	1.76	0.08
Floe.patch.number	1	797.1	2.63	0.05

Table 4.3 Comparison between the top model and the single covariate models of fine scale sea ice habitat resource selection of satellite collared female polar bears, Foxe Basin, Nunavut, Canada (November-April, 2008-2010).

Model	**Log-Likelihood**	**Chi-Square**	**df**	**P-value**
Floe.patch.density + lead.patch.density	-395.195			
Floe.patch.density	-396.738	3.086	1	0.08
Lead.patch.density	-396.949	3.507	1	0.06

Table 4.4 Beta estimates and confidence intervals for top model covariates for the fine scale sea ice habitat resource selection model of satellite collared female polar bears, Foxe Basin, Nunavut, Canada (November-April, 2008-2010).

Covariate	**Beta**	**SE**	**Upper**	**Lower**
Floe.patch.density	-0.289	0.160	0.023	-0.602
Lead.patch.density	0.622	0.341	1.290	-0.045

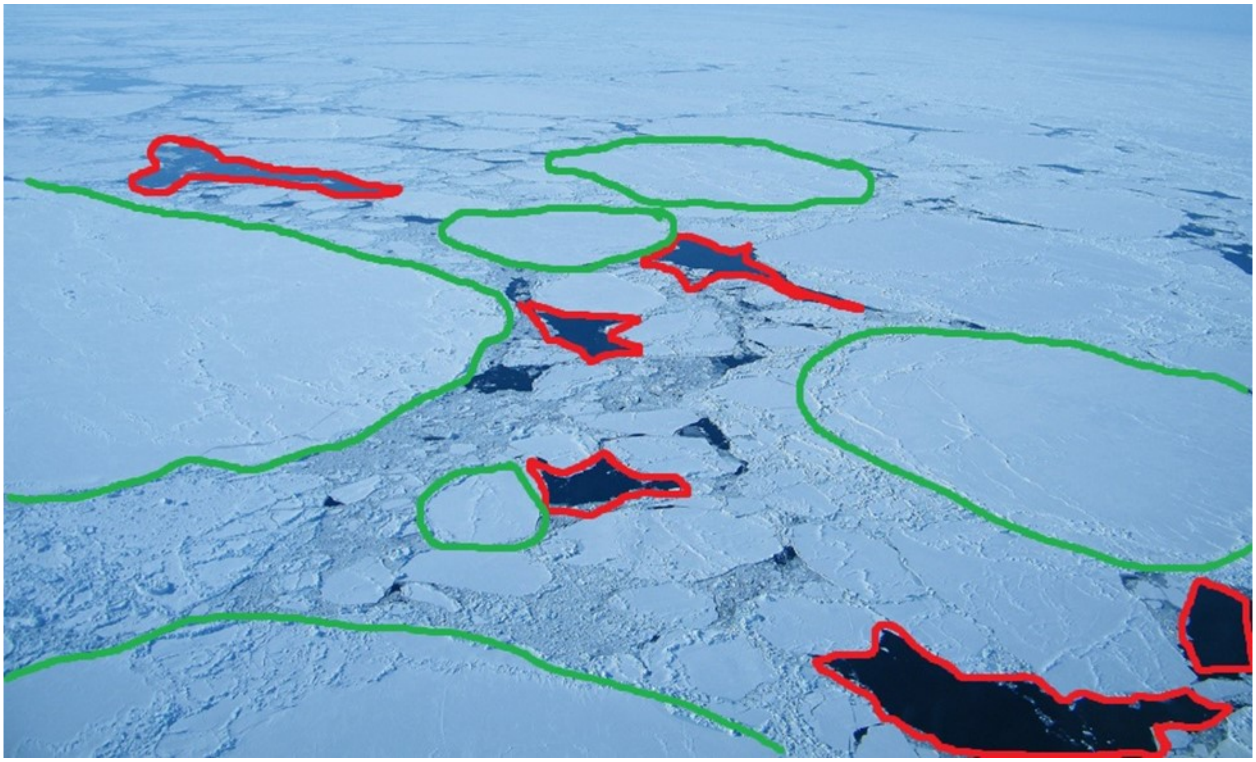


Figure 4.1 Sea ice floes (green outline) and leads (red outline), Foxe Basin, Nunavut, Canada. (photograph taken, April 2009).

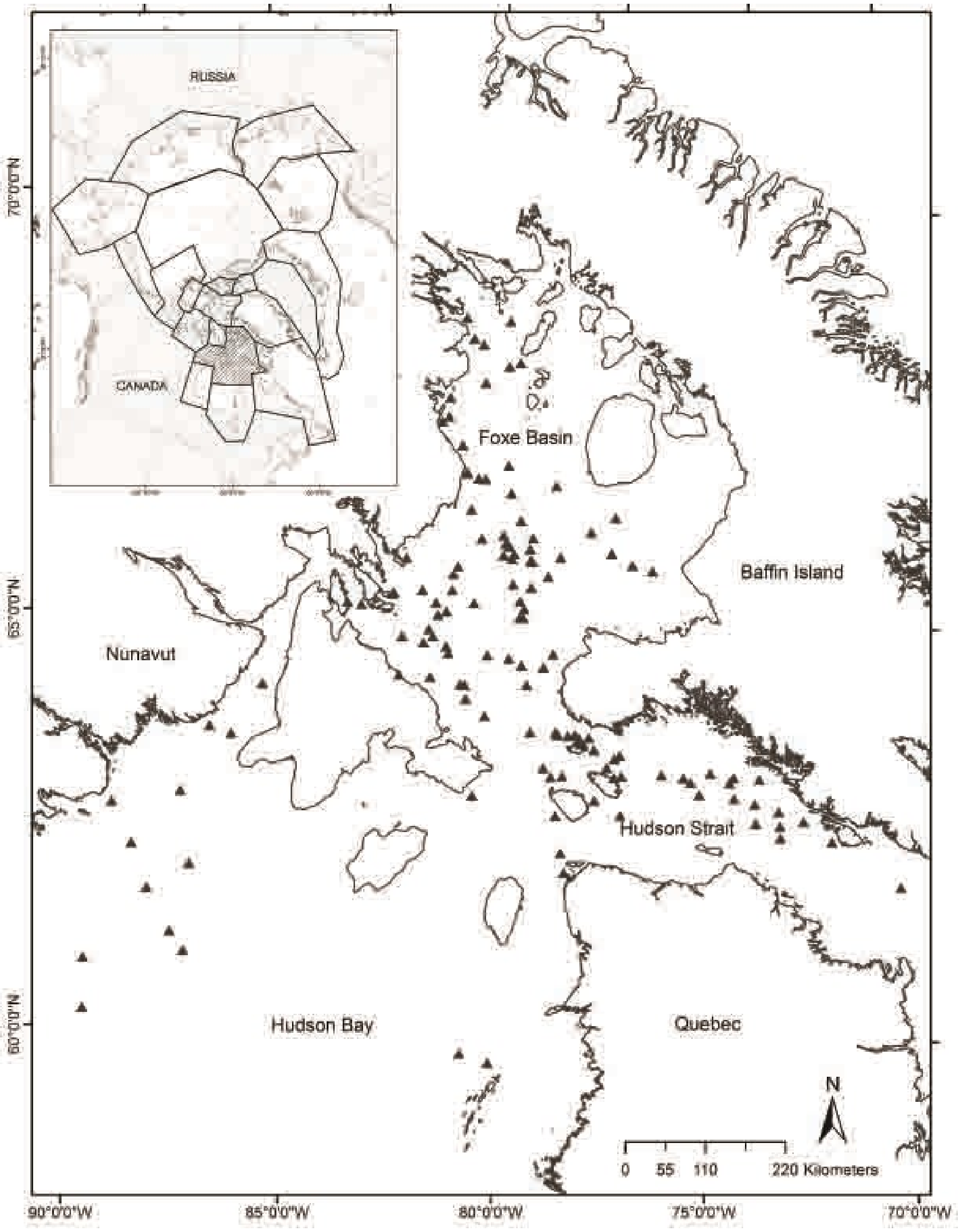


Figure 4.2 Study area with locations of satellite collared female polar bears, Foxe Basin, Nunavut, Canada (November-April, 2008-2010).

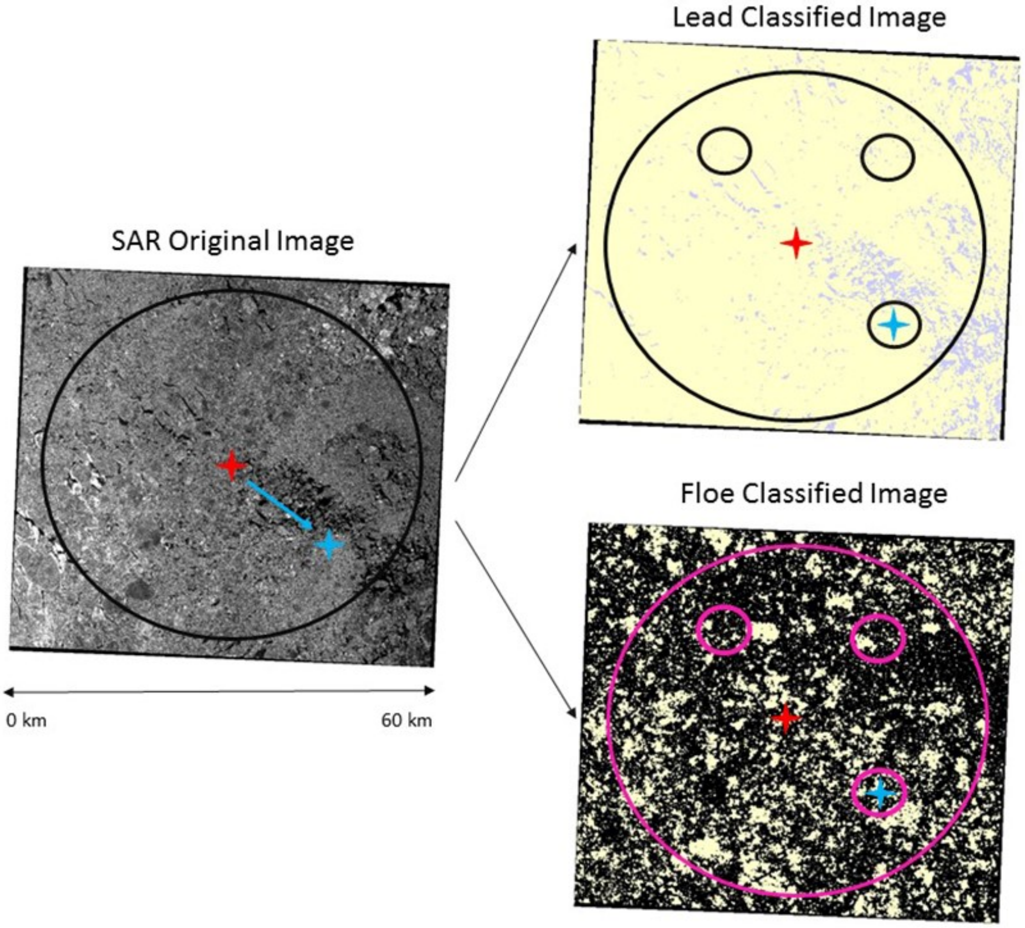


Figure 4.3 Classification of SAR imagery to create lead and floe images. The red star is the bear location at T_1 and the blue star at T_2 (selected location). The large black circle delineates the available sea icescape and the small black circles are a subset of the small buffers within which lead and floe ice characteristics were calculated.

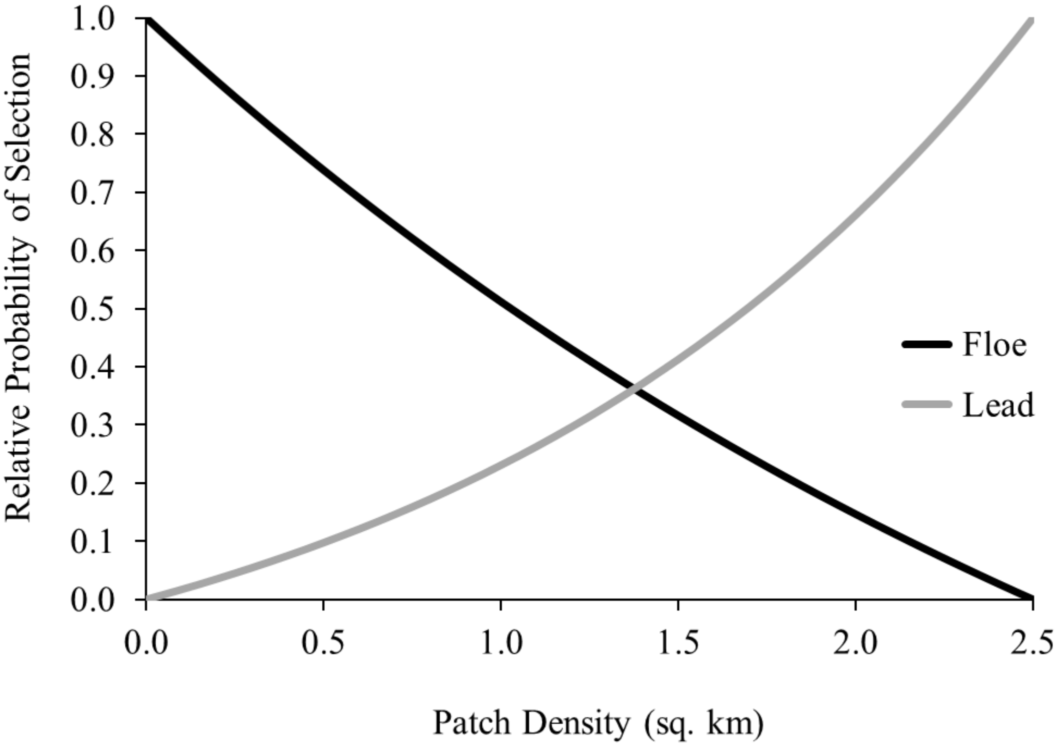


Figure 4.4 The relative probability of selection of sea ice habitat as a function of floe and lead patch density (/km²) for satellite collared female polar bears, Foxe Basin, Nunavut, Canada (November-April, 2008-2010).

Chapter 5

5 Factors influencing terrestrial movements and distribution of polar bears during the ice-free season

5.1 Introduction

Movements of individual animals are affected by four main components: external factors (abiotic and biotic environment), internal state, navigation capacity, and motion capacity (Nathan et al. 2008, Schick et al. 2008). It is challenging to study, interpret, and integrate all components in movement models (Nathan et al. 2008). As a result, many movement studies focus on one or a subset of components. There are, however, a growing number of empirically based integrative modeling approaches for movement (e.g., (Avgar et al. 2013, Bestley et al. 2013, Martin et al. 2013).

In high latitude ecosystems, seasonality imposes strong external influences on movements and distributions of wildlife in the form of extremes of daylight/darkness, climate, and, habitat availability and productivity. Each summer, in many parts of the Arctic, polar bears (*Ursus maritimus*) use terrestrial habitats when they are forced on land as their sea ice habitat melts and becomes unavailable (Derocher and Stirling 1990a, Schliebe et al. 2008). Of 19 polar bear populations in the circumpolar Arctic, five follow an annual cycle of moving off of sea ice when it melts and back onto ice when it reforms in the seasonal ice ecoregion (Amstrup et al. 2008, Thiemann et al. 2008a). The polar bear is a marine species that relies on sea ice as the platform for hunting, mating, travel, and in some areas, for denning (Smith 1980, Ramsay and Stirling 1986, Mauritzen et al. 2003b, Fischbach et al. 2007). The presence and nature of sea ice strongly influence energy intake in bears because their primary prey, ringed seals (*Pusa hispida*), are usually hunted from the surface of sea ice (Stirling and Archibald 1977, Smith 1980, Pilfold et al. 2012). Polar bears are rarely successful preying on seals without the aid of ice thus the energetic intake from such behaviour is considered to be minimal (Stirling 1974, Furnell and Oolooyuk 1980).

Understanding of polar bear terrestrial ecology is limited to a few populations (Knudsen 1978, Latour 1981b, Derocher and Stirling 1990a, b, Ferguson et al. 1997, Ovsyanikov 2005, Gleason and Rode 2009). On land, polar bears are sedentary, reducing movements to save energy and maintain fat reserves until denning or returning to the sea ice at freeze-up (Derocher and Stirling 1990a, Parks et al. 2006). Polar bears may segregate on the landscape by sex and reproductive status, with males nearest the coast and females inland (Derocher and Stirling 1990a). Males can be social, forming groups from 2-14 bears that physically interact in play fights and rest close together (Latour 1981a, Derocher and Stirling 1990b) but females are rarely social (Lunn 1986). Female and male polar bears show fidelity to terrestrial retreats and denning habitat (Parks et al. 2006, Cherry et al. 2013). The bears readily swim but most published accounts focus on movement between sea ice and shore during break-up (Durner et al. 2011, Pagano et al. 2012) or swimming across leads in the sea ice (Stirling 1974) but not during the ice-free season.

Polar bears typically consume little during terrestrial periods and rely on stored fat reserves accumulated while hunting on the sea ice (Stirling et al. 1977, Watts and Hansen 1987, Ramsay and Stirling 1988). Opportunistic foraging and scavenging by polar bears, however, is common (Russell 1975, Derocher et al. 1993, Dyck and Romberg 2007, Stempniewicz et al. 2013, Iverson et al. 2014), but these foods do not offset the net caloric deficit that occurs during the ice-free season (Ramsay and Hobson 1991, Rode et al. 2010b, Rode et al. 2015). As climate continues to warm and the ice-free period lengthens (Galbraith and Larouche 2011, Hochheim and Barber 2014, Stroeve et al. 2014a) polar bears are on shore longer (Stirling et al. 1999). The increased open water period has been correlated with declines in survival, reproductive rates, and population decline (Stirling et al. 1999, Regehr et al. 2007, Regehr et al. 2010, Bromaghin et al. 2015). Increased time on land is also associated with increased human-bear conflict (Stirling and Parkinson 2006, Towns et al. 2009).

The objective of this study was to examine the terrestrial movement patterns and behaviour of polar bears during the annual period of minimum ice cover in the seasonal sea ice ecoregion of Foxe Basin in Nunavut, Canada. Using satellite telemetry, I examined female and male polar bear distribution, movement paths and metrics, swimming behaviour, and fidelity to terrestrial range.

5.2 Methods

Study Area

The Foxe Basin polar bear population includes the coastal areas of Foxe Basin, northern Hudson Bay and western Hudson Strait, Nunavut, Canada (Fig. 5.1). All three marine water bodies are shallow (predominantly <200 metres deep), productive seas that undergo an annual phenological cycle from ice-free to almost total ice cover (Prinsenberg 1986b). Freeze-up begins in October and is complete in late December or January; break-up and melt begins in May and continues into August. Sea ice in the area is undergoing significant changes in response to climate change (Saucier et al. 2004, Sahanatien and Derocher 2012, Hochheim and Barber 2014). During break-up, when the sea ice concentration declines to approximately 30%, polar bears leave the ice for land and use terrestrial habitats until the sea ice refreezes (Cherry et al. 2013).

The coastline of Foxe Basin and Hudson Strait coastlines are complex with many offshore islands ranging in size from a few hundred square metres to Baffin Island at 507,450 km^{2}and fjords (Martini 1986). Hudson Bay, in contrast, is comparatively smooth with few offshore islands. The topography of the coast and adjacent land is diverse: from flat to rolling semi-mountainous terrain up to 600 m. The diet of polar bears include: ringed seals, bearded seals (*Erignathus barbatus*), harbour seals (*Phoca vitulina*), harp seals (*Pagophilus groenlandicus*), walrus (*Odobenus rosmarus*), bowhead (*Balaena mysticetus*), narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*), although ringed seals comprise about 70% of the diet (Sergeant 1986, Thiemann et al. 2008b).

Capture and Deployment of Satellite Collars and Ear-Tags

Polar bears were caught using tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Laboratories, Fort Dodge, IA, USA) at a concentration of 250 mg/ml and administered at approximately 5mg/kg delivered by remote injection from a helicopter. All bears were caught on land, during the ice-free season, following standard capture and handling methods (Stirling et al. 1989). Animal handling protocols were approved by the University of Alberta Animal Care and Use Committee for Biosciences.

Global positioning system (GPS) satellite collars, Telonics, Inc., Mesa, AZ, USA) linked to Argos satellites (CLS America, Lanham, MD, USA) were deployed on adult female polar bears with cubs-of-the-year, yearlings, and 2 females without offspring in August-October, 2007–2009. Collars had a potential lifespan of 1 to 2 years. Argos satellite linked GPS ear-tag transmitters (Wildlife Computers, Redmond, WA, USA) with a potential lifespan of 6 months were deployed on adult males. The number of active collars and ear tags varied over time due to battery longevity and failures (Appendix C). The satellite collars were monitored until October 2011.

Collar location data were collected at 3 or 4 hour intervals with GPS location accuracy <10 m with the exception of 2 bears whose collars provided only Argos locations for part of the year, of which I used locations with accuracy

<350 m. Ear-tag location data, collected once per day, had an accuracy <350 metres.

ArcGIS 9.3.1 (ESRI, Redlands, CA, USA) was used to plot location data, plot movement paths, and measure elevation (m) of locations using CanVec 1:50,000 NTS layers (http://geogratis.gc.ca/geogratis/Home?lang=en). Hawth's Tools (Beyer 2004) was used to calculate step length (km) and direction (°), displacement distance (km) between selected locations, total distance (km) moved on land, and path sinuosity index. Log_{10} transformation for non-normal distributions were used for: distance to coast, elevation, total distance moved, displacement, and swim distance. Elevation and sinuosity index could not be normalized. I compared group means using paired t-test and one-way ANOVA with Tukey's HSD post hoc multiple comparison test for normal and transformed data, and Mann-Whitney U-test and Kruskal-Wallis ANOVA for non-normalized data. All statistical tests were performed in OriginPro 9 (OriginLab Corp., Northampton, MA, USA). Analyses were considered statistically significant at $P \leq 0.05$ and $\bar{x}$ are ±1 standard error of the mean.

Movement behaviours, metrics and terrestrial distribution were compared between sex, family groups, and month. The family groups compared were: female & COY (cubs-of-the-year), females & YRLG (cubs>one year old), and solitary females (females without offspring). Analyses were constrained to August to November when sea ice concentrations were at their lowest and polar bears were on land.

Terrestrial Distribution

All ice-free terrestrial locations of satellite collared female polar bears and ear-tagged male polar bears from 2007-2011 were included to describe terrestrial distribution. Distance to coast and elevation were used to assess spatial segregation by sex and family group. Temporal comparisons of bear distribution were made between months (August – November) to investigate changes in bear distribution over the ice-free season.

Terrestrial Movement Behaviour

All locations of male and female polar bears were used to calculate terrestrial movement metrics: terrestrial days (number of days from collaring date or first day on land at break-up to last day on land at freeze-up), total distance (km) moved, and movement rate (km/d). The ice-free season movement path sinuosity index was used to describe landscape scale polar bear movement behaviours. Sinuosity index was calculated using Hawth's Tools (total path length/straight line distance from first location to last location: 1.0 is a straight line and higher values are more sinuous). I compared the movement metrics by sex, family group, and between months.

Long distance overland movements were identified as a bear moving from one body of water to another across land. These movements contrasted with the common coastal movements of collared bears. Overland movements were described using a path sinuosity index, duration (days), month, bearing (°), and total distance (km). The annual ice-free season movement path index was used to describe landscape scale polar bear movement behaviours. Oriana v4 (Kovach Computing Services, Anglesey, Wales) was used to calculate circular statistics and Rayleigh's uniformity test (Batschelet 1981) was used to determine if the step bearings making up each overland movement path were distributed uniformly or directionally about the mean step bearing.

Fidelity to summer range was measured using: 1) the distance (km) from capture location or first location on land at break-up to the last location on land at freeze-up, and, 2) the inter-annual distance (km) from the last location on land at freeze-up in year one to the first location on land at break-up the next year.

Swimming Movements

Swimming events were identified by movements from the ice edge to land, and between islands and coastal areas during the ice-free season. Daily and weekly sea ice charts (http://iceweb1.cis.ec.gc.ca/Archive20/?lang=en) were used to document open water conditions for each swimming event. For sex and family group swim distance comparisons I used each swim bout distance/bear.

5.3 Results

Satellite collars were deployed on 58 adult females and ear tags on 5 adult males, providing 19,295 terrestrial locations from 19 August 2007 – 22 October 2011 (Fig. 5.1).

Terrestrial Distribution

Females and males remained near the coast during the ice-free season, with 82% (15803/19295) of all locations <6 km of the coast. The mean distance-to-coast of all bears was 4.2 ± 0.1 km (median 1.1 km, range 0 – 65 km). Females were significantly further inland than males (t_{19293}= 5.11, P<0.001; Table 5.1). Family groups were found further from the coast than males ($F_{3,\ 19291}$=74.4, P<0.001; Table 5.1), and of the family groups, solitary females were nearest the coast, then females & YRLG and furthest females & COY (Tukey HSD, P<0.001 for all mean comparisons). Mean distance-to-coast varied monthly (August to November) for both females ($F_{3,\ 19058}$=58.9, P<0.001) and males ($F_{3,\ 229}$=3.3, P=0.02). All family groups except females & COY were closer to the coast in November than in August, September and October (Tukey HSD, P<0.001 for multiple mean comparisons; Fig. 5.2a).

Males and females were found on flat, steep, and high elevations (range 0-480 m; Table 5.1) on islands and the mainland, although most locations were recorded at lower elevations (Appendix C). Monthly mean elevations of males and female bears were variable (Fig. 5.2b).

Terrestrial Movements Metrics

The movement metrics of female and male bears did not differ: mean number of days on (t_{71}=0.32, P=0.75), mean total distances moved (t_{71}=1.52, P=0.13) and mean movement rates (t_{195}=1.25, P=0.21) (Table 5.2). When family group (females & COY, females & YRLG, solitary females) metrics were compared no differences were found: mean number of days on land ($F_{2, 65}$= 2.0, P=0.15), mean total distance moved ($F_{2, 65}$=1.67, P=0.20) and mean movement rates ($F_{2, 180}$=1.78, P=0.17) (Table 5.2). When comparing the movement rates between months, male rates were not different ($F_{2, 11}$=0.88, P=0.44) but female rates were ($F_{3, 179}$=10.91, P<0.001) with August (5.9 ± 0.8 km/d) being lowest and November highest (12.7±1.7 km/d). Some family group mean monthly movement rates differed: females & COY ($F_{3, 76}$=5.48, P=0.002) and female & YRLG ($F_{3, 83}$=6.56, P<0.001) with the November rate being highest and August (female & COY, Tukey HSD, P=0.02) and September (female & YRLG, Tukey HSD, P=0.003) rates lowest (Fig. 5.2c). Solitary female ($F_{3, 12}$=0.43, P=0.73) mean monthly movement rates did not differ.

Terrestrial Movement Behaviour

Foxe Basin polar bears displayed two terrestrial movement patterns: tortuous and meandering (Fig. 5.3). Tortuous movement behaviour was characterized by paths with high turning angles in a small area near and along the coast, and short inland forays. Meandering behaviour was characterized by smooth movement paths that followed the coast and sometimes included long distance overland components. The majority (72%, 46/64, Appendix C) of female bear movement paths were meandering (sinuosity index <10).

Male and female path sinuosity indices were not different (Mann-Whitney $U_{5, 64}$=178, P=0.69; Table 5.3) and did not differ by family group status (Kruskal-Wallis chi-square$_2$=1.3, P=0.52). The terrestrial movement paths of females that primarily used islands (excluding the large islands of Southampton and Baffin) were more compact and tortuous with higher sinuosity indices than bears on the mainland and large islands (Mann-Whitney $U_{26, 38}$=298.0, P=0.008; Table 5.3). The mean movement rates of the tortuous and meandering behaviours were not different (t_{75}=1.67, P=0.10) and sinuosity index and movement rate were not correlated ($F_{1, 165}$=0.12, P=0.73).

Long Distance Overland Movements

There were 18 long distance overland movements by 14 females (24%, 14/58) and none by males (Fig. 5.4). Overland movements were observed each year and in all ice-free months (August (n=1), September (n=5), October (n=6) and November (n=6)). The movements were across peninsulas on the mainland and large islands. The mean distance of the overland movements was 133 ± 15 km (range 47-244 km), crossing semi-mountainous terrain up to 480 m ($\bar{x}$ =182 ± 5 m) and duration of 2 to 25 days ($\bar{x}$ =5.6 ± 1.3 d, n=18). The overland sinuosity index was significantly different from the annual female movement path index (Mann Whitney $U_{18, 64}$=1149, P<0.001; Table 5.3). The overland movement mean sinuosity was 1.04 ± 0.01 (straight line=1.0) and the mean bearings of each overland movement was significantly directional (Appendix C). Many of the overland movements ended at the Gulf of Boothia (n=5 of 18) where sea ice historically remains late in the season or at Roes Welcome Sound (n=4 of 18) and the near shore islands of northern Hudson Strait (n=3 of 18) where land fast sea ice forms early at freeze-up. One bear traversed the Melville Peninsula in three consecutive years along similar paths, and several bears crossed peninsulas following similar paths and in different years (Fig.

5.4). Most overland movements (n=10 of 18) were the shortest paths across peninsulas.

Fidelity to Terrestrial Habitat

Some Foxe Basin polar bears showed annual and inter-annual landscape scale site fidelity. Sixty-three percent (46/73) of bears left land for the sea ice at freeze-up within 100 km of their capture location or first location on land at break-up. Female and male mean seasonal displacement (km) distances were not different (t_{71}=1.53, P=0.13; Table 5.2), nor were family group mean displacement distances ($F_{2,65}$=0.88, P=0.42).

Thirteen females had sufficient location data to evaluate inter-annual (2008-09, 2009-10 and 2010-2011) range fidelity. The mean inter-annual displacement distance was 190±43 km (range 4-296 km; n=17). Five females returned to land by swimming to within 110 km of the location where they left land the previous year at freeze-up; one of these bears returned to a small island in north central Foxe Basin where she denned later that year. Another bear returned by long distance swims (214 and 93 km) in two separate years to an island in Hudson Strait where she also denned in one year. A third bear followed a long distance overland route across the Melville Peninsula in three consecutive years (Fig. 5.4) and in the third year denned near the end of this route.

Swimming Movements

Swimming by females (25/58) and males (3/5) was observed in each month and year of the ice-free season. I observed two types of swimming: “return”, an obligate movement (only observed in females because male data was not available for this period) from the sea ice to land at break-up and “daily”, a facultative movement from land to land, across bays, between islands and from the mainland to islands (Fig. 5.5). Return and daily swims were recorded for all family groups. Mean female return swim distance ($\bar{x}$ =80.7±23.1 km; range 30-214 km; n=8) was significantly longer than mean female daily swim distance ($\bar{x}$ =7.8±1.0 km; range 0.2-115 km; n=196) (t_{202}= -6.72, P<0.001). There was a significant difference between the mean daily swim distance of family groups ($F_{2, 193}$=6.64, P=0.002), with solitary females ($\bar{x}$ =48.8±28.2 km) swimming greater distances than females & COY ($\bar{x}$ =9.5±1.8 km; Tukey HSD, P=0.004) and females & YRLG ($\bar{x}$ =9.1±2.0; Tukey HSD, P=0.001). Eleven females and 2 male bears had one daily swim bout/season, 8 females and 1 male had 2-10 swim bouts/season and 4 females swam between 10-50 times/season. Males swam further per daily bout ($\bar{x}$ =48.1±12.8 km, range 16-79 km; n=4) than females ($\bar{x}$ =7.8±1.0 km, range <1-115 km, n=196) (t_{198}=-4.09, P<0.001).

5.4 Discussion

The movements and distribution of Foxe Basin polar bears during the ice-free season were unlike those of other populations. I propose that movements are a result of foraging opportunities, increased energy reserves (decreased time on shore) and cooler temperatures (Fig. 5.6). In the southern Hudson Bay population, bears rested most of the time (86%) with little time (3.2%) allocated to feeding and scavenging activities (Knudsen 1978). In contrast, the Foxe Basin females moved extensively and covered longer distances (259 – 465 km) than western Hudson Bay bears (70 – 87 km) (Parks et al. 2006) despite the Foxe Basin bears spending approximately 40 fewer days on land (compared to Cherry et al. (2013)). The family group mean movement rates in Foxe Basin (6.6–9.2 km/d) were faster than in western Hudson Bay (0.7–4.8 km/d) (Derocher and Stirling 1990a, Parks et al. 2006) and comparable to Baffin Bay bears (5.9 -15.8 km/d) (Ferguson et al. 1997). I acknowledge that the temporal frequency of location data collection in both western Hudson Bay and Baffin Bay were lower than that of Foxe Basin but these are the only results to compare with at this time. Coastal movement behaviours were tortuous or meandering but despite the differences, the movement rates did not differ. The terrestrial movements of Foxe Basin bears suggest that there is an energetic reward and they may be actively scavenging and opportunistically foraging throughout the ice-free season and/or they are in better body condition coming off the ice, in contrast to the relatively inactive, energy saving behaviour of the Hudson Bay bears further south.

Terrestrial habitat for polar bears is resource-poor, as food is sparsely distributed (e.g., carcasses, resting seals or walrus, remnant ice floes to hunt from) or clumped and ephemeral (e.g., bird colonies, migrating birds, walrus haul-outs). The predominant meandering, somewhat linear movement pattern of Foxe Basin bears may be may the most efficient for foraging and reflect resource distribution (Gurarie and Ovaskainen 2011, Laidre et al. 2012, de Jager et al. 2014). Bears with tortuous movements may have found a rich food source, such as a whale carcass, to scavenge which would be a sufficient attractant to keep bears in close proximity for an extended period (Schliebe et al. 2008, Herreman and Peacock 2013). None of our collared or ear-tagged polar bears were recorded at the three main walrus haul-outs (South Ooglit, Manning, and Walrus Islands) nor spent much time at the three major bird colonies (Dewey Soper, Harry Gibbons and East Bay Migratory Bird Sanctuaries) in Foxe Basin.

Air temperature may be a critical external factor affecting polar bear movements. The air temperature of Foxe Basin is cooler than western Hudson Bay because it is further north (675-1450 km), and has higher landscape albedo (tundra barrens, graminoid and prostrate shrub tundra (Walker et al. 2005) versus erect and tall shrub, and taiga forest vegetation (Brook 2001)). Landscape albedo is one controlling parameter of surface energy budget and air temperature (Loranty et al. 2011, Pearson et al. 2013). Polar bears are prone to over-heating when active in warm temperatures (Øritsland 1970, Best 1982, Lunn and Stirling 1985) and reduce activity or use micro-habitat (e.g., earth dens dug to permafrost, temporary dens on glaciers, day beds on raised beaches, ocean spits, swimming) to reduce thermal stress (Jonkel et al. 1976, Schweinsburg 1979, Derocher and Stirling 1990a). Cold adapted terrestrial mammals will select habitat and change movement patterns to escape or take shelter from high temperatures in summer (Aublet et al. 2009, van Beest et al. 2012, Street et al. 2015).

Most Foxe Basin bears arrived on shore in August when the air temperature had begun to cool (Coral Harbour 8°C mean daily and 11.7°C mean maximum, Hall Beach mean daily 5°C and mean maximum 7.7°C) but in Hudson Bay temperatures were still at the summer peak (Churchill mean daily 12°C and mean maximum 16.8°C) (Appendix C). Temperatures decline in both regions from September-November but Foxe Basin remains 3-7°C cooler and has fewer days >10°C than Hudson Bay (Appendix C). Terrestrial movement rate increased from August–November in Foxe Basin and western Hudson Bay possibly in response to declining temperature and preparation to return to the sea ice (Derocher and Stirling 1990a).

The distribution of bears can be affected by conspecific interactions between male and female bears that can result in aggression, injury, death, and infanticide (Bellemain et al. 2005, Amstrup et al. 2006, Stirling and Ross 2011, Steyaert et al. 2013a). Segregation by sex and reproductive status by bears has been observed and may function to reduce risk, particularly to cubs, from infanticidal or predatory males (Taylor et al. 1985, Derocher and Stirling 1990a, Wielgus and Bunnel 1994, Derocher and Wiig 1999, Stirling et al. 2004, Martin et al. 2013). In brown bears (*U. arctos*), females with cubs reduced the infanticide risk by segregation and reducing movement activity (Ben-David et al. 2004, Martin et al. 2013, Steyaert et al. 2013b). I observed sex and family group segregation in Foxe Basin but the separation distances between males and females were low (Table 5.1) compared to western Hudson Bay where females were 5-28 km further inland than males (Derocher and Stirling 1990a). The Foxe Basin coastline is >5 times longer than western Hudson Bay, even with a larger number of bears (estimate 2585) (Stapleton et al. 2015) than western Hudson Bay (estimate 1030) (Stapleton et al. 2014) bear density in Foxe Basin was lower. It is possible that the lower bear density allows Foxe Basin female bears to remain near the coast and potential food resources (e.g., marine carrion) because the chance of a conspecific encounter is low. In addition, the Foxe Basin landscape topography is rugged, which creates more coastal habitat through three dimensional space that further reduces the potential for conspecific interactions (Schweinsburg 1979, Ferguson et al. 1997, Andersen et al. 2012). Further, the numerous islands and inlets in Foxe Basin may allow bears to swim to a lower risk location. Differential use of landscape features by males and females has been observed in Foxe Basin (Lunn and Stenhouse 1987, Taylor et al. 1990a) and other regions (Derocher and Stirling 1990a, Ovsyanikov 2005).

Directional or oriented overland movements and routes used by polar bears are rarely reported. Directional overland movements have only been recorded in western Hudson Bay when females emerge from maternity dens and move to the sea ice for foraging (Ramsay and Andriashek 1986, Derocher and Stirling 1990a, Parks et al. 2006). To date, polar bear movement routes have only been described by Inuit hunters and only for the Foxe Basin region where the Inuit observations were coincident with this study (Sahanatien 2011). Travel routes have been recorded for black bears (*U. americanus*) and it was hypothesized that knowledge of the routes were transmitted through social cues, likely chemical communication (Noyce and Garshelis 2014). It is possible that polar bears also use chemical communication on land as it occurs on sea ice when males follow female tracks in spring but this has not been studied in the terrestrial environment (Derocher 2012, Owen et al. 2015). Another possibility is that information about overland routes is culturally transmitted from female to cubs as postulated for denning habitat (Derocher and Stirling 1990a).

The overland directional movements I observed required navigational abilities as the targets or end points were distant (47-244 km) and probably beyond the sensory perception of the bears. Navigation ability was likely essential during the long distance swimming movements from sea-ice to land (29-214 km) and island to island (30-93 km) as a bear's visual, olfactory and auditory fields would be limited when swimming in open ocean waters. Navigation ability has been ascribed to polar bears and site fidelity requires it, but it has not been studied (Derocher 2012). It is recognized that large terrestrial and marine mammals navigate (Rogers 1987, Brooks and Harris 2008, Horton et al. 2011, Papastamatiou et al. 2011) but the mechanisms (e.g., cognitive maps, internal compass, magnetic fields) are poorly understood in large mammals (Gould and Gould 2012).

Sea ice is an attractant for polar bears as this is their primary foraging habitat and it is possible that the overland routes developed in response to historic patterns of early and late season occurrence of sea ice, to which bears developed a habitat expectancy value (Spencer 2012) based on experience (Dall et al. 2005, Schmidt et al. 2010, Merkle et al. 2013). Directional movements and navigation require memory and previous information about the resource distribution (Mueller et al. 2011a, Fagan et al. 2013). Memory and information plays a significant role in movements (Spencer 2012) and based on the fidelity of polar bears to summer ranges after many months on the sea ice, they do have well developed navigation abilities. Foxe Basin females demonstrated site fidelity to individual ice-free season home range similar to other areas (Lentfer 1983, Mauritzen et al. 2001, Stirling et al. 2004, Parks et al. 2006, Zeyl et al. 2010). Polar bears are dependent on their mothers for two-three years and during that time they learn through experience the locations of denning habitat (Derocher and Stirling 1990a, Zeyl et al. 2010) and likely foraging habitat as noted in other species (Davis and Stamps 2004, Nielsen et al. 2013).

Swimming was a regular form of ice-free season movement in Foxe Basin. Short and long distance swim movements may be an efficient option for moving between locations. The four bears that swam 10-50 times inhabited large, deep bays and inlets with highly convoluted coastlines, where swimming across would be faster and possible more energetically efficient than walking and a means to avoid conspecific interactions. Short distance swim movements were observed in the high arctic during spring before sea ice break-up, when bears swam across and in sea ice leads as part of their regular movements or when stalking seals and in other regions during summer when bears swam across channels and bays (Stirling 1974, Donaldson et al. 1981, Durner et al. 2011, Pagano et al. 2012, Stapleton 2013, Stirling and van Meurs 2015).

Long-distance swimming (>50 km) occurred when Foxe Basin female and male bears moved between islands or returned to land from the sea ice at break-up. Directional swimming movements toward land and sea ice have been reported (Durner et al. 2011, Pagano et al. 2012) but not directional swimming movements between islands. Long distance swim movements were hypothesized to be behavioural responses to declining sea ice in regions (Beaufort and Chukchi Seas) where polar bears have not historically swum to land (Pagano et al. 2012), and swimming had negative effects on body condition (Durner et al. 2011). Monnett and Gleason (2006) reported bears drowned after swimming during a storm, suggesting risks of long-distance swims. My observations of long-distance swimming supports Pagano et al. (2012) behavioural plasticity hypothesis and provides additional insight into swimming behaviour. In, 2010, two bears swam ashore to Southampton and Coats Islands within a few days of early movement of the ice away from the coast into Hudson Bay (http://iceweb1.cis.ec.gc.ca/Archive20/?lang=en). The 6 other long distance return swims occurred in late break-up (August of 2009-2011) and it appeared that the bears stayed with the deteriorating sea ice until they had to swim ashore and leave the prime foraging habitat, as might be expected in bears that have adapted to seasonal sea ice. Long-distance swim bouts (8) between islands provides further evidence that swimming is a regular ice-free season movement behaviour and not specifically a response to changing sea ice conditions. Further, the proximate reason for long-distance swimming in Foxe Basin differs from other regions (Durner et al. 2011, Pagano et al. 2012) where bears often swam in search of sea ice rather than land.

Foxe Basin polar bear terrestrial distribution and movement behaviours during the ice-free season were diverse in response to the physical and terrestrial environmental characteristics of the region and internal factors affecting individual bears (Fig. 5.6). My results have implications for polar bear conservation, research, and movement modeling. Increasing air temperature resulting from climate change will not only reduce available sea ice habitat (Durner et al. 2009, Sahanatien and Derocher 2012, Hamilton et al. 2013) but could have important physiological, movement and distribution impacts on polar bears during the ice-free season. More research and monitoring of ice-free season body condition and diet is needed in the northern seasonal ice ecoregion (Foxe Basin, Davis Strait and Baffin Bay) bear populations (Thiemann et al. 2008b, Rode et al. 2012) to describe how bears in these colder, more complex environments are responding to limited food resources in light of the observed and anticipated negative effects of longer ice-free seasons (Regehr et al. 2007, Molnár et al. 2010, Rode et al. 2010a, Robbins et al. 2012, Rode et al. 2015, Whiteman et al. 2015).

Polar bears are vulnerable to disturbance when in terrestrial habitat. As an IUCN classified (vulnerable) species (http://www.iucn.org/) and Canadian species-of-concern (http://www.cosewic.gc.ca), they should be given protection during the ice-free season (Peacock et al. 2011). At this time there are no polar bear specific guidelines or restrictions in Canada to mitigate the impacts of the extensive annual mineral exploration and tourism activities that occur in the seasonal sea ice ecoregion. Arctic national and territorial parks provide some polar bear terrestrial habitat protection but these are small relative to the range and occurrence of polar bears in Canada. In addition, incidents of human-polar bear conflict during the ice-free season have increased in Manitoba, Nunavut (Stirling and Parkinson 2006, Towns et al. 2009, Peacock et al. 2010) and other regions (Obbard et al. 2010). Knowledge and understanding of regional terrestrial bear movement and behaviour is essential for developing human-bear conflict and mitigation strategies.

Table 5.1 Terrestrial distribution of satellite-tagged female and male polar bears during the ice-free season, Foxe Basin, Nunavut (2007-2011).

	Distance to coast (km)			**Elevation (m)**			
Group	Mean (SE)	Median	Range	Mean (SE)	Median	Range	n[1]
Female	4.2 (0.1)	1.0	0-65	44.5 (0.5)	10	0-480	19062
Male	2.6 (0.4)	0.6	0-30	42.1 (4.7)	10	0-310	233
Female & COY	4.5 (0.1)	1.1	0-54	36.4 (0.6)	10	0-480	8379
Female & YRLG	4.1 (0.1)	0.8	0-57	45.9 (0.7)	10	0-400	8980
Solitary female	3.9 (0.2)	2.3	0-65	77.1 (2.5)	30	0-480	1703
All bears	4.2 (0.1)	1.1	0-65	44.5 (0.5)	10	0-480	19295

[1] Number of GPS satellite collar and ear tag locations.

Table 5.2 Movement metrics of satellite collared female and ear tagged male polar bears during the ice-free season, Foxe Basin, Nunavut (2007-2011).

Group	**Terrestrial days (d)**			**Displacement[1] (km)**			**Total distance moved (km)**			**Movement rate (km/d)**			**n[2]**
	Mean (SE)	Median	Range	Mean (SE)	Median	Range	Mean (SE)	Median	Range	Mean (SE)	Median	Range	
Female	70.8 (3.5)	67	30-141	111 (14.4)	74.1	1-511	421 (29.9)	338	38-1125	8.3 (0.5)	7.0	0.1-45.8	69
Male	66.6 (8.2)	65	41-91	65 (35.4)	43.9	1-201	250 (59.4)	306	64-376	5.1 (0.9)	4.3	0.8-13.1	5
Female & COY	64.1 (3.8)	57	39-130	103 (15.7)	83.6	2-425	410 (30.9)	423	161-788	7.8 (0.7)	6.8	0.1-24.7	30
Female & YRLG	78.4 (6.3)	73	30-141	134 (26.9)	70.1	1-511	465 (55.1)	309	38-1125	9.2 (0.8)	7.9	0.3-45.8	31
Solitary female	66.1 (8.6)	69	32-92	82 (28.8)	68.1	5-218	291 (70.4)	233	89-676	6.6 (1.5)	4.5	0.8-19.1	8

[1] Displacement from capture location or first location on land at break-up.

[2] Number of active satellite collars and ear tags used to calculate metrics (2007-2011).

Table 5.3 Movement path sinuosity index of satellite-collared female and ear tagged male polar bears during the ice-free season, Foxe Basin, Nunavut (2007-2011).

Group	**Mean (SE)**	**Median**	**Range**	**n**[1]
Female	15.33 (3.68)	4.37	1.06-128.28	64
Male	72.96 (67.13)	3.31	1.44-341.21	5
Island[2]	22.27 (7.29)	6.27	2.0-128.28	26
Mainland[2]	10.57 (3.57)	3.27	1.06-119.28	38
Overland[2]	1.04 (0.006)	1.03	1.008-1.11	19

[1] Number of active collars and ear tags used to calculate metrics (2007-2011)

[2] Females only

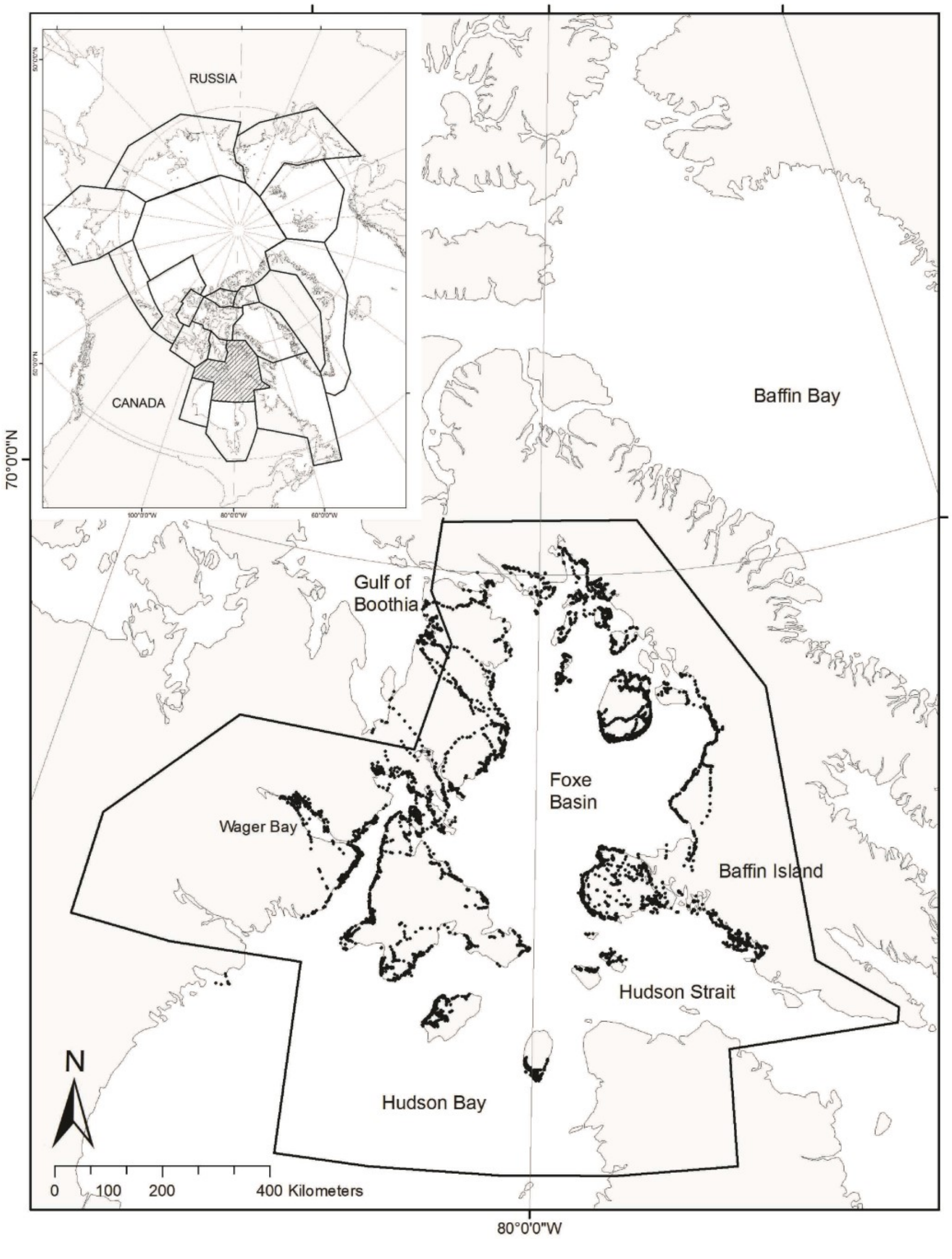
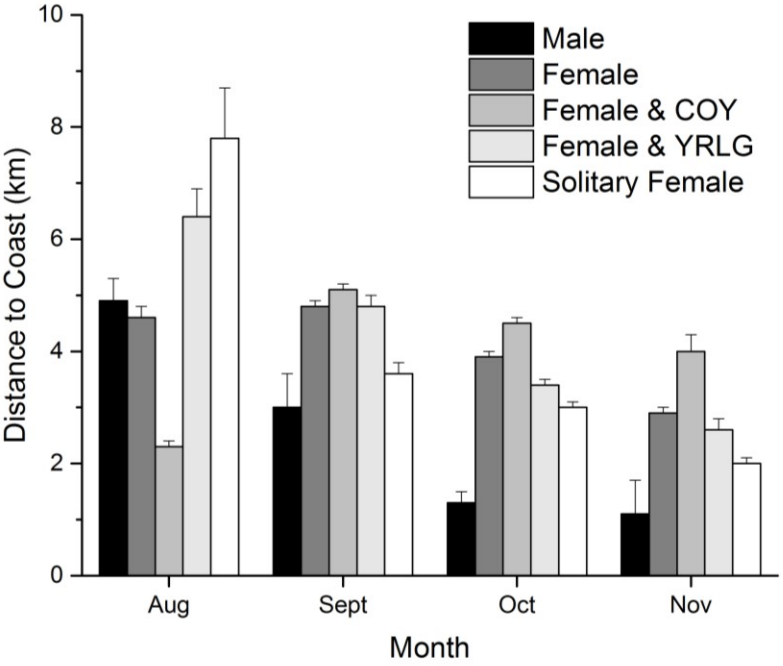
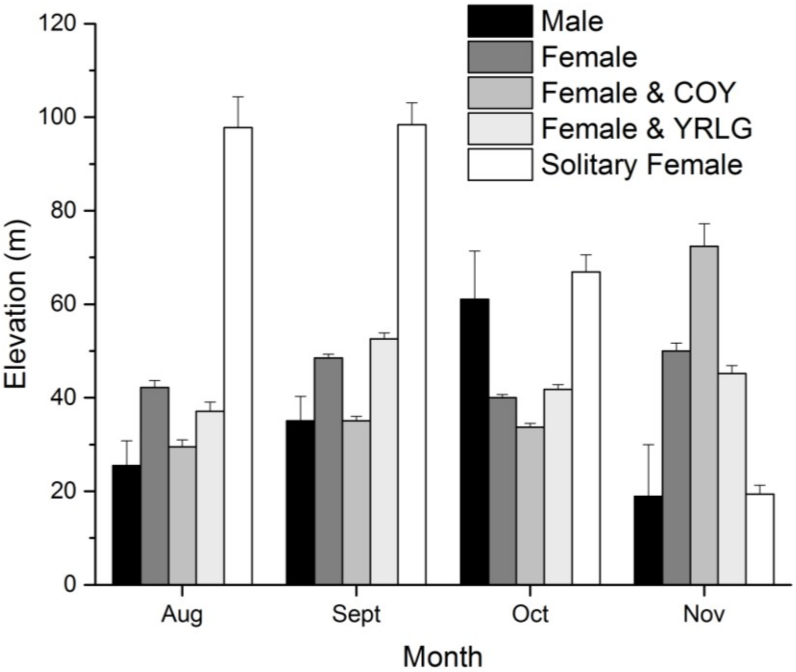


Figure 5.1 Map of study area with locations (black dots) of satellite-collared female polar bear and ear tagged male polar bear during ice-free seasons (2007-2011), Foxe Basin, Nunavut, Canada. The Foxe Basin population is outlined in black following (Obbard et al. 2010).

a)


Male
Female
Female & COY
Female & YRLG
Solitary Female
Distance to Coast (km)
0
2
4
6
8
10
Aug
Sept
Oct
Nov
Month

b)


Male
Female
Female & COY
Female & YRLG
Solitary Female
Elevation (m)
0
20
40
60
80
100
120
Aug
Sept
Oct
Nov
Month

c)

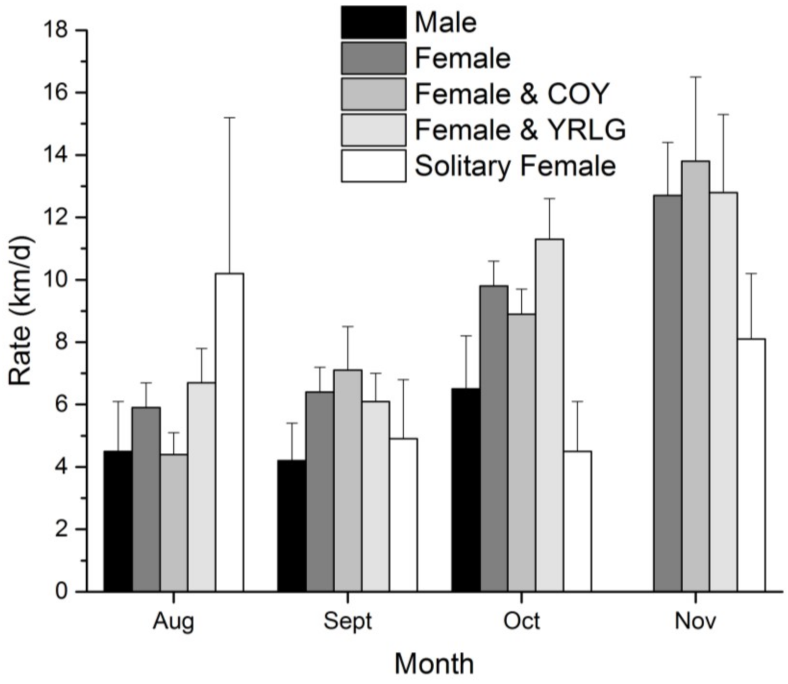


Figure 5.2 Terrestrial distribution of satellite tagged female and male polar bears during the ice-free season, Foxe Basin, Nunavut, Canada (2007-2011): a) mean monthly distance to coast (km) ± s.e., b) mean monthly elevation (m) ± s.e., and c) mean monthly movement rate (km/d) ± s.e.

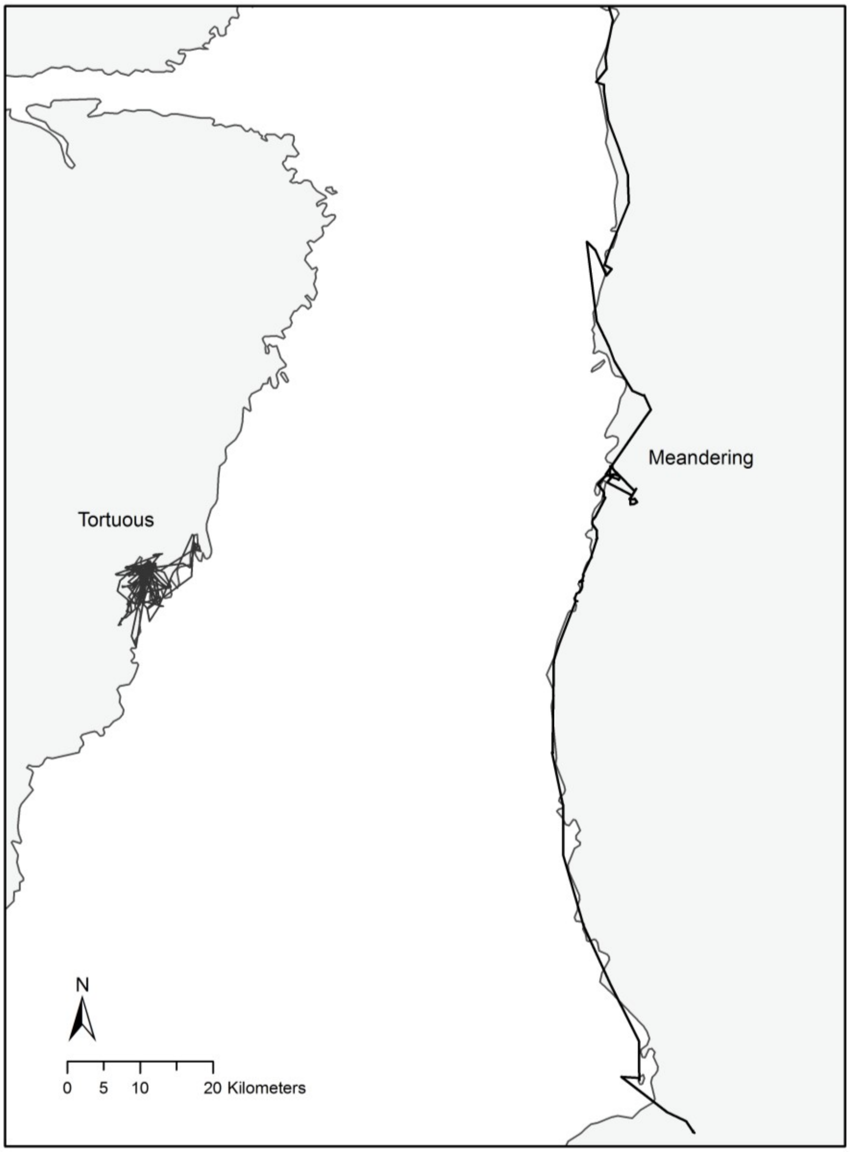


Figure 5.3 An example of tortuous and meandering terrestrial movement behaviours of satellite collared female polar bears during the ice-free season, Foxe Basin, Nunavut, Canada: tortuous with sinuosity index of 71.7 and meandering with sinuosity index of 2.4.

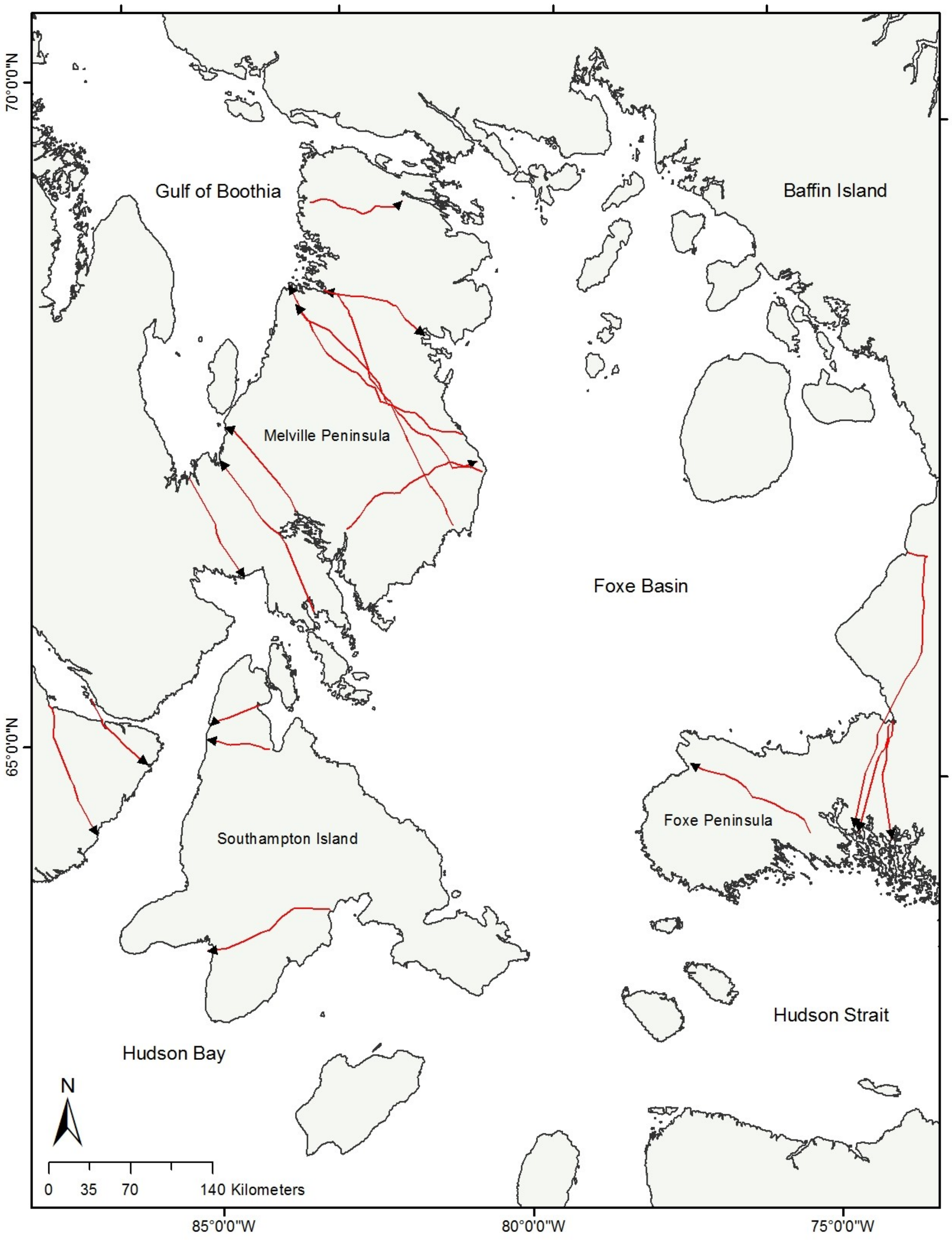


Figure 5.4 Map of long distance overland movements (n=18) by satellite collared female polar bears (n= 14) during the ice-free season, Foxe Basin, Nunavut, Canada (2007-2011). The mean sinuosity index of overland movements was 1.04 ± 0.01.

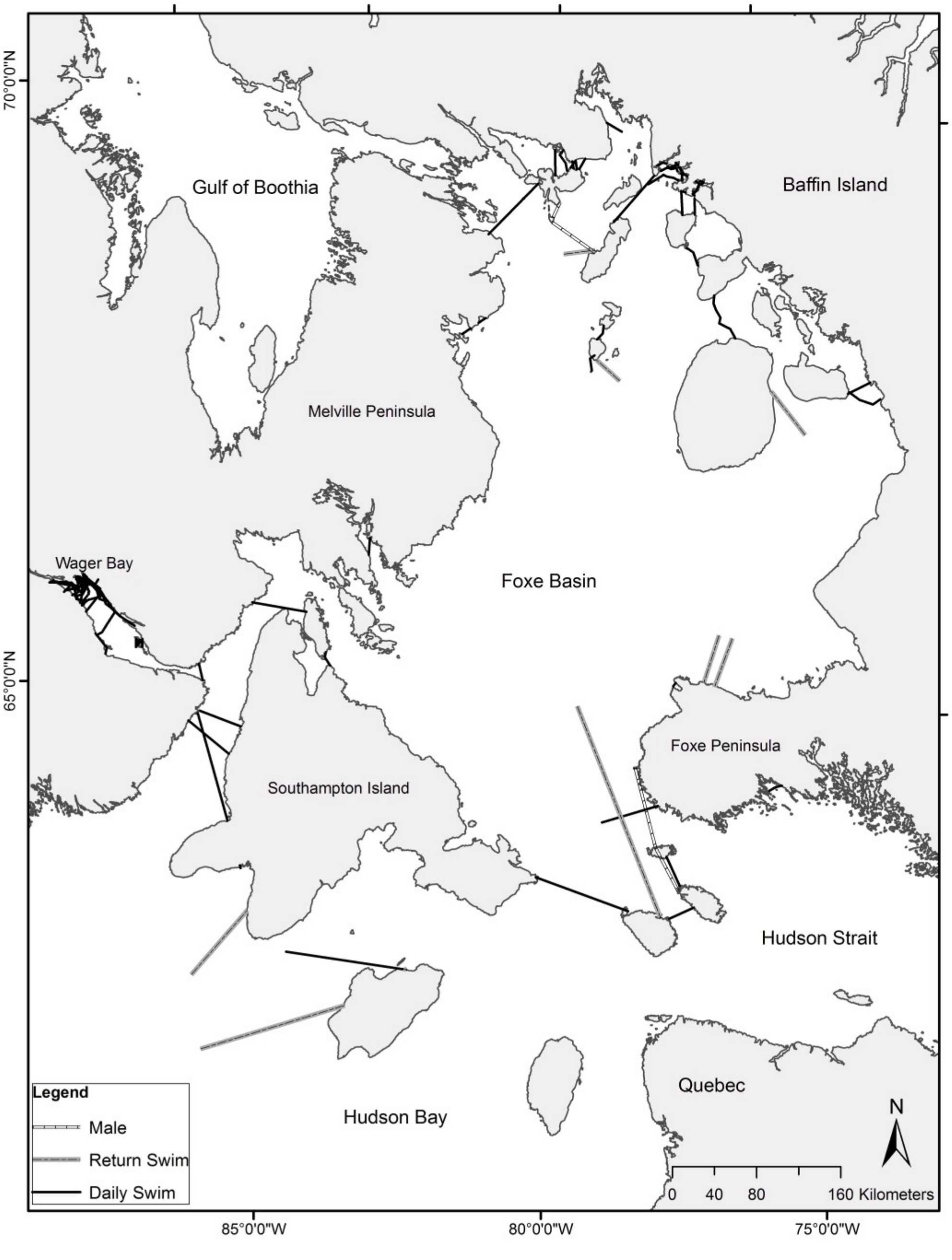


Figure 5.5 Swim movements of satellite collared female and ear-tagged male polar bears during the ice-free season, Foxe Basin, Nunavut, Canada (2007-2011).

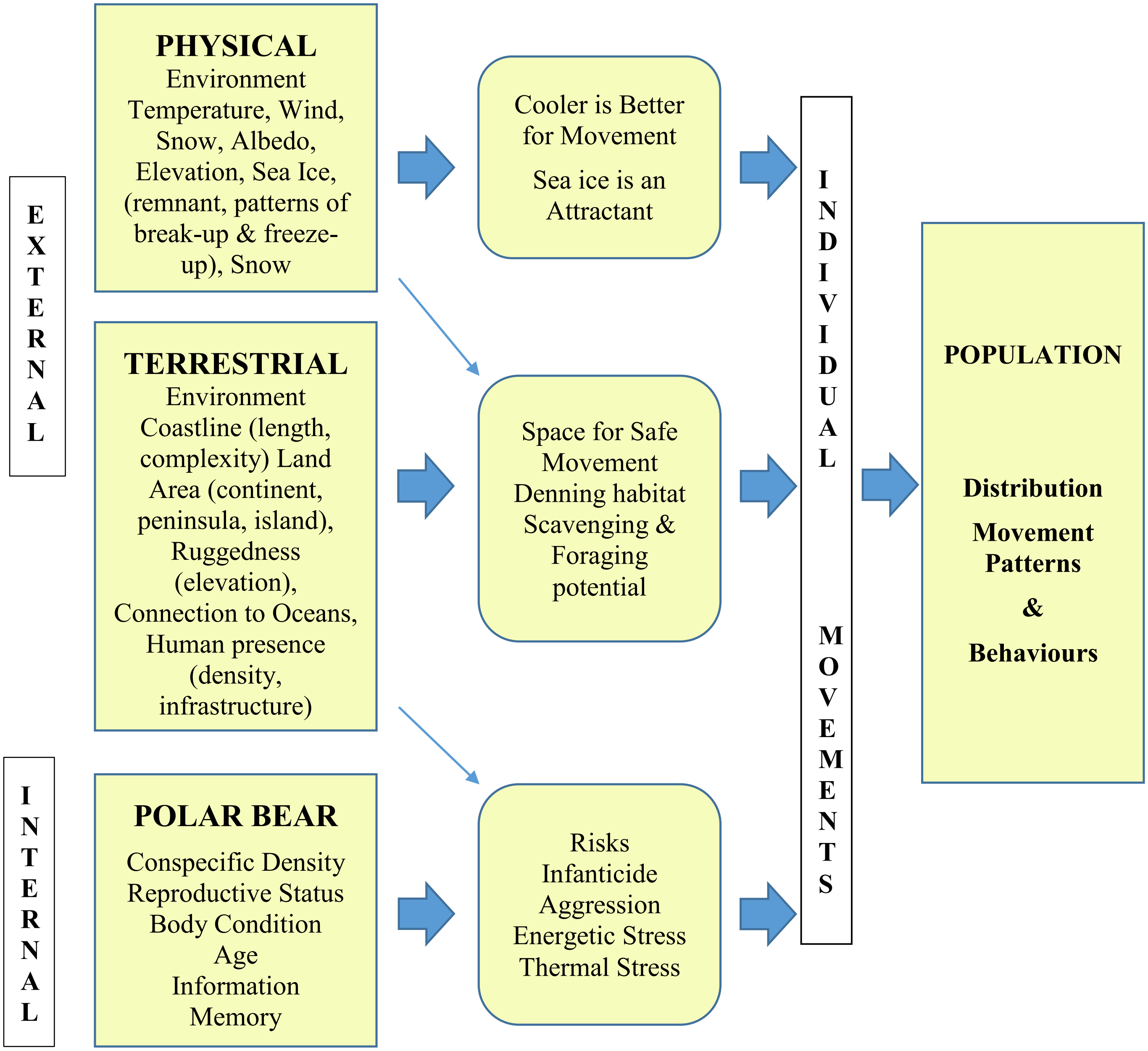


Figure 5.6 External and internal factors influencing ice-free season polar bear movement ecology. (Adapted from, (Nathan et al. 2008, Martin et al. 2013).

Chapter 6

6 Sea ice, Polar bears and The Future

6.1 Introduction

My research provides the first detailed observations of the spatial ecology, movement behaviours and sea ice habitat of the Foxe Basin polar bear (*Ursus maritimus*) population. My objectives were to bring sea ice habitat to the forefront (Chapters 2, 3 and 4), to provide insights into the functional relationships of bears with ice (Chapters 3 and 4), to introduce new approaches for quantifying and monitoring polar bear habitat (Chapters 2 and 4), and to interpret bear movement patterns and behaviour within the frameworks of animal movement research (Chapters 3 and 5). My results contribute to the overall understanding of polar bear ecology, and provide context and baseline information for management of this harvested polar bear population.

In this final chapter I will consider my findings in light of newly published research, as they apply to polar bears in their circumpolar range, and discuss information gaps and research needs.

6.2 Thresholds and the Relative Position of Foxe Basin

I measured significant negative trends (1979-2008) in the amount and quality of polar bear sea ice habitat in Foxe Basin (Chapter 2, Sahanatien and Derocher (2012) and these have continued (Hochheim and Barber 2014). I hypothesized that this bear population may show future reduced body condition and cub production as observed in western Hudson Bay (Stirling et al. 1999, Regehr et al. 2007) the adjacent polar bear population to the south which has been correlated with the changing sea ice conditions. A new Foxe Basin population estimate (2,585, S.E.=277; including adults, cubs of the year and yearlings) was recently published (Stapleton et al. 2015). The previous estimate (2,200, S.E.=260) occurred in the late 1980s-1990s (Taylor et al. 2006) and Stapleton et al. (2015) concluded that the Foxe Basin population size has remained stable over the past 20 years. If so, the documented changes in sea ice habitat have not affected bear abundance. Stapleton et al. (2015) results are informative as they can be interpreted within the broader context of the Hudson Bay System (Hudson Bay, Hudson Strait and Foxe Basin), and the sea ice and marine ecosystem responses to climate change of each marine water body. As it is possible for adjacent polar bear populations to respond differently to changing sea ice habitat conditions as observed in the Chukchi Sea and Beaufort Sea: in the Chukchi, bears remain in good condition but in the Beaufort bears have declined (Rode et al. 2014b, Bromaghin et al. 2015).

In light of the apparent stability of the Foxe Basin polar bear population, I hypothesize that Foxe Basin polar bears have not reached their sea ice habitat threshold, which can be measured as the number of days on land without access to marine mammal prey or conversely, the number of days on ice with access to prey. Foxe Basin bears were on land for an average of 71 days (2007-2012, Chapter 5) and this time period overlapped with the Stapleton et al. (2015) aerial survey. Western Hudson Bay (WHB) bears in comparison were on land for approximately 110 days in the 1990s and 120 days in the 2000s (Cherry et al 2013). Declines in body condition and demographics were recorded in the 1990s (Stirling et al. 1999), so we may assume that the WHB bears surpassed their habitat threshold earlier or during the 1990s. The decline in WHB bear body condition and demographic trends continued in the 2000s (Regehr et al. 2007), with concurrent declines in sea ice (Stirling et al. 2004, Stirling and Parkinson 2006, Hochheim and Barber 2014). The body condition of bears on Southampton Island and the mainland coast of northern Hudson Bay portions of the Foxe Basin population should be monitored because these bears were on land for 126 days, a period similar to WHB bears. Models have predicted that extended fasting will affect adult survival and litter size but such effects are most significant beyond 180 days of ice-free time (Molnár et al. 2010, Molnár et al. 2011, Molnár et al. 2014).

However, it is not just the number of days on land or on the sea ice that is important but timing of break-up and freeze-up. Spring and early summer sea ice habitat is most important for polar bear foraging (Watts and Hansen 1987, Ramsay and Stirling 1988). During this period, polar bears are hyperphagic because they have relatively easy access to ringed and bearded seal pups, subadults and adults on the ice in pupping lairs, and when they bask and moult (Smith 1980, Kingsley and Stirling 1991, Pilfold et al. 2012). Autumn and winter foraging on the sea ice is also vital but likely less rewarding as seals are more difficult to access while still in their pelagic behavioural state and they do not use the ice surface as regularly. Winter foraging ecology, however, is poorly understood due to the challenges associated with conducting research during winter darkness and inclement weather. Delayed freeze-up date trends can impact polar bear body condition and cub survival but relatively less than earlier break-up dates (Molnár et al. 2011). Coming off the ice in good body condition at break-up is critical for polar bears, especially lactating or pregnant females, to survive fasting for 3-8 months (Ramsay and Stirling 1988, Atkinson and Ramsay 1995).

In the Hudson Bay System and circumpolar Arctic, the trends in sea ice loss are stronger in the autumn than in the spring (Perovich and Richter-Menge 2009, Sahanatien and Derocher 2012, Hochheim and Barber 2014, Meier et al. 2014). Focusing on the Hudson Bay system, my results and others (Saucier et al. 2004, Moore 2006, Stirling and Parkinson 2006, Galbraith and Larouche 2011) were echoed by recent analyses by Hochheim and Barber (2014). They compared 1980-1995 to 1996-2010 and found that the open water season of Hudson Bay increased an average of 3.1±0.6 weeks (freeze-up 1.6 weeks, breakup 1.5 weeks), Hudson Strait by 4.9±0.8 weeks (freeze-up 2.4 weeks, break-up 2.5 weeks), and Foxe Basin by 3.5±0.9 weeks (freeze-up 2 weeks, break-up 1.5 weeks). The loss of sea ice was strongly correlated with increasing surface air temperature and this physical forcing was greater in the autumn than the spring. Most Foxe Basin bears arrived on land in August, the exceptions were the bears that ranged into northern Hudson Bay and they arrived on land in July (Chapter 5). This suggests that Foxe Basin bears still experience a sufficient period on ice during the hyperphagic period to accumulate fat, reflected by the overall good body condition that was observed during the aerial survey (Stapleton et al. 2015).

On the local and regional scales, sea ice habitat is of variable quality for polar bears and other pagophilic species. Foxe Basin and Hudson Strait are more productive than Hudson Bay (Ferland et al. 2011, Estrada et al. 2012, Cyr and Larouche 2014). Changing sea ice conditions are also increasing marine primary productivity in many Arctic regions, including Foxe Basin, because of earlier and more open water in spring arctic (Arrigo and van Dijken 2015). It is possible that the increases in productivity may offset the loss of sea ice habitat and foraging opportunities for higher trophic species, like polar bears. Such dynamics, however, may be transient as in the longer term, with continued sea ice loss and change, ecosystem shifts can occur that can be detrimental to ice dependent species (Grebmeier et al. 2006, Bluhm and Gradinger 2008, Harwood et al. 2015).

Complacency is not warranted in regards to the future status of the Foxe Basin polar bear population and harvest management. The current total allowable harvest may be sustainable but sea ice habitat is dynamic, and it will continue to decline because atmospheric temperatures will continue to rise as greenhouse gas emissions continue unabated (Meier et al. 2014). As a more southerly seasonal sea ice system, the Hudson Bay System has changed rapidly and the ice responses were more strongly correlated to atmospheric forcing than other Arctic regions (Hochheim and Barber 2014). The Foxe Basin polar bear population may be at a lower risk of declining habitat (Peacock et al (2010) but it is still at risk and requires monitoring. At some point, with continued warming, the sea ice will likely cross a threshold that will reduce the ability of polar bears to thrive in the region. We should heed Vongraven et al. (2012) warning that harvest management must be adaptive to changing habitat conditions (Laidre et al. 2015b).

6.3 Seasonal Sea Ice in the Big Picture

As seasonal sea ice continues to dominate the Arctic (Stroeve et al. 2012), more polar bear populations will be forced to use terrestrial habitat in summer. The bear populations of the divergent, convergent and archipelago ecoregions (Amstrup et al. 2008) have little experience on land aside from maternity denning (Durner et al. 2006, Andersen et al. 2012), although this is changing with the sea ice declines of recent years (Ovsyanikov 2005, Schiebe et al. 2008, Gleason and Rode 2009, Rogers et al. 2015). Most bears of these ecoregions probably do not have established movement patterns in terrestrial habitat. Which begs the question, what will the perennial sea ice polar bears do when they are forced on land during the ice-free season?

If my model of external and internal factors (Fig. 5.6) has general application, then we could expect archipelago ecoregion bears to move extensively because the physical and terrestrial factors are favourable for movement. Including swim movements between archipelago islands, mainland Canada and Greenland, and overland movements across islands. Extensive terrestrial movements without established patterns could cause breakdown of population structure if the bears do not return to their traditional sea ice habitat ranges. Loss of historically available perennial sea ice habitat could disrupt the fidelity that polar bears have shown to the delineated populations of the archipelago (Schweinsburg et al. 1982, Taylor et al. 2001). At this time there is no regular monitoring of bear distribution in the archipelago ecoregion.

Loss of multi-year ice in the divergent ecoregions has already created changes in the summer distribution of polar bears, as bears are increasingly using terrestrial habitat rather than staying with the ice as it retreats into the Arctic

Basin. The Russian and Alaskan continental coasts and the islands off Russia and Norway are receiving more bears in summer (Ovsyanikov 2005, Kochnev 2006, Schiebe et al. 2008, Gleason and Rode 2009, Rogers et al. 2015). The distribution of bears in this ecoregion is monitored in the Southern Beaufort Sea, Chukchi Sea and Barents Sea populations. Bears are observed gathering around marine mammal carcasses and congregations of shore bound walruses.

If Stroeve et al. (2007) and Overland and Wang (2013) are correct and summer sea ice will be no longer be in existence as of 2030, we will observe large changes in polar bear terrestrial distribution and abundance. All jurisdictions need to plan ahead and consider polar bear summer retreat refuges, special management areas and legislation for long term conservation of bear populations (Ragen et al. 2007, Peacock et al. 2011, Boltunov et al. 2012, Hamilton et al. 2013, Moritz and Agudo 2013).

6.4 Information Gaps & Research Needs

Foxe Basin was the last polar bear population in Canada to undergo detailed study of distribution, abundance and habitat (this study and Stapleton et al. (2015)). The size of the region, climate, logistics, cost, and inability to do spring on ice capture work (Foxe Basin has little landfast ice and most bears were on the active floe ice), all served to deter research efforts. The early challenges were chronicled in the field research reports from the 1980s and 1990s (Davidge 1980, Stenhouse and Lunn 1987, Taylor et al. 1990a). But one of the most detailed polar bear denning studies occurred on Southampton Island, Foxe Basin, when there was cooperation with community members and use of traditional knowledge (Harington 1968).

My research answered long standing and fundamental questions about the Foxe Basin bear ecology: where do Foxe Basin bears go in the winter? (Taylor et al. 1990a), what overlap in distribution is there with the Hudson Bay populations during winter and spring? (Taylor and Lee 1995), and is there subpopulation structure within the Foxe Basin population (Stirling and Ramsay 1986, Taylor et al. 1990b). But my four year study is only a baseline and should be continued.

Research and monitoring of Foxe Basin polar bears and other Nunavut bear populations are difficult to undertake without capturing, marking, and satellite tagging. However, in Nunavut there is significant opposition from Inuit hunters and organizations to capture, handling, marking, and satellite collaring of polar bears (Dowsley and Wenzel 2008, Peacock et al. 2011). The opposition is rooted in culture, politics in a post-colonial time, observations of bear deaths during the early years of capture work, and misinformation about the effects of capture drugs on bear behaviour and physiology. To address concerns regarding capture effects of modern immobilization drugs, studies found that bear movement rates were normal within 3-5 days post capture, and there were no effects on body condition, reproduction and cub survival (Thiemann et al. 2013, Rode et al. 2014a). Approval for capture and tagging research does occur if it is clear that the questions can only be answered using intrusive research methods and that the information collected will benefit polar bear management.

Alternative approaches for collecting biological material (biopsy darting, hair snagging, fecal samples, and hunter collected samples) are increasingly used for monitoring diet (stable isotopes, fatty acids) and populations (genetic mark-recapture) (Thiemann et al. 2008b, Peacock et al. 2012, de Groot et al. 2013, Herreman and Peacock 2013). Researchers have incorporated traditional ecological knowledge in polar bear research for many years e.g., (Harington 1968, Furgal et al. 1996) particularly to inform research methods, formulate hypothesis and interpret results but there have been few systematic, analytical studies (Born et al. 2011). Vongraven et al. (2012) suggested that traditional ecological knowledge should be collected for monitoring local and regional polar bear distribution, behaviour, body condition and reproduction.

Polar bears rely upon sea ice to obtain the majority of their nutrition and calories. It is fundamental that polar bear sea ice habitat be monitored at the population level at a minimum (Stirling and Derocher 2012, Vongraven et al. 2012, Laidre et al. 2015b). Depending on the geographic extent of a population, habitat monitoring may be more appropriate at a subpopulation or oceanographic unit. My results (Chapter 2) demonstrate one approach to monitoring and interpreting sea ice habitat trends that can be applied throughout the range of polar bears. Habitat selection studies should be conducted by population (Sahanatien and Derocher 2012, Vongraven et al. 2012) because sea ice conditions and quality are driven by regional climate and physical oceanographic conditions. Satellite imagery of sea ice is available for the entire Arctic at high and low resolutions, and from various sensors, it just needs to be put to use by management agencies.

One of the biggest challenges of my research was the overall lack of information about the Foxe Basin study area. In particular, lack of information on prey species distribution and abundance but also detailed bathymetric maps, recent oceanography, and benthic and under ice biodiversity all hamper understanding this diverse ecosystem. The International Polar Year (2007-2009) research efforts were concurrent with my research and recently new information on productivity and pelagic biodiversity were published (Ferland et al. 2011, Estrada et al. 2012). The seasonal sea ice ecosystem of the Hudson Bay System needs significant research attention to describe sea ice and marine food webs, similar to the efforts just completed in the Chukchi Sea and Beaufort Sea (Moore and Stabeno 2015). The inland seas, of Foxe Basin, Hudson Strait and Hudson Bay are essential year round habitat for walrus (*Odobenus rosmarus*), bowhead whale (*Balaena mysticetus*), beluga *(Delphinus leucas*), narwhal (*Monodon monoceros*) and polar bear, all sentinel Arctic species.

References

Ainley, D. G., C. T. Tynan, and I. Stirling. 2003. Sea ice: critical habitat for polar marine mammals and birds. Pages 240-266 *in* D. N. Thomas and G. S. Dieckmann, editors. Sea Ice: An Introduction to its Physics, Chemistry, Biology and Geology. Blackwell Science, Oxford, UK.

Amstrup, S. 2003. Polar bear. Pages 587-610 *in* G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. Wildlife Mammals of North America: Biology, Management, and Conservation. John Hopkins University Press, Baltimore, Maryland, USA.

Amstrup, S. C., E. T. DeWeaver, D. C. Douglas, B. G. Marcot, G. M. Durner, C. M. Bitz, and D. A. Bailey. 2010. Greenhouse gas mitigation can reduce sea-ice loss and increase polar bear persistence. Nature **468**:955-958.

Amstrup, S. C., G. M. Durner, T. L. McDonald, D. M. Mulcahy, and G. W. Garner. 2001. Comparing movement patterns of satellite-tagged male and female polar bears. Canadian Journal of Zoology **79**:2147-2158.

Amstrup, S. C., G. M. Durner, I. Stirling, N. J. Lunn, and F. Messier. 2000. Movements and distribution of polar bears in the Beaufort Sea. Canadian Journal of Zoology **78**:948-966.

Amstrup, S. C., B. G. Marcot, and D. C. Douglas. 2008. A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. Pages 213-264 *in* E. DeWeaver, C. Bitz, and L. Tremblay, editors. Arctic sea ice decline: observations, projections, mechanisms, and implications. American Geophysical Union, Washington, DC.

Amstrup, S. C., T. L. McDonald, and G. M. Durner. 2004. Using satellite radiotelemetry data to delineate and manage wildlife populations. Wildlife Society Bulletin **32**:661-679.

Amstrup, S. C., I. Stirling, T. Smith, C. Perham, and G. W. Thiemann. 2006. Recent observations of intraspecific predation and cannibalism among polar bears in the southern Beaufort Sea. Polar Biology **29**:997-1002.

Andersen, M., A. E. Derocher, Ø. Wiig, and J. Aars. 2012. Polar bear (*Ursus maritimus*) maternity den distribution in Svalbard, Norway. Polar Biology **35**:499-508.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71**:355-366.

Arrigo, K. R. 2014. Sea ice ecosystems. Annual Review of Marine Science **6**:439-467.

Arrigo, K. R. and G. L. van Dijken. 2015. Continued increases in Arctic Ocean primary productivity. Progress in Oceanography **136**:60-70.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology **77**:215-227.

Atkinson, S. N. and M. A. Ramsay. 1995. The effects of prolonged fasting of the body composition and reproductive success of female polar bears. Functional Ecology **9**:559-567.

Aublet, J. F., M. Feista-Bianchet, D. Bergero, and B. Bassano. 2009. Temperature constraints on foraging behaviour of male alpine ibex (*Capra ibex*) in summer. Oecologia **159**:237-247.

Avgar, T., R. Deardon, and J. M. Fryxell. 2013. An empirically parameterized individual based model of animal movement, perception and memory. Ecological Modelling **251**:158-172.

Baascha, D. M., A. J. Tyrea, J. J. Millspaugh, S. E. Huygnstrom, and K. C. Vercauteren. 2010. An evaluation of three statistical methods used to model resource selection. Ecological Modelling **221**:565-574.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, New York, NY USA.

Bellemain, E., J. E. Swenson, and P. Taberlet. 2005. Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. Ethology **112**:238-246.

Ben-David, M., K. Titus, and R. B. LaVern. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? Oecologia **138**:465-474.

Bengtson, J. L., L. M. Hiruki-Raring, M. A. Simpkins, and P. L. Boveng. 2005. Ringed and bearded seal densities in the eastern Chukchi Sea, 1999-2000. Polar Biology **28**:833-845.

Best, R. C. 1982. Thermoregulation in resting and active polar bears. Journal of Comparative Physiology **146**:63-73.

Bestley, S., I. D. Jonsen, M. A. Hindell, C. Guinet, and J.-B. Charrassin. 2013. Integrative modelling of animal movement: incorporating *in situ* habitat and behavioural information for a migratory marine predator. Proceedings of the Royal Society of London, Series B: Biological Sciences **280**:20122262.

Bethke, R., M. Taylor, S. Amstrup, and F. Messier. 1995. Population delineation of polar bears using satellite collar data. Ecological Applications **6**:311-317.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://spatialecology.com/htools (accessed January 2008).

Bhatt, U. S., D. A. Walker, J. E. Walsh, E. D. Carmack, K. E. Frey, W. N. Meier, S. E. Moore, F.-J. W. Parmentier, E. Post, V. E. Romanovsky, and W. R. Simpson. 2014. Implications of Arctic sea ice decline for the Earth system. Annual Review Environment and Resources **39**:57-89.

Blix, A. S. and J. W. Lentfer. 1979. Modes of thermal protection in polar bear cubs - at birth and on emergence from the den. American Journal of Physiology **236**:R67-R74.

Bluhm, B. A. and R. Gradinger. 2008. Regional variability in food availability for arctic marine mammals. Ecological Applications **18**:S77-S96.

Boltunov, A., V. Nikiforov, and V. Semenova. 2012. Community-based surveys and management of walruses and polar bears in the area of Cape Kozhevnikov (Chukotka, Russia). Pages 161-170 *in* F. Huettmann, editor. Protection of the Three Poles. Springer, New York.

Born, E. W., A. Heilmann, L. Hom, and K. Laidre. 2011. Polar Bears in Northwest Greenland: An Interview Survey about the Catch and the Climate. Museum Tusculanum Press, Copenhagen.

Born, E. W., Ø. Wiig, and J. Thomassen. 1997. Seasonal and annual movements of radio-collared polar bears (*Ursus maritimus*) in northeast Greenland. Journal of Marine Systems **10**:67-77.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions **12**:269-276.

Bromaghin, J. F., T. L. McDonald, I. Stirling, A. E. Derocher, E. S. Richardson, E. V. Regehr, D. C. Douglas, G. M. Durner, T. Atwood, and S. C. Amstrup. 2015. Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. Ecological Applications **25**:634-651.

Brook, R. K. 2001. Structure and dynamics of the vegetation in Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba: community and landscape scales. University of Manitoba, Winnipeg, MB.

Brooks, C. J. and S. Harris. 2008. Directed movement and orientation across a large natural landscape by zebras, *Equus burchelli antiquorum*. Animal Behaviour **76**:277-285.

Bump, J. K. and J. R. Lovvorn. 2004. Effects of lead structure in Bering Sea pack ice on the flight costs of wintering spectacled eiders. Journal of Marine Systems **50**:113-139.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd edition. Springer, New York, NY USA.

Burns, J. J. 1970. Remarks on distribution and natural history of pagophilic pinnipeds in Bering and Chukchi Seas. Journal of Mammalogy **51**:445-454.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy **24**:346-352.

Canadian Ice Service. 2008. Annual Arctic Ice Atlas, Winter 2007. Canadian Ice Service, Environment Canada, Ottawa, ON CA.

Canadian Ice Service. 2009. Annual Arctic Ice Atlas, Winter 2008. Canadian Ice Service, Environment Canada, Ottawa, ON CA.

Canadian Ice Service. 2010. Annual Arctic Ice Atlas - Winter 2009. Canadian Ice Service, Environment Canada, Ottawa, ON CA.

Canadian Ice Service. 2011. Annual Arctic Ice Atlas - Winter 2010. Canadian Ice Service, Environment Canada, Ottawa, ON CA.

Castro de la Guardia, L., A. E. Derocher, P. G. Myers, A. D. Terwisscha van Schletinga, and N. J. Lunn. 2013. Future sea ice conditions in western Hudson Bay and consequences for polar bears in the 21st century. Global Change Biology **19**:2675-2687.

Cavalieri, D. J., C. L. Parkinson, P. Gloersen, and H. J. Zwally. 1996. Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data. NASA DAAC. Updated yearly. National Snow and Ice Data Center, Boulder, CO USA.

Chambellant, M., N. J. Lunn, and S. H. Ferguson. 2012a. Temporal variation in distribution and density of ice-obligated seals in western Hudson Bay, Canada. Polar Biology **35**:1105-1117.

Chambellant, M., I. Stirling, W. A. Gough, and S. H. Ferguson. 2012b. Temporal variations in Hudson Bay ringed seal (*Phoca hispida*) life-history parameters in relation to environment. Journal of Mammalogy **93**:267-281.

Cherry, S., A. E. Derocher, G. W. Thiemann, and N. J. Lunn. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. Journal of Animal Ecology **82**:912-921.

Comiso, J. 2003. Large-scale characteristics and variability of the global sea ice cover.*in* D. N. Thomas and G. S. Dieckmann, editors. Sea Ice An Introduction to its Physics, Chemistry, Biology and Geology. Blackwell Science, Oxford, UK.

Comiso, J. 2010. Polar Oceans from Space. Springer, New York, NY USA.

Conover, W. J. 1980. Practical nonparametric statistics. 2nd edition. John Wiley and Sons, New York, NY, USA.

Coops, N. C., S. N. Gillanders, M. A. Wulder, S. E. Gergel, T. Nelson, and N. R. Goodwin. 2010. Assessing changes in forest fragmentation following infestation using time series Landsat imagery. Forest Ecology and Management **259**:2355-2365.

Crawford, J. A., K. J. Frost, L. T. Quackenbush, and A. Whiting. 2012. Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. Polar Biology **35**:241-255.

Crawford, J. A., L. T. Quackenbush, and J. J. Citta. 2015. A comparison of ringed and bearded seal diet, condition and productivity between historical (1975-1984) and recent (2003-2012) periods in the Alaskan Bering and Chukchi Seas. Progress in Oceanography **136**:133-150.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology **16**:488-502.

Crooks, K. R., C. Burdett, D. Theobald, C. Rondinini, and L. Boitani. 2011. Global patterns of fragmentation and connectivity of carnivore habitat. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences **366**:2642-2651.

Cyr, F. and P. Larouche. 2014. Thermal fronts atlas of Canadian coastal waters. Atmosphere-Ocean **53**:212-236.

Dall, S. R. X., L. A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens. 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology & Evolution **20**:187-193.

Darnis, G., D. Robert, C. Pomerleau, H. Link, P. Archambault, R. J. Nelson, M. Geoffroy, J.-E. Tremblay, C. Lovejoy, S. H. Ferguson, B. P. V. Hunt, and L. Fortier. 2012. Current state and trends in Canadian Arctic marine systems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. Climatic Change **115 Special Issue S1**:179-205.

Davidge, K. 1980. Polar bear denning survey - Wager Bay - 1978. NWT Wildlife Service Report.

Davis, J. M. and J. A. Stamps. 2004. The effect of natal experience on habitat preferences. Trends in Ecology & Evolution **19**:411-416.

de Groot, P. V. C., P. B. Y. Wong, C. Harris, M. Dyck, L. Kamookak, M. Pages, J. Michaux, and P. T. Boag. 2013. Toward a non-invasive Inuit polar bear survey: genetic data from polar bear hair snags. Wildlife Society Bulletin **37**:394-401.

de Jager, M., F. Bartumeus, A. Kolzch, F. J. Weissing, G. M. Hengeveld, B. A. Nolet, P. M. J. Herman, and J. van de Koppel. 2014. How superdiffusion gets arrested: ecological encounters explain shift from Levy to Brownian movement. Proceedings of the Royal Society of London, Series B: Biological Sciences **281**:20132605.

DeMaster, D. P. and I. Stirling. 1981. *Ursus maritimus*. Mammalian Species **145**:1-7.

Derocher, A. E. 2012. Polar bears: a complete guide to their biology and behavior. The Johns Hopkins University Press, Baltimore, MD, USA.

Derocher, A. E., J. Aars, S. C. Amstrup, A. Cutting, N. J. Lunn, P. K. Molnar, M. E. Obbard, I. Stirling, G. W. Thiemann, D. Vongraven, Ø. Wiig, and G. S. York. 2013. Rapid ecosystem change and polar bear conservation. Conservation Letters **6**:368-375.

Derocher, A. E., M. Andersen, Ø. Wiig, and J. Aars. 2010. Sexual dimophism and the mating ecology of polar bears (*Ursus maritimus*) at Svalbard. Behaviorial Ecology and Sociobiology **64**:939-946.

Derocher, A. E., D. Andriashek, and I. Stirling. 1993. Terrestrial foraging by polar bears during the ice-free period in western Hudson Bay. Arctic **46**:251-254.

Derocher, A. E., N. J. Lunn, and I. Stirling. 2004. Polar bears in a warming climate. Integrative and Comparative Biology **44**:163-176.

Derocher, A. E. and I. Stirling. 1990a. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Canadian Journal of Zoology **68**:1395-1403.

Derocher, A. E. and I. Stirling. 1990b. Observations of aggregating behaviour in adult male polar bears (*Ursus maritimus*). Canadian Journal of Zoology **68**:1390-1394.

Derocher, A. E., I. Stirling, and W. Calvert. 1997. Male-biased harvesting of polar bears in western Hudson Bay. Journal of Wildlife Management **61**:1075-1082.

Derocher, A. E. and Ø. Wiig. 1999. Infanticide and cannibalism of juvenile polar bears (*Ursus maritimus*) in Svalbard. Arctic **52**:307-310.

Donaldson, J., D. Heard, and G. Calef. 1981. Summer polar bear observations around Wager Bay, Northwest Territories. N.W.T. Wildlife Service, Yellowknife.

Dowsley, M. and G. Wenzel. 2008. "The time of the most polar bears": a co-management conflict in Nunavut. Arctic **61**:177-189.

Durner, G. M., S. C. Amstrup, and K. J. Ambrosius. 2006. Polar bear maternal den habitat in the Arctic National Wildlife Refuge, Alaska. Arctic **59**:31-36.

Durner, G. M., S. C. Amstrup, R. Nielson, and T. McDonald. 2004. Using discrete choice modeling to generate resource selection functions for female polar bears in the Beaufort Sea.*in* S. Hurzurbazar, editor. Resource selection methods and applications. First International Conference on Resource Selection. The University of Wyoming, Laramie, WY USA.

Durner, G. M., D. C. Douglas, R. M. Nielson, S. C. Amstrup, T. L. McDonald, I. Stirling, M. Mauritzen, E. W. Born, Ø. Wiig, E. DeWeaver, M. C. Serreze, S. E. Belikov, M. M. Holland, J. Maslanik, J. Aars, D. E. Bailey, and A. E. Derocher. 2009. Predicting 21st century polar bear habitat distribution from global climate models. Ecological Monographs **79**:25-58.

Durner, G. M., J. P. Whiteman, H. J. Harlow, S. C. Amstrup, E. V. Regehr, and M. Ben-David. 2011. Consequences of long-distance swimming and travel over deep-water pack ice for a female polar bear during a year of extreme sea ice retreat. Polar Biology **34**:975-984.

Dyck, M. G. and S. Romberg. 2007. Observations of a wild polar bear successfully fishing Arctic charr and fourhorned sculpin. Polar Biology **30**:1625-1628.

Edwards, M. A., A. E. Derocher, and J. A. Nagy. 2013. Home range size variation in female arctic grizzly bears relative to reproductive status and resource availability. PLoS ONE **8**:e68130.

Estrada, R., M. Harvey, M. Gosselin, M. Starr, P. Galbraith, and F. Straneo. 2012. Late-summer zooplankton community structure, abundance, and distribution in the Hudson Bay system (Canada) and their relationship with environmental conditions. Progress in Oceanography **11**:121-145.

Fagan, W. F., M. A. Lewis, M. Auger-Methe, T. Avgac, S. Benhamou, G. Breed, L. LaDage, U. E. Schlagel, W. Tang, Y. P. Papastamatiou, J. Forester, and T. Mueller. 2013. Spatial memory and animal movement. Ecology Letters **16**:1316-1329.

Fequet, D., L. Hache, S. McCourt, D. Langlois, C. Dicaire, B. Premont, A. Jolicoeur, and A. Minano. 2011. Sea Ice Climatic Atlas for Northern Canadian Waters 1981-2010. Canadian Ice Service, Environment Canada Ottawa, ON http://www.ec.gc.ca/glaces-ice/default.asp?lang=En&n=4B35305B-1.

Ferguson, S. H., L. Dueck, L. L. Loseto, and S. P. Luque. 2010. Bowhead whale *Balaena mysticetus* seasonal selection of sea ice. Marine Ecology Progress Series **411**:285-297.

Ferguson, S. H., M. K. Taylor, E. W. Born, A. Rosing-Asvid, and F. Messier. 1999. Determinants of home range size for polar bears (*Ursus maritimus*). Ecology Letters **2**:311-318.

Ferguson, S. H., M. K. Taylor, E. W. Born, A. Rosing-Asvid, and F. Messier. 2001. Activity and movement patterns of polar bears inhabiting consolidated versus active pack ice. Arctic **54**:49-54.

Ferguson, S. H., M. K. Taylor, and F. Messier. 1997. Space use by polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. Canadian Journal of Zoology **75**:1585-1594.

Ferguson, S. H., M. K. Taylor, and F. Messier. 2000. Influence of sea ice dynamics on habitat selection by polar bears. Ecology **81**:761-772.

Ferland, J., M. Gosselin, and M. Starr. 2011. Environmental control of summer primary production in the Hudson Bay system: the role of stratification. Journal of Marine Systems **88**:385-400.

Finley, K. J., G. W. Miller, R. A. Davis, and W. R. Koski. 1983. A distinctive large breeding population of ringed seals (*Phoca hispida*) inhabiting the Baffin Bay pack ice. Arctic **36**:162-173.

Fischbach, A., S. Amstrup, and D. Douglas. 2007. Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. Polar Biology **30**:1395-1405.

Fischer, J. and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography **16**:265-280.

Freitas, C., K. M. Kovacs, M. Andersen, J. Aars, S. Sandven, M. Skern-Mauritzen, O. Pavlova, and C. Lydersen. 2012. Importance of fast ice and glacier fronts for female bears and their cubs during spring in Svalbard, Norway. Marine Ecology Progress Series **447**:289-304.

Frost, K. J., L. F. Lowery, G. Pendleton, and H. R. Nute. 2004. Factors affecting the observed densities of ringed seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996-1999. Arctic **57**:115-128.

Furgal, C. M., S. Innes, and K. M. Kovacs. 1996. Characteristics of ringed seal, *Phoca hispida*, subnivean structures and breeding habitat and their effects of predation. Canadian Journal of Zoology **74**:858-874.

Furnell, D. and D. Oolooyuk. 1980. Polar bear predation on ringed seal in ice-free water. Canadian Field-Naturalist **94**:88-89.

Galbraith, P. S. and P. Larouche. 2011. Sea-surface temperature in Hudson Bay and Hudson Strait in relation to air temperature and ice cover breakup, 1985-2009. Journal of Marine Systems **87**:66-78.

Garćia-Martín, E. E., P. Serret, and R. J. G. Leakey. 2014. Plankton community and bacterial metabolism in Arctic sea ice leads during summer 2010. Deep-Sea Research I **92**:152-161.

Gaston, A. J., H. G. Gilchrist, and J. M. Hipfner. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Bunnich's guillemot (*Uria lomvia* L.). Journal of Animal Ecology **74**:832-841.

Gilg, O., K. M. Kovacs, J. Aars, J. Fort, G. Gauthier, D. Gremillet, R. A. Ims, H. Meltofte, J. Moreau, E. Post, N. M. Schmidt, G. Yannic, and L. Bollache. 2012. Climate change and the ecology and evolution of Arctic vertebrates. Annals of the New York Academy of Sciences **1249**:166-190.

Gjertz, I. and C. Lydersen. 1986. Polar bear predation on ringed seals in the fast-ice of Hornsund, Svalbard. Polar Research **4**:65-68.

Gleason, J. S. and K. D. Rode. 2009. Polar bear distribution and habitat association reflect long-term changes in fall sea ice conditions in the Alaskan Beaufort Sea. Arctic **62**:405-417.

Gould, J. L. and C. G. Gould. 2012. Nature's Compass. Princeton University Press, Princeton, NJ USA.

Gradinger, R., B. Bluhm, and K. Iken. 2010. Arctic sea-ice ridges - safe havens for sea ice fauna during periods of extreme ice melt? Deep Sea Research II **57**:86-95.

Gradinger, R. R. and B. A. Bluhm. 2004. In-situ observations on the distribution and behavior of amphipods and arctic cod under the sea ice of the high Arctic Canada Basin. Polar Biology **27**:595-603.

Grebmeier, J. M., J. E. Overland, S. E. Moore, E. V. Farley, E. C. Carmack, L. W. Cooper, K. E. Frey, J. H. Helle, F. A. McLaughlin, and S. L. McNutt. 2006. A major ecosystem shift in the northern Bering Sea. Science **311**:1461-1464.

Greenwood, P. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour **28**:1140-1162.

Gu, W., R. Heikkila, and I. Hanski. 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecology **17**:699-710.

Gurarie, E. and O. Ovaskainen. 2011. Characteristic spatial and temporal scales unify models of animal movement. The American Naturalist **178**:113-123.

Gustafson, E. J. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems **1**:143-156.

Hamilton, S. G., L. Castro de la Guardia, A. E. Derocher, V. Sahanatien, B. Tremblay, and D. Huard. 2013. Projected polar bear sea ice habitat in the Canadian Arctic Archipelago PLoS ONE **9**:e11371.

Hammill, M. O. and T. G. Smith. 1989. Factors affecting the distribution and abundance of ringed seal structures in Barrow Strait, Northwest Territories. Canadian Journal of Zoology **67**:2212-2219.

Hammill, M. O. and T. G. Smith. 1991. The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. Marine Mammal Science **7**:123-135.

Hanski, I. and O. Ovaskainen. 2002. Extinction debt at extinction threshold. Conservation Biology **16**:666-673.

Harington, C. R. 1968. Denning habits of the polar bear (*Ursus maritimus* Phipps). No. 5, Canadian Wildlife Service, Ottawa, ON, CA.

Harwood, L. A., T. G. Smith, J. C. George, S. J. Sandstrom, W. Walkusz, and G. J. Divoky. 2015. Change in the Beaufort Sea ecosystem: diverging trends in body condition and/or production in five marine vertebrate species. Progress in Oceanography **136**:263-273.

Heide-Jorgensen, M. P., L. M. Burt, R. G. Hansen, N. H. Nielsen, M. Rasmussen, S. Fossette, and H. Stern. 2012. The significance of the North Water Polynya to Arctic top predators. Ambio **42**:596-610.

Herreman, J. and E. Peacock. 2013. Polar bear use of a persistent food subsidy: insights from non-invasive genetic sampling in Alaska. Ursus **24**:148-163.

Higdon, J. and S. Ferguson. 2009. Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. Ecological Applications **19**:1365-1375.

Hobson, K. A. and H. E. Welch. 1992. Determination of trophic relationships within a high arctic marine food web using delta 13C and 15N analysis. Marine Ecology Progress Series **84**:9-18.

Hochheim, K. P. and D. G. Barber. 2010. Atmospheric forcing of sea ice in Hudson Bay during the fall period, 1980-2005. Journal of Geophysical Research. C. Oceans **115**:C05009.

Hochheim, K. P. and D. G. Barber. 2014. An update on the ice climatology of the Hudson Bay system. Arctic, Antarctic, and Alpine Research **46**:66-83.

Horton, T. W., R. N. Holdaway, A. N. Zerbini, N. Hauser, C. Garrigue, A. Andriolo, and P. J. Clapham. 2011. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. Biology Letters **7**:674-679.

Hostetler, J., J. McCown, E. Garrison, A. Neils, M. Barrett, M. Sunquist, S. Simek, and M. Oli. 2009. Demographic consequences of anthropogenic influences: Florida black bears in north-central Florida. Biological Conservation **142**:2456-2463.

Hunter, C., H. Caswell, M. Runge, E. Regehr, S. Amstrup, and I. Stirling. 2010. Climate change threatens polar bear populations: a stochastic demographic analysis. Ecology **9**:2883-2897.

Iacozza, J. and S. H. Ferguson. 2014. Spatio-temporal variabililty of snow over sea ice in western Hudson Bay, with reference to ringed seal pup survival. Polar Biology **37**:817-832.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY USA.

ITTVIS. 2009. ENVI-EX User's Guide, ITT Visual Information Solutions. Boulder, CO USA.

Iverson, S. A., H. G. Gilchrist, P. A. Smith, A. J. Gaston, and M. R. Forbes. 2014. Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. Proceedings of the Royal Society of London, Series B: Biological Sciences **281**:20133128.

Iverson, S. J., I. Stirling, and S. L. C. Lang. 2006. Spatial and temporal variation in the diets of polar bears across the Canadian Arctic: indicators of changes in prey populations and environment. Pages 98-117 *in* I. L. Boyd, S. Wanless, and C. J. Camphuysen, editors. Top Predators in Marine Ecosystems. Cambridge University Press, Cambridge, UK.

Jay, C. V., J. M. Grebmeier, A. S. Fischbach, T. L. McDonald, L. W. Cooper, and F. Hornsby. 2014. Pacific walrus (*Odobenus rosmarus divergens*) resource selection in the Northern Bering Sea. PLoS ONE **9**:e93035.

Jay, C. V., M. S. Udevitz, R. Kwok, A. S. Fischbach, and D. Douglas. 2010. Divergent movements of walrus and sea ice in the northern Bering Sea. Marine Ecology Progress Series **407**:293-302.

Johannessen, O. M., V. Y. Alexandrov, I. Y. Frolove, S. Sandven, L. H. Pettersson, L. P. Bobyleve, K. Kloster, V. G. Smirnov, Y. U. Mironov, and N. G. Babich. 2007. Remote Sensing of Sea Ice in the Northern Sea Route Studies and Application. Springer - Praxis, Chichester, UK.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**:65-71.

Johnson, M. 2007. Measuring habitat quality: a review. Condor **109**:489-504.

Jonkel, C., P. Smith, I. Stirling, and G. B. Kolenosky. 1976. The present status of the polar bear in the James Bay and Belcher Islands area. Canadian Wildlife Service.

Kahru, M., V. Brotas, M. Manzano-Sarabia, and B. Mitchell. 2011. Are phytoplankton blooms occurring earlier in the Arctic? Global Change Biology **17**:1733-1739.

Kelly, B. P., O. H. Badajos, M. Kunnasranta, J. R. Moran, M. Martinez-Bakker, D. Wartzok, and P. Boveng. 2010. Seasonal home range and fidelity to breeding sites among ringed seals. Polar Biology **33**:1095-1109.

Kenward, R. E., S. Walls, A. South, and N. Casey. 2008. Ranges8: for the analysis of tracking and location data. v2.8. Anatrack, Ltd., Wareham, UK.

Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J. M. Gaillard, and P. R. Moorcroft. 2010. The home range concept: are traditional estimators still relevant with modern telemetry technology. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences **365**:2221-2231.

Kingsley, M. C. S. and I. Stirling. 1991. Haul-out behaviour of ringed and bearded seals in relation to defence against surface predators. Canadian Journal of Zoology **69**:1857-1861.

Knudsen, B. 1978. Time budgets of polar bears (*Ursus maritimus*) on North Twin Island, James Bay, during summer. Canadian Journal of Zoology **56**:1627-1628.

Kochnev, A. A. 2006. Research on polar bear autumn aggregations on Chukotka, 1989-2004. Pages 157-165 *in* J. Aars, N. J. Lunn, and A. E. Derocher, editors. Polar Bears, Proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 20-24 June 2005, Seattle, Washington, USA. IUCN, Gland, Switzerland.

Kotliar, N. B. and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**:253-260.

Kovacs, K. M., C. Lydersen, and I. Gjertz. 1996. Birth-site characteristics and prenatal molting in bearded seals (*Erignathus barbatus*). Journal of Mammalogy **77**:1085-1091.

Kovacs, K. M., C. Lydersen, J. E. Overland, and S. E. Moore. 2011. Impacts of changing sea ice conditions on Arctic marine mammals. Marine Biodiversity **41**:181-194.

Krafft, B. A., K. M. Kovacs, and C. Lydersen. 2007. Distribution of sex and age groups of ringed seals *Pusa hispida* in the fast-ice breeding habitat of Kongsfjorden, Svalbard. Marine Ecology Progress Series **335**:199-206.

Kwok, R., G. F. Cunningham, M. Wensnahan, I. Rigor, H. J. Zwally, and D. Yi. 2009. Thinning and volume loss of the Arctic Ocean sea ice cover: 2003-2008. Journal of Geophysical Research. C. Oceans **114**:C07005.

Laidre, K. L., E. W. Born, E. Gurarie, Ø. Wiig, R. Dietz, and H. Stern. 2012. Females roam while males patrol: divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*). Proceedings of the Royal Society of London, Series B: Biological Sciences **280**:20122371.

Laidre, K. L., E. W. Born, P. Heagerty, Ø. Wiig, H. Stern, R. Dietz, J. Aars, and M. Andersen. 2015a. Shifts in female polar bear (*Ursus maritimus*) habitat use in East Greenland. Polar Biology **38**:879-893.

Laidre, K. L. and M. P. Heide-Jorgensen. 2011. Life in the lead: extreme densities of narwhals *Monodon monoceros* in the offshore pack ice. Marine Ecology Progress Series **423**:269-278.

Laidre, K. L., H. Stern, K. M. Kovacs, L. Lowry, S. E. Moore, E. V. Regehr, S. H. Ferguson, Wiig, P. L. Boveng, R. P. Angliss, E. W. Born, D. Litovka, L. Quakenbush, C. Lydersen, D. Vongraven, and F. Ugarte. 2015b. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conservation Biology **29**:724-737.

Laidre, K. L., I. Stirling, L. F. Lowry, Ø. Wiig, M. P. Heide-Jorgensen, and S. H. Ferguson. 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. Ecological Applications **18 (Supplement)**:S97-S125.

Latour, P. B. 1981a. Interactions between free-ranging, adulat male polar bears (*Ursus maritimus* Phipps): a case of adult social play. Canadian Journal of Zoology **59**:1775-1783.

Latour, P. B. 1981b. Spatial relationship and behavior of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. Canadian Journal of Zoology **59**:1763-1774.

Lentfer, J. W. 1973. Discreteness of Alaskan polar bear populations. Pages 323-329 *in* I. Kjerner and P. Bjurholm, editors. Proceedings of the XI International Congress of Game Biologists. National Swedish Environmental Protection Board, Stockholm, Sweden.

Lentfer, J. W. 1983. Alaskan polar bear movements from mark and recovery. Arctic **36**:282-288.

Lima, S. L. and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution **11**:131-135.

Lindenmayer, D. and J. Fischer. 2006. Habitat fragmentation and landscape change: an ecological and conservation synthesis. Island Press, Washington, DC, USA.

Liu, H., H. Guo, and L. Zhang. 2014. Sea ice classification using dual polarization SAR data. Earth and Environmental Science **17**:012115.

Lone, K., J. Aars, and R. A. Ims. 2012. Site fidelity of Svalbard polar bears as revealed by mark-recapture locations. Polar Biology **36**:27-39.

Loranty, M. M., S. J. Goetz, and P. S. A. Beck. 2011. Tundra vegetation effects on pan-Arctic albedo. Environmental Research Letters **6**:024014.

Ludwig, J. A. and J. F. Reynolds. 1988. Statistical Ecology. Wiley, New York, NY USA.

Lunn, N. J. 1986. Observations of nonaggressive behaviour between polar bear family groups. Canadian Journal of Zoology **64**:2035-2037.

Lunn, N. J. and G. B. Stenhouse. 1987. Foxe Basin polar bear research program - 1985 Field Report. Government of Northwest Territories, Department of Renewable Resources Report, Yellowknife, NWT.

Lunn, N. J. and I. Stirling. 1985. The signficance of supplemental food to polar bears during the ice-free period of Hudson Bay. Canadian Journal of Zoology **63**:2291-2297.

Lydersen, C. and K. M. Kovacs. 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. Marine Ecology Progress Series **187**:265-281.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. Nature **301**:379-384.

MANICE. 2005. Manual of standard procedures for observing and reporting ice conditions. Canadian Ice Service, Environment Canada, Ottawa, ON, CA.

Marcq, S. and J. Weiss. 2012. Influence of sea ice lead-width distribution on turbulent heat transfer between the ocean and the atmosphere. The Crysophere **6**:143-156.

Markus, T., J. Stroeve, and J. Miller. 2009. Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. Journal of Geophysical Research. C. Oceans **114**:C12024.

Martin, J., B. van Moorter, E. Revilla, P. Blanchard, S. Dray, P. Quenette, D. Allaine, and J. E. Swenson. 2013. Reciprocal modulation of internal and external factors determines individual movements. Journal of Animal Ecology **82**:290-300.

Martini, I. P. 1986. Coastal features of Canadian inland seas. Pages 117-142 *in* I. P. Martini, editor. Canadian Inland Seas. Elesvier, Amsterdam.

Matthews, C. J. D., S. P. Luque, S. D. Petersen, R. D. Andrews, and S. H. Ferguson. 2011. Satellite tracking of a killer whale (*Orcinus orca*) in the eastern Canadian Arctic documents ice avoidance and rapid, long distance movement into the North Atlantic. Polar Biology **34**:1091-1096.

Mattisson, J., J. Persson, H. Andren, and P. Segerstrom. 2011. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Canadian Journal of Zoology **89**:79-89.

Mauritzen, M., S. E. Belikov, A. N. Boltunov, A. E. Derocher, E. Hansen, R. A. Ims, Ø. Wiig, and N. Yoccoz. 2003a. Functional responses in polar bear habitat selection. Oikos **100**:112-124.

Mauritzen, M., A. E. Derocher, O. Pavlova, and Ø. Wiig. 2003b. Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. Animal Behaviour **66**:107-113.

Mauritzen, M., A. E. Derocher, and Ø. Wiig. 2001. Space-use strategies of female polar bears in a dynamic sea ice habitat. Canadian Journal of Zoology **79**:1704-1713.

Mauritzen, M., A. E. Derocher, Ø. Wiig, S. E. Belikov, A. N. Boltunov, E. Hansen, and G. W. Garner. 2002. Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. Journal of Applied Ecology **39**:79-90.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience **16**:238-247.

McCall, A. G., A. E. Derocher, and N. J. Lunn. 2015. Home range distribution of polar bears in western Hudson Bay. Polar Biology **38**:343-355.

McDermid, G. J., N. C. Coops, M. A. Wulder, S. E. Franklin, and N. E. Seitz. 2010. Critical remote sensing contributions to spatial wildlife ecological knowledge and management.*in* S. A. Cushman and F. Huettmann, editors. Spatial Complexity, Informatics and Wildlife Conservation. Springer, New York, NY USA.

McDonald, T., B. Manly, R. Nielson, and L. Diller. 2006. Discrete choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. Journal of Wildlife Management **70**:375-383.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, MA, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html.

McGarigal, K. and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 122 p., Portland, OR, USA.

McGarigal, K., S. Tagil, and S. A. Cushman. 2009. Surface metrics: an alternative to patch metrics for the quantification of landscape structure. Landscape Ecology **24**:433-450.

McLoughlin, P. and S. Ferguson. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience **7**:123-130.

Meier, W. N., G. K. Hovelsrud, B. E. H. van Oort, J. R. Key, K. M. Kovacs, C. Michel, C. Haas, M. A. Granskog, S. Gerland, D. K. Perovich, A. Makshtas, and J. D. Reist. 2014. Arctic sea ice transformation: a review of recent observed changes and impacts on biology and human activity. Review of Geophysics **51**:185-217.

Melentyev, V. V. and V. I. Chernook. 2010. Multi-spectral satellite-airborne management of ice form marine mammals and their habitat in the presence of climate change using a "hot spots" approach.*in* S. A. Cushman and F. Huettmann, editors. Spatial Complexity, Informatics and Wildlife Conservation. Springer, New York, NY, USA.

Merkle, J. A., D. Fortin, and J. M. Morales. 2013. A memory-based foraging tactic reveals an adaptive mechanism for retricted space use. Ecology Letters **17**:924-931.

Messier, F., M. Taylor, and M. A. Ramsay. 1992. Seasonal activity patterns of female polar bears (*Ursus maritimus*) in the Canadian Arctic as revealed by satellite telemetry. Journal of Zoology London **226**:219-229.

Metzger, J., A. Martensen, M. Dixo, L. Bernacci, M. Ribeiro, A. Teixeira, and R. Pardini. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation **142**:1166-1177.

Meyer, C. B. and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions **12**:288-297.

Miles, M. W. and R. G. Barry. 1998. A 5-year satellite climatology of winter sea ice leads in the western Arctic. Journal of Geophysical Research. C. Oceans **103**:21,723-721,734.

Minasny, B. and A. B. McBratney. 2002. FUZME version 3.0. Australian Centre for Precision Agriculture, University of Sydney, Sydney, Australia.

Mizerek, T., H. Regan, and K. Hovel. 2011. Seagrass habitat loss and fragmentation influence management strategies for a blue crab, *Callinectes sapidus*, fishery. Marine Ecology Progress Series **427**:247-257.

Molnár, P. K., A. E. Derocher, T. Klanjscek, and M. A. Lewis. 2011. Predicting climate change impacts on polar bear litter size. Nature Communication **2**:186.

Molnár, P. K., A. E. Derocher, M. A. Lewis, and M. K. Taylor. 2007. Modelling the mating system of polar bears: a mechanistic approach to the Allee effect. Proceedings of the Royal Society of London, Series B: Biological Sciences **275**:217-226.

Molnár, P. K., A. E. Derocher, G. W. Thiemann, and M. A. Lewis. 2010. Predicting survival, reproduction and abundance of polar bears under climate change. Biological Conservation **143**:1612-1622.

Molnár, P. K., A. E. Derocher, G. W. Thiemann, and M. A. Lewis. 2014. Corrigendum to "Predicting survival, reproduction and abundance of polar bears under climate change." Biological Conservation **177**:230-231.

Monnett, C. and J. S. Gleason. 2006. Observations of mortality associated with extended open-water swimming by polar bears in the Alaskan Beaufort Sea. Polar Biology **29**:681-687.

Moore, C. W., D. Obrist, A. Steffen, R. M. Staebler, T. A. Douglas, A. Richter, and N. S. V. 2014. Convective forcing of mercury and ozon in the Arctic boundary layer induced by leads in the sea ice. Nature **506**:81-85.

Moore, G. W. K. 2006. Reduction in seasonal sea ice concentration surrounding southern Baffin Island 1979-2004. Geophysical Research Letters **33**:L20501.

Moore, S. E. and H. P. Huntington. 2008. Arctic marine mammals and climate change: impacts and resilience. Ecological Applications **18 (Supplement)**:S157-S165.

Moore, S. E. and P. J. Stabeno. 2015. Synthesis of Arctic Research (SOAR) in marine ecosystems of the Pacific Arctic. Progress in Oceanography **136**:1-11.

Moritz, C. and R. Agudo. 2013. The future of species under climate change: resiliance or decline? Science **341**:504-508.

Mortelliti, A., G. Amori, and L. Boitani. 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia **163**:535-547.

Mortelliti, A., G. Amori, D. Capizzi, C. Cervone, S. Fagiani, B. Pollini, and L. Boitani. 2011. Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. Journal of Applied Ecology **48**:153-162.

Moulton, V. D., W. J. Richardson, T. McDonald, R. E. Elliott, and M. T. Williams. 2002. Factors influencing local abundance and haulout behavior of ringed seals (*Phoca hispida*) on landfast ice of the Alaskan Beaufort Sea. Canadian Journal of Zoology **80**:1900-1917.

Moyer, M. A., J. W. McCown, and M. K. Oli. 2007. Factors influencing home-range size of female Florida black bears. Journal of Mammalogy **88**:468-476.

Mueller, T. and W. F. Fagan. 2008. Search and navigation in dynamic environments - from individual behaviors to populations distributions. Oikos **117**:654-664.

Mueller, T., W. F. Fagan, and V. Grimm. 2011a. Integrating individual search and navigation behaviors in mechanistic movement models. Theoretical Ecology **4**:341-355.

Mueller, T., K. A. Olson, G. Dressler, P. Leimgruber, T. K. Fuller, C. Nicolson, A. J. Novaro, M. J. Bolgeri, D. Wattles, S. DeStefano, J. M. Calabrese, and W. F. Fagan. 2011b. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography **20**:683-694.

Nagy, J. A., D. L. Johnson, N. C. Larter, M. W. Campbell, A. E. Derocher, A. Kelly, M. Dumond, D. Allaire, and B. Croft. 2011. Subpopulation structure of caribou (*Rangifer tarandus* L.) in arctic and subarctic Canada. Ecological Applications **21**:2334-2348.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences, USA **105**:19052-19059.

Newsome, T. M., G.-A. Ballard, D. R. Dickman, P. J. S. Fleming, and R. van de Ven. 2013. Home range, activity and sociality of a top predator, the dingo: a test of the resource disperson hypothesis. Ecography **36**:914-925.

Nielsen, S. E., A. B. A. Shafer, M. S. Boyce, and G. B. Stenhouse. 2013. Does learning or instinct shape habitat selection? PLoS ONE **8**:e53721.

Noyce, K. V. and D. L. Garshelis. 2014. Follow the leader: social cues help guide landscape-level movement of American black bears (*Ursus americanus*). Canadian Journal of Zoology **92**:1005-1017.

O'Corry-Crowe, G. 2008. Climate change and the molecular ecology of arctic marine mammals. Ecological Applications **18 (Supplement)**:S56-S76.

Obbard, M. E., M. R. L. Cattet, T. Moody, L. R. Walton, D. Potter, J. Inglis, and C. Chenier. 2006. Temporal trends in the body condition of southern Hudson Bay polar bears. Research Information Note #3. Ontario Ministry of Natural Resources. http://www.ontla.on.ca/library/repository/mon/16000/268686.pdf, Peterborough, ON, CA.

Obbard, M. E. and K. R. Middel. 2012. Bounding the southern Hudson Bay polar bear subpopulation. Ursus **23**:134-144.

Obbard, M. E., G. W. Thiemann, E. Peacock, and T. D. DeBruyn. 2010. Polar Bears: Proceedings of the 15th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, Copenhagen, Denmark, 29 June-3 July 2009, vii + 235., IUCN, Gland, Switzerland and Cambridge, UK.

Ochilov, S. 2012. Operational SAR sea-ice image classification. IEEE Transactions on Geoscience and Remote Sensing **50**:4397-4408.

Øritsland, N. A. 1970. Temperature regulation of the polar bear (*Thalarctos maritimus*). Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology **37**:225-233.

Overland, J. E. and M. Wang. 2013. When will the summer Arctic be nearly ice free? Geophysical Research Letters **40**:2097-2101.

Ovsyanikov, N. 2005. Behavior of polar bears in coastal congregations. Zoologicheskij zhurnal **84**:94-103.

Owen, M. A., R. R. Swaisgood, C. Slocomb, S. C. Amstrup, G. M. Durner, K. Simac, and A. P. Pessier. 2015. An experimental investigation of chemical communication in the polar bear. Journal of Zoology **295**:36-43.

Paetkau, D., S. C. Amstrup, E. W. Born, W. Calvert, A. E. Derocher, G. W. Garner, F. Messier, I. Stirling, M. K. Taylor, Ø. Wiig, and C. Strobeck. 1999. Genetic structure of the world's polar bear populations. Molecular Ecology **8**:1571-1584.

Pagano, A. M., G. M. Durner, S. C. Amstrup, K. S. Simac, and G. S. York. 2012. Long-distance swimming by polar bears (*Ursus maritimus*) of the southern Beaufort Sea during years of extensive open water. Canadian Journal of Zoology **90**:663-676.

Papastamatiou, Y. P., D. P. Cartamil, C. G. Lowe, C. G. Meyer, B. M. Wetherbee, and K. N. Holland. 2011. Scales of orientation, directed walks and movement path structure in sharks. Journal of Animal Ecology **80**:864-874.

Parks, E. K., A. E. Derocher, and N. J. Lunn. 2006. Seasonal and annual movement patterns of polar bears on the sea ice of Hudson Bay. Canadian Journal of Zoology **84**:1281-1294.

Parmesan, C. 2006. Ecological and evolutionary reponses to recent climate change. Annual Review of Ecology and Systematics **37**:637-669.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.

Peacock, E., A. E. Derocher, N. J. Lunn, and M. E. Obbard. 2010. Polar bear ecology and management in Hudson Bay in the face of climate change.*in* S. H. Ferguson, L. L. Loseto, and M. L. Mallory, editors. A Little Less Arctic. Springer, Netherlands.

Peacock, E., A. E. Derocher, G. W. Thiemann, and I. Stirling. 2011. Conservation and management of Canada's polar bears (*Ursus maritimus*) in a changing Arctic. Canadian Journal of Zoology **89**:371-385.

Peacock, E., J. Laake, K. L. Laidre, E. W. Born, and S. N. Atkinson. 2012. The utility of harvest recoveries of marked individuals to assess polar bear (*Ursus maritimus*) survival. Arctic **65**:391-400.

Peacock, E., S. A. Sonsthagen, M. E. Obbard, A. Boltunov, E. V. Regehr, N. Ovsyanikov, J. Aars, S. N. Atkinson, G. K. Sage, A. G. Hope, E. Zeyl, L. Bachmann, D. Ehrich, K. T. Scribner, S. C. Amstrup, S. Belikov, E. Born, A. E. Derocher, I. Stirling, M. K. Taylor, Ø. Wiig, D. Peatkau, and S. L. Talbot. 2015. Implications of the circumpolar genetic structure of polar bears for their conservation in a rapidly warming Arctic. PLoS ONE **10**:e112021.

Peacock, E., M. K. Taylor, J. Laake, and I. Stirling. 2013. Population ecology of the polar bears in Davis Strait, Canada and Greenland Journal of Wildlife Management **77**:463-476.

Pearson, R. G., S. J. Phillips, M. M. Loranty, P. S. A. Beck, T. Damoulas, S. J. Knight, and S. J. Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nature Climate Change **3**:673-677.

Pedersen, A. 1945. Der eisbar (*Thalarctos maritimus* Phipps): verbreitung und lebensweise. Aktieselskabet E Bruun and Co., Copenhagen, DK.

Perovich, D. K. and J. A. Richter-Menge. 2009. Loss of sea ice in the Arctic. Annual Review of Marine Science **1**:417-441.

Pettorelli, N., W. F. Laurence, T. G. O'Brien, M. Wegmann, H. Nagendra, and W. Turner. 2014. Satellite remote sensing for applied ecologists: opportunities and challenges. Journal of Applied Ecology **51**:839-848.

Pilfold, N. W., A. E. Derocher, and E. Richardson. 2014a. Influence of intraspecific competition on the distribution of a wide-ranging, non-territorial carnivore. Global Ecology and Biogeography **23**:425-435.

Pilfold, N. W., A. E. Derocher, I. Stirling, and E. Richardson. 2014b. Polar bear predatory behaviour reveals seascape distribution of ringed seal lairs. Population Ecology **56**:129-138.

Pilfold, N. W., A. E. Derocher, I. Stirling, and E. Richardson. 2015. Multi-temporal factors influence predation for polar bears in a changing climate. Oikos **124**:1098-1107.

Pilfold, N. W., A. E. Derocher, I. Stirling, E. Richardson, and D. Andriashek. 2012. Age and sex composition of seals killed by polar bears in the eastern Beaufort Sea. PLoS ONE **7**:e41429.

Post, E., U. S. Bhatt, C. M. Bitz, J. F. Brodie, T. L. Fulton, M. Hebblewhite, J. Kerby, S. J. Kutz, I. Stirling, and D. A. Walker. 2013. Ecological consequences of sea ice decline. Science **341**:519-524.

Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science **325**:1355-1358.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65-110 *in* L. Boitani and T. K. Fuller, editors. Research Techniques in Animal Ecology Controversies and Consequences. Columbia University Press, New York.

Prinsenberg, S. J. 1986a. The circulation and current structure of Hudson Bay. Pages 187-204 *in* I. P. Martini, editor. Canadian Inland Seas. Elesvier Oceanography Series, Amsterdam, Netherlands.

Prinsenberg, S. J. 1986b. On the physical oceanography of Foxe Basin. Pages 217-236 *in* I. P. Martini, editor. Canadian Inland Seas. Elesvier, Amsterdam, Netherlands.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabe-Hesketh, S. and B. S. Everett. 2007. A handbook of statistical analyses using STATA. Fourth edition. Chapin & Hall/CRC, Boca Raton, Florida USA.

Ragen, T., H. Huntington, and G. Hovelsrud. 2007. Conservation of arctic marine mammals faced with climate change. Ecological Applications **18 (Supplement)**:S166-S174.

Ramsay, M. A. and D. Andriashek. 1986. Long distance route orientation of female polar bears (*Ursus maritimus*) in spring. Journal of Zoology London **208**:63-72.

Ramsay, M. A. and K. Hobson. 1991. Polar bears make little use of terrestrial food webs - evidence from stable carbon isotope analysis. Oecologia **86**:598-600.

Ramsay, M. A. and I. Stirling. 1986. On the mating system of polar bears. Canadian Journal of Zoology **64**:2142-2151.

Ramsay, M. A. and I. Stirling. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). Journal of Zoology **214**:601-634.

Ramsay, M. A. and I. Stirling. 1990. Fidelity of female bears to winter-den sites. Journal of Mammalogy **71**:233-236.

Ray, G. C., J. E. Overland, and G. L. Hufford. 2010. Seascape as an organizing principle for evaluating walrus and seal sea-ice habitat in Beringia. Geophysical Research Letters **37**:1-6.

Regehr, E. V., C. M. Hunter, H. Caswell, S. C. Amstrup, and I. Stirling. 2010. Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. Journal of Animal Ecology **79**:117-127.

Regehr, E. V., N. J. Lunn, S. C. Amstrup, and I. Stirling. 2007. Effects of earlier sea ice breakup on survival and population size of polar bears in Western Hudson Bay. Journal of Wildlife Management **71**:2673-2683.

Revilla, E. and T. Wiegand. 2008. Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. Proceedings of the National Academy of Sciences, USA **105**:19120-19125.

Robbins, C., C. Lopez-Alfaro, K. D. Rode, Ø. Toien, and O. L. Nelson. 2012. Hibernation and seasonal fasting in bears: the energetic costs and consequences for polar bears. Journal of Mammalogy **93**:1493-1503.

Rode, K. D., S. C. Amstrup, and E. V. Regehr. 2010a. Reduced body size and cub recruitment in polar bears associated with sea ice decline. Ecological Applications **20**:768-782.

Rode, K. D., A. M. Pagano, J. F. Bromaghin, T. C. Atwood, G. M. Durner, K. S. Simac, and S. C. Amstrup. 2014a. Effects of capturing and collaring on polar bears: findings from long-term research on southern Beaufort Sea population. Wildlife Research **41**:311-322.

Rode, K. D., E. Peacock, M. Taylor, I. Stirling, E. W. Born, K. L. Laidre, and Ø. Wiig. 2012. A tale of two polar bear populations: ice habitat, harvest, and body condition. Population Ecology **54**:3-18.

Rode, K. D., E. V. Regehr, D. C. Douglas, G. Durner, A. E. Derocher, G. W. Thiemann, and S. M. Budge. 2014b. Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. Global Climate Change **20**:76-88.

Rode, K. D., J. D. Reist, E. Peacock, and I. Stirling. 2010b. Comments in response to "Estimating the energetic contribution of polar bear (*Ursus maritimus*) summer diets to the total energy budget" by Dyck and Kebreab (2009). Journal of Mammalogy **91**:1517-1523.

Rode, K. D., C. T. Robbins, L. Nelson, and S. C. Amstrup. 2015. Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities. Frontiers in Ecology and the Environment **13**:138-145.

Rodgers, A. R., A. P. Carr, H. L. Beyer, L. Smith, and J. G. Kie. 2007. HRT: Home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre of Northern Forest Ecosystem Research, Thunder Bay, ON CA.

Rogers, L. L. 1987. Navigation by adult black bears. Journal of Mammalogy **68**:185-188.

Rogers, M. C., E. Peacock, K. Simac, M. B. O'Dell, and J. M. Welker. 2015. Diet of female polar bears in the southern Beaufort Sea of Alaska: evidence for an emerging alternative foraging strategy in response to environmental change. Polar Biology **38**:1035-1047.

Rose, R. A., D. Byler, J. R. Eastman, E. Fleishman, G. Geller, S. Goetz, L. Guild, H. Hamilton, M. Hansen, R. Headley, J. Hewson, N. Horning, B. A. Kaplin, N. Laporte, A. Leidner, P. Leimgruber, J. Morisette, J. Musinsky, L. Pintea, A. Prados, V. C. Radeloff, M. Rowen, S. Saatchi, S. Schill, K. Tabor, W. Turner, A. Voacek, J. Vogelmann, M. Wegmann, D. Wilkie, and C. Wilson. 2015. Ten ways remote sensing can contribute to conservation. Conservation Biology **29**:350-359.

Russell, R. H. 1975. The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. Arctic **28**:117-129.

Sahanatien, V. 2011. Interview Database: Inuit knowledge of polar bears, Foxe Basin, Nunavut. University of Alberta, Edmonton, AB, CA.

Sahanatien, V. and A. E. Derocher. 2012. Monitoring sea ice habitat fragmentation for polar bear conservation. Animal Conservation **15**:397-406.

Sahanatien, V., E. Peacock, and A. E. Derocher. 2015. Population substructure and space use of Foxe Basin polar bears. Ecology and Evolution **14**:2851-2864.

Santora, J. A. 2014. Environmental determinants of top predator distribution within the dynamic winter pack ice zone of the northern Antarctic Peninsula. Polar Biology **37**:1083-1097.

Saucier, F. J., S. Senneville, S. Prinsenberg, F. Roy, G. Smith, P. Gachon, D. Caya, and R. Laprise. 2004. Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada. Climate Dynamics **23**:303-326.

Scales, K. L., P. I. Miller, L. A. Hawkes, S. N. Ingram, D. W. Sims, and S. C. Votier. 2014. On the front line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. Journal of Applied Ecology **51**:1575-1583.

Schaefer, J., A. Veitch, F. Harrington, W. Brown, J. Theberge, and S. Luttich. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. Oecologia **126**:507-514.

Schaefer, J. and C. Wilson. 2002. The fuzzy structure of populations. Canadian Journal of Zoology **80**:2235-2241.

Schaefer, J. A. and S. P. Mahoney. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. Canadian Journal of Zoology **91**:767-774.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters **11**:1338-1350.

Schiebe, S., K. D. Rode, J. S. Gleason, J. Wilder, K. Proffitt, T. J. Evans, and S. Miller. 2008. Effects of sea ice extent and food availability on spatial and temperal distribution of polar bears during the fall open-water period in the Southern Beaufort Sea. Polar Biology **31**:999-1010.

Schipper, J. and J. S. Chanson and F. Chiozz and N. A. Cox and M. Hoffman and V. Katariya and J. Lamoreux and A. S. L. Rodrigues and S. N. Stuart and H. J. Temple and J. Baillie and L. Boitani and T. E. J. Lacher and R. A. Mittermeier and A. T. Smith and D. Absolon and J. M. Aguiar and G. Amori and N. Bakkour and R. Baldie and R. J. Berridge and J. Bielby and P. A. Black and J. J. Blanc and T. M. Brooks and J. A. Burton and T. M. Butynski and G. Catullo and R. Chapman and Z. Cokeliss and B. Collen and J. Conroy and J. G. Cooke and G. A. B. da Fonseca and A. E. Derocher and H. T. Dublin and J. W. Duckworth and L. Emmons and R. H. Emslie and M. Festa-Blanchet and M. Foster and S. Foster and D. Garshelis and C. Gates and M. Gimenz-Dixon and S. Gonzalez and J. F. Gonzalez-Maya and T. C. Good and G. Hammerson and P. S. Hammond, et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science **332**:225-230.

Schliebe, S., K. D. Rode, J. S. Gleason, J. Wilder, K. Proffitt, T. J. Evans, and S. Miller. 2008. Effects of sea ice extent and food availability on spatial and temporal distribution of polar bears during the fall open-water period in the Southern Beaufort Sea. Polar Biology **31**:999-1010.

Schmidt, K., W. Jedrzejewski, H. Okarma, and R. Kowalczyk. 2009. Spatial interactions between grey wolves and Eurasian lynx in Bailowieza Primeval Forest, Poland. Ecological Research **24**:207-214.

Schmidt, K. A., S. R. X. Dall, and J. A. van Gils. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos **119**:304-316.

Schooley, R. and L. Branch. 2011. Habitat quality of source patches and connectivity in fragmented landscapes. Biodiversity and Conservation **20**:1611-1623.

Schweinsburg, R. E. 1979. Summer snow dens used by polar bears in the Canadian High Arctic. Arctic **32**:165-169.

Schweinsburg, R. E. and L. J. Lee. 1982. Movement of four satellite-monitored polar bears in Lancaster Sound, Northwest Territories. Arctic **35**:504-511.

Schweinsburg, R. E., L. J. Lee, and P. B. Latour. 1982. Distribution, movement and abundance of polar bears in Lancaster Sound, Northwest Territories. Arctic **35**:159-169.

Sergeant, D. 1986. Sea mammals. Pages 327-340 *in* I. P. Martini, editor. Canadian Inland Seas. Elsevier Oceanography Series, Amsterdam, Netherlands.

Smith, S. D., R. B. Muench, and C. H. Pease. 1990. Polynyas and leads: an overview of physical processes and environment. Journal of Geophysical Research. C. Oceans **95**:9461-9479.

Smith, T. and B. Sjare. 1990. Predation of belugas and narwhals by polar bears in the nearshore areas of the Canadian High Arctic. Arctic **43**:99-102.

Smith, T. G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology **58**:2201-2209.

Smith, T. G. and M. O. Hammill. 1981. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Canadian Journal of Zoology **59**:966-981.

Smith, T. G. and I. Stirling. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology **53**:1297-1305.

Spencer, W. D. 2012. Home ranges and the value of spatial information. Journal of Mammalogy **93**:929-947.

Stapleton, S., S. N. Atkinson, D. Hedman, and D. Garshelis. 2014. Revisiting Western Hudson Bay: using aerial surveys to update polar bear abundance in a sentinel population. Biological Conservation **170**:38-47.

Stapleton, S., E. Peacock, and D. Garshelis. 2015. Aerial surveys suggest long-term stability in the seasonally ice-free Foxe Basin (Nunavut) polar bear population. Marine Mammal Science:10.1111/mms.12251.

Stapleton, S. P. 2013. Alternative methods for monitoring polar bears in the North American Arctic. University of Minnesota, St. Paul, MN USA.

Stempniewicz, L., D. Kidawa, M. Barcikowski, and L. Iliszko. 2013. Unusual hunting and feeding behaviour of polar bears on Spitzbergen. Polar Record **50**:216-219.

Stenhouse, G. B. and N. J. Lunn. 1987. Foxe Basin polar bear research program - 1984 field report. . Northwest Territories Department of Renewable Resources Report, Yellowknife, NT, CA.

Stewart, D. B. and W. L. Lockhart. 2005. An overview of the Hudson Bay marine ecosystem overview. Department of Fisheries and Oceans, Ottawa, ON, CA.

Stewart, R. E. A., J. W. Hamilton, and J. B. Dunn. 2013. Results of Foxe Basin walrus (*Odobenus rosmarus rosmarus*) surveys: 2010-2011. Fisheries and Oceans Canada, Winnipeg, MB, CA.

Steyaert, S. M. J. G., J. Kindberg, J. E. Swenson, and A. Zedrosser. 2013a. Male reproductive strategy explains spatiotemporal segregation in brown bears. Journal of Animal Ecology **82**:836-845.

Steyaert, S. M. J. G., C. Reusch, S. Brunberg, J. E. Swenson, K. Hacklander, and A. Zedrosser. 2013b. Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. Biology Letters **9**:20130624.

Stirling, I. 1974. Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). Canadian Journal of Zoology **52**:1191-1198.

Stirling, I. 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. Journal of Marine Systems **10**:9-21.

Stirling, I. 2011. Polar Bears The Natural History of a Threatened Species. Fizhentry & Whiteside, Markham, ON, CA.

Stirling, I., D. Andriashek, and W. Calvert. 1993. Habitat preference of polar bears in the western Canadian Arctic in late winter and spring. Polar Record **29**:13-24.

Stirling, I., D. Andriashek, P. Latour, and W. Calvert. 1975. Distribution and abundance of polar bears in the eastern Beaufort Sea. Canadian Wildlife Service, Ottawa, ON, CA.

Stirling, I. and W. F. Archibald. 1977. Aspects of predation of seals by polar bears. Journal of Fisheries Research Board of Canada **34**:1126-1129.

Stirling, I. and A. E. Derocher. 1993. Possible impacts of climate warming on polar bears. Arctic **46**:240-245.

Stirling, I. and A. E. Derocher. 2012. Effects of climate warming on polar bears: a review of the evidence. Global Change Biology **18**:2694-2706.

Stirling, I., C. Jonkel, P. Smith, R. Robertson, and D. Cross. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay Canadian Wildlife Service, Ottawa, ON, CA.

Stirling, I. and P. Latour. 1978. Comparative hunting abilities of polar bear cubs of different ages. Canadian Journal of Zoology **56**:1768-1772.

Stirling, I., N. J. Lunn, and J. Iacozza. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. Arctic **52**:294-306.

Stirling, I., N. J. Lunn, J. Iacozza, C. Elliot, and M. Obbard. 2004. Polar bear distribution and abundance on the southwestern Hudson Bay coast during open water season, in relation to population trends and annual ice patterns. Arctic **57**:15-26.

Stirling, I. and N. A. Øritsland. 1995. Relationships between estimates of ringed seal and polar bear populations in the Canadian Arctic. Canadian Journal of Fisheries and Aquatic Sciences **52**:2594-2612.

Stirling, I. and C. L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. Arctic **59**:261-275.

Stirling, I. and M. A. Ramsay. 1986. Polar bears in Hudson Bay and Foxe Basin: present knowledge and research opportunities. Pages 341-354 *in* I. P. Martini, editor. Canadian Inland Seas. Elsevier Science, Amsterdam, The Netherlands.

Stirling, I. and J. E. Ross. 2011. Observations of cannibalism by polar bears (*Ursus maritimus*) on summer and autumn sea ice at Svalbard, Norway. Arctic **64**:476-482.

Stirling, I. and P. Smith. 1974. Polar bear management in Canada. Pages 61-67 *in* Polar Bear Specialist Group, editor. Polar Bears, Proceedings of the Fifth Working Meeting of the Polar Bear Specialist Group. IUCN, Morges, Switzerland.

Stirling, I., C. Spencer, and D. Andriashek. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. Journal of Wildlife Diseases **25**:159-168.

Stirling, I. and R. van Meurs. 2015. Longest recorded underwater dive by a polar bear. Polar Biology **published online: 25 March 2015**:DOI 10.1007/s00300-00015-01684-00301.

Street, G. M., A. R. Rodger, and J. M. Fryxell. 2015. Mid-day temperature variation influences seasonal habitat selection by moose. Journal of Wildlife Management **79**:505-512.

Stroeve, J., M. M. Holland, W. Meier, T. Scambos, and M. Serreze. 2007. Arctic sea ice decline: faster than forecast. Geophysical Research Letters **34**:L09501.

Stroeve, J., T. Markus, L. Boisvert, J. Miller, and A. Barrett. 2014a. Changes in Arctic melt seson and implications for sea ice loss. Geophysical Research Letters **41**:1216-1225.

Stroeve, J. C., T. Markus, L. Boisvert, J. Miller, and A. Barrett. 2014b. Changes in Arctic melt season and implications for sea ice loss. Geophysical Research Letters **41**:1216-1225.

Stroeve, J. C., M. C. Serreze, M. M. Holland, J. E. Kay, J. Malanik, and A. P. Barrett. 2012. The Arctic's rapidly shrinking sea ice cover: a research synthesis. Climate Change **110**:1005-1027.

Sturm, M., J. A. Maslanik, D. K. Perovich, J. C. Stroeve, J. A. Richter-Menge, T. Markus, J. Holmgren, J. F. Heinrichs, and K. Tape. 2006. Snow depth and ice thickness measurements from the Beaufort and Chukchi seas collected during the AMSR-Ice03 campaign. IEEE Transactions on Geoscience and Remote Sensing **44**:3009-3020.

Sunquist, M. E. and F. Sunquist. 2001. Changing landscapes: consequences for carnivores. Pages 399-418 *in* J. Gittleman, S. Funk, D. Macdonald, and

R. Wayne, editors. Carnivore Conservation. Cambridge University Press, Cambridge, UK.

Swift, T. and S. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. Biological Reviews **85**:35-53.

Taylor, M., T. Larsen, and R. E. Schweinsburg. 1985. Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). Arctic **38**:303-309.

Taylor, M. and J. Lee. 1995. Distribution and abundance of Canadian polar bear populations: a management perspective. Arctic **48**:147-154.

Taylor, M. K., S. Akeeagok, D. Andriashek, W. Barbour, E. W. Born, W. Calvert, H. D. Cluff, S. Ferguson, J. Laake, A. Rosing-Asvid, I. Stirling, and F. Messier. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. Canadian Journal of Zoology **79**:690-709.

Taylor, M. K., J. Lee, and L. Gray. 1990a. Foxe Basin polar bear research program - 1987 field report. Government of Northwest Territories, Department of Renewable Resources Report, Yellowknife, NWT, CA.

Taylor, M. K., J. Lee, J. Laake, and P. D. McLoughlin. 2006. Estimating population size of polar bears in Foxe Basin, Nunavut using tetracycline biomarkers. Wildlife Report. Nunavut Department of Environment, Iqaluit, NU, CA.

Taylor, M. K., J. Lee, and R. Mulders. 1990b. Foxe Basin polar bear research program - 1988 field report. Government of Northwest Territories, Department of Renewable Resources Report, Yellowknife, NWT.

Taylor, M. K., P. D. McLoughlin, and F. Messier. 2008. Sex-selective harvesting of polar bears *Ursus maritimus*. Wildlife Biology **14**:52-60.

Thiemann, G., A. Derocher, and I. Stirling. 2008a. Polar bear *Ursus maritimus* conservation in Canada: an ecological basis for identifying designatable units. Oryx **42**:504-515.

Thiemann, G. W., A. E. Derocher, S. G. Cherry, N. J. Lunn, E. Peacock, and V. Sahanatien. 2013. Effects of chemical immobilization on the movements rates of free-ranging polar bears. Journal of Mammalogy **94**:386-397.

Thiemann, G. W., S. J. Iverson, and I. Stirling. 2008b. Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. Ecological Monographs **78**:591-613.

Thomas, C. D. and W. E. Kunin. 1999. The spatial structure of populations. Journal of Animal Ecology **68**:647-657.

Towns, L., A. E. Derocher, I. Stirling, N. J. Lunn, and D. Hedman. 2009. Spatial and temporal patterns of problem polar bears in Churchill, Manitoba. Polar Biology **32**:1529-1537.

Trenberth, K. E., P. D. Jones, and P. Ambenje. 2007. Observations: surface and atmospheric climate change.*in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Avery, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY USA.

Tynan, C. T. and D. P. DeMaster. 1997. Observations and prediction of Arctic climate change: potential effects on marine mammals. Arctic **50**:308-322.

van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour **84**:723-735.

Vancoppenolle, M., K. M. Meiner, C. Michel, L. Bopp, F. Brabant, G. Carnat, B. Delille, D. Lannuzel, G. Madec, S. Moreau, J.-L. Tison, and P. van der Merwe. 2013. Role of sea ice in global biogeochemical cycles: emerging views and challenges. Quaternary Science Reviews **79**:207-230.

Vaughn, D. G., J. C. Comiso, I. Allison, J. Carrasco, G. Kaser, R. Kwok, P. Mote, T. Murray, F. Paul, J. Ren, E. Rignot, O. Solomina, K. Steffen, and T. Zhang. 2013. Observations: Cryosphere *in* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allan, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, U.K. and New York, USA.

Visconti, P. and C. Elkin. 2009. Using connectivity metrics in conservation planning - when does habitat quality matter? Diversity and Distributions **15**:602-612.

Vongraven, D., J. Aars, S. Amstrup, S. N. Atkinson, S. Belikov, E. W. Born, T. D. DeBruyn, A. E. Derocher, G. Durner, M. Gill, N. Lunn, M. E. Obbard, J. Omelak, N. Ovsyanikov, E. Peacock, E. Richardson, V. Sahanatien, I. Stirling, and Ø. Wiig. 2012. A circumpolar monitoring framework for polar bears. Ursus **5**:1-66.

Walker, D. A., M. K. Raynolds, F. J. A. Daniels, E. Einarsson, A. Elvebakk, W. A. Gould, A. E. Katenin, S. S. Kholod, C. J. Markon, E. S. Melnikov, N. G. Moskalenko, S. S. Talbot, B. A. Yurtsev, and C. Team. 2005. The circumpolar Arctic vegetation map. Journal of Vegetation Science **16**:267-282.

Wassmann, P., C. M. Duarte, S. Agusti, and M. K. Sejr. 2011. Footprints of climate change in the Arctic marine ecosystem. Global Change Biology **17**:1235-1249.

Watts, P. D. and S. E. Hansen. 1987. Cyclic starvation as a reproductive strategy in the polar bear. Pages 305-318 *in* A. S. I. Loudon and P. A. Racey, editors. Reproductive energetics in mammals. Symposia of the Zoological Society of London. Clarendon Press, Oxford, UK.

Whiteman, J. P., H. J. Harlow, G. M. Durner, R. Anderson-Sprecher, S. E. Albeke, E. V. Regehr, S. C. Amstrup, and M. Ben-David. 2015. Summer declines in activity and body temperature offer polar bears limited energy savings. Science **349**:295-298.

Wielgus, R. B. and F. L. Bunnel. 1994. Sexual segregation and female grizzly bear avoidance of males. Journal of Wildlife Management **58**:405-413.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review Ecology and Systematics **7**:81-120.

Wiig, Ø., E. W. Born, and L. T. Pederson. 2003. Movements of female polar bears (*Ursus maritimus*) in the East Greenland pack ice. Polar Biology **26**:509-516.

Wiig, Ø., A. E. Derocher, and S. Belikov. 1999. Ringed seal (*Phoca hispida*) breeding in the drifting pack ice of the Barents Sea. Marine Mammal Science **15**:595-598.

Wilson, R. R., J. S. Horne, K. D. Rode, E. V. Regehr, and G. M. Durner. 2014. Identifying polar bear resource selection patterns to inform offshore development in a dynamic and changing Arctic. Ecosphere **5**:Article 136.

Wolf, M., J. Frair, E. H. Merrill, and P. Turchin. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. Ecography **32**:401-410.

World Meterological Organization. 1970. Sea ice nomenclature. WMO, Geneva, Switzerland.

Zakhvatkina, N. Y., V. Y. Alexandrov, O. M. Johannessen, S. Sandven, and I. Y. Frolov. 2013. Classification of sea ice types in ENVISAT synthetic aperture radar images. IEEE Transactions on Geoscience and Remote Sensing **51**:2587-2600.

Zalewski, A. and B. Jedrzejewka. 2006. Spatial organization and dynamics of the pine marten *Martes martes* population in Bialowieza Forest (E Poland) compared with other European woodlands. Ecography **29**:31-43.

Zeyl, E., D. Ehrich, J. Aars, L. Bachmann, and Ø. Wiig. 2010. Denning-area fidelity and mitochondrial DNA diversity of female polar bears (*Ursus maritimus*) in the Barents Sea. Canadian Journal of Zoology **88**:1139-1148.

Appendix A

Table A1. The number of clusters and individual bear cluster affiliations based on fuzzy clustering using fuzziness weighting exponent value (m) of 1.5 for the location data of satellite collared female polar bears, Foxe Basin, Nunavut, Canada (October – March, 2007-2011). FB=Foxe Basin cluster, HS=Hudson Strait cluster and HB=Hudson Bay cluster. The table values indicate strength of a bear's cluster affiliation and the highest values are bolded for each set of clusters.

	2 Clusters		3 Clusters			4 Clusters			
BearID	**FB/HS**	**HB/HS**	**FB**	**HS**	**HB**	**FB**	**HS**	**HB1**	**HB2**
B600661	0.0035	**0.9965**	0.0011	0.00161	**0.99729**	0.00147	0.00206	0.28817	**0.70829**
B618529	**0.99792**	0.00208	**0.95917**	0.03769	0.00314	**0.95365**	0.03925	0.00447	0.00264
B618532	**0.99838**	0.00162	**0.98148**	0.01646	0.00206	**0.97728**	0.01773	0.00316	0.00183
B618535	**0.90231**	0.09769	0.00109	**0.99856**	0.00036	0.00137	**0.99766**	0.00048	0.00049
B618537	**0.97506**	0.02494	0.0086	**0.99041**	0.00099	0.00617	**0.99228**	0.00083	0.00072
A618542	**0.99832**	0.00168	**0.9359**	0.0603	0.0038	**0.92849**	0.06313	0.00511	0.00326
A631643	**0.97262**	0.02738	**0.98693**	0.00991	0.00315	**0.98407**	0.00924	0.00434	0.00235
A631681	0.00703	**0.99297**	0.00572	0.0101	**0.98418**	0.00335	0.00565	**0.75822**	0.23278
A631682	**0.52356**	0.47644	0.17031	**0.60576**	0.22392	0.1413	**0.46562**	0.16263	0.23046
A631684	**0.98688**	0.01312	**0.7669**	0.20218	0.03092	**0.72578**	0.2001	0.04756	0.02656
A631687	**0.89016**	0.10984	0.09546	**0.88357**	0.02097	0.08385	**0.87781**	0.01928	0.01906
A631688	0.23363	**0.76637**	0.03684	**0.80378**	0.15939	0.03439	**0.66699**	0.11833	0.18029
A631691	0.35409	**0.64591**	0.02462	**0.90856**	0.06682	0.02563	**0.83235**	0.05717	0.08484
A631692	**0.99564**	0.00436	**0.97925**	0.01707	0.00368	**0.97085**	0.01916	0.00658	0.00341
A631694	**0.96414**	0.03586	**0.98695**	0.00892	0.00413	**0.98143**	0.00888	0.00635	0.00334
A631695	**0.88756**	0.11244	0.02131	**0.97265**	0.00604	0.01776	**0.9716**	0.00543	0.00521
A631716	**0.96031**	0.03969	**0.73523**	0.21466	0.05011	**0.68288**	0.20516	0.06785	0.0441
A631718	0.01197	**0.98803**	0.00562	0.00759	**0.98679**	0.00403	0.00526	**0.68591**	0.3048
A631720	0.0264	**0.9736**	0.01862	0.01219	**0.96919**	0.00127	0.00081	**0.97774**	0.02018
B618532a	**0.99402**	0.00598	**0.99522**	0.00413	0.00065	**0.99494**	0.00376	0.00081	0.00049
B618535a	**0.88707**	0.11293	0.00078	**0.99894**	0.00027	0.00072	**0.99875**	0.00027	0.00026
B618537a	**0.98992**	0.01008	0.06683	**0.92909**	0.00408	0.05571	**0.93673**	0.00428	0.00328
A631643a	**0.9681**	0.0319	**0.95351**	0.03776	0.00873	**0.94546**	0.0364	0.01111	0.00703
A631684a	**0.88704**	0.11296	**0.72981**	0.17337	0.09682	**0.62619**	0.15214	0.15343	0.06824
A631692a	**0.99141**	0.00859	**0.97206**	0.02223	0.00572	**0.96028**	0.02443	0.01014	0.00515
A631694a	**0.90413**	0.09587	**0.95497**	0.02525	0.01978	**0.92984**	0.02424	0.03115	0.01477
A617098	0.00601	**0.99399**	0.00312	0.00476	**0.99212**	0.0025	0.00365	0.22397	**0.76988**
A618527	0.03138	**0.96862**	0.02057	0.01458	**0.96485**	0.00245	0.00169	**0.95684**	0.03903
A618536	**0.95891**	0.04109	**0.97262**	0.0202	0.00718	**0.96558**	0.0192	0.00961	0.00561
A618542a	**0.99612**	0.00388	**0.80354**	0.18593	0.01052	**0.7838**	0.19316	0.01371	0.00933
A34046	0.00476	**0.99524**	0.00225	0.00389	**0.99387**	0.00056	0.00092	0.03345	**0.96508**
A34051	**0.83502**	0.16498	0.1269	**0.82673**	0.04638	0.12138	**0.78403**	0.04398	0.05061
A34056	0.00587	**0.99413**	0.00497	0.01266	**0.98237**	0.00121	0.00292	0.04785	**0.94802**
A34058	0.00284	**0.99716**	0.00212	0.0049	**0.99297**	0.00054	0.00118	0.03529	**0.96299**
A77012	0.00805	**0.99195**	0.00497	0.00717	**0.98786**	0.00279	0.00385	0.16094	**0.83242**

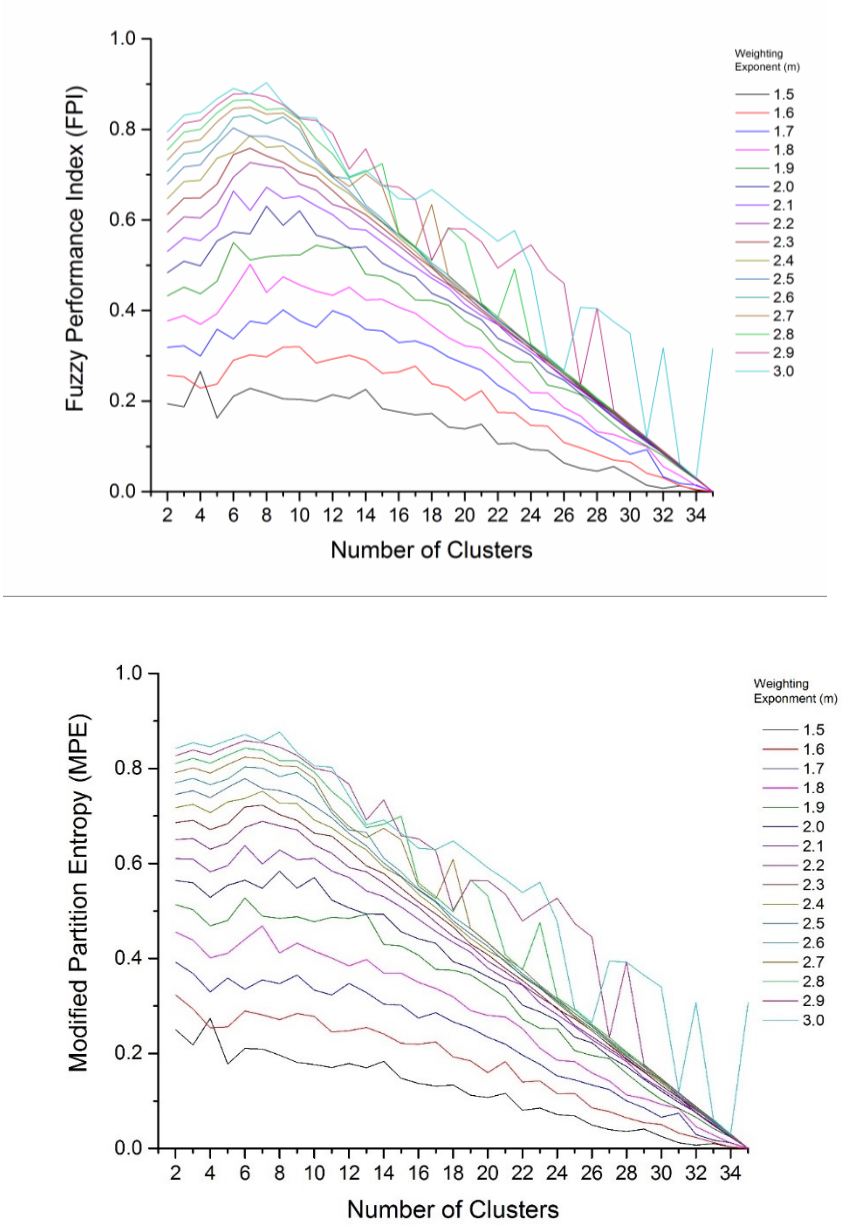


Figure A1. Fuzzy c-means validity functions: fuzziness performance index (FPI) and modified partition entropy (MPE) vs potential number of subpopulation clusters. The diagonal metric distance was used in the calculations along with fuzzy weighting exponent (m) $1.5 \leq m \leq 3.0$ for satellite collared female polar bears, Foxe Basin, Nunavut, Canada (October-March 2007-2011). The purpose of the plots is to identify the FPI and MPE minima as a means to determine movement behaviour: independent or coordinated. The minima for each exponent value (m) occurred at 34 clusters which is equal to the total sample size, thus each polar bear moved independently of all other bears.

Appendix B

Table B1. List and definitions of covariates for fine scale sea ice habitat resource selection analysis of satellite collared female polar bears, Foxe Basin, Nunavut (November-April, 2008-2010).

Habitat Covariate	**Definition**
Floe.mean	Proportion of floe pixels that are non-background[1]
Floe.area.non.bkg	Area (km^2) of all pixels not floe and not land (background)[1]
Floe.patch.number	Number of floe patches[1]
Floe.patch.area	Area (km^2) of all floe pixels[1]
Floe.patch.density	Density (patch/km^2) of floe patches[1]
Floe.patch.mean.size	Mean size (km^2) of floe patches[1]
Floe.patch.SD.size	Standard deviation of mean floe patch size[1]
Floe.edge.tot	Total length (km) of edge or perimeter of all floe patches[1]
Floe.edge.density	Length (km/km^2) of floe patch edge per small buffer[1]
Floe.centre.value	Value (0=not in floe, 1=in floe) of pixel at the used or available location[1]
Floe.distance.edge	Distance (km) from centre of small buffer to nearest edge between floe and non-floe pixels[1]
Floe.distance.patch	Distance (km) from centre of small buffer to nearest floe patch[1]
Lead.mean	Proportion of pixels that are lead pixels that are non-
Lead.area.non.bkg	background
Lead.patch.number	Area (km^2) of all pixels not lead and not land (background)
Lead.patch.area	Number of lead patches[1]
Lead.patch.density	Area (km^2) of all lead pixels[1]
	Density (patch/km^2) of lead patches[1]
Lead.mean.patch.size	Mean size (km^2) of lead patches[1]
Lead.patch.SD.size	Standard deviation of the mean lead patch size[1]
Lead.edge.tot	Total length (km) of edge or perimeter of all lead patches[1]
Lead.edge.density	Length (km) of lead patch edge per small buffer (km/km^2)[1]
Lead.centre.value	Value (0=not in lead, 1=in lead) of pixel at the used or available location[1]
Lead.distance.edge	Distance (km) from centre of small buffer to nearest edge between lead and non-lead pixels[1]
Lead.distance.patch	Distance (km) from centre of small buffer to nearest lead patch[1]
Distance.to.Land	Distance (km) from used or available location to land
Depth	Depth (m) of ocean at used or available location[2]
Ice.Concentration	Ice concentration (%) at used or available location[3]

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[1] Source: SAR satellite imagery, [2] Source: GEBCO bathymetric chart, [3] Source: SSM/I satellite imagery

Table B2. Collinearity of sea ice fine-scale and broad-scale sea ice habitat covariates using Pearson's correlation matrix of satellite collared female polar bears, Foxe Basin, Nunavut (November-April, 2008-2010; n = 2751).

i) Floe patch metric correlation coefficients before removal of |r|>0.6.

	f.area.non.bkg	f.patch.num	f.patch.area	f.patch.dn	f.patch.mean.size	f.patch.sd.size	f.edge.tot	f.edge.dn	f.centre.value	f.dist.edge	f.dist.patch
f.mean	-.061**	0.465**	**0.958****	-0.217**	**0.611**** `	**0.730****	0.242**	0.277**	0.463**	-0.076**	-0.271**
f.area.non.bkg		0.229**	0.188**	-0.221**	0.02*	0.074**	0.309**	0.002*	0.013*	-0.282**	-0.271**
f.patch.num.			-0.408**	0.435**	-0.424**	-0.529**	0.510**	0.458**	-0.250**	-0.230**	-0.099**
f.patch.area				-0.272**	**0.612****	**0.746****	0.316**	0.269**	0.460**	-0.122**	-0.297**
f.patch.dn					-0.228**	-0.295**	0.157**	0.204**	-0.106**	-0.011*	-0.023
f.patch.mean.size						0.356**	-0.207**	-0.221**	0.291**	0.091**	-0.103**
f.patch.sd.size							-0.015*	-0.037*	0.385**	-0.021*	-0.174**
f.edge.tot								**0.940****	0.078**	-0.347**	-0.294**
f.edge.dn									0.076**	-0.307**	-0.265**
f.centre.value										-0.061**	-0.287**
f.dist.edge											**0.934****

*correlation not significant; **correlation significant at the 0.01 level (2-tailed); bolded values are >|0.6|

ii) Floe patch metric correlation coefficients used in habitat selection models.

	f.patch.num	f.patch.area	f.patch.dn	f.edge.dn	f.centre.value	f.dist.patch
f.area.non.bkg	0.009**	0.188**	-0.221**	0.002*	0.013*	-0.229**
f.patch.num		-0.408**	0.435**	0.458**	-0.250**	-0.099**
f.patch.area			-0.272**	0.269**	0.460**	-0.297**
f.patch.dn				0.204**	-0.106**	-0.023*
f.edge.dn					0.076**	-0.265**
f.centre.value						-0.287**

*not significant; ** significant at the 0.01 level (2-tailed)

iii) Lead patch metric correlation coefficients before removal of |r|>0.6.

	l.area.non.bkg	l.patch.num	l.patch.area	l.patch.dn	l.patch.mean.size	l.patch.sd.size	l.tot.edge	l.edge.dn	l.centre.value	l.dist.edge	l.dist.patch
l.mean	-0.68**	0.284**	__0.985__**	0.303**	__0.799__**	__0.649__**	__0.610__**	__0.622__**	__0.641__**	-0.268**	-0.376**
l.area.non.bkg		0.072**	0.026*	-0.107**	0.004*	0.005*	0.067**	__-0.025__*	-0.009*	-0.087**	-0.063**
l.patch.num			0.292**	__0.948__**	-0.056**	0.147**	__0.783__**	__0.773__**	0.142**	-0.525**	-0.521**
l.patch.area				0.275**	__0.811__**	__0.654__**	__0.626__**	__0.621__**	0.639**	-0.281**	-0.377**
l.patch.dn					-0.055**	0.141**	__0.734__**	__0.765__**	0.147**	-0.499**	-0.503**
l.patch.mean.size						0.272**	0.148**	0.148**	0.545**	-0.083**	-0.207**
l.patch.sd.size							0.520**	0.518**	0.423**	-0.232**	-0.252**
l.tot.edge								__0.988__**	0.372**	-0.496**	-0.498**
l.edge.dn									0.373**	-0.497**	-0.499**
l.centre.value										-0.172**	-0.257**
l.dist.edge											__0.971__**

*not significant; **significant at the 0.01 level (2-tailed); bolded values are >|0.6|

iv) Lead patch metric correlation coefficients used in habitat selection models.

	l.patch.dn	l.patch.mean.size	l.patch.sd.size	l.centre.value	l.dist.patch
l.area.non.bkg	-0.107**	0.004*	0.005*	-0.009*	-0.063**
l.patch.dn		-0.055**	0.141**	0.147**	-0.503**
l.patch.mean.size			0.272**	0.545**	-0.207**
l.patch.sd.size				0.423**	-0.252**
l.centre.value					-0.257**

*not significant; **significant at the 0.01 level (2-tailed)

v) Broad scale covariate correlations coefficients used in habitat selection models.

	Depth	Ice.conc
Dist.land	0.03*	0.179**
Depth		-0.017*

*not significant; **significant at the 0.01 level (2-tailed)

Table B3. List of *a priori* fine scale sea ice habitat resource selection models ranked according to ΔAICc for satellite collared female polar bears, Foxe Basin, Nunavut, Canada (November-April 2008-2010).

Model	Covariate	LL	AIC	k	AICc	ΔAICc
20	f.patch.dn + l.patch.dn	-395.20	794.39	2	794.48	0.00
4	f.patch.dn	-396.74	795.48	1	795.51	1.02
23	f.patch.n + f.patch.dn + l.patch.dn	-394.70	795.40	3	795.59	1.11
9	l.patch.dn	-396.95	795.90	1	795.93	1.44
26	f.patch.dn + f.edge.dn + l.patch.dn	-395.03	796.05	3	796.24	1.76
2	f.patch.num	-397.54	797.08	1	797.11	2.61
3	f.patch.area	-398.05	798.10	1	798.13	3.65
1	f.area.non.bkg	-398.09	798.18	1	798.21	3.73
16	ice.conc	-398.13	798.26	1	798.29	3.81
12	l.centre.val	-398.24	798.48	1	798.51	4.03
13	l.dist.patch	-398.26	798.51	1	798.54	4.06
15	depth	-398.38	798.75	1	798.78	4.30
8	l.area.non.bkg	-398.40	798.80	1	798.83	4.35
11	l.patch.sd.size	-398.68	799.27	1	799.30	4.82
7	f.dist.patch	-398.76	799.36	1	799.39	4.91
5	f.edge.dn	-398.81	799.53	1	799.56	5.07
10	l.patch.mean.size	-398.81	799.63	1	799.67	5.17
14	dist.land	-398.83	799.63	1	799.66	5.18
6	f.centre.val	-398.83	799.66	1	799.69	5.20
21	depth + ice.conc	-397.83	799.65	2	799.75	5.26
17	f.area.non.bkg + l.area.non.bkg	-398.09	799.91	2	800.01	5.52
19	f.dist.patch + l.dist.patch	-398.09	800.17	2	800.27	5.78
18	f.centre.val + l.centre.val	-398.24	800.47	2	800.57	6.08

Model	Covariate	LL	AIC	k	AICc	ΔAICc
27	f.centre.val + l.centre.val + ice.conc	-397.58	801.16	3	801.35	6.87
24	dist.land + depth + ice.conc	-397.73	801.46	3	801.65	7.17
32	f.area.non.bkg + l.area.non.bkg + depth	-397.73	801.47	3	801.66	7.17
22	f.patch.area + l.patch.mean.size + l.patch.sd.size	-397.84	801.67	3	801.86	7.38
25	f.dist.patch + l.dist.patch + dist.land	-398.07	802.14	3	802.33	7.84
29	f.patch.area + l.patch.mean.size + l.patch.sd.size + f.patch.num	-397.33	802.65	4	802.97	8.49
31	f.patch.num + f.patch.area + l.patch.mean.size + l.patch.sd.size	-397.33	802.65	4	802.97	8.49
28	f.area.non.bkg + l.area.non.bkg + f.centre.val + l.centre.val	-397.38	802.75	4	803.07	8.59
30	f.edge.dn + dist.land + depth + ice.conc	-397.63	803.26	4	803.58	9.10
34	l.area.non.bkg + l.patch.dn + l.patch.mean.size + l.patch.sd.size + l.centre.val + l.dist.patch	-395.64	803.28	6	803.96	9.47
33	f.edge.dn + f.dist.patch + l.dist.patch + dist.land	-398.01	804.02	4	804.33	9.85
35	f.area.nonbkg + f.patch.num + f.patch.area + f.patch.dn + f.edge.dn + f.centre.val + f.dist.patch	-395.85	805.71	7	806.62	12.13
36	l.area.non.bkg + l.patch.dn + l.patch.mean.size + l.patch.sd.size + l.centre.val + l.dist.patch +dist.land + depth + ice.conc	-394.84	807.69	9	809.18	14.70
37	f.area.non.bkg + f.patch.num + f.patch.area + f.patch.dn + f.edge.dn + f.centre.val + f.dist.patch + dist.land + depth + ice.conc	-395.07	810.15	10	811.98	17.50
38	f.area.non.bkg + f.patch.num + f.patch.area + f.patch.dn + f.edge.dn + f.centre.val + f.dist.patch + l.area.non.bkg + l.patch.dn + l.patch.mean.size + l.patch.sd.size + l.centre.val + l.distpatch	-393.32	812.64	13	815.76	21.27
39	Global	-392.14	816.27	16	821.04	26.56

Appendix C

Table C1. Number of transmitting satellite collars on female and ear tags on male polar bears that were on land during the ice-free season, Foxe Basin, Nunavut (2007-2011).

Sex	Year	August	September	October	November
Female	2007	12	12	12	9
	2008	20	22	20	8
	2009	4	25	25	17
	2010	10	10	10	6
	2011	3	4	1	0
	Total	49	73	68	40
Male	2008	3	4	4	2
	2009	1	1	1	0
	Total	4	5	5	2

Table C2. Long distance overland movement sinuosity index and test of movement path directionality of satellite collared female polar bears, Foxe Basin (2007-2011).

BearID	**Year**	**Month**	**Family Group**	**Sinuosity Index**	**Mean Bearing**	**SE**	**Raleigh Test**	**n_{test}**
34045	2007	Nov	YRLG	1.0081	157.5	11.5	Z=8.58, P<0.001	13
34046	2007	Oct	COY	1.0134	270.8	21.0	Z=3.16, P=0.04	8
34049	2007	Nov	COY	1.0273	148.1	11.3	Z=6.52, P<0.001	8
617087A	2008	Sept	YRLG	1.0561	311.2	7.6	Z=20.72, P<0.001	45
617087A	2008	Nov	YRLG	1.1080	96.8	10.4	Z=12.34, P<0.001	37
618527A	2008	Sept	COY	1.0080	322.8	4.1	Z=7.79, P<0.001	8
618527A	2008	Sept	COY	1.0138	156.4	7.9	Z=3.88, P=0.01	4
618534A	2008	Oct	YRLG	1.0113	208.6	8.9	Z=11.19, P<0.001	17
618538A	2008	Nov/Dec	YRLG	1.0485	300.9	5.9	Z=13.53, P<0.001	16
631687A	2009	Oct	YRLG	1.0200	178.4	20.0	Z=3.73, P=0.02	12
631694A	2009	Sept	YRLG	1.0402	335.8	7.0	Z=22.28, P<0.001	84
631716A	2009	Oct/Nov	COY	1.0185	315.8	6.3	Z=8.35, P=0.001	9
631716A	2009	Nov	COY	1.0501	111.5	12.6	Z=8.07, P<0.001	14
631718A	2009	Nov	YRLG	1.0434	252.3	6.3	Z=8.34, P<0.001	9
631720A	2009	Oct	YRLG	1.0138	282.7	3.8	Z=7.82, P<0.001	8
634586A	2009	Oct	YRLG	1.0234	200.0	9.8	Z=11.85, P<0.001	24
631694A	2010	Aug	NOCUB	1.0740	312.5	7.9	Z=18.84, P<0.001	41
631643A	2011	Sept	COY	1.0760	64.9	9.6	Z=13.31, P<0.001	32

Table C3. Mean number of days/month with temperatures above 10°C and 20°C in Churchill, MB, Coral Harbour NU and Hall Beach NU. Data downloaded from http://climate.weather.gc.ca/

	Churchill		**Coral Harbour**		**Hall Beach**	
Month	>10°C	>20°C	>10°C	>20°C	>10°C	>20°C
June	16.4	5.4	6.3	0.2	1.2	0
July	27.5	11.3	26.1	3.7	14.7	0.4
August	28.0	8.6	19.8	0.6	7.3	0.2
September	11.1	1.5	3.4	0	0.5	0
October	1.5	0	0	0	0	0
November	0	0	0	0	0	0

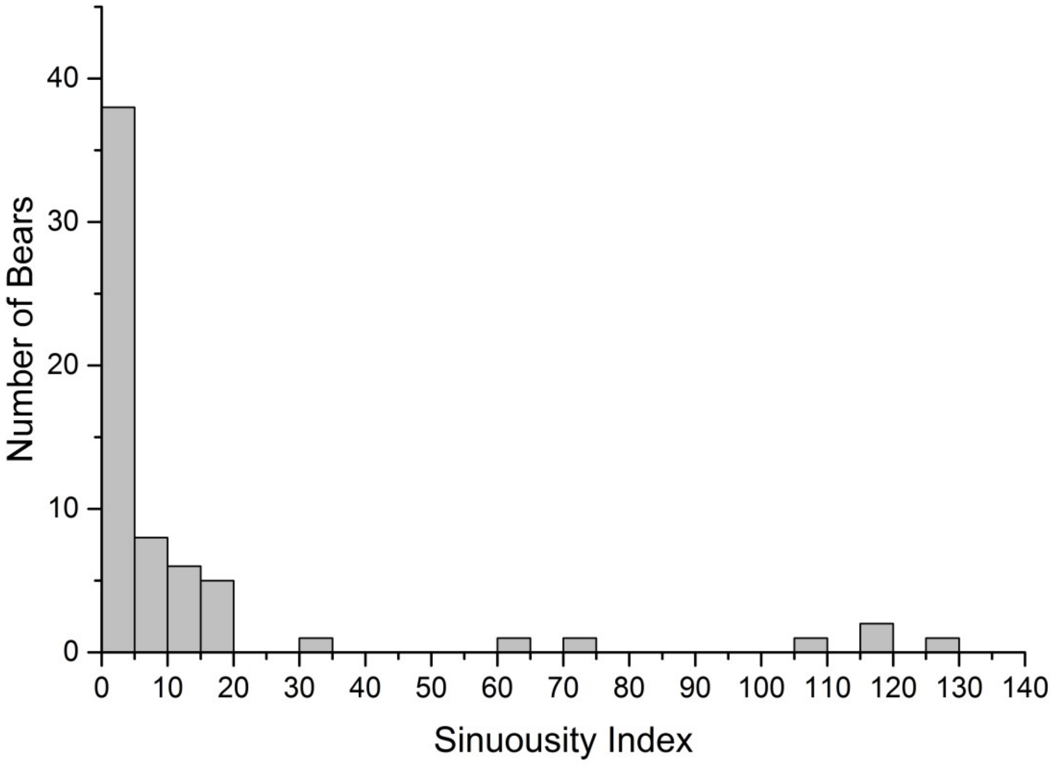

Figure C1. Histogram of movement path sinuosity index of satellite collared female polar bears (n=64) during the ice free season, Foxe Basin, Nunavut, Canada (2007-2011).

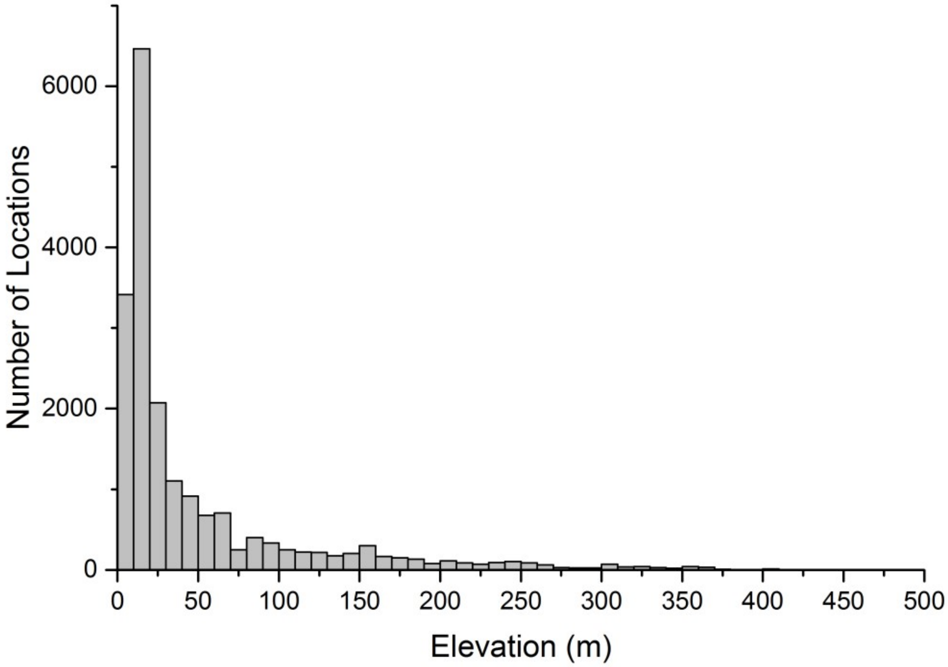

Figure C2. Histogram of elevations that satellite collared female polar bears used during the ice free season, Foxe Basin, Nunavut, Canada (2007-2011).

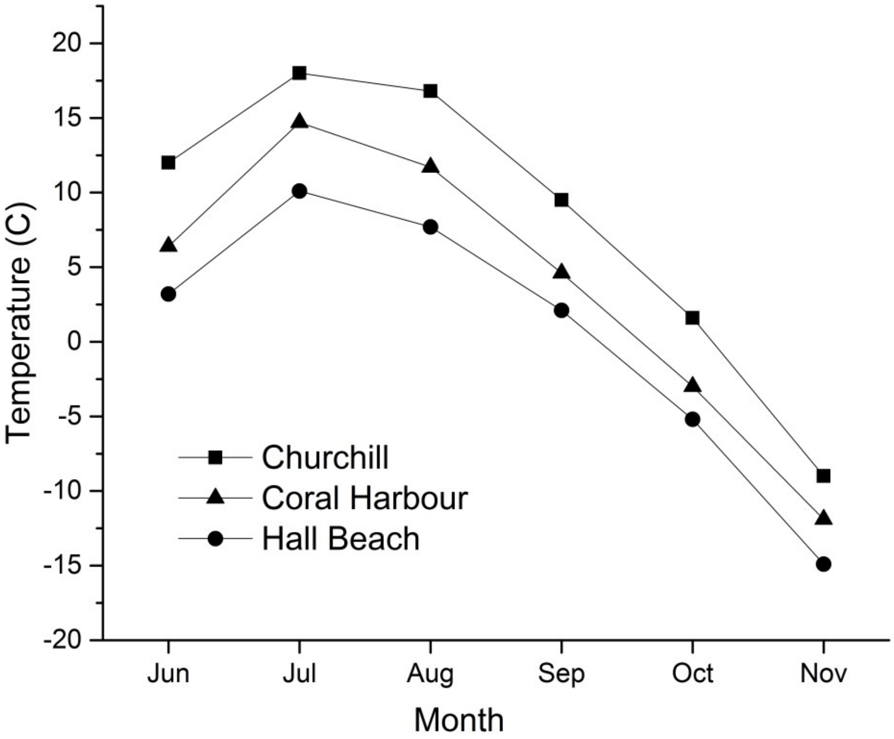

Figure C3. Mean maximum monthly temperatures (1981-2010) for the sea ice break-up and freeze-up months at Churchill, MB, Coral Harbour, NU and Hall Beach, NU, Canada. Data downloaded from http://climate.weather.gc.ca/