University of Alberta

Movement patterns of polar bears (*Ursus maritimus*) on the sea ice of Hudson Bay

by

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A thesis submitted to the Faculty of Graduate Studies and Research in
partial fulfillment of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall 2005

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ISBN: 0-494-09258-0
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ISBN: 0-494-09258-0

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Dedication

For Moragh

ABSTRACT

Animal movement can be an important determinant in population dynamics. Polar bears (*Ursus maritimus*) move over thousands of kilometers of dynamic sea ice hunting seals, but recent decreases in sea ice thickness and extent are affecting the population in western Hudson Bay. The purpose of this research was to examine polar bear movement patterns on the ice of Hudson Bay in relation to individual reproductive status, temporal variations in sea ice, and prey distribution. Overall, movement patterns were not dependent on reproductive status, but changed significantly with season. Annual distance moved by bears in Hudson Bay has decreased since 1991, which suggests that measured declines in bear condition and numbers are due to reduced prey intake. This study is the first to quantitatively examine polar bear movement on the sea ice of Hudson Bay and presents new insights into polar bear ecology in a rapidly changing arctic ecosystem.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Andrew Derocher, for giving me the opportunity to be involved in such exciting research and to see polar bears and Canada's north first-hand. I thank Dr. Derocher along with Dr. Stirling for their willingness to share their insights into polar bear ecology with me. Their combined wealth of experience with polar bears, seals, and arctic ecosystems was a great source of guidance. I thank my entire committee for their suggestions and comments at various stages of the process. Special thanks are due to Charlene Nielson, who was always ready to sit with me for hours as I stumbled through the process of learning GIS. I am grateful to my family for their constant support and care packages. Sometimes all I needed was chocolate. Thanks to everyone in the Derocher lab for being there to discuss ideas, figure out how to format documents, or just gab. Finally, I would like to thank John Brzustowski, without whose love, support, and statistical help I could not have completed this thesis. This research was completed in part by funding from NSERC PGSA scholarship.

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°C	degrees Celsius
ANOVA	analysis of variance
COY	cub-of-the-year
CWS	Canadian Wildlife Service
gC	grams of carbon
GIS	geographic information system
GPS	global positioning system
h	hour
kg	kilogram
km	kilometer
m	meter
MCP	minimum convex polygon
n	sample size
SE	standard error
WH	western Hudson Bay
$\bar{x}$	mean

CHAPTER ONE - GENERAL INTRODUCTION

Animal movement and distribution

How individual animals move and distribute themselves across a landscape over time has a profound influence on population growth rates, abundance and genetic structure (Marsh and Jones 1988, Turchin 1991, Wiens *et al.* 1993). Animals move in order to acquire resources such as food, mates, and shelter and to avoid predators or competitors (Pyke *et al.* 1977, Turchin 1998). Therefore, patterns of animal movement can reveal aspects of the landscape important to the animal, the energetic costs and benefits of acquiring resources within that landscape, and information about intra- and interspecific relationships (e.g. Moen *et al.* 1997, South 1999, Frair *et al.* in press). Studies of animal movement and distribution can facilitate the understanding of evolutionary relationships (e.g. Graham and Grimm 1990), and are essential for effective wildlife management (e.g. Taylor *et al.* 2001, Phillips *et al.* 2004).

Animal movement studies have traditionally examined small scale movement patterns of insects or other small animals due to the logistic difficulties of tracking larger animals over greater distances (e.g. Richerson and Borden 1972, Kareiva 1983, McIntyre and Wiens 1999). Studies of animal distribution have relied on mark-recapture techniques for similar reasons (Cormack 1972, DeMaster *et al.* 1980), and while these studies are useful, they provide a static picture of distribution at one point in time. Recent advances in satellite tracking technology have allowed researchers to follow large, wide-ranging animals effectively (e.g. Berthold and Terrill 1991, Papi and Luschi 1996). Furthermore, improvements in geographic information systems (GIS) and global positioning systems (GPS) enable the analysis of relationships between animal movements and environmental variables on several spatial and temporal scales (e.g. Arthur *et al.* 1996, Johnson *et al.* 2004). Satellite and GPS tracking facilitate analyses of the dynamic distribution of animals over large spatial and temporal scales, providing insights into the causes of observed patterns of distribution. These developments are especially useful when studying large or wide-ranging animals that inhabit landscapes inaccessible to researchers. One such animal is the polar bear (*Ursus maritimus*), which wanders over thousands of kilometers of arctic sea ice in winter darkness.

Polar bear background

History and current status of polar bears

Polar bears evolved from brown (or grizzly) bears (*U. arctos*) during the late-Pleistocene era, and genetic evidence shows that polar bears are most closely related to the grizzly bear population of southeast Alaska (Talbot and Shields 1996). Polar bears appear to have undergone rapid evolution during their short history, developing a more carnivorous dentition than other ursid species (Kurtén 1964), thicker, lighter coloured fur, elongated skulls, and shorter claws. Early polar bear ancestors moved further northward, and were no longer dependent on the seasonal availability of terrestrial vegetative productivity, but relied almost solely on northern phocid species for food (Amstrup and DeMaster 1988).

According to Inuit oral history, polar bears have been hunted by humans since the two species first shared space, between 25 000 and 23 000 years ago (Feazel 1990). During most of the 20th century, polar bear hunting was completely unregulated, and during the 1950s and 60s, when snowmobiles became common, the number of kills jumped to unprecedented levels (Prestrud and Stirling 1994). Although population estimates were uncertain, it became clear that polar bear populations might be in serious danger. In 1973, the International Agreement on the Conservation of Polar Bears was signed in Oslo, Norway, and was ratified by all five circumpolar countries by 1976. The polar bear is currently listed as a "species of special concern" under the new definitions of the Committee on the Status of Endangered Wildlife in Canada.

At present, the circumpolar distribution of polar bears is divided into 19 relatively discrete populations based on both telemetry and genetics (Bethke *et al.* 1996). Although demographic data is not complete for several of these regions and some population estimates may be unreliable, the worldwide polar bear population is generally agreed to be between 21 500 and 25 000 (Lunn et al. 2002).

Polar bear diet

Polar bears are the largest non-aquatic carnivores alive today (Stirling *et al.* 1977) and they hunt their primary prey, ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*), from the platform of sea ice (Stirling and Archibald 1977, Smith 1980). Other phocid species are taken occasionally, depending on the region, and bears have been known to feed on whale carcasses, or kill whales that become trapped in the pack ice (Lowry *et al.* 1987). During the summer, bears have also been observed eating kelp (Russell 1975). However, the majority of the polar bear diet consists of ringed and bearded seals hunted on the ice (Stirling and McEwan 1975, Derocher *et al.* 1993). Ringed seals are small, ranging in mass from 60 – 110 kg, and they are associated with high ice cover in relatively shallow water of 5 – 150 m depth (Frost *et al.* 2004). They are found in higher densities near fast ice edges or pressure ridges in consolidated pack ice, especially from March through July when pupping and moulting brings more seals onto the ice (Frost and Lowry 1981, Kingsley *et al.* 1985, Wiig *et al.* 1999). Ringed seals generally dig breathing holes as ice is forming in the fall, and maintain them throughout the winter (Frost and Lowry 1981). In April, pregnant females enlarge these holes and excavate lairs beneath snow drifts in which they haul out and give birth to their young (Kingsley and Stirling 1991). Pups are nursed for five to seven weeks during which time they more than double their weight, 50% of which can be fat (Frost and Lowry 1981). Bearded seals are larger, from 300 – 400 kg, and prefer active ice edges and leads since they can only maintain their own breathing holes in very thin ice (Smith 1980, Burns 1981). Bearded seals are benthic feeders and can dive to depths of up to 400 m but are found in higher densities at depths less than 100 m (Kingsley *et al.* 1985, Gjertz *et al.* 2000). Kingsley *et al.* (1985) found that bearded seals preferred large floes of broken and rotting ice during break-up, and were not associated with fast ice. Adults may be found hauled out on large ice floes throughout the year, but larger numbers haul out in loose aggregations during pupping and moulting, which occur between April and August (Burns 1981). Both ringed and bearded seals are found in higher densities on annual ice than on multi-year ice (Kingsley *et al.* 1985).

Two major seal hunting strategies used by polar bears have been identified (Stirling 1974, Stirling and Latour 1978, Smith 1980). The most common method is “still-hunting”, during which bears sit or lay at a breathing hole or ice edge, waiting for a seal to emerge. The second method, “stalking,” occurs when a bear creeps slowly toward a basking seal and makes a sudden dash when it is within 15-30 m of the seal. Stalking has been observed much less often than still-hunting, and fewer successful kills result (Stirling 1974). During break-up, bears may also dig into sub-nivean birth lairs in attempts to catch pups (Smith 1980). Most of a polar bear’s annual seal kill is made during break-up, when young-of-the-year are fat but still relatively naïve (Stirling and Øritsland 1995).

Reproduction and survival

Male polar bears generally weigh from 300 to 800 kg and measure 200 to 250 cm from tail tip to nose, while females weigh between 150 and 300 kg and measure 180 to 200 cm (DeMaster and Stirling 1981). Weight varies significantly throughout the season, as bears put on large amounts of fat during hunting periods and fast through months when food is scarce or unavailable. Adults can accumulate between five and ten cm of subcutaneous fat over a few months of hunting (Ramsay and Stirling 1988).

Females become sexually mature at three and a half or four years of age, with first production of cubs occurring between the ages of four and eight years (Ramsay and Stirling 1988). The majority of male bears reach sexual maturity around the age of six years (Rosing-Asvid *et al.* 2002). Mating occurs between March and June, depending on the region (Løno 1970, Rosing-Asvid *et al.* 2002). Females dig and enter maternity dens in the fall where they give birth to cubs while in a state of torpor (DeMaster and Stirling 1981). Litters generally consist of two cubs, but single cubs or, less often, triplets, can also occur (Amstrup and DeMaster 1988). The family group emerges in February or March, and shortly afterwards, the mother begins hunting on the sea ice again. Cubs stay with their mothers for one to two and a half years, after which time they are weaned (DeMaster and Stirling 1981). Mortality rates are low overall, although mortality rates for cubs prior to weaning are variable and between 10 and 50% (Amstrup and Durner 1995, Derocher and Stirling 1995). Adult annual mortality has been estimated to be between 2 and 16% (DeMaster and Stirling 1981, Amstrup and Durner 1995) and Stirling *et al.* (1977) estimated maximum life span to be between 25 and 30 years, although older bears have been recorded.

Distribution patterns

Polar bears are non-territorial and, with the exception of family groups, are typically solitary (Ramsay and Stirling 1988). During the past three decades, thousands of bears have been tagged and recaptured, and, more recently, followed using radio and satellite telemetry, and these methods have revealed much about polar bear movements and ranging behaviour (e.g. Garner *et al.* 1991, Mauritzen *et al.* 2001, Wiig *et al.* 2003). Females show fidelity to general denning areas over their lifetime regardless of wide ranging movements during non-denning periods (Amstrup and Gardner 1994, Derocher and Stirling 1990). Movement patterns are variable both within and between sub-populations. For example, polar bear home ranges were between 11 610 km^2 and 616 800 km^2 in the northern Beaufort Sea (Amstrup *et al.* 2000), and between 168 480 km^2 and 467 937 km^2 in eastern Greenland (Wiig *et al.* 2003). In the Greenland study, Wiig *et al.* (2003) showed that individual bears' home ranges varied dramatically between years as well. These variations in movement patterns are not trivial; polar bears use over twice as much energy to move as is predicted by general calculations based on body size (Hurst *et al.* 1982). Movement rates and distribution appear to be dependent on several factors, including the availability of food (e.g. Messier *et al.* 2001), local ice conditions (e.g. Ferguson *et al.* 2000) and individual variation (e.g. Mauritzen *et al.* 2001).

Sea ice and climate change

Sea ice is the primary habitat for polar bears, and it is highly dynamic, varying significantly both within and between years (Ferguson *et al.* 2000). Even within a single season ice grows and melts, breaks into floes, drifts with currents and wind, converges and diverges. Recent studies have shown that sea ice extent (total area covered by sea ice, including ice-free areas) and area (total area of ice alone, not including open water) have both declined over the past 20 years in almost all regions of the Arctic, and these trends are predicted to continue in the coming years (Parkinson *et al.* 1999, Maslowski *et al.* 2001, Comiso and Parkinson 2004). The summers of 1998, 2002, and 2003 set records for low sea ice extent in the Arctic Ocean (Rigor and Wallace 2004). There is also evidence that sea ice is thinning as more multiyear ice melts than builds up each year (Rothrock *et al.*1999). These patterns appear to be partially the result of warming atmospheric temperatures, which induce ice melt earlier, and delay ice formation, both of which reduce the duration of the ice season (Comiso 2002). Shorter ice seasons mean that there is less time for ice to grow and thicken, and areas of open water increase (Etkin 1991). Larger areas of open water reduce reflectance and increase absorption of energy from the sun, further increasing water temperatures and slowing ice formation (Comiso 2002).

Climate warming is already significantly impacting wildlife around the globe (Parmesan and Yohe 2003) and it is predicted to have even greater effects on northern species (Hansell *et al.* 1998, Humphries *et al.* 2004, Ims and Fuglei 2005). Changes in the distribution and abundance of arctic species have already been recorded and attributed to climate. For example, black guillemot (*Cepphus grylle*) numbers off the coast of Alaska have declined because they are forced to fly further to reach the ice edge where they forage (Krajick 2001) and decreased snow depth and earlier ice break-up has led to reduced seal recruitment in Hudson Bay (Ferguson *et al.* 2005, Stirling 2005). Polar bears will likely be affected by climate changes primarily through changes in ice structure and condition and its consequent effects on the ice-dependent species of seals they prey upon (Derocher *et al.* 2004). Greater fragmentation and thinner ice will lead to higher ice drift velocities, more areas of open water where seals can emerge to breath, and longer ice-free seasons (Derocher *et al.* 2004, Gagnon and Gough 2005). These climatic impacts will be felt first near the southern edges of polar bear ranges (Stirling and Derocher 1993, Humphries *et al.* 2004).

Hudson Bay

Hudson Bay and James Bay represent the southern limit of polar bear distribution in Canada (Stirling *et al.* 1977). Hudson Bay is a shallow inland sea that occupies the central region of the Canadian Shield. Strong prevailing northwesterly winds bring large masses of arctic air into the area and are not obstructed by any large topographical structures (Maxwell 1986), leading to long cold winters and short cool summers (Stirling *et al.* 1977). Ice begins to form in the Bay in about mid-October, with maximum ice cover (nearly 100%) occurring from February to April. From May to mid-August, ice begins to melt and September is generally ice-free (Houser and Gough 2002). Overall ice cover has decreased in Hudson Bay from 1972 to 1996 (Parkinson *et al.* 1999, Stirling *et al.* 1999), and break-up is occurring earlier (Stirling *et al.* 1999, Gagnon and Gough, in press). Because Hudson Bay is essentially a closed system, the most important factors regulating ice conditions are atmospheric (Parkinson *et al.* 1999). Between 1950 and 1990, air temperatures increased at a rate of 0.2-0.3°C per decade (Skinner *et al.* 1998), and the decreasing ice cover can most likely be attributed to this rise (Etkin1991).

Little is known about primary productivity in Hudson Bay, but satellite images reveal relatively high phytoplankton abundance throughout the Bay (Smith and Sakshaug 1990). Roff and Legendre (1986) suggest an average annual primary productivity rate of 35 gC/m^2 in the open waters of Hudson Bay, but with production as high as 175 gC/m^2

in areas around the Belcher Islands (Grainger 1982). For comparison, typical annual production on Arctic shelves is 13-45 gC/m^2 (Jones and Anderson 1994). The mixing of southward moving Arctic waters and incoming westward moving Atlantic waters and a mean depth of only 125 m contribute to these high levels of productivity (Smith and Sakshaug 1990). The seal species present in Hudson Bay are ringed, bearded, and to a lesser extent, harp (*P. groenlandica)*, hooded (*Cystophora cristata*), and harbour (*P. vitulina*) (Stirling *et al.* 1977). In 1995, 1980 bearded and 140 880 ringed seals were estimated to be hauled out on the ice (Lunn *et al.* 1997) in western Hudson Bay. Other marine mammals present are Atlantic walrus (*Odobenus rosmarus*), bowhead (*Balaena mysticetus*) and beluga whales (*Delphinapterus leucas*) and polar bears (Stirling *et al.* 1977).

The polar bears of western Hudson Bay

The polar bears of western Hudson Bay (WH) have been the subject of study since the 1960s (Stirling *et al.* 1977, Derocher *et al.* 2004). Regular surveys have been done in the area by the Canadian Wildlife Service (CWS), Manitoba Department of Renewable Resources and Transportation Services, and the Ontario Ministry of Natural Resources (Stirling *et al.* 1977, Stirling *et al.* 1999). Lunn *et al.* (1997) estimated the western Hudson Bay population to be about 1200 ± 250, but new evidence suggests that the population is currently less than 1000

(Regehr *et al.* in preparation). Due to a male-biased harvest the population is estimated to be 58% female and 42% male (Derocher *et al.* 1997). Over 60% of the adult population is marked with uniquely numbered ear tags and tattoos (Lunn *et al.* 2002). Despite some overlap between the WH bears and those of the southern Hudson Bay population during the on-ice period, individuals show a high degree of fidelity to particular coastal areas and there has been very little immigration or emigration between the summering areas of the two populations (Derocher and Stirling 1990, Stirling *et al.* 2004).

Unlike many polar bear sub-populations, bears from Hudson Bay populations are forced ashore each summer when ice cover melts completely (Russell 1975, Derocher *et al.* 1993). Once on land, the bears segregate by age and sex class; adult males and subadults stay close to the coast line and adult females, whether solitary or accompanied by cubs, move further inland (Stirling *et al.* 1977, Latour 1981, Derocher and Stirling 1990). In fall, pregnant females dig maternity dens in peat banks and other bears move back onto the ice (Stirling *et al.* 1977, Lunn *et al.* 2004). Cubs are born in mid-November to mid-December and emerge with their mothers from their dens in February or March (Derocher *et al.* 1992). Within a few weeks the family group makes its way back onto the sea ice to feed until break-up in June or July (Ramsay and Stirling 1988).

Since the early 1980s there have been declines in condition, reproductive rates, and numbers of WH polar bears, all of which have been linked to earlier ice break-up and later ice freeze-up (Stirling *et al.* 1999, Derocher *et al.* 2004, Regehr *et al.* in preparation). The combination of a shorter hunting period and a longer fasting period means that bears may not be able to accumulate sufficient fat reserves to survive the ice-free season (Derocher *et al.* 2004). Females emerging from maternity dens later in the winter have an even shorter hunting period coupled with increased energy demands of providing for cubs as well as for themselves.

Thesis objectives

The primary objective of this thesis is to examine the movement patterns of polar bears from the western Hudson Bay population over time and in relation to changes in climatic conditions in Hudson Bay. Although the WH population has been well-studied for over 40 years, very little is known about their behaviour on the sea ice, and what factors affect that behaviour. These variables can now be quantified more easily with GPS-satellite-linked collars and in this thesis I use location data from satellite collars to examine polar bear movement on the ice.

In chapter two, I analyse satellite collar data from 1991 to 1999 collected by CWS along with data from new GPS collars deployed in 2004. The purpose is to describe the general and large-scale patterns of movement for bears in this region by examining differences between reproductive classes, seasons, and years. By comparing trends in bear movement on the ice to previously documented trends in ice condition, I attempt to examine how movement may be affected by changes in ice in Hudson Bay. I also compare my data to data collected from other sub-populations of bears in an attempt to identify the underlying determinants of polar bear movement patterns.

Chapter three presents a more detailed investigation of the movement paths and search strategies of a sample of polar bears from the western Hudson Bay population. I characterize polar bear search strategies by examining the distribution of move lengths and turning angles and identifying the spatial and temporal scales at which polar bear movement changes. I discuss the results in terms of hunting efficiency, energy budgets, and future changes to polar bear habitat.

Chapter four summarizes the results from the entire thesis, and synthesizes the findings in relation to large scale environmental factors. I suggest future work that is required for a better understanding of polar bear movement and how it will be affected as climate continues to change.

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CHAPTER TWO – SEASONAL AND ANNUAL MOVEMENT PATTERNS OF POLAR BEARS ON THE SEA ICE OF HUDSON BAY

Introduction

Animal movement is influenced both by the distribution of resources such as food or breeding habitat, and by the physical structure of the landscape (Kareiva 1982, McIntyre and Wiens 1999). Analysis of animal movement and distribution across a landscape and through time can provide insights into resource use patterns, foraging strategies, energy expenditure, and population dynamics (e.g. Jones 1977, Johnson *et al.* 2002, Fortin *et al.* 2003). The increased use of satellite and global positioning system (GPS) technology in recent years has made it easier to examine the movement patterns of large, wide-ranging animals, particularly if their habitat is difficult to access by humans (e.g. Jouventin and Weimerskirch 1990, Fritz *et al.* 2003).

Polar bears (*Ursus maritimus*) are non-territorial carnivores that travel thousands of kilometers over arctic sea ice hunting their principal prey, ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980). Earlier research on polar bear movement relied on mark-recapture data alone or together with radio telemetry when the bears were close to or on land (e.g. Lentfer 1983, Stirling *et al.* 1980, Derocher and Stirling, 1995); however, satellite and GPS technology have improved our ability to understand the structure and dynamics of polar bear distribution. The circumpolar population has been divided into 19 relatively discrete sub-populations based on satellite location data (Bethke *et al.* 1996, Taylor *et al.* 2001) and satellite-tracking studies in the Beaufort Sea, the Eastern high Arctic, Greenland and the Barents Sea have revealed a significant degree of variation in movement patterns both within and between sub-populations (Born *et al.* 1997, Messier *et al.* 2001, Mauritzen *et al.* 2003a, Durner *et al.* 2004).

Variations within sub-populations are due to differences both in the energetic demands of individual bears and in local ice conditions. Females have greater energetic demands when they are accompanied by offspring than when they are not, and therefore may adopt different space-use strategies or be unable to exert as much energy as other bears (Amstrup *et al.* 2000, Mauritzen *et al.* 2001). In addition, seasonal changes in ice conditions create different landscapes through which bears must move, and their movement rates and habitat preferences often shift cyclically with the seasons (Ferguson *et al.* 2000a).

The variation between polar bear sub-populations is most likely due to regional differences in ocean productivity, seal distribution, and sea ice. For instance, levels of marine primary productivity vary with water depth, vertical mixing and freshwater input and areas of high primary productivity can support higher densities of other marine organisms (Jones and Anderson 1994). Seal distribution is dependent on local productivity as well as on sea ice dynamics, both of which vary substantially throughout the Arctic (Kingsley *et al.* 1985, Lunn *et al.* 1997, Frost *et al.* 2004). Sea ice structure and dynamics are determined by regional air and water circulation patterns, temperature fluctuations, and bathymetry (Thomas and Dieckmann 2003).

In addition to this existing variability, climate change is affecting ecosystem dynamics across the Arctic (Hansell *et al.* 1998, Derocher *et al.* 2004). Sea ice extent, concentration, and thickness have all declined since the 1970s (Parkinson *et al.* 1999, Maslowski *et al.* 2001, Comiso 2002), and these changes have been attributed to large scale climatic shifts in air temperature and global ocean and atmosphere circulation (Parkinson *et al.* 1999, Comiso and Parkinson 2004). Negative effects of climate change on arctic wildlife have already been documented in several species, such as declining reproductive success in geese, cod, and seals (MacInnes *et al.* 1990, Portner *et al.* 2001, Stirling 2005). Because climatic influences will affect ice conditions and seal distributions differently in different regions of the Arctic (Gough and Wolfe 2001, Maslowski *et al.* 2001), it is likely that individual polar bear sub-populations will also vary in their responses.

The polar bears of western Hudson Bay (WH) are unique because they live close to the southern limit of polar bear distribution and may be affected by a warming climate sooner and more severely than other sub-populations (Stirling and Derocher 1993, Derocher *et al.* 2004). Each summer, the entire sea ice cover in the Bay melts and bears are forced ashore where they spend several months fasting on land (Stirling *et al.* 1977, Derocher and Stirling 1990). The WH bears show strong fidelity to specific denning areas on land and return year after year despite wide ranging movements on the ice during winter (Ramsay and Stirling 1990, Derocher and Stirling 1990). When the ice reforms in October and November, bears move back out onto the ice to hunt, with the exception of pregnant females, who dig and enter dens (Ramsay and Stirling 1988). Cubs are born sometime between mid-November to mid-December (Derocher *et al.* 1992), and the family group emerges in February or March to move out onto the ice together. The most critical hunting period for all WH bears may be between April and July, when both ringed and bearded seals haul out onto the ice to moult or pup and fat, naïve seal pups become abundant (Stirling and McEwan 1975, Kingsley and Stirling, 1991, Stirling and Øritsland 1995). During this period, bears must acquire sufficient fat stores to sustain their metabolic requirements throughout the ice-free period when food is not available (Ramsay and Stirling 1988, Atkinson and Ramsay 1995).

Recent studies have shown that ice break-up in Hudson Bay has been occurring progressively earlier over the past 30 years (Gough *et al.* 2004, Gagnon and Gough in press), and that this may be the cause of a measured decline in polar bear condition, as they are forced ashore before they can accumulate adequate fat stores (Stirling *et al.* 1999). The trend toward earlier break-up is projected to continue, as are declines in ice cover and concentration (Etkin 1991, Gagnon and Gough in press). Patterns of bear movement in Hudson Bay are predicted to change as this happens, in response to changes in prey distribution, prey species and ice structure (Derocher *et al.* 2004); however, little is known about the present movement patterns of bears while they are on the sea ice.

The purpose of this study is to describe the annual and seasonal movement patterns of satellite radio-collared female bears from the WH population throughout the on-ice period. I hypothesized that females with offspring would move less than solitary females due to the increased energetic demands of caring for young, that changes in ice due to seasonal shifts would affect movement patterns, and that bear movement may have changed over time in response to changes in ice conditions.

Methods

Study area

The boundary of the WH polar bear population includes coastal areas of Manitoba, Nunavut, and western Ontario, and is bounded by 63°10'N and 88°30'W (Stirling *et al.* 1977, Stirling *et al.* 1999). The capture area for this study was south of Churchill, Manitoba (Figure 2.1), between 57°00' and 58°50'N latitude and 92°25' and 94°15'W longitude (Derocher and Stirling 1995).

Hudson Bay is a shallow inland sea with a mean depth of 125 m and an area of about 10^6 km^2 (Jones and Anderson 1994). Productivity has mainly been estimated in southeast Hudson Bay and is 35 gC/m^2/year on average, with the highest levels (175 gC/m^2/year) found around the Belcher Islands (Roff and Legendre 1986). In comparison, the average production on Arctic shelves is 5-13 gC/m^2/year (Roff and Legendre 1986). Ocean currents in the Bay follow a large scale counter-clockwise gyre which moves south from Foxe Basin, and exits through the Hudson Strait (Prinsenberg 1986). Ice formation begins mid-October in the northwest and early ice is pushed by the gyre southward along the west coast towards James Bay. Ice velocities during freeze-up are between 0.36 and 0.54 km/h (Saucier *et al.* 2004). From late December until the end of April, ice cover is greater than nine tenths throughout the Bay and the maximum extent occurs in April. Break-up occurs from May to mid-August, as the southern most ice begins to melt due to warmer temperatures, and ice from the northwest is pushed by the gyre along the west coast (Maxwell 1986, Saucier *et al.* 2004). The last ice floes are generally found along the southern coast in Ontario and in James Bay, and by September the whole Bay is ice-free (Gough *et al.* 2004).

Data collection

Between 1991 and 1998, 41 adult female bears from the WH population were captured and collared. Polar bears were caught in either September or March using standard helicopter capture methods (e.g. Derocher and Stirling 1996) and were immobilized using Telazol® (Fort

Dodge Laboratories, Fort Dodge, Iowa) according to Stirling *et al.* (1989). Animal handling procedures were approved by the University of Alberta BioSciences Animal Policy and Welfare Committee. Bears were classified as belonging to one of the following groups: females with cubs-of-the-year (COYs), females with yearlings, solitary adult females 5 years or older, adult males 5 years or older, or sub-adult males or females (2-4 years). A sample of adult females was fitted with Telonics (Mesa, Arizona) satellite radio collars linked to the Argos system (Service Argos, Inc. Lynnwood, Washington). Males were not tracked because their necks are wider than their heads, and collars cannot be secured. The satellite collars were programmed with different duty cycles in different years depending on immediate study objectives. Argos provided quality indices for each location: 3 - accuracy < 150 m, 2 - accuracy = 150 - 350 m, 1 - accuracy = 350 - 1000 m, 0 - accuracy > 1000 m, A or B - too few satellites to estimate accuracy, but locations may be accurate.

In September 2004, 11 Telonics Gen III GPS - Argos satellite linked collars were deployed in the same capture area. Accuracy of these newer collars is within 30 m (M. Edwards, pers. comm.). The collars were programmed to acquire 6 GPS locations per day every 4 hours. Only adult females accompanied by offspring were fitted with collars because solitary females may have been pregnant and would have gone into maternity dens for the fall and early winter. Collared bears were all classified according to reproductive status as above at the time of collaring. For all bears, status was updated if bears were recaptured; otherwise, bears were classified as "unknown reproductive status" one year after capture.

I obtained daily ice extent measurements for Hudson Bay from the National Oceanic and Atmospheric Administration at the National Snow and Ice Data Centre for each year from 1991 to 1999 (Arctic Climatology Project 2000). From these daily ice extent measurements I calculated average annual area as well as average monthly and seasonal ice areas within each year.

Statistical analysis

I used the North American Datum 1983 coordinate system for plotting bear locations in Hudson Bay. All bear locations were originally plotted as latitude north and longitude west, but were converted to Universal Transverse Mercator (UTM) coordinates for zone 15 in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) so that locations are positive and in meters for all spatial analyses.

For seasonal analyses, I divided the year into 4 biologically relevant seasons based on both bear behaviour and ice conditions: freeze-up, winter, break-up, and summer. Because movement and behaviour changes when bears move onto the ice from land (Ramsay and Andriashek 1986, Durner *et al.* 2004), the first day of freeze-up was defined for each bear as its first location on the ice after summer and the last day was defined as December 31 for all bears. From January to May, the ice in Hudson Bay is at its maximum concentration, and continues to thicken until April, when it is at its maximum concentration and thickness; therefore, I defined winter as January 1 until April 30. After April, ice concentration begins to decline throughout the Bay, and both ringed and bearded seals begin to pup and moult (Stirling and Øritsland 1995, Lunn *et al.* 1997). Therefore, I defined break-up as beginning May 1 and ending for each bear on the last day it was located on the ice before returning to land. Once on land, bears in Hudson Bay move little (Latour 1981) and I defined this period from first to last land location as summer.

Because polar bears do not defend territories, the term "home range" in this paper refers only to the general area occupied by a bear within a given time period. Annual and seasonal home range size were estimated by the minimum convex polygon (MCP) method (Hayne 1949) using Hawth's Tools 3 (http://www.spatialecology.com/htools) for ArcGIS 9.2. This method of home range estimation was chosen both because of its simplicity and because it facilitates comparison of WH bears with other populations since MCP has been the most commonly used method in other studies. Annual home range was estimated when there were at least 25 locations within a year for a given bear and where the first and last locations were at least 292 days apart (80% of a 365 day year). If there were data for a single bear beyond 365 days, a second bear-year was started at the 366th day. This situation occurred less than 5% of the time in annual comparisons, and usually data existed for a single bear in only one year. Seasonal home range was estimated when there were at least 20 locations in a season and if the first and last locations were at least 20 days apart. To compare the more frequent GPS data with the satellite data, I randomly sub-sampled the newer data 1000 times with replacement and found the average MCP size using the mean number of locations available in the satellite data for calculations of MCPs.

Annual and seasonal net displacements were calculated by measuring the straight-line distance between the first and last location for the given period. Because WH bears are known to show site fidelity when they return to land after being on the ice, I was interested in the distance between where bears left land and where they returned after the on-ice period. For females collared on land in September, this distance was calculated from September to the following September. However, for females collared as they emerged from dens on land in March, net annual displacement was calculated from March, when they left the denning area, until September, by which time all bears had returned to land.

Hourly movement rates were calculated by dividing the straight-line distance from one location to the next by the hours elapsed between them. To determine how much the interval between locations influenced the derived movement rate, I plotted the hour interval between consecutive locations against the derived mean rate for that interval and found the best fit curve to describe the relationship. I used the curve to help determine whether hourly rates should be divided into short-term and long-term rates, and where those divisions should occur.

I estimated total annual distance moved as the sum of all straight-line distances for a particular bear within a year. I used only bears for which there were at least 12 locations, with no gap greater than 30 days between two locations, and for which the first and last locations were at least 292 days apart. In analyses of total seasonal distance, I used bears for which there were at least 4 locations in a season, and at least 20 days between the first and last location. Because locations were much more frequent in the GPS collar dataset than in the satellite dataset, to compare results from the two datasets, I sub-sampled the GPS collar data 1000 times with replacement to match the frequency of the satellite data.

For all analyses, I used individual bear as the sampling unit. I tested the null hypothesis that measured variables were independent of reproductive class or season using one-way ANOVAs when data conformed to statistical assumptions of normality and equal variance. If data were not distributed normally, or if they showed heteroskedasticity, I used the Kruskal-Wallis or Mann-Whitney U non-parametric tests (Sokal and Rohlf 2001). In seasonal comparisons, the same bear was measured in consecutive seasons in a year, so I used Friedman's non-parametric test for related samples (test statistic reported as X^2_r). I also correlated all variables with year to identify temporal relationships. When I found time trends, I tested whether these were correlated with mean ice extent for the period of interest. I used Pearson's product-moment correlation (correlation coefficient reported as r) if data were distributed normally; otherwise I used Spearman's rank correlation (reported as r_S) which produces a more conservative estimate, but lifts the assumption of normality (Sokal and Rohlf 2001). Because the number of bears collared each year varied, sample sizes vary for each analysis. All ANOVAs or non-parametric tests of multiple differences were followed by either Bonferroni or non-parametric Tukey's tests (Zar 1999, p. 225) to determine which variable(s) differed significantly from others. For all analyses, sample sizes are reported and means are given ± one standard error (SE); a result was considered significant if its probability was less than 0.05. All linear statistics were performed with SPSS 13.0 for Windows. Sub-sampling was performed using R 2.0 for Linux and Tukey's tests were calculated using Microsoft Excel 2003.

Mean angles and r (a vector between 0 and 1 that indicates strength of directionality where 1 is perfect directionality with no variance and 0 is uniform distribution of angles) were computed for each season according to Zar (1999). The null hypothesis of uniform distribution was calculated using Rayleigh's z-test for circular uniformity. I tested the effect of reproductive status on mean angles using the Watson-Williams multi-sample test of mean angles (Zar 1999, p.625), which is a test analogous to ANOVA in linear statistics. Circular statistics were calculated using Microsoft Office Excel 2003.

Results

Collars were deployed on 46 adult females between March 1991 and September 1998 and 6083 locations were obtained. Of these, 16% had a quality index of 0 (>1000 m error) and were omitted from analyses. After these were removed, 12% of locations had A or B ratings and most of these were also removed; however, they were retained if movement rates between locations were less than 10 km/hr (the maximum movement rate recorded). No B locations filled this criteria, but some A locations did. The frequency of locations varied; however, the mean time between two locations was 195 ± 8 hours (about 8 days) and the median was 117 hours (5 days).

For analyses of bears with GPS collars, one good location for each fix time was taken, when available. Due to collar malfunctions, weather and bear behaviour, there were commonly less than 6 locations per day. The mean number of fixes per day was 4.3 ± 0.04, and fixes were obtained, on average, every 7.2 ± 0.3 hours, 27 times more frequently than in the older dataset. Life span of the 11 collars deployed in September 2004 ranged from 68 to 309 days; therefore, I did not use 2005 data in any break-up or annual comparisons. However, seven collars transmitted consistently through freeze-up and winter, so these data were combined and compared with the satellite data.

Home ranges

Mean annual home range size for WH bears was 106 614 km^2 ± 12 314 (n = 29). Females with COYs had both the smallest (8470 km^2) and largest (311 646 km^2) home ranges (Table 2.1). There were no significant differences between reproductive classes (ANOVA $F_{2, 26} = 0.52$, $P = 0.60$) so all bears were pooled for further analyses. Annual home range size decreased by 55%, from 149 576 km^2 in 1992 to 68 321 km^2 in 1998 ($r = -0.51$, $P = 0.005$; Figure 2.2). There was also a significant decline in average annual ice extent in Hudson Bay over the same time period ($r = -0.938$, $P < 0.0001$). Annual home range size was positively correlated with average annual ice extent ($r_s = 0.575$, $n = 29$, $P = 0.001$).

Seasonal MCPs were created from means of 38 locations in freeze-up, 33 in winter, 24 in break-up and 38 in summer. I sub-sampled the 2004-2005 data and made MCPs using the appropriate number of locations per season in order to facilitate comparison. However, the sub-sampled MCPs were not significantly different from the MCPs created for the same bears using all of the points in a season, despite the fact that there were hundreds of locations per season in the raw GPS data (Kruskal-Wallis $H = 0.63$, $P = 0.43$). Home ranges varied significantly with season (Table 2.2) for all reproductive classes of bears (Friedman's test $X^2_r = 24.05$, $P < 0.0001$) and were smallest in summer. Home ranges in all other seasons were not significantly different from each other (Tukey's test).

There were no significant differences between reproductive classes for home ranges in summer (Kruskal-Wallis H = 1.94, P = 0.38), or break-up (Kruskal-Wallis H = 1.02, P = 0.60), and no changes over time (summer r_s = -0.14, P = 0.41; break-up r_s = -0.07, P = 0.71). During freeze-up, there were significant differences between females with COYs or yearlings, but there were not enough solitary females to include them in the analysis (Mann Whitney U = 34.0, P= 0.003). Females with COYs had the larger home ranges. This difference was dependent on an increase in freeze-up home range size in 2004 for females with COYs (r_s = 0.69, n = 18, P = 0.001). There was only one female with yearlings in the 2004 data, so I could not determine whether this increase in freeze-up home range size occurred for all reproductive classes of bears. In winter, reproductive class had a significant effect on home range size (Kruskal-Wallis H = 8.73, P = 0.013). Tukey's test for multiple comparisons showed that females with yearlings had significantly larger winter home ranges than did females with COYs, but solitary females were not significantly different from either group. There were no trends over time in winter home range size (r_s = -0.114, n = 58, P = 0.39).

Net displacement

Mean annual net displacement was 82 ± 17 km (n = 48), but the data were highly skewed and median net displacement was 39 km (Figure 2.3). In other words, bears returned to land less than 40 km from where they had left. There were no differences between the medians of reproductive classes (Kruskal-Wallis H = 4.38, P = 0.11), although there were differences between the means (Kruskal-Wallis H = 6.35, P = 0.04). Females with COYs ($\bar{x}$ = 113 ± 35 km, n = 20) and females with yearlings ($\bar{x}$ = 112 ± 41 km, n = 9) had similar mean displacement, but solitary females had significantly lower displacements ($\bar{x}$ = 34 ± 4 km, n = 19). The high means for females with offspring were strongly influenced by two bears who had net annual displacements of 696 (01005C in 1994), 306 (01008C in 1995) and 406 (01008C in 1996) km respectively. Although 01008C returned to land 306 km from where she left land in 1995, the following year, she did return to the Churchill area. When these two individuals were removed from analysis, there were no differences between classes (Kruskal-Wallis H = 4.4, P = 0.11). Annual net displacement did not change over time for any reproductive class (r_s = -0.15, P = 0.32).

For all reproductive classes, net displacement depended on season (Friedman's test X^2_r = 36.73, P < 0.0001). Tukey's test for multiple comparisons showed that in summer, displacement was significantly lower than in all other seasons, and displacement in freeze-up was higher than in winter (Table 2.3). During freeze-up, mean net displacement was 336 ± 18 km there were no significant differences between reproductive classes (ANOVA $F_{1,30}$ = 1.54, P = 0.22) or over time (r = 0.056, P = 0.76). During winter, there were significant differences between classes (ANOVA $F_{2,56}$ =

16.5, $P < 0.0001$). Bonferroni test for multiple comparisons showed that females with COYs ($\bar{x} = 354 \pm 23$ km) had larger net displacements in winter than other females (solitary females $\bar{x} = 195 \pm 23$; females with yearlings $\bar{x} = 195 \pm 24$). There were no changes in net winter displacement over time for any reproductive class (females with COYs $r_s = -0.15$, $P = 0.46$; solitary females $r_s = -0.13$, $P = 0.66$; females with yearlings $r_s = 0.14$, $P = 0.57$). There were no significant differences between classes in net displacement during break-up (Kruskal-Wallis $H = 4.6$, $P = 0.1$) or summer (Kruskal-Wallis $H = 5.7$, $P = 0.06$) and there were no changes with time in either season (break-up $r_s = -0.80$, $P = 0.64$; summer $r_s = 0.02$, $P = 0.91$).

Directional patterns

Bears only showed significant directional movement when they were leaving land and moving onto the ice (Table 2.4), and overall, reproductive class had little effect on direction of movement. During freeze-up, there were no differences between reproductive classes (Watson-Williams $F_{2,32} = 0.44$, $P > 0.25$), and bears of all classes moved significantly northeast (mean direction = 52°, $r = 0.33$; Rayleigh's $z = 4.64$, $n = 42$, $P < 0.01$). During winter, reproductive class affected direction of movement (Watson-Williams $F_{2,64} = 12.03$, $P < 0.0005$), and females with COYs moved significantly northeast (mean direction = 52°, Rayleigh's $z = 5.1$, $n = 31$, $P < 0.01$), while all other females showed no directionality (solitary females: Rayleigh's $z = 0.14$, $n = 23$, $P > 0.25$; females with yearlings: Rayleigh's $z = 0.05$, $n = 20$, $P > 0.25$). During break-up there were no significant differences between classes (Watson-Williams $F_{2,46} = 0.26$, $P > 0.25$), and no significant directionality, although there was weak support for a mean angle of 240° (Rayleigh's $z = 2.35$, $n = 67$, $0.05 < P < 0.1$). Solitary females had the strongest directionality during break-up (mean angle = 230°, $r = 0.38$); however, it was not strong enough to reject the null hypothesis of uniform distribution (Rayleigh's $z = 2.12$, $P > 0.1$). During summer there were no significant differences between classes (Watson-Williams $F_{2,71} = 0.56$, $P > 0.25$), and bears did not show significant directionality (Rayleigh's $z = 2.72$, $n = 72$, $P > 0.25$).

Rates of movement

Rate was strongly dependent on interval until approximately 100 hours separated two points (Figure 2.4). Because most of the 2004-2005 GPS locations were less than 8 hours apart, and because the point separating an extremely steep slope from a lesser one appeared to occur at around 10 hours, I decided to separate the rates into short-term (less than 8 hours between locations) and mid-term (between 8 and 100 hour intervals). However, because most other studies on polar bear movement have used satellite collars that provided locations only every 4-7 days, I also calculated long term movement rates when the interval between locations was 100 to 200 hours to facilitate comparisons.

Long-term movement rates (100-200 hours between consecutive locations) did not differ between classes (Kruskal Wallis H = 0.71, P = 0.70), but did vary significantly with season (Friedman's test $X^2_r = 23.18$, $P < 0.0001$; Table 2.5). Tukey's post-hoc tests showed that summer movement rates were significantly lower than those of all other seasons (Figure 2.5). During break-up and summer, movement rates did not change over time. During winter, however, there was a significant decline over time in long term rates ($r_s = -0.061$, n = 18, P = 0.008).

Mid range hourly movement rates (8-100 hours between consecutive locations) varied significantly with season (Friedman's test $X^2_r = 9.96$, P = 0.019; Table 2.5), but did not vary with reproductive class in any season (Kruskal-Wallis tests: freeze-up H = 1.97, P = 0.37; winter H = 5.6, P = 0.06; break-up H = 1.47, P = 0.48; summer H = 0.84, P = 0.66). Movement rates were highest during freeze-up ($\bar{x} = 1.06 \pm 0.11$ km/hr) and lowest during summer ($\bar{x} = 0.10 \pm 0.02$ km/hr), but Tukey's post hoc tests showed that only summer movement rates were significantly different from rates in other seasons ($P < 0.0001$). There were no changes in mid-range movement rates over time in any season (freeze-up $r_s = 0.38$, P = 0.18; winter $r_s = -0.08$, P = 0.72; break-up $r_s = 0.31$, P = 0.24; summer $r_s = 0.28$, P = 0.46). The highest mid-range rate recorded was 4.12 km/hr and was achieved by a solitary female in winter, but the mean overall rate was 0.61 ± 0.08 km/hr.

Short-term movement rates (<8 hours between consecutive locations) were consistently higher than longer term rates in all seasons (Figure 2.5, and summarized in Table 2.5). There were significant differences between seasonal short-term movement rates (Friedman's test $X^2_r = 13.56$, $P = 0.004$) and Tukey's test for multiple comparison showed that summer was significantly lower than winter. Reproductive classes did not affect short-term movement rates in any season (Kruskal-Wallis tests: freeze-up $H = 0.50$, $P = 0.48$; winter $H = 1.76$, $P = 0.42$; break-up $H = 2.59$, $P = 0.27$; summer $H = 1.84$, $P = 0.40$). There were no changes in short-term movement rate over time in freeze-up ($r_s = -0.23$, $P = 0.50$), but rates declined in winter ($r_s = -0.74$, $n = 19$, $P < 0.0001$) and summer ($r_s = -0.79$, $n = 13$, $P = 0.001$) and there was also weak evidence for a decline in break-up movement rates ($r_s = -0.63$, $P = 0.052$). The highest observed short-term movement rate was 10.86 km/hr and was recorded for a female with yearlings in winter. There were only three instances of rates as high as 10 km/hr and all three occurred when bears were on the ice and the time between consecutive locations was less than 2 hours.

Total distances

The mean distance traveled annually was 2080 ± 170 km ($n = 35$). The shortest distance traveled was 547 km by a solitary female and the greatest distance was 4935 km by a female with COYs (Table 2.6). There were no significant differences between reproductive classes (ANOVA

$F_{2,32}$ = 1.13, P = 0.335), so classes were pooled for further analyses. There was a 45% decline in total annual distance traveled over time from 2885 km in 1991 to 1581 km in 1998 (r = -0.47, n = 35, P = 0.004; Figure 2.6).

The total seasonal distances calculated for bears with GPS collars were two to three times greater than those calculated for bears with satellite collars due to the much higher frequency of locations available from GPS collar data. Total seasonal distances were calculated from the satellite data using 12 locations for freeze-up, 16 for winter, 11 for break-up and 12 for summer. Once GPS data were sub-sampled to match these numbers of locations, distances moved were comparable. There were significant differences between seasonal distances traveled (Friedman's test X^2_r = 37.12, P<0.0001) and Tukey's post hoc test showed that total distance traveled in winter were higher than during break-up and distances traveled in summer were lower than those in every other season (Table 2.7). During freeze-up, there was no difference between the distance traveled by females with COYs or yearlings (Mann-Whitney U = 1.11, P = 0.57), and there were not enough data for solitary females in freeze-up to include them in the analysis. Distance traveled in freeze-up did not change over time (r_s = 0.14, P = 0.53). In winter, females with yearlings traveled a greater total distance ($\bar{x}$ = 1090 ± 99) than other females (solitary $\bar{x}$ = 898 ± 99; females with COYs $\bar{x}$ = 568 ± 47; Kruskal-Wallis H = 17.6, P < 0.0001). Total distance traveled in winter by solitary females did not change significantly over time (r_s = -0.30, n = 17, P = 0.24); however, there was weak evidence that the total distance traveled by females with offspring in winter has declined over time (females with COYs: r_s = -0.35, n = 27, P = 0.071; females with yearlings: r_s = -0.44, n = 19, P = 0.059). During break-up, females with COYs traveled a greater total distance than did other females (Kruskal-Wallis H = 7.48, P = 0.024), and there were no changes in distance traveled by any class over time. There were no significant differences between reproductive classes for total distance moved in the summer (Kruskal-Wallis H = 0.67, P=0.72). The total distance traveled in summer did not change over time (r_s = -0.15, P = 0.31).

Discussion

Movement patterns of individual animals affect population distribution and dynamics (Jones 1977, Zollner and Lima 1999), and are affected by resource availability and landscape structure (McIntyre and Wiens 1999). Therefore, understanding animal movements is a key component in understanding the ecology of the whole population. In the Hudson Bay region, polar bear condition has been declining due to changes in the bears' sea ice habitat (Stirling *et al.* 1999); however, previous studies on Hudson Bay polar bears have focussed on the ice-free period when bears are on land (e.g. Latour 1981, Stirling *et al.* 2004) and relatively little is known about bear movements on the ice when they are far from shore. This study is the first to quantitatively examine bear movement on the ice of Hudson Bay, and because both hunting and mating occur exclusively on the ice (but see Derocher *et al.* 1993) this period is critical to bear survival and reproductive success (Atkinson and Ramsay 1995).

Sample sizes in many analyses were small due to variation in location frequency, but in most cases, effect sizes were large relative to sample variation and results were clear. Sub-sampling the GPS data allowed valid comparisons between these and the satellite data; however, differences over time in movement rates may have been affected by differences in the datasets. For instance, GPS locations always had at least four hours separating them, while satellite collars had no lower limit to the time between locations. Therefore, declines over time in short-term movement rates may have been due to longer location intervals in 2004-2005. Other than this, I could not find evidence that combining the GPS and satellite datasets would produce misleading results.

Effects of reproductive class and season

Polar bears from the WH population used space differently depending on the season and the most apparent differences in movement were seen in summer. Consistent with other studies which show Hudson Bay bears are not active while on land in summer (Knudsen 1978, Derocher and Stirling 1990, Lunn *et al.* 2004), home ranges in summer were small, distances moved were minimal, and hourly movement rates were low. Although my results show high mean net displacements for females with young, these were influenced by only two bears that did not return to the Churchill area when the ice melted, and median displacements were less than 40 km for all groups, which is similar to the net annual displacements of 30-32 km found by Derocher and Stirling (1990). Despite one bear's return to land almost 700 km from where she left, she did return to the her original denning area the following year. These results are consistent with the hypothesis that females return to the same area in order to familiarize their cubs with suitable denning habitat (Scott and Stirling 2002).

During freeze-up, polar bears had high hourly movement rates, high net and total distances covered, small home ranges, and significant directionality, all of which describe travelling behaviour (Kareiva and Shigesada 1983, Fritz *et al.* 2003). Bears moved with a mean direction of 52° which agrees with the mean directions of 53° and 39° found by Derocher and Stirling (1990) and Ramsay and Andriashek (1986) respectively for bears as they moved onto the ice. However, due to logistic constraints, bears in previous studies were either followed on land only, or were relocated up to 195 km offshore, and it is now evident that bears move more than 300 km offshore, and maintain their northeast directionality until late December. Ice drift contributes to observed movement rates and directions because bears are walking on a moving platform (Mauritzen *et al.* 2003b). In Hudson Bay, ice drift velocities are highest during freeze-up and early winter, at 0.4 – 0.5 km/hr in a southeast direction (Saucier *et al.* 2004), so bears probably move faster and in a more northerly direction than is apparent by their observed paths.

By winter, bears moved more slowly in random directions, covered less net distance, and had larger home ranges than during freeze-up, suggesting that hunting became the main activity after December. Net displacement during break-up for all classes was similar to net displacement during freeze-up, indicating that over the winter, bears moved neither closer to nor farther from the Cape Churchill area, and only began to move toward land after May 1. The similarity between freeze-up and break-up rates, total distances and home range sizes support this pattern of movement.

Females with COYs did not have lower hourly movement rates than other females in any season, and, in fact, moved greater total distances in a year than other females, despite being accompanied by small cubs which might be expected to have more limited mobility. Evidence that females caring for dependent young use different movement strategies has been found in polar bears (Mauritzen *et al.* 2003a) as well as in other mammals (e.g. Beier *et al.* 1995, Loretta and Vieira 2005). Daily energy expenditure of female mammals with young are about four times their basal metabolic rate because of energy lost through food-sharing and lactation (Ricklefs *et al.* 1996); therefore, female polar bears with COYs need to eat more than other females in winter and break-up. Emergence from maternity dens may coincide with seal pupping and moulting to maximize the productivity of a shorter hunting period (Ramsay and Andriashek 1986, Amstrup and Gardner 1994). Still, it is likely difficult for females with young to store as much fat as other classes of females and Atkinson and Ramsay (1995) found that female polar bears with offspring had significantly less body mass, less total body fat, and less fat per unit lean body mass than solitary females.

Comparisons to other populations

The annual home range size of Hudson Bay polar bears has not been previously documented, although satellite collars have been used to measure home ranges of bears in the eastern high Arctic (Ferguson *et al.* 1999), the Bering and Chukchi seas (Garner *et al.* 1991) the Beaufort Sea (Amstrup *et al.* 2000), the Barents Sea (Mauritzen *et al.* 2001), and Northeast Greenland (Born *et al.* 1997). The largest annual home ranges have been identified in the Beaufort Sea ($\bar{x}$ = 166 694 km^2; Amstrup *et al.* 2000) and in the Canadian Archipelago ($\bar{x}$ = 125 500 km^2; Ferguson *et al.* 1999) and bears in both areas were highly variable, with some ranges up to 600 000 km^2. Home ranges for bears in the Archipelago were calculated using kernel methods of range estimation, which generally produce smaller areas than MCP methods, so it is likely that the mean MCP range for Archipelago bears is larger than 125 500 km^2. Unlike bears in the Beaufort Sea or Archipelago, WH bears had a mean home range size more similar to polar bear ranges in the Barents Sea (means from 28 000 to 96 302 km^2; Born *et al.* 1997; Mauritzen *et al.* 2001) although there was a lot of individual variability.

Polar bear home range size is largely determined by the availability and predictability of prey (Ferguson *et al.* 1999, Mauritzen *et al.* 2003a). Both ringed and bearded seals prefer annual ice and shallow water less than 200 m (Kingsley *et al.* 1985, Gjertz *et al.* 2000) and they are rarely found in multiyear ice or hauled out on land (Kingsley *et al.* 1985, Frost *et al.* 2004). Therefore, polar bear home ranges are large when they encompass substantial amounts of either multiyear ice or land, as is the case in both the Arctic Archipelago and the Beaufort Sea (Stirling and Øristland 1995, Ferguson *et al.* 1999). Because Hudson Bay is only 250 m at its deepest (Maxwell 1986) and is covered with annual ice only, productivity is high (Roff and Legendre 1986) and seals have access to the entire Bay. Lunn *et al.* (1997) found higher seal densities in Hudson Bay than have been found in other areas of the Arctic. Furthermore, in other parts of the Canadian Arctic, winter can be less productive for hunting because of lower prey availability and higher proportions of multi-year ice, and bears occasionally go into shelter dens on the ice to wait out inclement weather (Ferguson *et al.* 2000b). I found no evidence of long-term denning by bears on Hudson Bay sea ice, and bears were active throughout the winter.

Movement rates and distances traveled have only been measured in a few other polar bear populations (Born *et al.* 1997; Amstrup *et al.* 2000, Messier *et al.* 2001), but movement rates of WH bears were comparable, and bears reached maximum short-term speeds of about 10 km/hr which is similar to rates reported by Amstrup *et al.* (2000). However, reproductive status did not affect movement rate in Hudson Bay whereas in the southern Beaufort Sea, solitary females had higher movement rates than females with yearlings (Amstrup *et al.* 2000). The reason for this difference is unknown, but could pertain to more predictable hunting opportunities in Hudson Bay compared to the high Arctic.

Temporal trends in bear movement

Annual home range size of WH bears declined by 81 255 km^2 and total annual distance traveled declined by 1304 km from 1991 to 1998. The total distance moved and the annual home range size are obviously linked. However, lack of change in total distances covered during freeze-up and break-up suggest that home range size is more dependent on distance covered during winter than in the other two ice seasons. Support for this was evident in the decline in total distance traveled during winter for females with offspring by 42% from 1991 to 1999, and the possible declines in winter movement rates.

Home range size and total distance covered were both positively correlated with average annual ice area and minimum annual ice area in Hudson Bay, and both of these have also declined over time (Stirling *et al.* 1999). Stirling *et al.* (1999) showed that polar bears are returning to land with less fat than they have had in the past, which means they have lower energy reserves to get them through the ice-free season. A decrease in fat reserves means that bears are not maintaining an overall positive energy balance and that energy input is lower than energy output. I found that bears are moving less, suggesting that output has not increased; therefore, the proximate cause of declining bear condition must be a lower energy intake. This means that bears are eating less over the on-ice hunting period than they have in the past, and accumulating less fat as a result.

Fat storage is critical to polar bear survival, especially in the Hudson Bay region, where there are no hunting opportunities during the summer and pregnant females may not eat for up to eight months (Stirling and McEwan 1975, Derocher *et al.* 1993). During the ice-free season, bears lose between 0.70 and 0.85 kg/day (Watts *et al.* 1987), and loss of body fat accounts for 93% of the change in mass (Atkinson and Ramsay 1995). In black bears (*Ursus americanus*) insufficient fat stores during periods of dormancy lead to muscle metabolization, which forces the bear to urinate, and dehydration threatens survival (Maxwell *et al.* 1988). When polar bears metabolize fat, urea is recycled, creating both protein and water metabolically (Nelson *et al.* 1983), meaning that the amount of stored fat on a polar bear will largely determine its fitness. In addition, Atkinson and Ramsay (1995) showed that a direct positive relationship exists between a female polar bear's fat stores and the survival of her cubs; therefore, the decrease in fat accumulation by WH bears has consequences to population level fitness and may be contributing to observed declines in bear abundance in the area (Regehr *et al.* in preparation).

The reasons for lower energy intake are unclear, but may be related to recent declines in ringed seal survival and recruitment in Hudson Bay (Ferguson *et al.* 2005, Stirling 2005). These declines have been attributed to changes in Arctic climate, including increased temperatures and precipitation. Ringed seals require high concentrations of annual ice and enough snowfall to maintain stable birthing lairs on the pack ice and pups in lairs with thinner snow roofs are more vulnerable to predation (Furgal *et al.* 1996). There is also evidence that fish community composition has changed, with a decrease in a primary prey species for seals, the arctic cod (*Boreogadus saida*) (Gaston *et al.* 2003). Another factor that may affect polar bear prey intake is a decrease in the predictability of finding seals. When ice concentration is high, most breathing holes are actively maintained by seals, so a polar bear waiting at a hole has a high chance of actually catching a seal (Stirling and McEwan 1975), whereas when ice is more fragmented, there are more naturally occurring holes at which seals can emerge, and still-hunting by polar bears will be less productive (Derocher *et al.* 2004). Finally, an important factor contributing to lower polar bear energy intake is shorter ice season duration. In Hudson Bay, freeze-up is occurring later and break-up is occurring progressively earlier than it has in the past (Stirling *et al.* 1999, Gagnon and Gough in press). This means that bears in Hudson Bay have less time to hunt on the ice and accumulate fat, and a longer ice-free period during which they must rely on their fat stores.

Conclusions and future work

Since 1991, annual home range size and total distance traveled have decreased for all bears, and the proximate cause for this is likely decreased energy intake during the on-ice hunting period. The ultimate cause may be related to changes in ice cover, ice extent, and the duration of the ice season in Hudson Bay, all of which have affected seal recruitment and distribution in the Bay. Future research should include building energetics models for polar bears that incorporate both long term metabolic needs and short-term foraging strategies to identify the determinants of body mass and energy intake (e.g. Moen *et al.* 1997). To do this, we need a better understanding of polar bear movement and searching strategies (see Chapter 3) and a better understanding of seal abundance and distribution in Hudson Bay. Current data on seal population dynamics are building (Lunn *et al.* 1997, Ferguson *et al.* 2005), and the more detailed information available from GPS collars will also provide valuable insights into what drives bear movement on Hudson Bay. Some recent research has suggested that there may be "breeding areas" on the ice to which particular individuals are faithful (Obbard 2005). If this is the case, it will be important to collar related individuals (i.e. cubs of females that have been collared) to see if they show fidelity to certain breeding areas on the ice. This information will be critical to understanding the responses of polar bears to changing ice conditions in the future.

Table 2.1. Annual home range size (km^2) for female polar bears from the western Hudson Bay population collared between 1991 and 1998.

Reproductive class	$\bar{x}$ **± SE**	**n**	**min**	**max**
Females with COYs	109 491 ± 21 255	14	8470	311 646
Solitary females	93 428 ± 14 932	11	24 034	158 236
Females with yearlings	132 800 ± 31 102	4	86 876	221 819
Total	*106 613 ± 12 314*	*29*	*8470*	*311 646*

Table 2.2. Seasonal minimum convex polygon home range sizes (km^2) of female polar bears from the WH population between 1991 and 2004.

Reproductive class	**Freeze-up**		**Winter**		**Break-up**		**Summer**	
	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n
Females with COYs	43 552 ± 5033	18	29 323 ± 5003	27	41 039 ± 12 452	19	733 ± 183	22
Solitary females	26 220	1	44 875 ± 7931	12	15 803 ± 5824	4	462 ± 301	7
Females with yearlings	13 824 ± 4168	11	52 808 ± 6482	19	18 565 ± 3781	7	553 ± 148	10
Total	*28 203 ± 3286*	*23*	*40 234* ± 3759	*58*	*32 430 ± 8157*	*30*	*638* ± 121	*39*

Table 2.3. Seasonal net displacement (km) of female polar bears from western Hudson Bay between 1991 and 2004.

Reproductive class	**Freeze-up**		**Winter**		**Break-up**		**Summer**	
	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n
Females with COYs	355 ± 22	19	354 ± 24	27	293 ± 42	20	44 ± 7	29
Solitary females	N/A	N/A	195 ± 23	14	146 ± 23	6	12 ± 3	7
Females with yearlings	308 ± 31	13	195 ± 24	18	220 ± 37	10	51 ± 11	20
Total	*336 ± 19*	*32*	*268 ± 17*	*59*	*248 ± 27*	*36*	*42 ± 6*	*43*

Table 2.4. Mean seasonal direction (in degrees true) and r (vector of mean direction) for female polar bears from western Hudson Bay.

Reproductive Class	**Freeze-up**			**Winter**			**Break-up**			**Summer**		
	θ	n	r	θ	n	r	θ	n	r	θ	n	r
Females with COYs	55	21	0.32	52	31	0.40	239	22	0.17	66	30	0.11
Solitary females	87	4	0.19	199	23	0.08	230	15	0.38	97	16	0.15
Females with yearlings	45	17	0.39	233	20	0.05	266	12	0.13	86	26	0.33
Total	*52*	*42*	*0.33*	*58*	*74*	*0.14*	*238*	*49*	*0.22*	*83*	*72*	*0.19*

Table 2.5. Hourly movement rates (km/hr) of female polar bears from western Hudson Bay for short-term (< 8 hrs between consecutive locations), mid term (> 8 hrs and < 100 hrs between consecutive locations), and long term (>100 hrs and < 200 hrs between consecutive locations) movements.

Reproductive class	**Freeze-up**		**Winter**		**Break-up**		**Summer**	
Short-term rates	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n
Females with COYs	1.8 ± 0.3	9	3.0 ± 1.4	4	1.6 ± 0.2	4	0.4 ± 0.2	10
Solitary females	N/A	0	2.5 ± 0.6	4	1.4	1	0.6	1
Females with yearlings	1.7 ± 0.3	2	1.7 ± 0.4	11	1.0 ± 0.3	5	1.9	2
Total	*1.8 ± 0.3*	*11*	*2.1 ± 0.4*	*19*	*1.3 ± 0.2*	*10*	*0.7 ± 0.3*	*13*
Mid term rates								
Females with COYs	1.1 ± 0.2	9	0.5 ± 0.1	10	0.5 ± 0.1	6	0.1 ± 0.1	9
Solitary females	0.3	1	0.9 ± 0.2	4	0.6 ± 0.1	4	0.1 ± 0.02	7
Females with yearlings	1.1 ± 0.2	4	0.9 ± 0.1	8	0.7 ± 0.2	6	0.2 ± 0.1	2
Total	*1.0 ± 0.1*	*14*	*0.7 ± 0.1*	*22*	*0.6 ± 0.1*	*16*	*0.1 ± 0.03*	*18*
Long term rates								
Females with COYs	0.5 ± 0.1	4	0.3 ± 0.1	9	0.4 ± 0.1	5	0.1 ± 0.02	5
Solitary females	0.7 ± 0.4	3	0.6 ± 0.1	5	0.4 ± 0.1	3	0.1 ± 0.03	5
Females with yearlings	0.4 ± 0.1	3	0.5 ± 0.02	4	0.4 ± 0.04	4	0.1 ± 0.03	5
Total	*0.5 ± 0.1*	*10*	*0.4 ± 0.1*	*18*	*0.4* ± 0.04	*12*	*0.1* ± 0.02	*15*

Table 2.6. Total distance moved annually (km) by female polar bears from western Hudson Bay between 1991 and 1999.

Reproductive class	$\bar{x}$ ± SE	n	min	max
Females with cubs	2516 ± 589	6	1060	4935
Solitary females	1843 ± 210	17	547	3714
Females with yearlings	2198 ± 269	12	674	3543
Total	*2080* ± 170	*35*	*547*	*4935*

Table 2.7. Total distance moved per season (km) by female polar bears from western Hudson Bay between 1991 and 2004.

Reproductive class	**Freeze-up**		**Winter**		**Break-up**		**Summer**	
	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n
Females with COYs	686 ± 35	19	568 ± 47	27	739 ± 91	19	84 ± 13	26
Solitary females	792	1	898 ± 99	17	420 ± 77	8	70 ± 21	8
Females with yearlings	702 ± 48	10	1090 ± 99	19	500 ± 137	12	87 ± 16	14
Total	*695* ± *27*	*30*	*814* ± 52	*63*	*600* ± 53	*39*	*82* ± 9	*48*

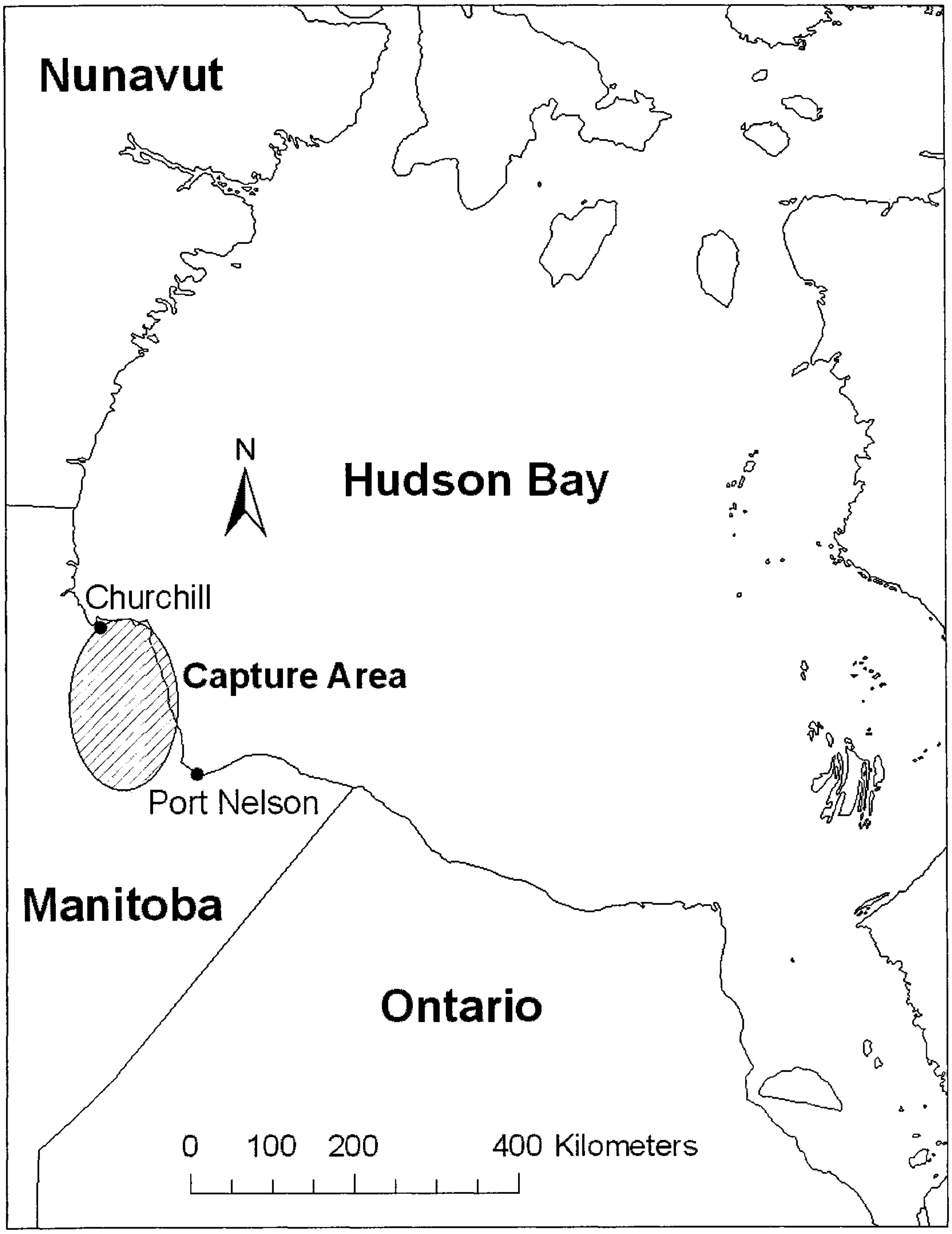

Figure 2.1. Map of the Hudson Bay region showing the area where polar bears from the western Hudson Bay population are captured by helicopter.

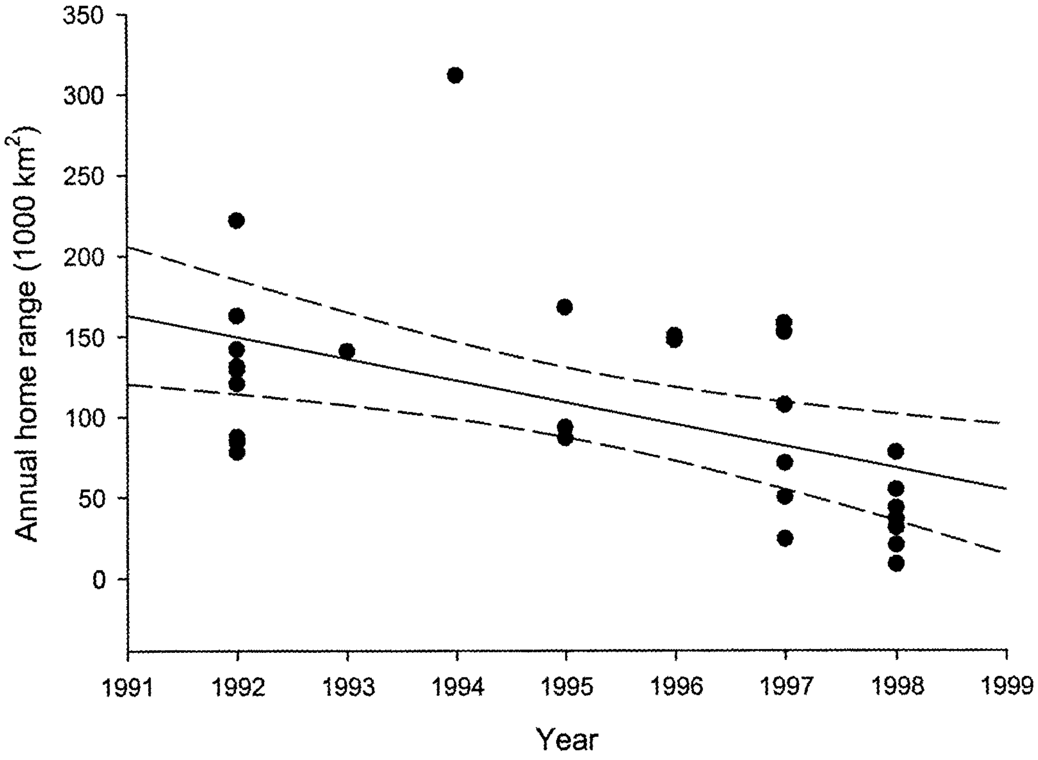

Figure 2.2. Annual home range size (km^2) of female polar bears from western Hudson Bay in 1992 to 1998. Regression line (solid) is shown with 95% confidence interval (dashed lines).

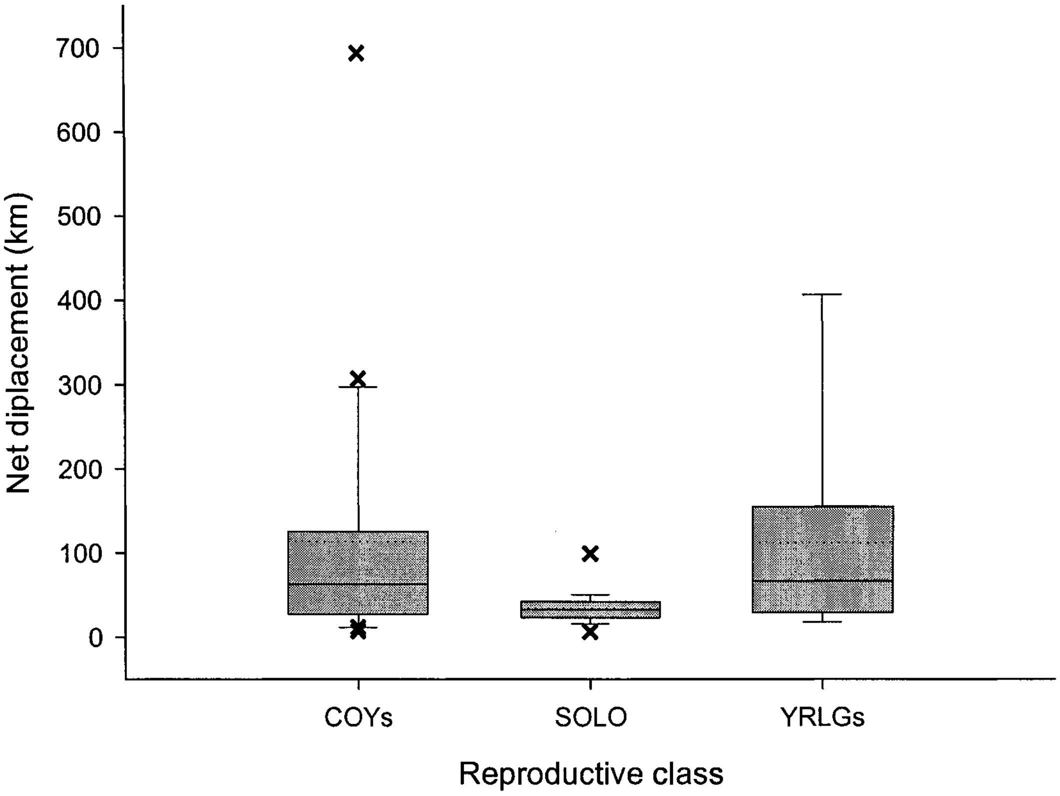

Figure 2.3. Annual net displacement (km) by female polar bears from the western Hudson Bay population. Outliers are indicated with an "x", solid lines show the medians, and dotted lines show the means.

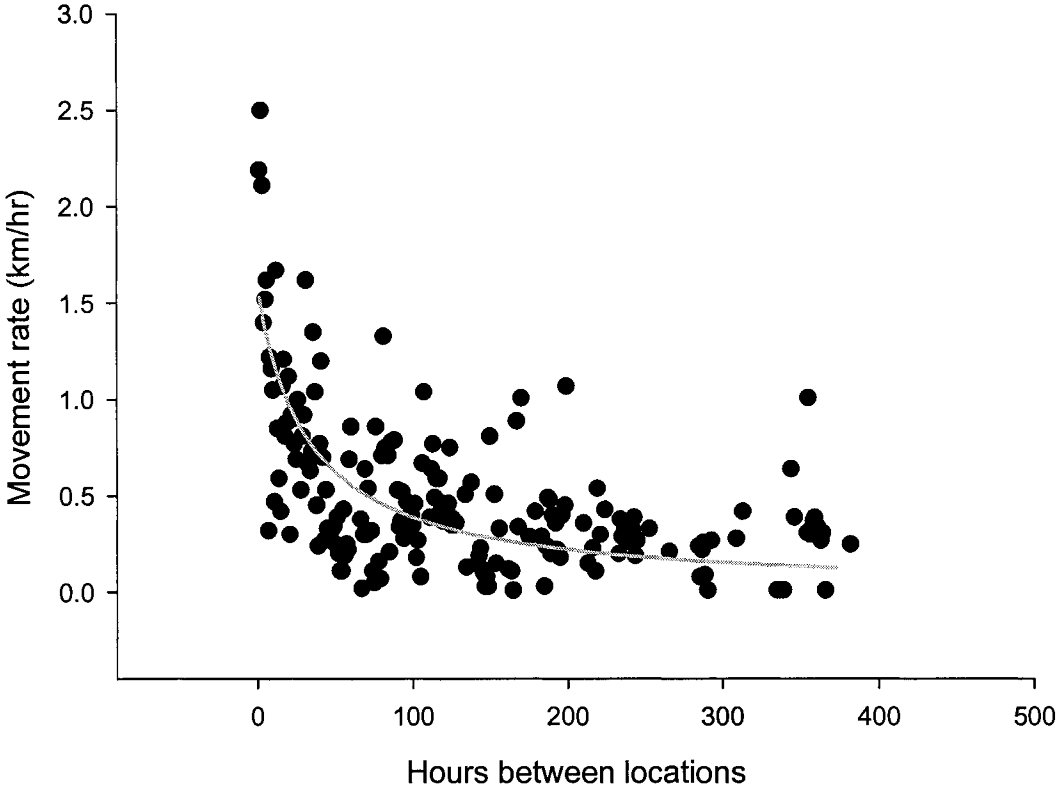

Figure 2.4. Relationship between the mean movement rates of western Hudson Bay polar bears and the time interval between locations. The solid line represents the best fit curve.

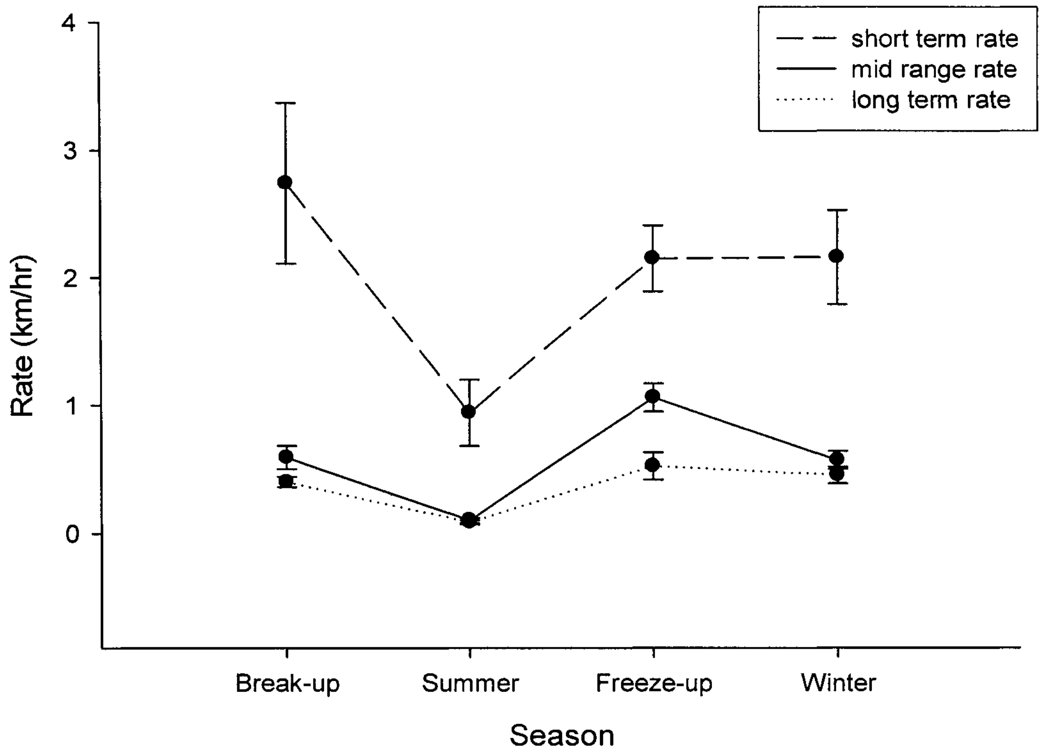

Figure 2.5. Seasonal movement rates (± SE) of female polar bears from western Hudson Bay in 1991-2005. Short-term rates were calculated from locations < 8 hours apart; mid range rates were calculated from locations > 8 hours and < 100 hours apart; long term rates were calculated from locations > 100 hours and < 200 hours apart.

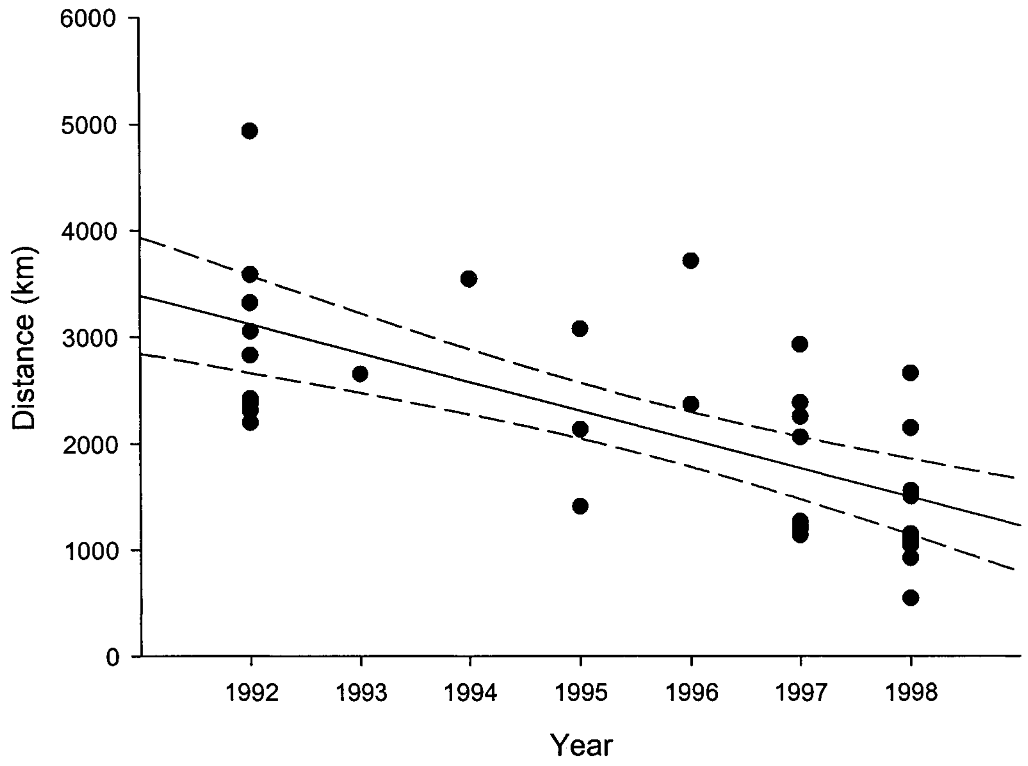

Figure 2.6. Total distance traveled annually by female polar bears from western Hudson Bay in 1992-1998. Regression is shown (solid line) with 95% confidence interval (dashed lines).

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CHAPTER THREE – SCALE-DEPENDENT SEARCH STRATEGIES OF FEMALE POLAR BEARS ON THE SEA ICE OF HUDSON BAY

Introduction

Most animals must move to find resources such as food, mates, or refuge from predators; therefore, animal movement patterns and searching efficiency will affect the fitness of both individuals and the population (Pyke *et al.* 1977, Kareiva and Shigesada 1983, Zollner and Lima 1999). However, movement strategies that maximize the probability of finding resources will vary depending on the size and distribution of both the searcher and the resource (Cain *et al.* 1985, Fauchald *et al.* 2000, Viswanathan *et al.* 2002), as well as on landscape structure (Zollner and Lima 1999, Goodwin and Fahrig 2002). For predators, foraging success is particularly dependent on search pattern in hierarchical systems, where small, high density patches of prey are nested within larger patches (Arditi and Dacorogna 1988, Fauchald 1999, Mauritzen *et al.* 2001).

Polar bears (*Ursus maritimus*) are non-territorial predators that travel over thousands of kilometers on sea ice searching for their primary prey, ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) (Stirling 1974, Smith 1980). Ringed seals are not normally gregarious and usually congregate in groups of only 2 or 3 animals (Frost and Lowry 1981). In late spring when seals are moulting, higher concentrations and larger group sizes may occur (Stirling *et al.* 1982, Frost *et al.* 2004). Bearded seals are also solitary, but form loose aggregations around cracks or leads in large ice floes (Burns 1981). Moulting and pupping, which occur between May and June in Hudson Bay (Lunn *et al.* 1997), bring high numbers of both ringed and bearded seals onto the ice. At this time, fat, naïve, recently weaned pups become abundant, so this may be the most important hunting period for polar bears (Messier *et al.* 1992, Kingsley and Stirling 1991, Stirling and Øritsland 1995). In some parts of their range, such as Hudson Bay, sea ice melts completely in summer, forcing bears to spend months on shore where they fast until ice forms again (Stirling *et al.* 1977, Stirling and Derocher 1993). Unlike terrestrial ursids, polar bears are essentially marine predators that do not typically hunt or even eat on land (Stirling and McEwan 1975, Ramsay and Hobson 1991, Derocher *et al.* 1993).

Recently, declines in polar bear condition and abundance have been reported for the western Hudson Bay (WH) population (Stirling *et al.* 1999, Regehr *et al.* in preparation), and the reasons are likely related to climate warming and aggravated by harvest impacts (Stirling and Derocher 1993, Stirling *et al.* 1999, Derocher *et al.* 2004). Earlier ice break-up may also be a cause of declines in ringed seal recruitment, and changes in ice conditions have led to lower ringed seal populations in recent years (Ferguson *et al.* 2005, Stirling 2005). Polar bear populations are closely tied to ringed seal numbers and behaviour (Stirling and

Øritsland 1995); however, little is known about seal spatiotemporal distributions in Hudson Bay (Lunn *et al.* 1997) or polar bear movement strategies when they are on the ice (Messier *et al.* 1992).

Advances in satellite and global positioning system (GPS) technology allow researchers to describe the movement paths of wide-ranging predators over great distances (Jouventin and Weimerskirch 1990, Bertrand *et al.* 2005), and the structure of the path can reveal the search strategies used by the predator (Pyke *et al.* 1977, Viswanathan *et al.* 2002). For instance, many marine predators show movement patterns that reflect searches for prey in a hierarchical patch system (Kotliar and Wiens 1990, Fauchald 1999), and these search patterns can be identified by the distribution of move lengths between turns in an animal's path (Fritz *et al.* 2003, Austin *et al.* 2004, Bertrand *et al.* 2005). In addition, detecting the spatial and temporal scales at which predator behaviour changes can indicate the scales at which prey aggregate (Bertrand *et al.* 2005, Fauchald and Tveraa 2003), and the scales at which other environmental factors affect predator movement decisions (Fritz *et al.* 2003, Frair *et al.* in press).

The purpose of this study was to examine the movement patterns of a sample of female polar bears on the sea ice of Hudson Bay and to identify the spatial and temporal scales at which bear movement behaviour changed. I used movement data from bears fitted with GPS collars to address two questions: (1) do polar bear moves reflect a strategy of hierarchical patch searching and (2) if so, at what spatial and temporal scales do patches occur? A more detailed knowledge of polar bears' movement on the ice may provide insights into their energetic requirements and the reasons for the recent declines in polar bear condition and numbers.

Methods

Study area

The WH polar bear population inhabits coastal areas of Manitoba, Nunavut, and western Ontario during the summer in an area bounded by 63°10'N and 88°30'W (Stirling *et al.* 1977, Stirling *et al.* 1999). The capture area for this study was located south of Churchill, Manitoba, between 57°00' and 58°50'N latitude and 92°25' and 94°15'W longitude (Derocher and Stirling 1995). Hudson Bay is a large inland sea on the Canadian Shield with a mean depth of 125 m and an area of about 10^6 km^2 (Jones and Anderson 1994). Each year ice covers greater than 9/10 of the Bay by March or April, and by September the waters are ice free (Saucier *et al.* 2004). Polar bears in the region spend November to July hunting for seals on the ice, and are forced ashore when the ice melts. From August to October bears remain on land and live off their fat reserves (Stirling and McEwan 1975, Stirling *et al.* 1977). Currently, the WH polar bear population is estimated to be less than 1000 and declining (Regehr *et al.* in preparation).

Data collection

In September 2004, we fitted 11 female bears with Telonics (Mesa, Arizona) Gen III Global Positioning System (GPS) collars linked to the Argos satellite system (Service Argos, Inc. Lynnwood, Washington). Only female bears were collared because the necks of male bears are wider than their heads so collars cannot be secured. Bears were located and captured using standard helicopter methods as part of an ongoing monitoring program and were immobilized with tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Company) according to Stirling *et al.* (1989). Animal handling procedures were approved by the University of Alberta BioSciences Animal Policy and Welfare Committee. Animals were classified as belonging to one of the following groups: females with cubs-of-the-year (COYs), females with yearlings, solitary adult females (5+ years), subadult males or females (2-4 years) or adult males. We were interested in bear movement on the ice and wanted to avoid uninformative data from pregnant females in maternity dens, so we only collared adult females that were accompanied by offspring. Dependent young were either 8 month old COYs or 20 month old yearlings. Each collar was programmed to obtain six GPS fixes per day, every four hours, and to transmit them to a data processing centre daily.

Statistical analyses

For the purposes of some analyses, I divided the on-ice period into 3 biologically relevant seasons: freeze-up (first on-ice location until December 31, when ice cover in the Bay typically reaches 9/10 throughout), winter (January 1 – April 30), and break-up (May 1, when ice cover begins to decline from maximum, until bears came off the ice). All bear locations were originally plotted as latitude north and longitude west, but were converted to Universal Transverse Mercator (UTM) coordinates for North American Datum (NAD) 1983 zone 15 in ArcGIS 9.2 (Environmental Systems Research Institute (ESRI), Redlands, California, USA) so that locations were positive and in meters for all spatial analyses. I created individual bear movement paths using Hawth's Tools 3 (http://www.spatialecology.com/htools) in ArcGIS and found the distances and bearings between locations with Jenness extensions 2005 (http://www.jennessent.com/arcview/path.htm) in ArcView 3.1. I estimated the total distance moved by each bear in each season by summing the straight-line distances between locations. I calculated daily distances traveled by dividing the total distance by the number of days in the period of interest. I tested whether daily distances varied with season using either Kruskal-Wallis or Mann-Whitney U non-parametric tests (Sokal and Rolf 2001).

To characterize polar bear movement strategies, I examined the probability distribution of the move lengths that made up each bear path

(Viswanathan *et al.* 1996, 1999). The distribution of move lengths is a structural feature of an animal's path (Figure 3.1; Klafter *et al.* 1996, Bergman *et al.* 2000) that can suggest the behavioural strategy used by the animal to find resources (Mårell *et al.* 2002, Austin *et al.* 2004). For instance, many search paths in nature can be described by a random walk in which move lengths within the path follow a Gaussian distribution (Figure 3.1a; Kareiva and Shigesada 1983, Bartumeus *et al.* 2002). Simulation experiments have confirmed that this type of walk is particularly successful when the searcher is looking for resources that are larger than itself or that occur at high densities (Viswanathan *et al.* 2002). However, when search targets, whether they are prey, mates, or another resource, are sparse and patchy, a more efficient search strategy is characterized by a Lévy distribution of move lengths and is called a Lévy walk (Figure 3.1b; Viswanathan *et al.* 1999, Bartumeus *et al.* 2002). Lévy walks have many more long moves than would be expected in a random walk (Klafter *et al.* 1996), and these long moves take the animal far from the previous patch, reducing the chances of patches being revisited. Move lengths within a patch are short as the searcher focuses its exploration until the patch becomes unproductive and the searcher uses another very long move to find a new patch. Lévy walks have been identified in several wide-ranging predators such as wandering albatross (*Diomedea exulans*) (Viswanathan *et al.* 1996), reindeer (*Rangifer tarandus*) (Mårell *et al.* 2002), and grey seals (*Halichoerus grypus*) (Austin *et al.* 2004).

To describe the distribution of polar bear moves, I grouped the arbitrary "steps" obtained from GPS locations, which may not reflect actual choices made by the bear, into independent "moves" using Turchin's (1998) method. I aggregated n steps into one move if the n-1 intermediate locations were no more than x m away from the line connecting the beginning of the first step to the end of the last one (Figure 3.2). The value of x was gradually increased until the path turning angles were no longer significantly autocorrelated at $\alpha = 0.05$ (Jammalamadaka and Sarma 1988).

Once each path was made up of a series of moves, I examined the distribution of move lengths to test whether it conformed to a Lévy walk. The statistical distribution of move lengths in a Lévy walk is described by the inverse power-law distribution:

$$P(l_j) \sim l_j^{-\mu}$$

where l is move length and μ is a natural parameter between 1 and 3 (Viswanathan *et al.* 1999). As μ goes to 1, long moves get longer and short moves get shorter, and when $\mu \geq 3$, move lengths follow a Gaussian distribution. In a patchy environment, searching efficiency is highest when $\mu = 2$ (Viswanathan *et al.* 2002). The value of μ can be estimated from the slope (β_1) of a log-log plot of move frequency versus length (Viswanathan *et al.* 1999). Therefore, I created a histogram of move lengths for each bear, but because the shape of a histogram is sensitive to bin size, I followed Scott's (1979) rule for estimating bin width (h):

$$h = 3.5sn^{-1/3}$$

where s is the standard deviation of the sample and n is the sample size. This method minimizes over-smoothing of the data and is robust to non-normal distributions (Scott 1979). I then fitted a least-squares linear regression through a plot of log (frequency) on log (move length) and estimated the parameter μ from the absolute value of the slope, β_1.

I further characterized polar bear search strategies by identifying the spatial scales at which patches occur. The paths of animals searching for patchy prey are often characterized by a specific pattern within a patch and another between patches (Fauchald 1999, Fritz *et al.* 2003). For instance, animals usually have a high turning rate within patches and a lower turn rate between them (Fauchald *et al.* 2000). Therefore, patch size can be identified by comparing consecutive steps in a path across spatial scales (Nams 2005). At scales smaller than the patch size, consecutive steps are more likely to be positively correlated because the two steps will be either both inside or both outside of the patch. At scales approximately equal to patch size, one step will more often be inside while the next is outside a patch and consecutive steps would be negatively correlated. Finally, at scales greater than patch size, steps will likely cover both patch and non-patch areas, so we would expect no correlation between consecutive steps. Nams (2005) tested this theory by correlating consecutive cosines of turning angles in simulated paths and found that patch sizes were consistently and correctly identified, even when patch size was variable and search patterns did not follow a correlated random walk. Other methods of identifying patch size such as first-passage time (Fauchald 1999) or fractal analysis (Nams and Bourgeois 2004) are conservative, especially if patch size varies, and do not consistently identify patches if search patterns are heterogeneous (Nams 2005). Furthermore, it is not clear what patterns would be observed using these methods if animals are not, in fact, using patches (Nams 2005). On the other hand, using the cosine of turning angles method, a clear null prediction for no patch use would be zero correlation at all scales.

To identify patch sizes searched by polar bears, I tested the correlation of cosines over a range of scales using the Fractal program by Nams (v. 4.09; http://www.nsac.ns.ca/envsci/staff/vnams/Fractal.htm). Bear paths were divided into steps of equal length so that two consecutive steps formed a "V" at the crux of which the angle was measured. The cosine of this angle was compared to the cosine at the next V, and these pairs of cosines were correlated for the entire path. This procedure was repeated for increasing step sizes from 100 m up to 150 km and the path correlation coefficients (r) were plotted against step size. Positive correlations of cosines indicated spatial scales below the patch size, and negative correlations occurred at patch size (Nams 2005). I added 95% confidence intervals to the plot using the Fractal program's bootstrapping method to help decide if correlations were significantly above or below zero.

I was also interested in whether there was a typical length of time bears spent searching an area before moving away. To my knowledge, there are currently no systematic methods available for identifying temporal search scales (but see Fauchald *et al.* 2000 for a qualitative approach). Therefore, I developed a method for examining the changes in variance of tortuosity over a range of temporal scales. The idea for this is based on the first-passage time method of identifying spatial search scales in which variance of time spent in a given area peaks at scales equivalent to patch sizes (Fauchald and Tveraa 2003, Frair *et al.* in press). I started with a window of 12 hours and moved it along each bear path, calculating the tortuosity as the total distance traveled divided by the net distance within the time window. This allowed me to calculate the variance in tortuosity over the whole path. I increased the window by four hour increments (the minimum time between two bear locations), and found the variance in tortuosity at each time scale up to 720 hours (30 days), then plotted the variance against the size of the temporal window. Variance in tortuosity for an entire path should be highest at scales comparable to temporal patch sizes because most windows will either capture areas where tortuosity in bear movement is very high (within patches) or areas where tortuosity is low (between patches). At time scales larger than typical search times, most windows will encompass areas of both high and low tortuosity, so the variance over the entire path will be lower. When temporal windows are smaller than search times, they will not be large enough to capture the very high tortuosity that results from a path turning back on itself within a patch (i.e. a large total but small net displacement) and so variance for the entire path will be lower. Therefore, peaks in tortuosity variance should occur when the temporal window matches the typical time spent searching an area. This procedure was written and performed in R 2.0 for Linux (J. Brzustowski pers. comm.).

Results

Life span of the 11 collars deployed in September 2004 ranged from 68 to 309 days. Because ice only reformed in late November, four collars that ceased transmission within 84 days (before 4 December 2004) were excluded from analyses. The seven remaining collars transmitted regularly until at least April, so full freeze-up and winter paths were available for these bears; however, complete break-up paths were not available (see Table 3.1 for dates of last locations). There were commonly less than six locations per day and the final location of the day, taken at 21:00, was the most frequently missed location. This might be related to the sleep patterns of bears since they sleep most often between 18:00 and 24:00 (Stirling *et al.* 1974) and collar antennae might be obstructed by bear position. The mean number of fixes per day was 4.3 ± 0.04, and fixes were obtained, on average, every 7.2 ± 0.3 hours. Total number of locations per bear path ranged from 337 to 860.

Distances traveled

Bears moved as far as 850 km from the denning area south of Churchill over the course of the on-ice seasons. Bear 47509 reached the Belcher Islands by February and stayed in that area until June. By May 1, all bears except 47509 were north or northeast of the denning area and within 300 km of it. Total distances traveled from freeze-up until collars ceased transmission during break-up were between 3000 and 5000 km, with mean daily distances traveled ranging from 11 to 43 km (Table 3.1). Bears moved significantly farther per day during freeze-up than winter (Mann-Whitney $U = 49$, $n_1 = 7$, $n_2 = 7$, $P = 0.001$).

Lévy walk analysis

Three bears' paths were not significantly autocorrelated; however the paths of bears 47509, 49184, 49187, and 49188 were, and steps were grouped into moves accordingly (Table 3.2). The values of x needed to remove significant autocorrelation were between 0.001 and 2.27 km, which are not large in relation to polar bear movement rates (typically 1-3 km/hr; chapter 2). All bear paths were composed of moves that followed Lévy distributions (Table 3.2). Values of μ ranged from 1.3 to 1.93, but for six of the seven bears, values of μ for winter paths were closer to 2.0 than μ for freeze-up paths. The bear path with μ closest to 2 was the overall path of bear 49188 ($\mu = 1.93$; Figure 3.3).

Spatial and temporal search scales

All bears showed patch use at two or more spatial scales (Table 3.3). Changes in movement behaviour at scales smaller than 3 or 4 km were not clearly identifiable because two consecutive locations were typically more than 3 km apart for all bears except 47509. Because of the small number of moves per path when large step sizes were used, confidence intervals became too wide at large scales to allow interpretation of changes in cosine correlation. However, at an intermediate range of scales (1 – 100 km), significant changes in correlation could be identified (Figure 3.4). Five of the seven bears showed patch use at around 10-15 km, and six showed patch use in the range of 40 – 60 km. One bear (49184) also searched at a scale of about 80 km, and bear 47509 showed strong patch use at a smaller scale than other bears (1.5 – 2 km). When compared visually to the movement paths of each bear, these scales of patch use are reflected in the sizes of areas where path tortuosity increases (Figure 3.5).

All bear paths showed increased variance in tortuosity at specific temporal scales (Figure 3.6), which may indicate typical times spent searching patches (Table 3.3). Six of the seven paths had high variance in tortuosity at a scale of 3 – 6 days, and six also had peaks at a scale of 19 – 25 days (Figure 3.7).

Discussion

New technology has increased our understanding of movements in wide-ranging animals (Fritz *et al.* 2003, Nams 2005) and quantitative models are now needed to help interpret movement paths obtained from GPS collar data (Bergman *et al.* 2000, Johnson *et al.* 2002, Frair *et al.* in press). The advantages of GPS collar data over satellite or radio telemetry data include more frequent locations and higher spatial accuracy, which provide researchers with a more complete picture of an animal path (e.g. Ryan *et al.* 2004, Pepin *et al.* 2004). The GPS collars used in this study captured two to three times more of the distance covered by bears than satellite collars have done in the past (Chapter 2). I found that bears can move at least 5000 km during the on-ice season, and this distance still underestimates the real distance traveled (Pepin *et al.* 2004). Although polar bears generally employ a "sit-and-wait" strategy to capture seals, and rarely stalk prey (Stirling 1974, Stirling and McEwan 1975, Smith 1980), it is clear that they must travel extensively to find areas where seals are available.

The metabolic cost of walking is higher in polar bears than other quadrupeds (Hurst *et al.* 1982) and bears may go for weeks between seal kills while on the ice, especially during winter when seals are less available (Stirling and Øritsland 1995). If an animal cannot maintain a positive energy balance, then its survival will be threatened (Moen *et al.* 1997, da Luz *et al.* 2001). Therefore, as optimal foraging theory suggests

(Pyke *et al.* 1977), we would expect bears to have evolved efficient movement patterns that maximize seal intake while minimizing walking time.

The lengths of moves within each polar bear path followed a Lévy distribution, and Lévy walk strategies are most successful when resources are sparse and patchily distributed (Viswanathan *et al.* 1996, Mårell *et al.* 2002, Viswanathan *et al.* 2002, Bertrand *et al.* 2005). Mårell *et al.* (2002) found that the moves of all reindeer paths studied followed Lévy distributions, whereas another common model of animal movement, correlated random walks, consistently underpredicted net displacements. Conversely, Austin *et al.* (2004) found that a correlated random walk model fit 50% of the seals studied, while only 15% had paths that fit a Lévy distribution. However, seal locations were taken every second day, and reindeer locations were determined every 30 seconds and with less spatial error (Marell *et al.* 2002). Furthermore, when Austin *et al.* (2004) increased the frequency of locations in an animals path, more animals' paths fit the Lévy walk model. This suggests that a lower resolution of data may miss important path features (Bergman *et al.* 2000), and highlights the benefits of increased location frequency and accuracy available with GPS (e.g. Pepin *et al.* 2004, Bertrand *et al.* 2005).

Because of the high cost of movement for polar bears (Hurst *et al.* 1982), they should move as directly as possible until they detect the presence of prey. Lévy walks are characterized by many more long moves than would be expected from a Gaussian distribution (Klafter *et al.* 1996, Viswanathan *et al.* 2002). These long moves take animals between patches quickly, but the shorter moves allow for efficient searching at smaller spatial scales (Fauchald *et al.* 2000, da Luz *et al.* 2001). This kind of strategy seems advantageous when searching for prey in sea ice habitat where the landscape and patches of prey are constantly changing, either because seals become more vigilant and less vulnerable, or they move away, shifting the location of the patch (Burns 1981, Kingsley and Stirling 1991). Within this kind of dynamic patchy habitat, polar bears will likely respond to environmental cues at different spatiotemporal scales (Kotliar and Wiens 1990, Mauritzen *et al.* 2001), so it is important to recognize the scales at which bear movement behaviour changes.

Several studies have identified multiple scales of patchiness within animal movement paths (Fauchald *et al.* 2000, Fritz *et al.* 2003, Nams and Bourgeois 2004, Frair *et al.* in press) and the spatial scales at which predator movement changes are linked to spatial characteristics of both habitat and prey (Fritz et al. 2003, Bertrand *et al.* 2005). For instance, Fritz *et al.* (2003) identified three scales at which tortuosity changed in the paths of wandering albatrosses and related these to elements of the albatross' environment. The largest scale indicated movement within large areas of suitable prey habitat, the intermediate scale revealed active foraging within patches of prey, and changes at the smallest scale reflected the influence of wind on the birds' paths. All polar bears also showed at least two, and most showed three spatial scales at which tortuosity changed, and these changes like reflect bear responses to variation in seal distribution and ice conditions. Both ringed and bearded seals are found in higher densities on large floes in active annual pack ice with 60-80% concentration during break-up (Kingsley and Stirling 1991, Lunn *et al.* 1997) but local abundances throughout the ice season are influenced by the amount of open water present, and weather and snow conditions of specific areas (Burns 1981, Moulton *et al.* 2002). Most bears searched at scales of 10-15 and 45-60 km. It may be that at the larger scale, bears use long moves to cover broad swaths across areas of possible seal habitat until they detect an area where seal density is higher. At a scale of 10-15 km, bears appeared to focus their searching, covering the area more thoroughly with shorter moves and higher turning angles, which might indicate the scale at which the energetic benefits of concentrated searching outweigh the benefits of traveling long distances. I did not detect any changes in movement patterns once ice began to break up, when the primary prey shifts from adult seals to pups (Stirling 1974, Stirling and Øritsland 1995). Bears may not change their general searching strategies during this time, but may adjust the systematic searching to focus on birth lairs.

The much smaller patch sizes found in four of the seven bears could reflect either the influence of landscape elements like leads or polynyas on movement paths, or avoidance of other bears (Stirling 1974, Stirling *et al.* 1993). Because individual polar bears may adopt specific movement strategies when hunting that differ from those of other bears in the same region (Mauritzen *et al.* 2001), it is likely that some factors affect particular bears' movement patterns more than others. Small scale searching might also indicate areas where seals are more dense, which might explain the small sizes of all three search scales identified for bear 47509 (Table 3.3). Of the winter paths, bear 47509 had the lowest value of μ (1.32), which reflects more tightly clumped movement and shorter moves (Bertrand *et al.* 2005; Figure 3.8). There is evidence that the waters around the Belcher Islands are highly productive (Roff and Legendre 1986) and polynyas that support a diversity of marine organisms are frequently present in the area (Gilchrist and Robertson 2000). Bear 47509 may have found a particularly productive patch of prey and remained in the area. However, to test this hypothesis, a more extensive knowledge of productivity in Hudson Bay is required and movement paths for the same bear in multiple years are needed to determine the degree to which paths are dependent on the individual regardless of external cues.

Predator behaviour might reflect the temporal scales of prey distribution as well as the spatial scales (Fauchald *et al.* 2000). For example, at intermediate and small spatial scales, the distribution of capelin (*Mallotus villosus*) changes with time, and the duration of observed aggregations of murres (*Uria* spp.) reflects the time scales of capelin patch occurrence (Fauchald *et al.* 2000). The temporal relationship between predator movement and prey distribution has been given little attention in the literature, so no standard method of identifying the time scales of searches exists. However, I found peaks in the variance of tortuosity at specific time scales for all bears, suggesting that this could be an objective method for detecting temporal search scales. Six of the seven bears appeared to search at a scale of 3-5 days and six bears also searched at a scale of 20-25 days. The smaller time scale might reflect the typical duration of local seal abundance, where several small groups of seals were hauled out on a large floe, but became aware of a polar bear's presence and became more vigilant or spent more time in the water. The larger temporal scale could indicate the rate of habitat change on the ice. If a polar bear finds ice conditions suitable for seals, it may search within that area until the ice shifts enough that suitability for seals decreases. However, little is known about the ice dynamics of Hudson Bay (Saucier *et al.* 2004) and this hypothesis needs to be tested using satellite ice images and ice drift data.

Conclusions and future work

The movement paths of polar bears in Hudson Bay suggest that seals are distributed in a hierarchical patch system of high density areas nested within larger areas of lower density. Bears exhibit changes of tortuosity at scales of about 45-55 km, 10-15 km, and possibly 2-5 km, which may reflect, respectively, searching between areas of suitable seal habitat, concentrated hunting within patches of higher prey density, and adjustments made in response to landscape features. It appears that bears spend about 3 days in concentrated searches, which suggests that seals may dissipate or alter their behaviour after that time, and 3 weeks searching larger areas, which may reflect the temporal scale at which substantial habitat changes occur.

Changes in sea ice conditions (Parkinson *et al.* 1999), earlier break-up and later freeze-up (Gagnon and Gough, in press), and declines in seal recruitment and survival (Ferguson *et al.* 2005, Stirling 2005) will undoubtedly affect polar bear movement strategies and their hunting success. An important next step will be to relate polar bear movement strategies to habitat variables such as the presence of leads and polynyas using satellite images and advances in ice classification (Riggs *et al.* 1999). More information about the distribution and abundance of ringed and bearded seals in Hudson Bay is also crucial if we are to better understand the relationships between polar bears, seals, and sea ice.

Table 3.1. Total and daily distances traveled (km) by female polar bears from western Hudson Bay in 2004-2005 wearing GPS-satellite linked collars that transmitted a mean of 4.3 ± 0.04 locations per day.

Bear	**Freeze-up path**		**Winter path**		**Full path**		**Date stopped**
	Total	Daily	Total	Daily	Total	Daily	
47509	2021	35.5	1340	11.3	3654	16.8	10 June
47514	1276	32.7	2600	21.8	4294	24.5	15 May
47515	1395	30.3	2822	23.7	5045	25.7	30 May
49184	1406	42.6	2794	23.7	4200	27.6	29 April
49187	1186	34.9	1587	17.3	2773	21.8	3 April
49188	1167	29.9	2160	18.1	4409	19.7	1 July
49189	1002	26.4	1925	16.2	3044	18.0	11 May
Mean ± SE	*1350±123*	*33.2±1.9*	*2175±223*	*18.8±1.7*	*3917±304*	*22.0±1.5*	*10 May ± 11 days*

Table 3.2. Results of Lévy distribution analysis of the paths of female polar bears from western Hudson Bay in 2004-2005. Significant autocorrelation was found in the paths of four bears, and steps between GPS locations were grouped into moves so that paths were no longer autocorrelated. Parameter μ was estimated from the slope of a log-log plot of move frequency vs. length. Lévy walks are characterized by $1 < \mu < 3$ and contain many more long movements than random walks.

Bear ID	**Number of steps**	**Reduced moves**	**Freeze-up μ**	**Winter μ**	**Total path μ**
47509	857	361	1.63	1.32	1.63
47514	623	--	1.45	1.69	1.71
47515	643	--	1.55	1.74	1.81
49184	370	156	1.65	1.75	1.35
49187	384	382	1.63	1.79	1.76
49188	710	698	1.52	1.77	1.93
49189	337	--	1.35	1.60	1.62

Table 3.3. Spatial and temporal scales of patch use by female polar bears from western Hudson Bay in 2004-2005. Spatial scales were determined by positive correlation of cosines of consecutive turning angles followed by negative correlation on a plot of correlation coefficient with increasing step size. Temporal scales were determined by peaks in tortuosity variance (tortuosity = total distance/net displacement) with increasing temporal step size.

Bear PTT ID	Age of accompanying cub in September	Number of locations	Spatial scale (km)	Temporal scale (days)
47509	COY	860	1.8 – 2 9 – 10 20 – 26	3.5 – 4 11 19 – 22
47514	Yearling	623	4 – 5 14 – 16 42 – 48*	2 – 3 8 – 9 22 – 23
47515	COY	643	14 – 16* 40 – 50	3 – 4 18 – 21
49184	COY	373	8 – 9 49 – 51 76 – 82	13 – 15 20 – 23
49187	COY	385	28 – 30 56 – 62	4 25 – 26
49188	COY	709	11 – 12 50 – 60	5.5 – 6 10 – 12 21 – 22
49189	COY	337	5 – 6 28 – 30 45 – 55	6 14 – 16

* Spatial scales where confidence intervals included zero but correlation coefficient did increase above zero then fall below.

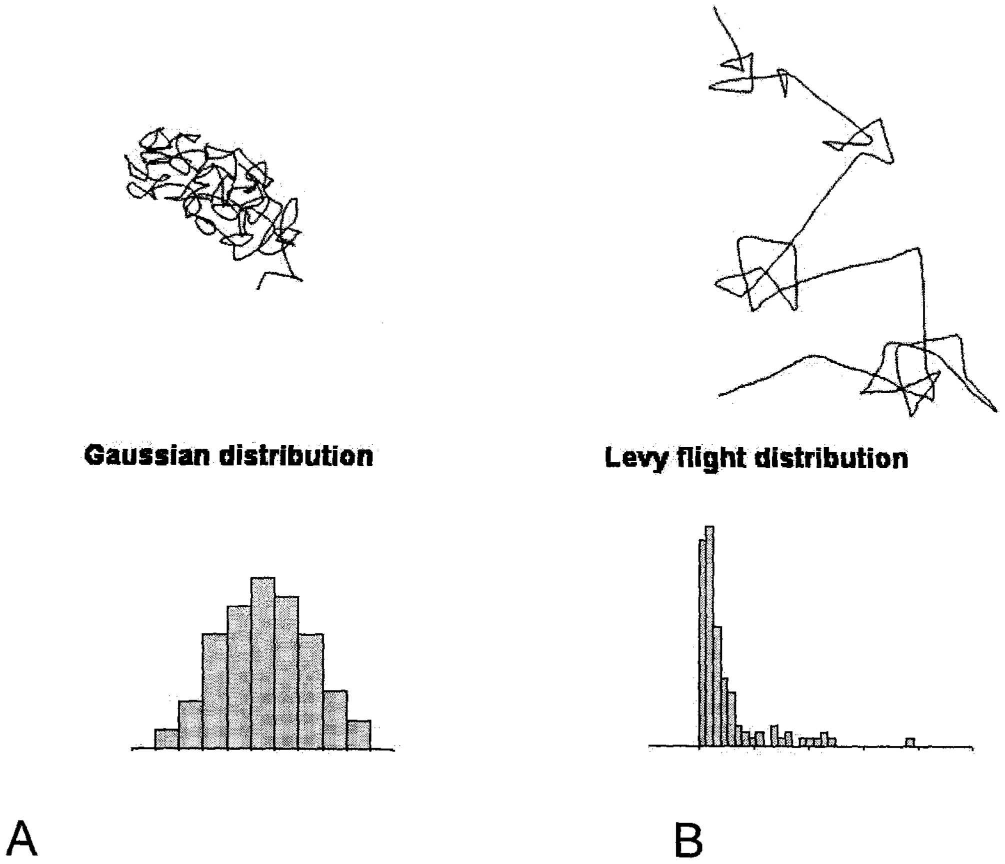

Figure 3.1. Illustration of two distributions of move lengths and their resulting paths. A Gaussian distribution (A) results in Brownian motion and is an efficient search strategy if targets are distributed randomly and frequently. A Lévy distribution (B) results in a Lévy walk, characterized by very long moves between patches, which is a more efficient search strategy when targets are found in sparsely distributed, high-density patches.

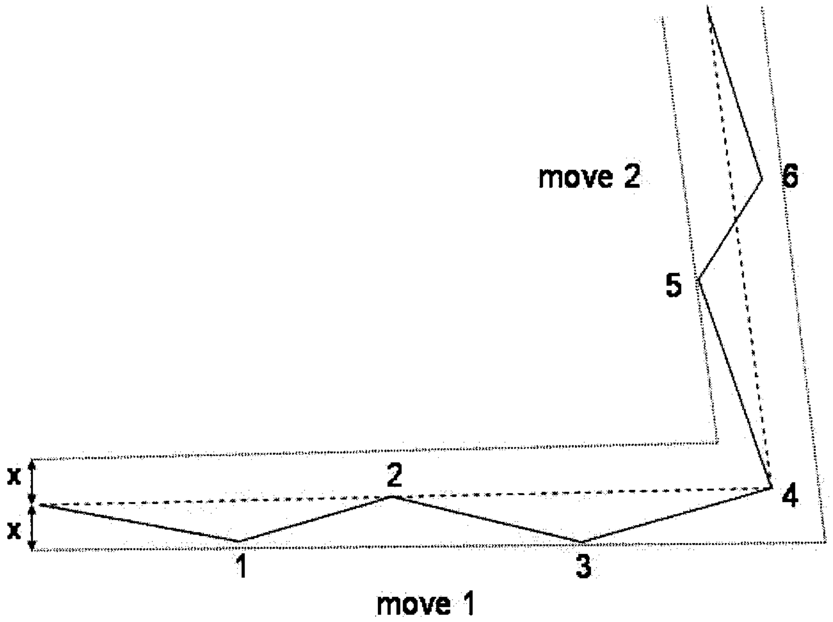

Figure 3.2. Method for grouping steps into discrete moves of unequal duration (Turchin 1998). The numbers 1-6 represent the GPS locations that define the "steps" of the path. "Moves" are made up of *n* steps if the *n*-1 intermediate locations are no more than *x* m away from a line connecting the beginning of the first step to the end of the last one. In this case 4 steps make the first move because locations 1-3 are not more than x m away from the line connecting the beginning to location 4. The size of x is chosen iteratively until the resulting path of moves is no longer autocorrelated.

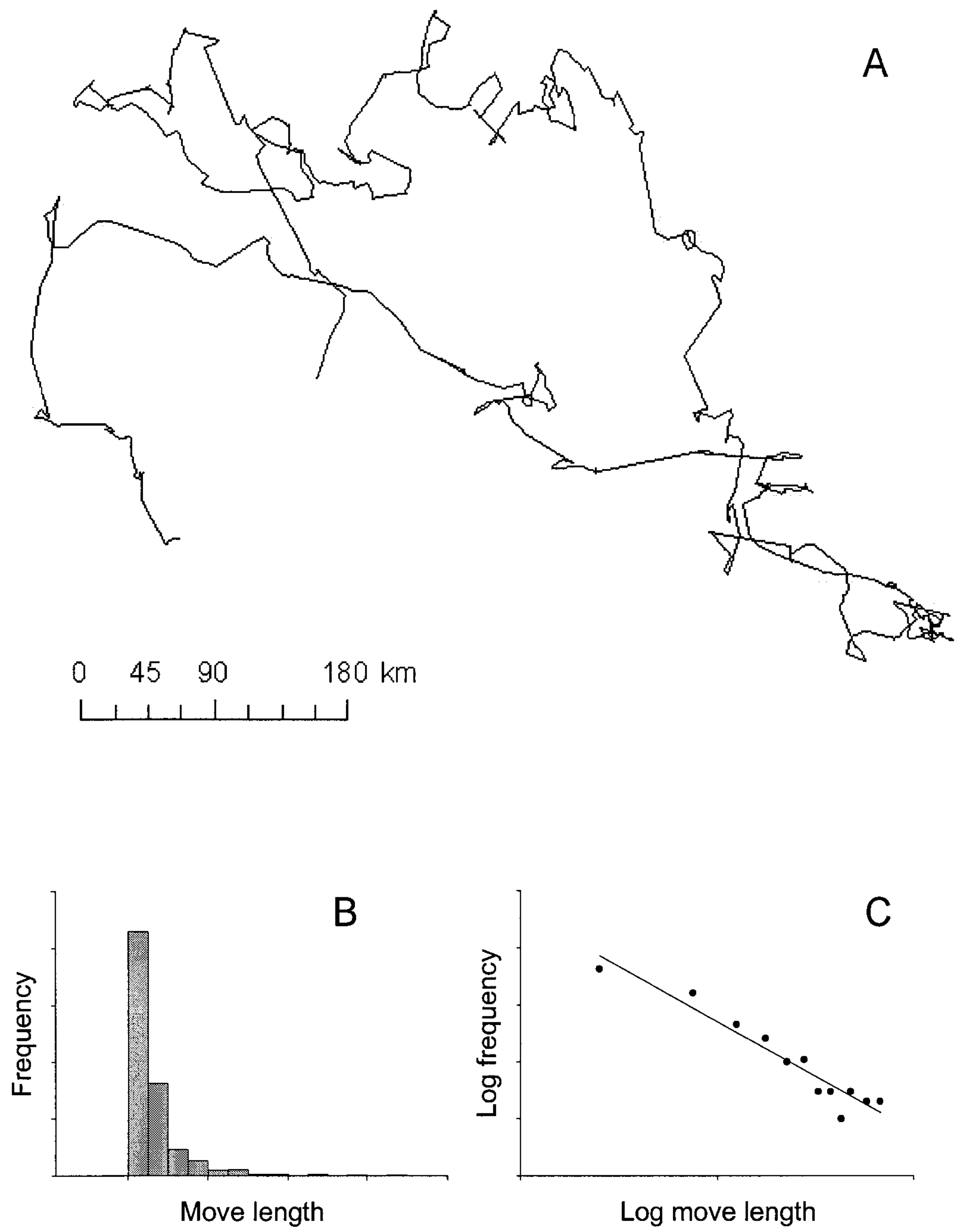

Figure 3.3. Characterization of the movement path of polar bear 49188 on Hudson Bay sea ice from November 2004 until July 2005. (A) illustration of the path, (B) distribution of move lengths and (C) the log-log plot of move frequency vs. length. The slope of the regression line is used to estimate the parameter μ in the power law distribution $P(l_j) \sim l_j^{-\mu}$ where l is move length. In the case of bear 49188, the slope is 1.93, which is close to optimal Lévy search efficiency.

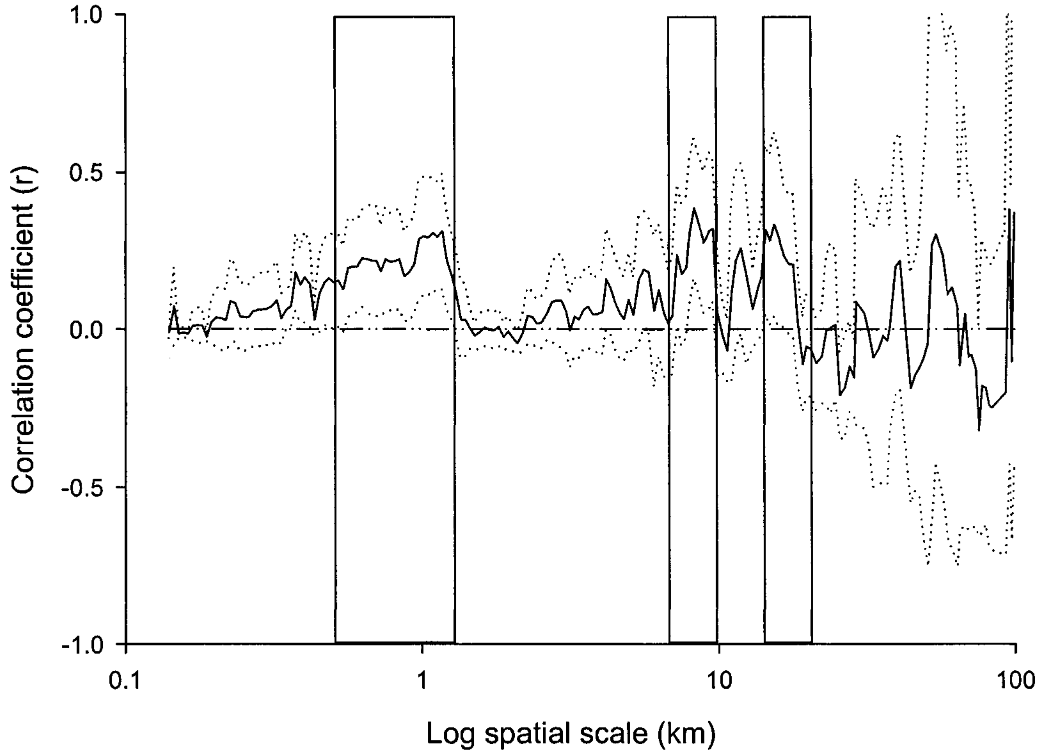

Figure 3.4. Path correlation (solid line) with 95% confidence interval (dotted line) for polar bear 47509 in 2004-2005 at increasing spatial scales. Regions of significant positive correlation (highlighted with rectangles) followed by negative or zero correlation indicate scales below patch size. For this bear positive correlation dropped at 1.8, 10, and 20 km.

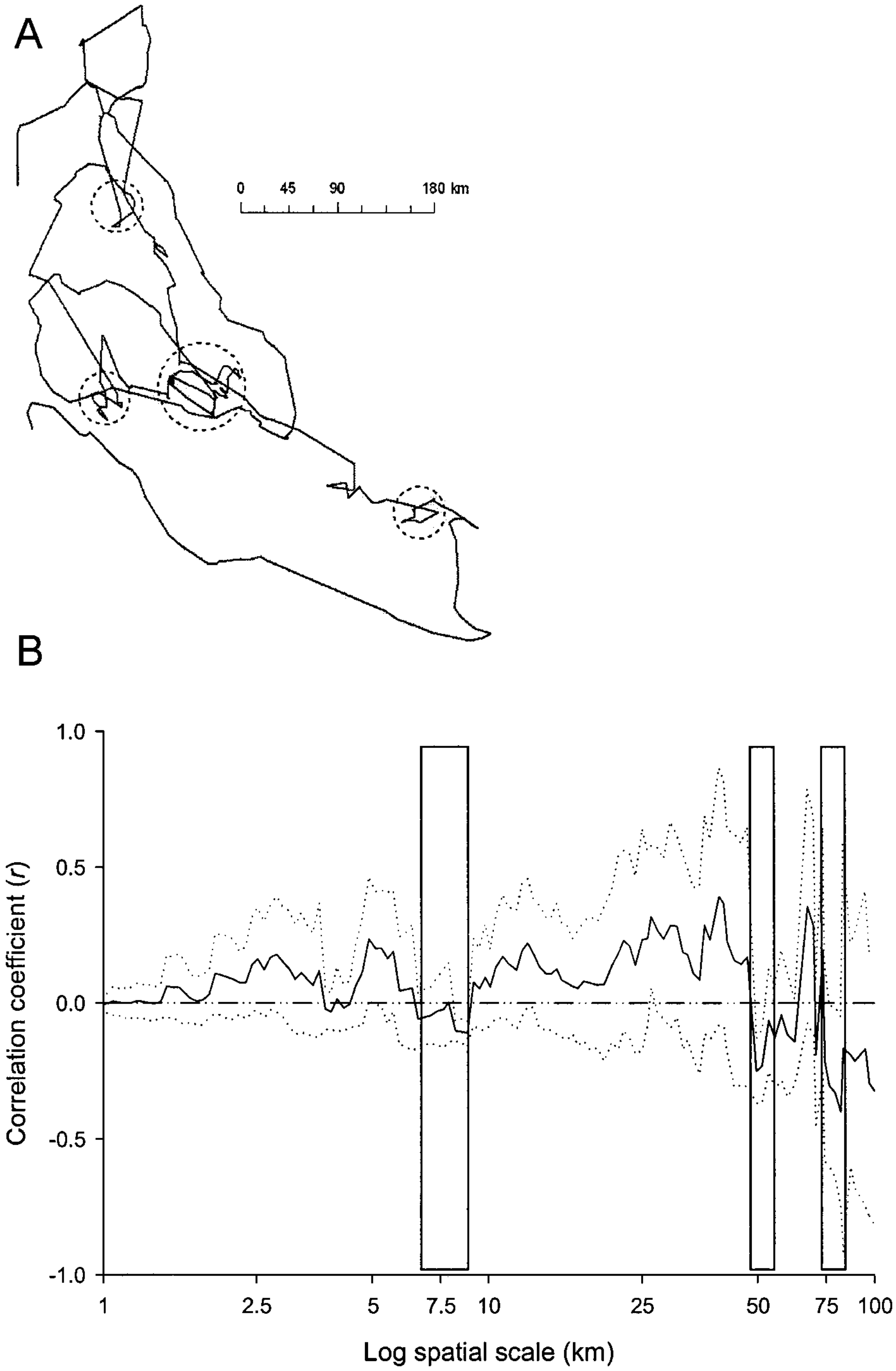

Figure 3.5. The total movement path of bear 49184 (A) and the change in path correlation (solid line) with 95% confidence intervals (dotted lines) at increasing spatial scale (B). Patch sizes of about 8, 50 and 75 km are suggested by regions of negative correlation (highlighted on the plot with clear rectangles) that follow regions of positive correlation. A few examples of searches within either 50 or 75 km are indicated on the path with dashed circles.

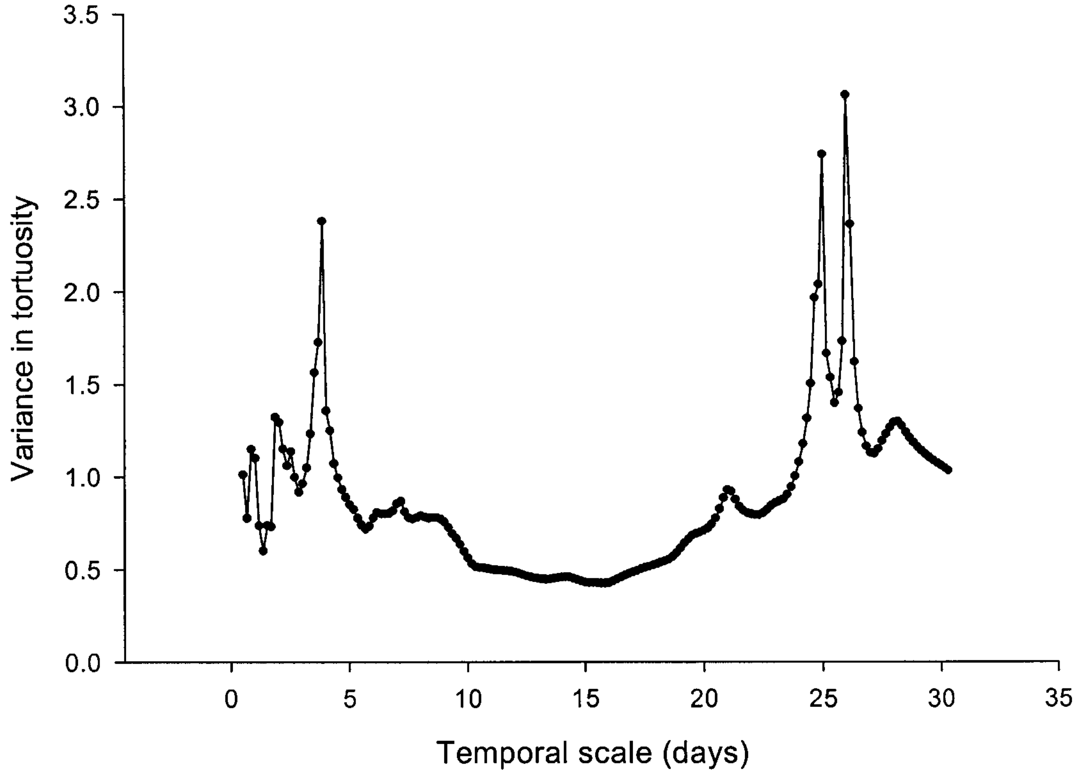

Figure 3.6. Variance in tortuosity (total distance/net distance) for bear 49187 at various temporal scales. The two large peaks occur at 4 days and 25 days.

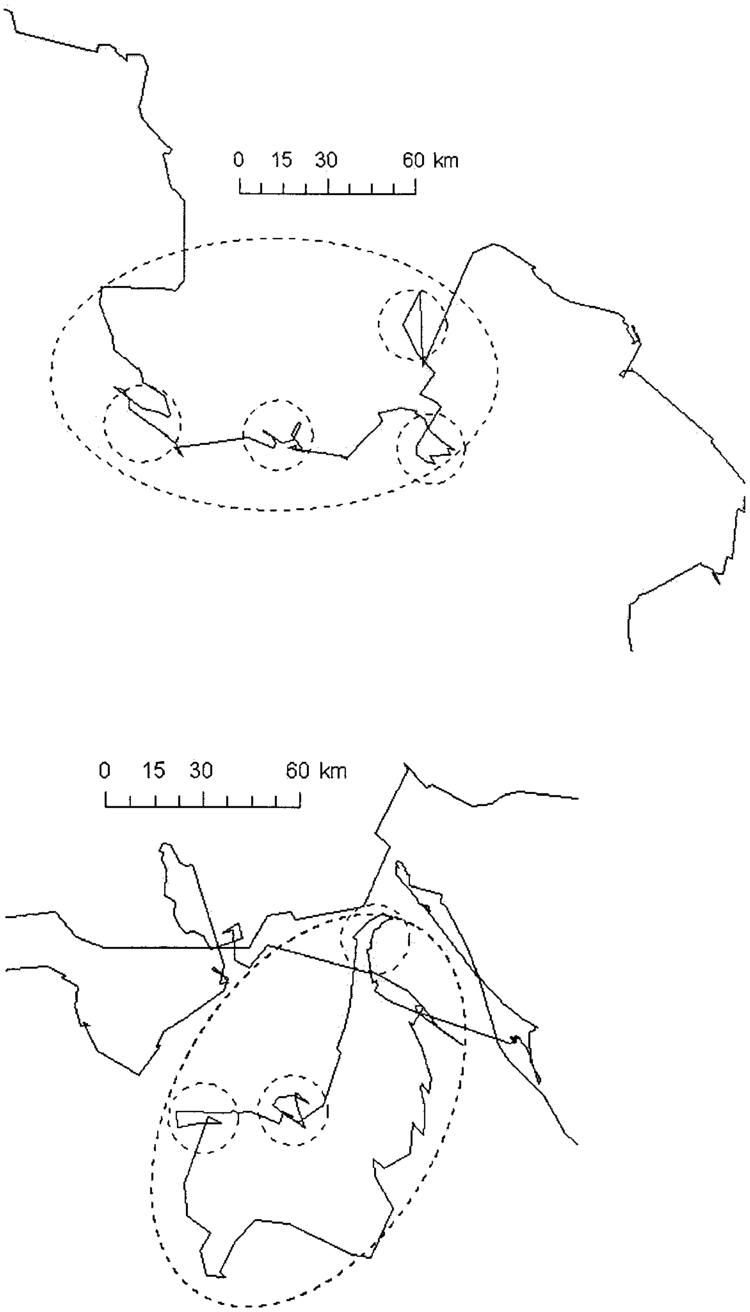

Figure 3.7. Temporal search scales of polar bears 47514 and 49187. Smaller dashed circles indicate areas searched in 3 days, larger dashed ovals indicate areas searched over 3 weeks.

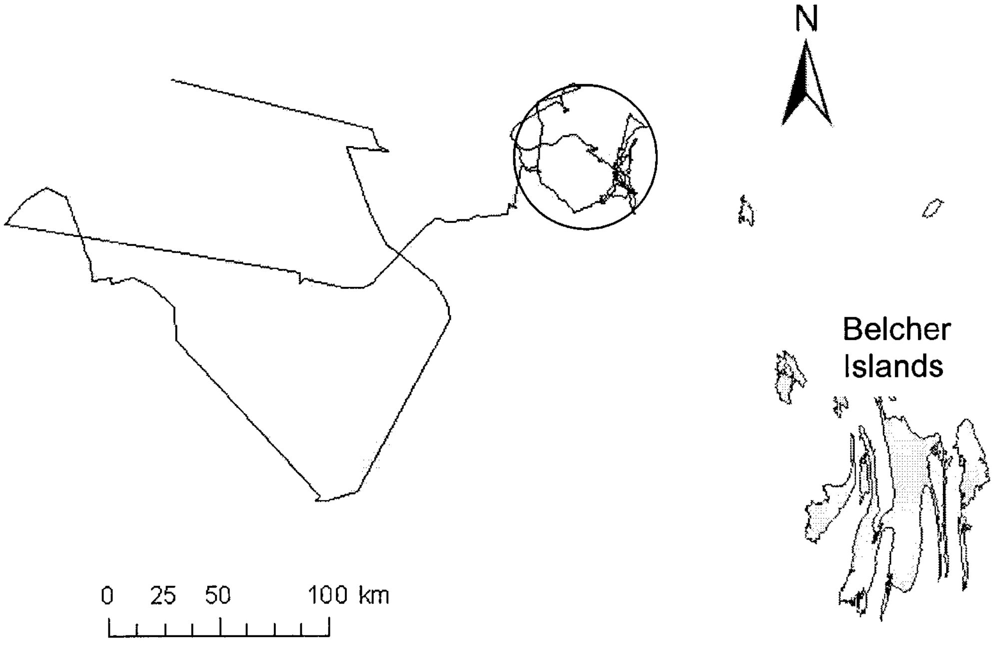

Figure 3.8. Winter and break-up path of bear 47509 on Hudson Bay. From February until June, the bear stayed within the area shown (radius 25 km). The rest of the path was covered in January.

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CHAPTER FOUR - GENERAL CONCLUSIONS AND FUTURE RESEARCH

Summary

In my thesis, I examined movement patterns of female polar bears on the sea ice of Hudson Bay by developing hypotheses about the effects of reproductive class and season, testing whether movement patterns have changed over time, and using movement theory to characterize hunting strategies. I found that while season had significant effects on movement patterns due to changes in sea ice structure and the consequent changes to prey availability, reproductive class had little effect on polar bear movement. Distances traveled by females of all reproductive classes declined from 1991 to 1998, coincident with a reduction in sea ice extent. This means that measured declines in polar bear condition and population size (Stirling *et al.* 1999, Regehr *et al.* in preparation) are most likely due to decreased prey intake rather than increased energy output. Polar bear movement paths can be characterized by a Lévy distribution of move lengths, which suggests a search strategy where long moves take bears between patches of prey and within patches many short moves concentrate searching behaviour. Bears appear to move in a hierarchical patchy environment, in which movement is concentrated at small spatial and temporal scales and these patches are nested within searches at larger scales. The identification of the patterns, scales and strategies of polar bear movement provides a framework in which to understand the relationship between bears, their sea ice habitat and their prey.

Animal movement technology and theory

This study makes use of advances in animal tracking technology and highlights the benefits of satellite-linked collars in research on the movement of wide-ranging animals. The addition of GPS to satellite-linked collars offer several further advantages over satellite technology alone, including greater accuracy and increased frequency of locations (Schwartz and Arthur 1999). A comparison between the total annual distances traveled as derived from satellite and those derived from GPS data in this study emphasize the difference. Distances were two to three times greater when locations were more frequent, revealing that polar bears travel much further than has been previously documented. In the Beaufort Sea, Amstrup *et al.* (2000) calculated annual distances of up to 6200 km from locations 3-7 days apart; which means that bears in that region may actually travel over 12 000 km in a year. Knowing the real distances traveled annually and daily by polar bears is critical if we are to predict how declines in ice extent and prey availability will affect a bears' ability to maintain a positive energy balance. As tracking technology continues to improve, advances in the application of movement theory are necessary to analyse increasingly accurate representations of animal paths over large ranges of spatial and temporal scales (e.g. Bergman *et al.* 2000, Johnson *et al.* 2002, Nams 2005).

Future research

This study identifies the probable reason for declines in both condition and numbers of western Hudson Bay polar bears and provides baseline information and a context from which further research into polar bear movement can proceed. There are many aspects yet to be understood about polar bear movement and several ways that future studies can build and improve on the methods of this research. Continued deployment of GPS collars in western Hudson Bay in the coming years will increase future sample sizes, adding power to statistical approaches and credibility to biological conclusions. As GPS technology begins to be used in other polar bear population studies (e.g. Durner *et al.* 2005) comparisons between regions will help to highlight the underlying ecological determinants of polar bear movement.

The next steps toward understanding polar bear ecology in Hudson Bay in the face of a changing climate involve relating bear movement to habitat and prey characteristics. Improvements in remote sensing and ice classification from satellite imagery, and advances in monitoring of wind and ocean currents will allow researchers to better quantify the dynamics of the sea ice system (Barber *et al.* 2003, Saucier *et al.* 2004). Because sea ice is constantly changing, daily images are required to realistically represent the actual habitat encountered by polar bears at any given place and time. Future studies should examine the extent to which small scale ice features, such as leads, pressure ridges and cracks influence direction and speed of polar bear travel. As the climate warms, the abundance and distribution of these features will change, and polar bear movement will be affected. In addition, more information about seal distribution and abundance in Hudson Bay, and how seal movement is affected by sea ice conditions, is needed. Because of the difficulty of visually tracking seals, GPS and satellite technology should be used along with mark-recapture techniques that allow for assessment of sex, age and condition.

As more complete paths of polar bear movement become known, and these are combined with information on sea ice and seal distribution, a more complete understanding of polar bear energy budgets will result (e.g. Moen *et al.* 1997). This information can help us identify how individual behaviour is related to population level dynamics (Lima And Zollner 1996) and will allow us to predict how polar bears may be affected as ice conditions change on both regional and global scales.

Final conclusions

This is the first study to quantitatively examine polar bear movement patterns on the sea ice, and among the first to use GPS technology to track polar bears. The results provide insight into how polar bears perceive their sea ice habitat and search for prey within it.

Furthermore, it is clear that sea ice is a dynamic habitat in which a positive energy balance is becoming increasingly difficult for bears to maintain. Changes in management policy may become necessary and hunting in some regions may have to cease altogether. Continued monitoring of polar bear movement will help us understand how bears and the entire Arctic marine ecosystem will respond to a rapidly changing habitat.

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