# Populations and Sources of Recruitment in Polar Bears

Final Report

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# Summary

Immature polar bears (*Ursus maritimus*) and adult female polar bears were caught in western Canada in the Beaufort Sea, instrumented with GPS satellite transmitters, and monitored to study dispersal patterns, population connectivity, habitat use, movement dynamics, and population structure. The data are used to investigate the discreteness of biological populations in the Beaufort Sea region and to examine patterns of dispersal. Current models of population delineation and dynamics are driven solely by internal population dynamics and issues of population emigration and immigration are ignored. The study examines polar bear distribution by season, movement patterns, and associated metrics relevant to polar bears ecology. A total of 65 bears (41 adult females, 12 sub-adult females, and 12 sub-adult males) were instrumented in 2007 to 2010 and monitored to spring 2011. The bears were caught from the Alaska-Yukon border eastward to Cape Dalhousie in the NWT. Collars deployed in 2011 will continue to provide data until 2013 so some analyses for this report will be expanded for peer reviewed publications.

Analysis of movement rates indicate that sub-adult polar bears tended to move more than adult females, and to occupy areas of shallower depths and lower sea-ice concentrations. In general, adult females moved the least, probably due to denning and cub-rearing behavior, while sub-adult females remained in areas with higher ice concentration and higher depths. In terms of home range size, there was significant seasonal variation in the extent of the polar bears' range, as well as the difference in extent between the 50% home range and the 95% area. In warmer months (June through November), the bears were more dispersed and used a much larger area than recognized by the IUCN sub-population boundary. Three summer refugia were evident for the bears: the Alaska coast, multiyear ice to the north of the Tuktoyaktuk Peninsula, and to the northeast near northwestern Banks Island. In colder months (December through May), the bears were more concentrated near the continental coastline and the home range size diminished noticeably. Substantial overlap with the adjacent populations in the Chukchi Sea, Northern Beaufort Sea, and the Arctic Basin were evident. Further eastward, some overlap with the Viscount Melville population was noted.

To assess habitat use, we employed a novel approach to resource selection functions to quantify patch quality from locations of seals killed by polar bears observed during capture and tracking. Using binary logistic regression, we weighted kill locations by the estimated biomass of the kill, instead of treating each location equally. We applied the model to compare the capture locations of different classes of polar bears relative to patch quality to assist in understanding the distribution of subadult polar bears. Patch quality was highest in active areas of sea ice, including edges of large leads, in newly formed ice, and at the shorefast ice boundary. Relative probability of a seal kill was negligible at regional sea ice concentrations <50%. The results corroborate previous observations of hunting polar bears, and suggest polar bear migratory cues and avoidance of low sea ice concentrations in spring is likely due to unproductive hunting conditions. Although subadult and adult polar bears differ in competitive ability, they were found in equal proportion in the highest quality patches. Large bodied prey items can satiate adults, allowing subadults access to carrion with significant biomass. We suggest scavenging opportunities for subadults may be the cause of a mixed distribution between unequal competitors.

To provide a longer-term perspective on the current tracking of polar bears, we used satellite telemetry information collected for polar bears in the Southern Beaufort Sea over a 25-year span to examine trends in movement rates and distribution. We hypothesized that because of the limited amount of land cover and coastline and the highly seasonal distribution of sea ice, polar bears in this region should have among the largest annual ranges in the circumpolar region. We further hypothesized that recent declines in the availability of sea ice would represent a decline in habitat quality and resource availability that should further increase the size of annual ranges and the distance and rates of polar bear movements. Determining the relationship between sea ice habitat quality and polar bear movement is key to developing predictive models that can quantitatively link habitat availability with polar bear energy budgets and population processes. The annual area occupied by individual polar bears in the Southern Beaufort Sea has increased in recent years. Our results indicate that although polar bear movement rates and annual distances travelled have not increased significantly over time, annual home ranges have increased by an average of 240% between 1985-93 and 2007-09. These trends suggest that rather than increasing movement rates or distances, polar bears now spread their movements over larger annual areas.

Recent evidence suggests that an increasing proportion of polar bears in the Southern Beaufort Sea population are electing to remain on land during the increasingly ice-free summer months. Part of this shift may be associated with anthropogenic sources of food available in the form of bowhead whale carcasses left on shore after local subsistence harvests in the autumn. The use of land-based refugia during the ice-free season may contribute to large annual ranges as polar bears tend to remain on the ice as long as possible and thereby increase the distance between winter and summer habitats. The main distributional shift of bears in recent years was to the north and west of the area occupied in the 1980s and 1990s. Of the 18 polar bears collared before 2007, only 4 moved beyond the northern boundary of the Southern Beaufort Sea population zone and no bear moved more than 125 km north of the line. In contrast, the majority of bears (7/13) collared in 2007 moved beyond the population area, utilizing ice more than 600 km north of the boundary (*ca*. 900 km offshore) and as far west as Wrangel Island in the Russian Chukchi Sea. These trends could be indicative of weakening population boundaries in response to habitat change and could have implications for mark-recapture population estimates and sustainable harvest management. It is clear that habitat loss in the Beaufort Sea has affected the way polar bears make their living on the sea ice.

To standardize data for movement analyses and to assess possible effects of handling on polar bears, we investigated the movement patterns of polar bears post-capture to measure their recovery from chemical immobilization. We used three individual-based metrics to assess their recovery: time to move 50 m, time to move 100 m, and time to reach a baseline movement rate threshold (km/d) derived from each individual's movements in a fully recovered state (i.e., 30-60 days post capture). There were no differences in recovery rate metrics across years or age classes. When compared across populations, only the time to 50 m differed, being shortest in the Southern Beaufort Sea. Bears captured on land during the ice-free period in western Hudson Bay and Foxe Basin appeared to be more variable in their response to capture than were those handled on the sea ice of the Southern Beaufort Sea, but in all three areas, bears showed gradual acceleration in movement, with rates reaching indicative of recovery 48 hours after capture. Sixty-nine percent (51/74) of bears appeared to be fully recovered in ≤ 3 d. Our results indicate that polar bears captured in different locations, seasons, and life history stages all recover predictably from chemical immobilization and typically resume normal movement rates within 2-3 days of capture.

This study suggests a profound change in the annual home range size of adult female polar bears in an area undergoing dramatic environmental change. Annual home range sizes more than tripled from 1985-93 to 2007-09. Although our analysis could not separate the walking movements of polar bears from the movement of their floating sea ice habitat, passive transport of polar bears on the ice will be significant. At present, it is clear that habitat changes in the Beaufort Sea have affected the way polar bears make their living on the sea ice.

Overall, we found limited evidence of age-dependent dispersal and consistent with existing information on population structure, it appears that polar bears exhibit natal area philopatry. Only one study animal, an adult female, appeared to emigrate from the Southern Beaufort Sea population to the Chukchi Sea population to the west. Nonetheless, it was clear that existing population boundaries do not adequately reflect the space use of polar bears in the Southern Beaufort Sea. We therefore recommend that the established borders of the Southern Beaufort Sea management unit be re-evaluated in light of ongoing environmental change. Integration of results from this study with recent GPS collaring the Chukchi Sea and north of the Alaskan coast in the Beaufort Sea would facilitate a more contemporary delineation of the Southern Beaufort Sea population. Ongoing analyses of the data collected during this study will continue to provide new insights into population structure and the factors affecting space use in the population.

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# Introduction

Polar bears (*Ursus maritimus*) are distributed throughout the ice-covered seas of the circumpolar Arctic (DeMaster and Stirling 1981) and are a specialized predator on two species of seals: ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Smith 1980; Stirling and Archibald 1977; Thiemann et al. 2008). The Arctic sea ice habitat is a dynamic environment and large temporal and spatial variation is common (Ådlandsvik and Loeng 1991; Shapiro et al. 2003; Barber and Iacozza 2004). Linkages between climate driven sea ice habitats and polar bears were first established from hunting returns in Greenland (Vibe 1967) and more recent research has linked the dynamics of polar bear populations to climatic events that reduce productivity of their primary prey, ringed seals (Stirling et al. 1982; Stirling 2002). Change in the productivity of ringed seals affects polar bear natality and survival through changes in body condition (Ramsay and Stirling 1988; Derocher and Stirling 1994; Stirling 2002; Rode et al. 2010; Stirling and Derocher 2012). These changes in environmental conditions result in strong and weak cohorts in the population that are reflected in population age structures but diminish over time possibly due to immigration from adjoining populations (Stirling 2002).

Remote locations, low density, and high research costs for monitoring polar bear populations have resulted in an incomplete understanding of their population dynamics. Researchers have pieced together a variety of elements to construct insight into the dynamics of many populations. Similar to other species of bears, polar bears have small litters, a prolonged mother-offspring bond, and delayed maturation that results in low population growth rates (Bunnell 1981; Taylor 1987). Adult survival rates are high and population trend is sensitive to changes in adult female survival rates (Eberhardt 1990; Amstrup Durner 1995; Taylor 1987). Studies have shown that reproductive rates are the most dynamic component of polar bear populations and variation in cub survival rates play a major role in determining reproductive interval (Derocher Stirling 1995; Derocher Stirling 1996; Stirling 1999). However, incomplete time series, small sample sizes, and biased samples have limited interpretation of some elements. Despite these limitations, the population ecology of polar bears is reasonably well understood with some notable exceptions. In particular, juvenile dispersal patterns have not been examined in polar bears.

Currently, 19 populations[1] of polar bears have been defined in the circumpolar Arctic (IUCN/SSC Polar Bear Specialist Group 2010) (**Figure 1**). Populations have been defined using several different methods and population boundaries have been revised many times as new information has been made available. Original population boundaries were based on subjective information obtained from field observations, from local people and geographic or political boundaries (e.g., Stirling et al. 1977). These population definitions were refined using mark-recapture methods and returns of tagged animals in the harvest (Lentfer 1973; Stirling et al. 1977). Development of radio telemetry techniques, initially VHF radios and then satellite radios, permitted a more rigorous assessment of population boundaries (Bethke et al. 1996; Taylor et al. 2001; Mauritzen et al. 2002). More recently, a modified clustering method was applied to satellite radio-telemetry to generate probabilities of occurrence for bears in one population occurring in another population (Amstrup et al. 2004). Genetic methods have also been applied to identifying populations and can provide different temporal perspectives and insights on gene flow (Paetkau et al. 1999; Cronin et al. 2009; Zeyl et al. 2010). The combination of genetic and telemetry methods likely provide an optimal approach to understanding population structure. Longer-term, there is concern that as the climate warms in the Arctic, population boundaries may

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[1] under the IUCN/SSC system, there are 19 “subpopulations” globally but for this document, the term “population” is used.

shift as sea ice patterns change, which might affect movement patterns (Derocher et al. 2004). Satellite radio-telemetry is now the accepted means of assessing population boundaries. However, a major problem with the current management of polar bear populations is the absolute bias towards adult females in all movement studies. The necks of adult males are wider than their heads and preclude radio collaring. Until recently, lack of reliable technology to allow radios to automatically fall off has excluded subadults from tracking studies. There is limited information to suggest that the movement patterns of adult males is similar to that of adult females (Amstrup et al. 2001) but no information is available on the movements of subadults which is the group most likely to move widely and possibly disperse.

## Beaufort Sea Population

The Beaufort Sea population is broadly defined as those bears living in Alaska and Canada in the Beaufort Sea and Amundsen Gulf, east to include southern and western Banks Island and western Victoria Island, and as far west as Icy Cape, Alaska (Lentfer 1983; Amstrup et al. 1986; Amstrup and DeMaster 1988; Stirling et al. 1988). The population is divided into two populations with the Southern Beaufort Sea population ranging from between Paulatuk and Baillie Island, Northwest Territories to Icy Cape, Alaska and the Northern Beaufort Sea population extending from the Paulatuk area eastwards into Coronation Gulf and Northwards to include western Victoria Island and Banks Island. To the west, the Southern Beaufort Sea population overlaps to some degree with the Chukchi Sea population and to the east, with the Northern Beaufort Sea population that abuts the Viscount Melville Sound and M'Clintock Channel populations (**Figure 1** and **Figure 2**). To the north, the Southern Beaufort Sea population abuts the poorly defined Arctic Basin population.

The Beaufort Sea and the Western Hudson Bay populations are the two best-studied populations worldwide. However, the dynamics of sea ice and the geographic setting of these two populations are fundamentally different. The Beaufort Sea is an open ocean system where polar bears can follow the sea ice year round while the Hudson Bay system is a closed area where the sea ice melts totally in summer. The reproductive patterns in these two populations substantially differ. Large changes in the condition and reproductive rates of polar bears in western Hudson Bay have occurred over the past 20 years and have been linked to possible density-dependent responses following recovery from over-harvest (Derocher and Stirling 1992; Derocher and Stirling 1995) and more recently to climate change (Stirling and Derocher 1993; Stirling 1999). In contrast, the dynamics of condition and reproduction in the Beaufort Sea are more closely tied to recovery from over-harvest and climatic variation (Amstrup et al. 1986; Stirling 2002). Increasingly, studies are indicating negative consequences for the Southern Beaufort Sea population as a result of sea ice loss (Stirling et al. 2008; Regehr et al. 2010; Rode et al. 2010; Hunter et al. 2010; Pagano et al. 2012). The Beaufort Sea population undergoes highly variable periods of high and low recruitment that are linked to ringed seal productivity (Stirling 2002). The sea ice dynamics of the Beaufort Sea population make research more challenging because the large area, inaccessibility of the population in summer, and logistic constraints. Regardless, the Beaufort Sea population is well studied and adequate logistics are available. Increasing oil exploration and development both in the USA and Canada (**Figure 3** and **Figure 4**) necessitate improving our understanding of vital population processes.

## Dispersal

Dispersal has important ramifications for population ecology and dynamics through the redistribution of animals. Patterns of natal area dispersal have important ramifications for evolution, ecology, and management of a species. The role of dispersal is often examined at the individual and population level. At the individual level, dispersal can work to minimize inbreeding, reduce competition among related individuals for resources, and reduce competition among related individuals for mates (Waser and Jones 1983; Pusey 1987). At the population level, dispersal can influence population gene flow, metapopulation dynamics, and population structure (Haila et al. 1989). Movement of young animals is the most common mechanism of redistribution in most mammals (Greenwood 1980; Dobson 1982; Rogers 1987; Chepko-Sade and Halpin 1987; McLellan and Hovey 2001). There is substantial evidence from theoretical and empirical studies to suggest that dispersal is density dependent and plays a major role in population demographics for a wide variety of taxa (e.g., Gaona 1998; Andreassen and Ims 2001; Gaggiotti et al. 2002; Bonenfant et al. 2002; Massot et al. 2002; Pedersen et al. 2004). Existing information on the dispersal patterns of polar bears is extremely limited. Population management assumes that the population dynamics of polar bears is largely driven by internal processes and patterns of immigration and emigration are ignored (Taylor and Lee 1995). An alternative view would advocate that management units are based on regions with genetically distinct traits (Moritz 1994). Using genetic markers, polar bears on a circumpolar basis were concluded to a single evolutionary significant unit (Paetkau et al. 1999). Current management plans for polar bears rely on populations delimited by the movements of adult females and no other age or sex classes are considered. This has been a necessity given the technology available. Limited information in studies suggests that movement between populations does occur (e.g., Stirling et al. 1977, 1980; Amstrup 2000) but this has been ignored in quantified population models and assumed to be negligible.

Polar bears in the Beaufort Sea are linked genetically to adjacent populations (Paetkau et al. 1999). The North and South Beaufort Sea polar bear populations were described as having low levels of genetic differentiation (*op. cit*). Minimal levels of genetic structure were observed in all populations surrounding the Polar Basin with the exception of apparent discontinuities in the Canadian Archipelago (*op. cit.*). Existing information on the movements of polar bears from radio telemetry are difficult to reconcile with the genetic patterns. Radio telemetry data suggest that adult females are highly philopatric but genetic exchange appears common. Despite many years of polar bear monitoring using satellite telemetry on adult females, dispersal events between populations have been extremely limited. Virtually all data collected on movement patterns, however, has been collected on adult females that are likely the single population element most likely to show philopatry to an established range.

Dispersal in other Ursidae is common. Studies of black bear (*U. americanus*) show that females are philopatric while dispersal is male biased (Rogers 1987; Elowe and Dodge 1989; Schwartz and Franzmann 1992; Onorato 2004). Similar results have been noted for grizzly bears (*U. arctos*) (Glenn and Miller 1980; Proctor et al. 2004). Polar bear life history traits of large body size, non-territorial behavior, asocial nature, relatively continuous distribution of prey species, and contiguous distribution of their primary habitat all combine to suggest that long-distance dispersal should be common.

Studies of dispersal in large mammals have been hampered by the difficulty of obtaining reliable locations on dispersing animals. Advances in satellite telemetry have opened this area of research as obtaining position information no longer requires extensive searching over broad geographic areas. The development of remote drop-off devices and improvements in satellite telemetry methods have greatly increased the potential for expanding radio telemetry to subadult bears which in the past were at risk should the researcher not be able to remove the collar at a predetermined time and the animal grow too large for its collar. Telonics (Mesa, Arizona) has developed the latest model of their remote release link the CR-2a which can be programmed to release at a date fixed by the researcher. This technology was successfully exploited during this study. A small number of bears could not be recaptured because they had dispersed beyond the study area (**Figure 5**) so we relied on the remote releases. Many collars were removed and none of the bears caught in the field in Canada showed any sign of injury (**Figure 6**). Bears feeding on the bowhead whale (*Balaena mysticetus*) carcasses in coastal Alaska did present problems associated with excessive weight gain and tight collars and necessitated intervention to remove some collars.

### Management

Internationally, polar bears have benefited from coordinated management of shared populations as outlined in the International Agreement on Polar Bears (1973) and the Marine Mammal Protection Act (1972) in the United States (Prestrud and Stirling 1994; Brower et al. 2002). The need for shared management between interested Alaskan and Canadian resource users of the Southern Beaufort Sea population resulted in the *Polar Bear Management Agreement for the Southern Beaufort Sea* being negotiated between the Inupiat hunters of Alaska and the Inuvialuit hunters of Canada. The agreement was ratified in 1988 and provides provisions for joint management and protection of the stock while allowing a sustainable harvest (Brower et al. 2002; Nageak et al. 1999).

The existing management framework for the Beaufort Sea area utilizes three relatively discrete populations: the North Beaufort Sea, the South Beaufort Sea, and the Chukchi Sea (**Figure 1**). Polar bear hunting quotas are allocated to communities based on where they hunt and the populations are managed as independent units. A revised management regime has been proposed that utilizes the probability of occurrence at a given location based on the movement patterns of adult females (Amstrup et al. 2004).

## Project rationale

A major shortcoming of the past methodology and analyses is the reliance on adult females for allocating space use and population boundaries. Hunting effort, or impact of a theoretical oil spill (Durner et al. 2000), can be assessed using adult females but the assumption is that adult females adequately represent the rest of the population. However, hunters are encouraged to not kill adult females and the space use of polar bears differs between the sexes and age classes (Stirling et al. 1993). Therefore, management of polar bears using existing population boundaries in the Southern Beaufort Sea was deemed questionable and provided rationale for further investigation.

The approximately 21,500-25,000 polar bears of the world are currently divided among 19 recognized “populations” the Arctic Region of the Northern Hemisphere. Although these units are referred to as “populations” there is no genetic or behavioral basis for assuming genuine isolation. Past studies of individual polar bear movements suggest that female adults occupy restricted home ranges. Data on males is severely limited because it is difficult to fit adult males with transmitter collars. The only study conducted on males suggests movement patterns similar to adult females but the very short time frame of monitoring (Amstrup et al. 2001) precludes any conclusive assessment. Adult movements may not accurately reflect population structure because natal dispersal is the dominant control against population isolation in most vertebrates, with male-biased natal dispersal dominant among mammals and particularly common in other ursid species (Rogers 1987; McLellan and Hovey 2001; Proctor et al. 2004). The designation of geographic populations has been influenced by political boundaries and management needs but greater investigation of the biological basis of contemporary population structure is warranted. The existing management units require evaluation for their effectiveness at defining population discreteness, for quantifying the relative role of internal and external demographic processes, for estimating population recovery from perturbations, setting harvest goals, and for understanding gene flow.

Juvenile polar bears had not been monitored by radio telemetry and this age group is the one most likely to emigrate or immigrate between populations. Long-range dispersal was observed in an adult female polar bear (Durner and Amstrup 1995), but these events are uncommon suggesting that adult female emigration is atypical. Long-term monitoring of juvenile polar bears has not previously been accomplished but recently developed technology now allows such studies. Thus, data on the movements of juvenile polar bears, including the location of their adult home-ranges relative to their natal home-ranges, was a missing critical element.

This study was designed to provide insight into polar bear movement that could limit effective dispersal and assist with understanding population boundaries. Using information on subadults is a novel approach and allowed insight into natal dispersal and tests of the current working hypothesis that polar bears are divided among relatively discrete populations (Bethke et al. 1996; Mauritzen et al. 2002; Amstrup et al. 2004). The study also provides new data on movement ecology that is being used to enhance analysis of oil-spill/polar bear mortality models. Oil spill models are not presented in this report but are ongoing as an additional element that evolved from the initial project. Collars deployed on adult females allowed for comparison with earlier studies and thus aspects of temporal trends in space use and movement ecology.

## Project Goals

The purpose of this study was to investigate and quantify the patterns of movement and dispersal of juvenile polar bears (2-5 years old) caught in eastern Alaska or western Canada in the Beaufort Sea to examine the working hypothesis that polar bears are divided among discrete populations and to offer alternative interpretations as appropriate. The study was designed to enhance analysis of oil-spill/polar bear mortality models although these elements are still being developed as an extension of the initial study. Goals were expanded during the study to include a representative sample of adult females of varying reproductive status to allow comparison with earlier studies and to provide a reference with subadults. The study aimed to analyze existing data on juvenile use area, dispersal, and philopatry to construct working hypotheses and deploy GPS satellite collars on juvenile polar bears captured near their natal area and follow the bears until settlement. Targets animals included 2 years-olds with their mothers, recently weaned 2 year-olds, and 3-4 year-olds in the primary capture areas of the Southern Beaufort Sea. It was assumed that study animals with their mothers were born in the area and the study includes natal area dispersal/philopatry but we were unable to document birth sites so there is some conjecture on this point. The intent of the study was to provide insights into barriers to population movement. In particular, patterns of sea ice formation, break-up, and drift were assessed with consideration of existing population boundaries and information from subadult polar bears.

## Report organization

The report is organized into 4 main components:

1) Seasonal distribution of polar bears,
2) Long-term changes in the movement patterns of polar bears,
3) The effect of unequal competition and unequal access on the distribution of polar bears,
4) A preliminary analysis of polar bear movements and habitat use.

The study methods are outlined in the individual components of the report to provide sufficient detail on data sources and analytical methods.

### Data management

All data collected during the study was recorded, validated, and will be made available to investigators for further analyses upon mutual agreement. All raw data was recorded on standardized polar bear capture forms and entered in formats that facilitate in-house data-storage and computation requirements. All data are integrated into the National Polar Bear Database managed by Environment Canada (Edmonton, Canada). An additional copy is maintained at the University of Alberta, Department of Biological Sciences and is backed-up on a regular basis. Copies of capture data were provided to the US Geological Survey for population estimation and monitoring and to the US Fish and Wildlife Service for comparisons with the Chukchi Sea population. Copies of the movement data (**Figures 7 - 10**) reside with the NWT Department of Natural Resources, Inuvik Region for management purposes. Discussions for data sharing are ongoing with the Yukon Government. Data was provided to the Northwest Territories, Environment Canada, and USGS for analyses in support of the Inuvialuit-Inupiat Agreement meetings to assist in population delineation analyses.

### Partnerships

The research was coordinated with agencies conducting polar bear research in the Beaufort Sea and adjacent areas (Environment Canada, NWT Department of Environment and Natural Resources, Biological Research Division of the US Geological Survey, and the US Fish and Wildlife Service).

### Permits

All methods used in this study were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee (Permits 408505, 409606, 409705, 600804, 600904, 6001004, 600/03/12). Guidelines followed by this Committee were established under the policies of the Canadian Council on Animal Care (CCAC) and existing legislation of the Province of Alberta and the Government of Canada. The Committee ensures that all animals associated with the activities of the research, regardless of species, are treated humanely, and not subjected to unnecessary or excessive pain, distress or discomfort. No significant trauma, injury or death to study animals occurred during the research. Collars were either remotely released from study animals or were removed.

Wildlife research permits were obtained from the Government of the Northwest Territories (Wildlife Research Permits WL003322 WL005372, WL005596, WL007376, WL 007425). Consultation with the local Hunters and Trappers Committees was facilitated by presentations to the Inuvialuit Game Council and the Wildlife Management Advisor Council (North Slope and NWT).

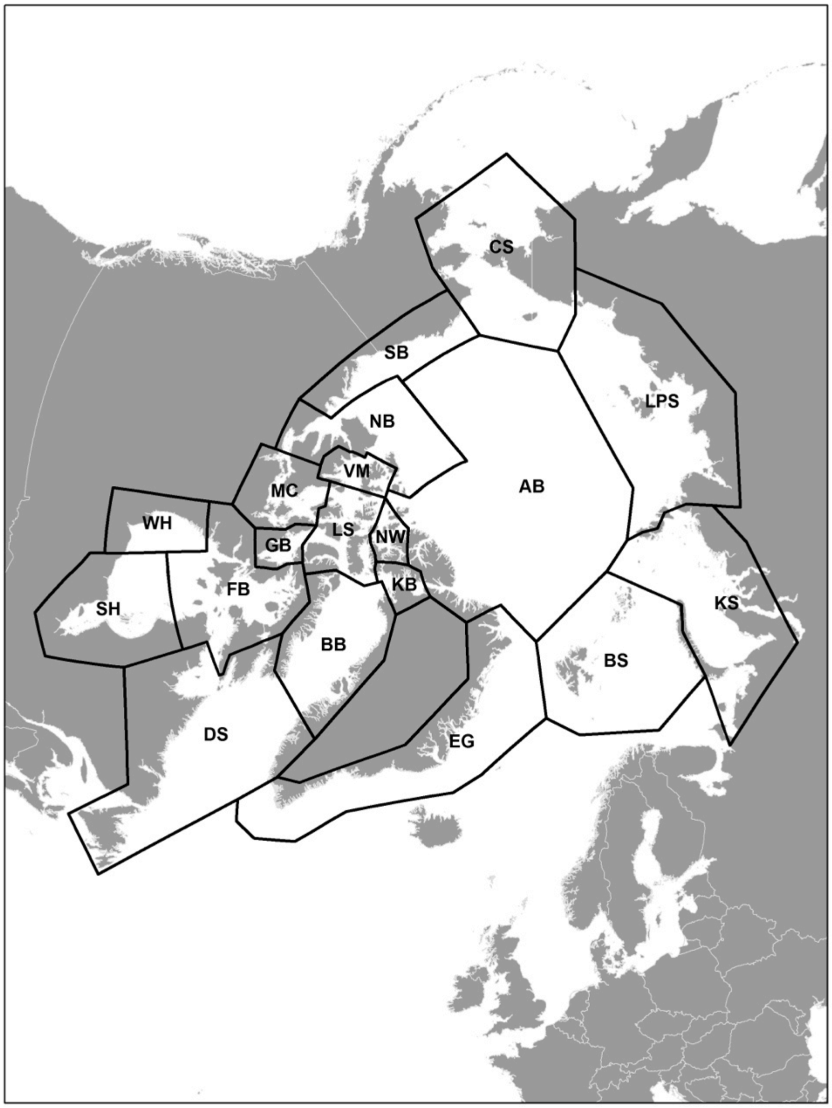

Figure 1 Circumpolar polar bear populations recognized by the IUCN/SSC Polar Bear Specialist Group (Obbard *et al.*, 2010). Counter clockwise from the top: CS - Chukchi Sea, SB - Southern Beaufort Sea, NB- Northern Beaufort Sea, VM - Viscount Melville Sound, MC - M'Clintock Channel, NW - Norwegian Bay, LS - Lancaster Sound, GB - Gulf of Boothia, FB - Foxe Basin, WH - Western Hudson Bay, SH - Southern Hudson Bay, DS - Davis Strait, BB - Baffin Bay, KB - Kane Basin, EG - East Greenland, BS - Barents Sea, KS - Kara Sea, LPS - Laptev Sea, AB - Arctic Basin (after Stirling and Derocher 2012). Note: the IUCN/SSC uses “subpopulation” for these 19 areas but throughout this report, the term “population” is used as the equivalent.

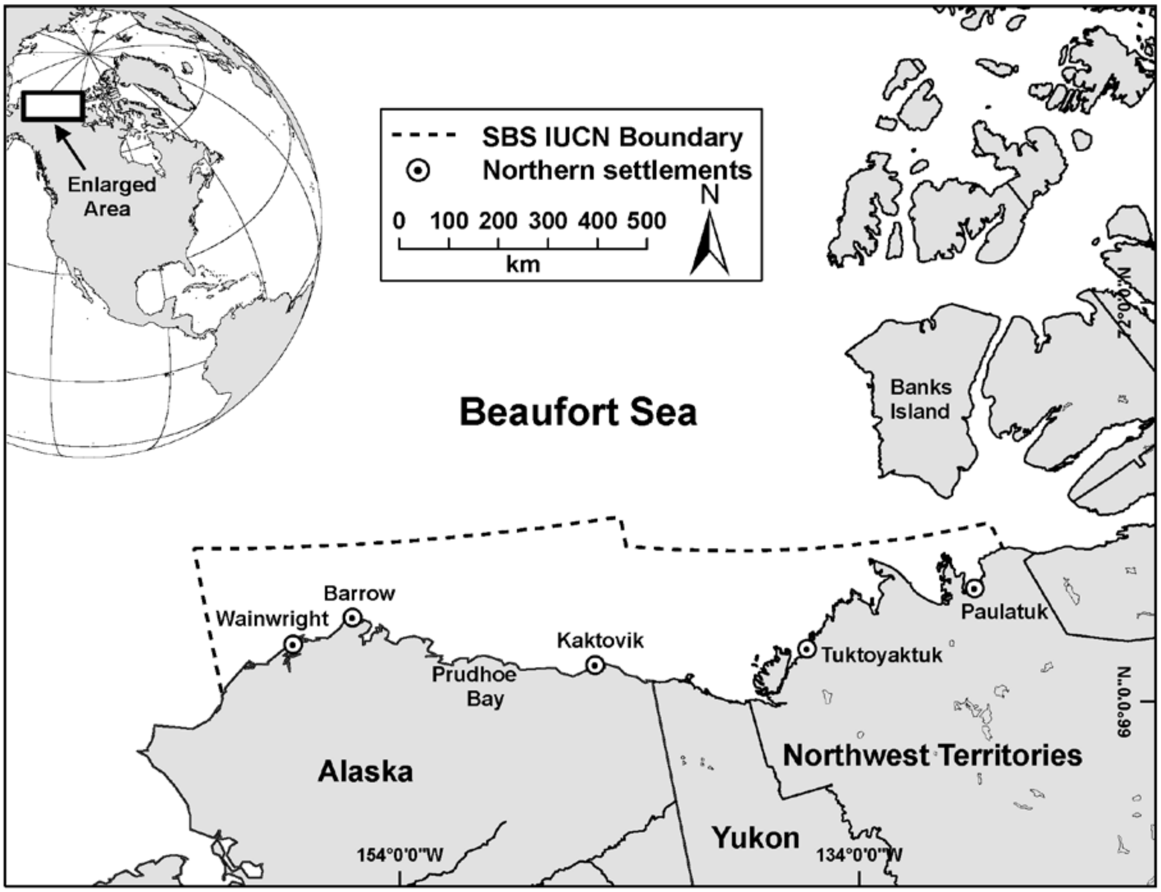

Figure 2 The Southern Beaufort Sea population boundary (dashed line) as recognized by the IUCN/SSC Polar Bear Specialist Group (2010).

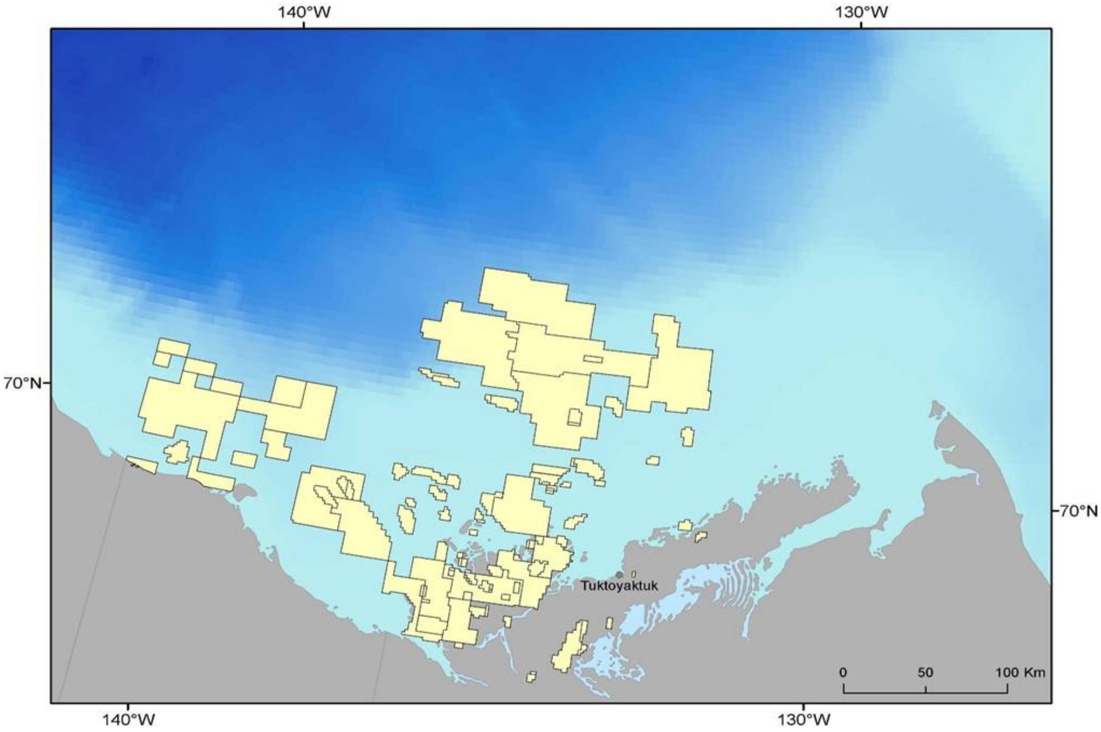

Figure 3 Location of Canadian hydrocarbon leases in the Beaufort Sea region.

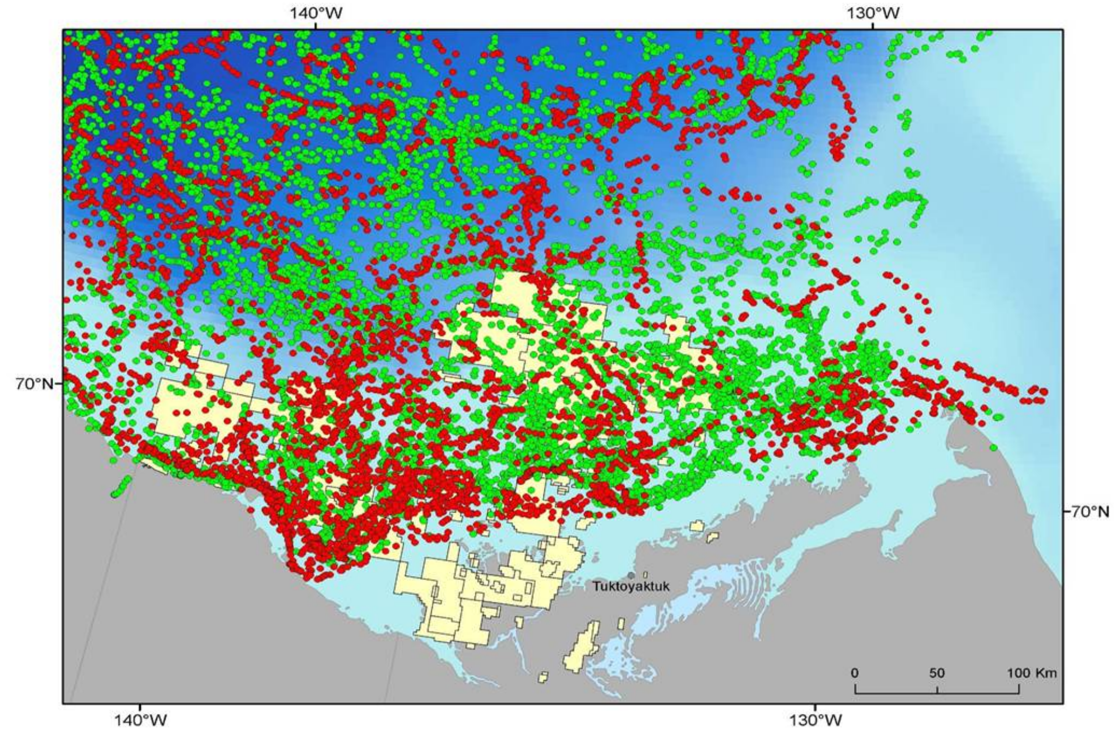

Figure 4 Locations of polar bears followed by GPS satellite telemetry (2007-08) relative to Canadian hydrocarbon leases in the Beaufort Sea. (2007 – green dots, 2008 – red dots).

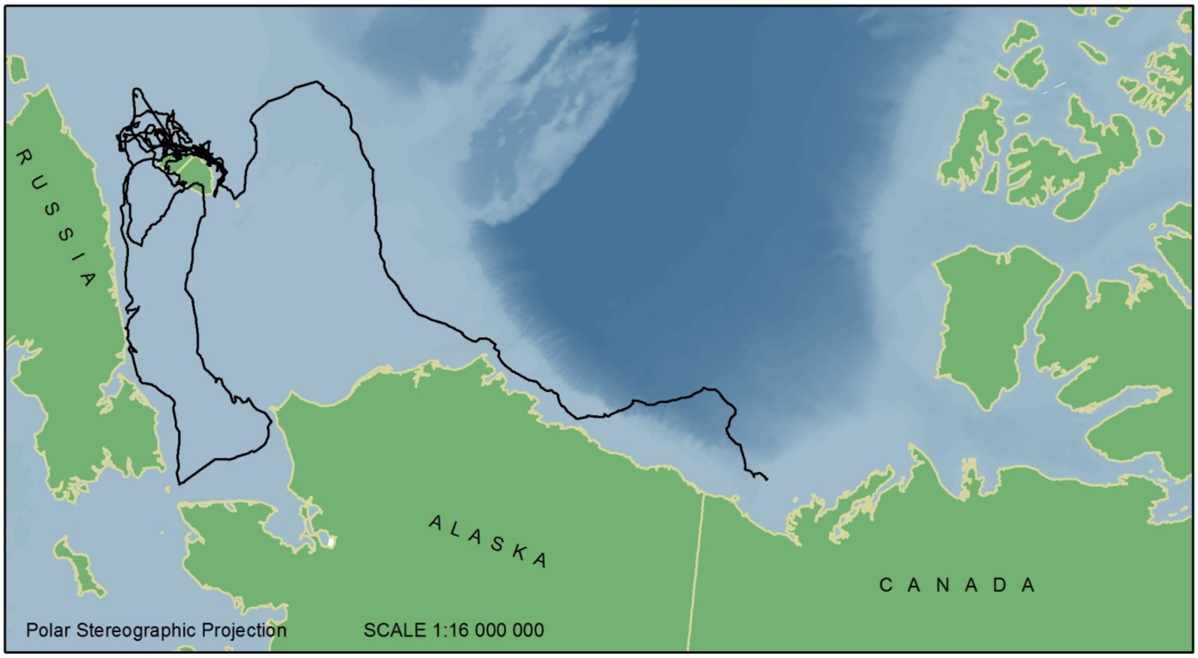

Figure 5 The movement path of bear X32690 a lone adult female when caught in April 2009. The bear showed no signs of a return movement when the collar ceased transmission in 2011.

Figure 6 Photographs of X32692 caught to remove a Telonics GPS satellite collar that had not released. No injury to bear was evident. The flattened hair is typical of any bear wearing a collar.

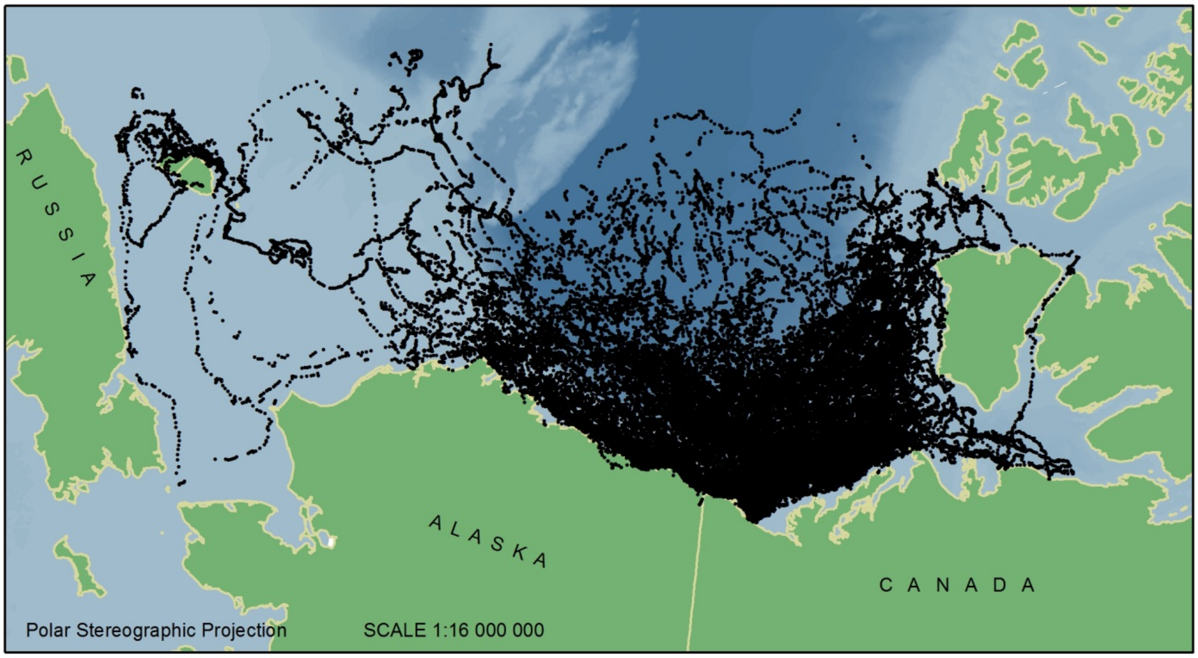

Figure 7 All locations for 65 polar bears in the Southern Beaufort Sea, collected between 2007 and 2010.

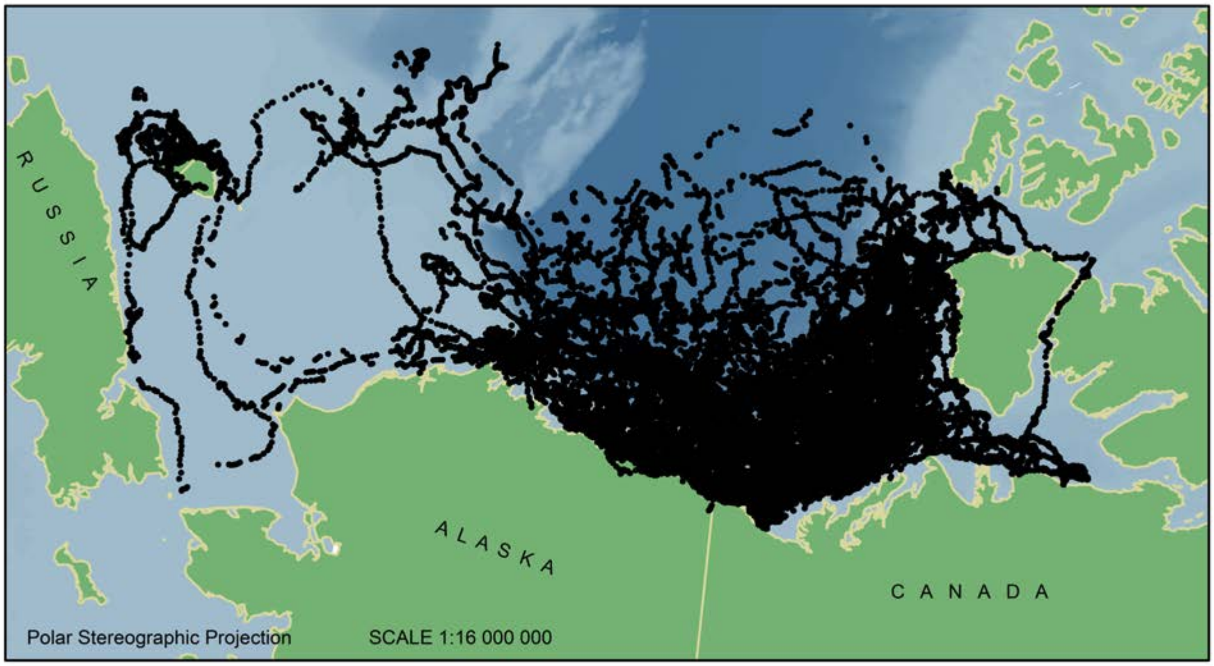

Figure 8 All locations (n=54,533) for adult female polar bears in the Southern Beaufort Sea, collected between 2007 and 2010.

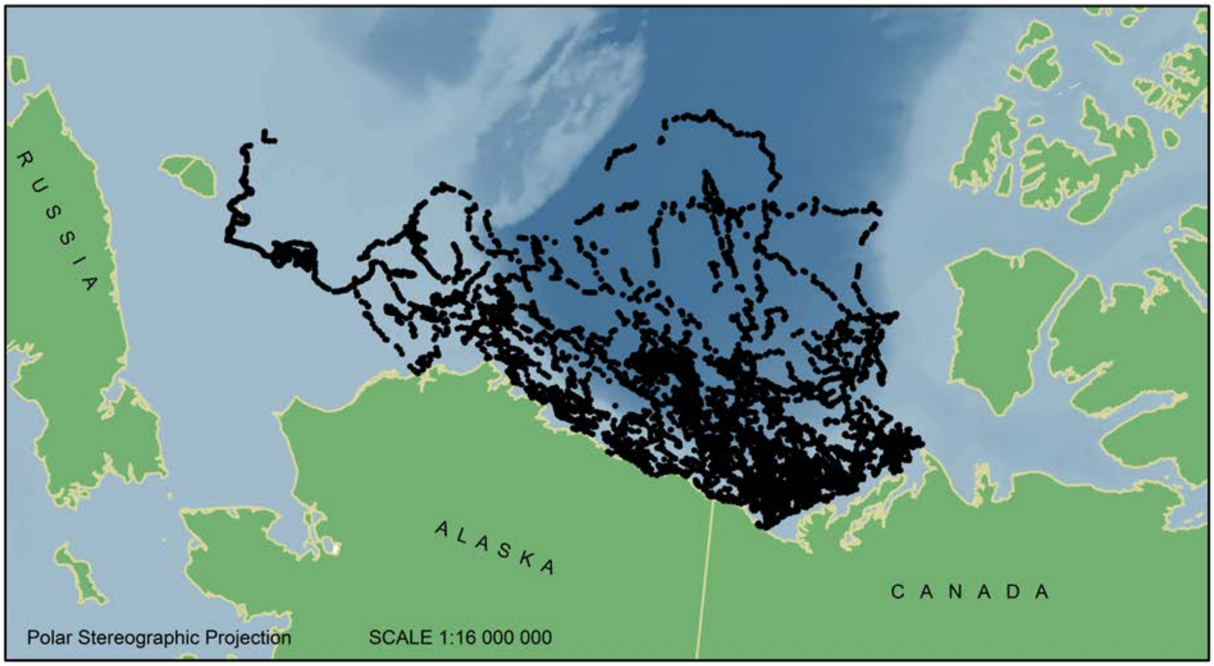

Figure 9 All locations (n=10,584) for subadult female polar bears in the Southern Beaufort Sea, collected between 2007 and 2010.

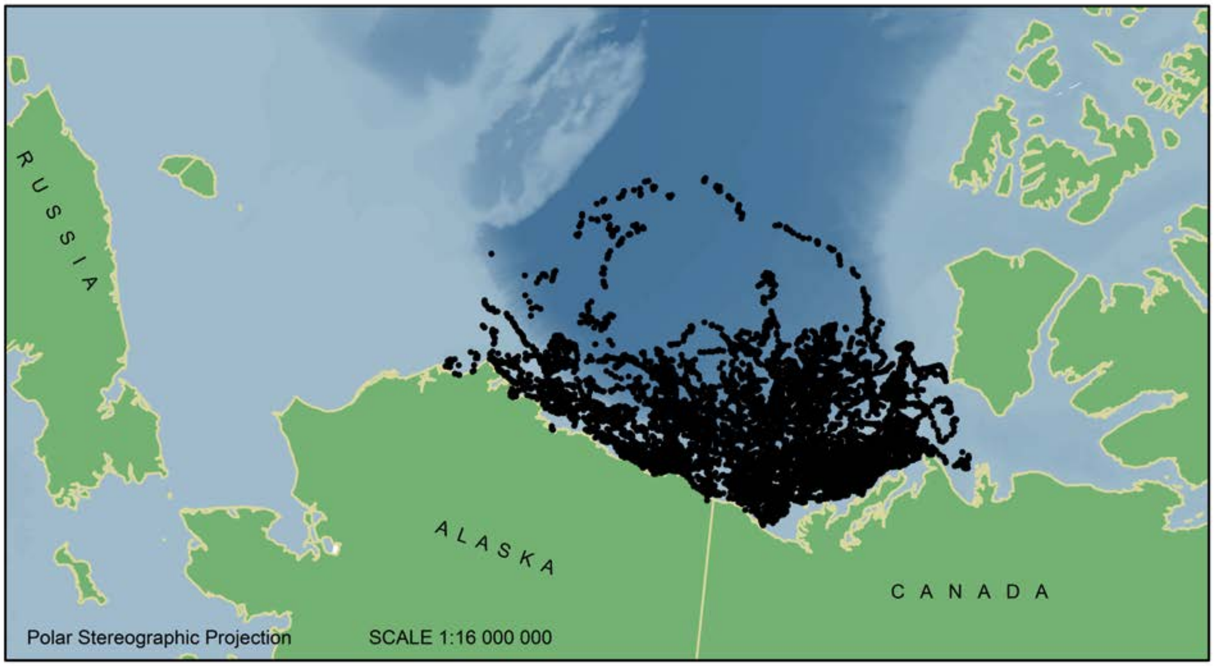

Figure 10 All locations (n=13,603) for subadult male polar bears in the Southern Beaufort Sea, collected between 2007 and 2010

# Seasonal distribution of polar bears[2]

Polar bears are entirely dependent on sea ice which they hunt, travel, mate (Smith 1980; Stirling and Derocher 1993), and in some cases, den on (Lentfer 1975; Amstrup and Gardner 1994). They are an obligate predator of seals, and their survival and reproduction are dependent on the acquisition of sufficient fat reserves through hunting success during late spring and early summer (Stirling et al. 2008). Ringed seals and bearded seals are the primary prey of polar bears in the Beaufort Sea (Smith 1980; Stirling and Archibald 1977; Thiemann et al. 2008). Seal distribution, and therefore polar bear distribution, is strongly influenced by shore leads, polynyas, areas of annual and multi-year sea ice, and patterns of freeze-up and break-up (Stirling 2002). Annual ice overlaying the continental shelf is the most biologically productive polar bear habitat, yielding greater seal abundances than deeper waters of the polar basin (Derocher et al. 2004; Durner et al. 2009).

The Southern Beaufort Sea polar bear population is experiencing notable declines in sea ice extent (Comiso and Parkinson 2004) and multiyear ice (Rothrock and Zhang 2005; Stroeve et al. 2007; Maslanik et al. 2011). Polar bears inhabiting this region are expected to be one of the populations most affected by climate warming (Regehr et al. 2007; Stirling and Derocher 2012).

In general, Southern Beaufort Sea bears respond to seasonal fluctuations in sea ice by moving north to multi-year pack ice when the annual ice melts, and returning south when it refreezes. The recent trend of later sea ice freeze-up and earlier sea ice break-up is forcing

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[2] A version of this segment of the report is in preparation as a peer reviewed publication as Pongracz, J., and Derocher, A.E. in prep. Seasonal distribution of polar bears in the Beaufort Sea.

Southern Beaufort Sea bears to either spend the summer on sea ice over deep waters where productivity is low or on land where food is limited (Amstrup et al. 2006; Schliebe et al. 2008). Recently, polar bears in the Beaufort Sea have shifted to denning on land from offshore regions and this shift was attributed to a decline in suitable sea ice substrate for denning (Fischbach et al. 2007). Changes in sea ice extent and condition in the Beaufort Sea were associated with declines in cub survival, instances of bears clawing through solid ice in an attempt to catch seals, cannibalism, drowning, and starvation (Amstrup et al. 2006; Monnett and Gleason 2006; Stirling et al. 2008; Regehr et al. 2010; Hunter et al. 2010; Rode et al. 2010).

It is well known that polar bears respond to seasonal and interannual variation in sea ice distribution (e.g., Stirling et al. 1993, Mauritzen et al. 2003, Durner et al. 2009), yet quantification of temporal variation in polar bear distribution has not been studied. How bears respond to seasonal and annual fluctuations in sea ice provides insight to how bears may respond to continued climatic changes. We examine polar bear distribution from June 2007 through May 2011, a period with four record breaking years of low sea ice extent (Stroeve et al. 2011a). Our main objective is to analyze distribution patterns to determine how polar bears respond to changing sea ice conditions. We focus on: 1) how the distribution of polar bears changes seasonally, 2) and identify areas of seasonal importance relative to sea ice cover, and 3) annual variability in the distribution of polar bears. We predict polar bears will use habitat of increasing distance to shore and thus increasing ocean depths as ice cover decreases seasonally and in years of low sea ice extent over time.

## Methods

## Study Area

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

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

Break-up begins in late April at the headwaters of the Mackenzie River and extends northward (Carmack and MacDonald 2002). Along the continental shelf, break-up spreads from the shore lead (Carmack and MacDonald 2002). Freeze up begins in early to mid-October.

## Polar Bear Location Data

Location data were obtained from polar bears fitted with global positioning system (GPS)

Argos® satellite-linked collars. Two types of collars were used: Telonics Gen III GPS collars and Telonics Gen IV GPS collars (Telonics, Mesa, Arizona). Polar bears were located using a helicopter (Bell 206 or A-Star B2) and immobilized with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®) following standard procedures (Stirling et al. 1989). Capture and handling methods were in accordance with the Canadian Council on Animal Care guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee. Nine adult females and 9 subadults were collared in 2007; 5 adult females and 6 subadults were collared in 2008; 17 adult females and 8 subadults were collared in 2009; and 10 adult females were collared in 2010 (**Figure 11**). Collaring was extending into 2011 and 2012 with support outside of this contract. Collars were deployed between mid-April and mid-May, and programmed to acquire GPS locations every 4 hours.

## Location Processing

For GEN III collars, 95% of position fixes are within 13-36 meters of the actual location (Telonics 2004), GEN IV collars have a typical accuracy of 2-10 meters (Telonics 2009). Location paths of bears tracked were scrutinized, and erroneous locations were removed. Location data from collars thought to be dropped on ice were excluded from analysis; suspect collars were identified from high similarity to sea ice movement rate and patterns, and in consideration of previous bear movements and seasonal activities.

Seasons were defined based on bear biology, bear movement patterns, and patterns of sea ice freeze up and break up. Spring included March – May, summer: June – September, autumn: October - November, and winter: December – February.

## Kernel Densities

We examines polar bear space use using kernel densities, which provide an estimated probability density function corresponding to an animal's utilization distribution (UD) (Kernohan et al. 2001; Van Winkle 1975; Worton 1987). The UD, which is the intensity or intensity of use over an animal's home range (Kernohan et al. 2001; Van Winkle 1975), is first used to measure space use on an individual level, and then used to measure joint space use of multiple animals.

The kernel estimator can be visualized as the sum of bumps placed over each bear location, where the shape of the bumps is determined by the function, and the width of the bumps is determined by the smoothing parameter or bandwidth selected (Silverman 1986). The probability density at a given location within the study area is the sum of all kernels at that location. The kernel density approach is nonparametric, thus no assumptions about the underlying distribution are made. Autocorrelation of location data likely causes home range estimates bias (Swihart and Slade 1985). However, when the study period is fixed, autocorrelation is less important than the representative sample and subsampling decreases home range estimation (Fieberg 2007; Otis and White 1999).

Kernel density is sensitive to the bandwidth. Bandwidth selection is important because an over-smoothed (too large of a bandwidth) will extend the home range of an animal beyond realistic boundaries and bandwidth too small will produce a fragmented utilization distribution resulting in inadequate connection of space within a home range (Blundell et al. 2001; Gitzen et al. 2006; Kernohan et al. 2001). Bandwidth should be selected based on data characteristics because no bandwidth method is superior in all situations (Gitzen et al. 2006). We used the plug-in bandwidth calculation method which performs as well as or better than least squares cross validation (LSCV) (Gitzen et al. 2006), which has a tendency to cause data to fragment (Blundell et al. 2001; Kernohan et al. 2001; Kie et al. 1996) and can fail if many points have the same or close to the same value (Silverman 1986). Furthermore, the plug-in method performs best with partially-clumped data, and is recommended when examining species that range widely across the home range (Gitzen et al. 2006). The plug-in method was chosen *a priori* for the current study because 1) polar bears range widely across the home range, and 2) location data tend to be clumped at differing time scales (seasonally and on a smaller scale due to foraging activities). Bandwidth was constant for each density estimate (fixed kernel), resulting in a bandwidth that may be unique for each bear for each month. The two stage plug-in approach used to estimate bandwidth calculates a preliminary bandwidth based on the covariance matrix. This initial bandwidth is plugged into a function estimating the first stage bandwidth, and the resultant bandwidth is plugged into a lower-derivative function; this second stage bandwidth is then used to estimate the final bandwidth (Gitzen et al. 2006; Wand and Jones 1994). Bandwidth was calculated in R using package ‘ks’ (Duong 2007). The plug in approach used the asymptotic integrated mean squared error approach (Duong and Hazelton 2003), the bandwidth matrix was diagonal (constrained to smooth in directions parallel to the co-ordinate axes), and the data were pre-scaled. To accommodate kernel density analysis, the study area was overlaid with a grid of 2.5 $km^2$ cells with a modified Albers projection with a central meridian of 138.3˚ W and standard parallels of 67.9˚ and 75.7˚ N latitude.

Number of locations per bear per day varied between 0 and 6. A monthly kernel density was estimated for each bear with >40 locations in 20 days. In general, bias and variance asymptote at about 50 locations for kernel densities (Seaman Monthly kernel densities were calculated to measure the joint space use of multiple animals. Because bear locations per month varied, monthly bear kernel densities were assigned a weighted contribution according to the number of monthly locations per bear. Hence, grouped monthly kernel densities were determined by multiplying each bear density by the proportion of data contributed during that month and summing all resulting kernel densities. Seasonal kernel densities were calculated by summing months within the season, where each month was weighted equally. Kernel densities were calculated using the ‘kde’ function in Geospatial Modelling Environment (Hawthorne 2010).

Kernel densities are depicted using percent contours that with the 10, 50, and 95% intensity of use calculated using Hawths Tools (Hawthorne 2006).

## Bathymetry

Bathymetry data with a 2.5 $km^2$ resolution (Jakobsson et al. 2008) was reclassified to categorical values as land or water by 100 m increment to 4000 m and then pooled for greater depths. The volume of the UD for each season in each of the differing categorical values was used to classify selected bathymetries.

## Results

A total of 41 adult females were collared with 17 alone, 5 with cubs-of-the-year (COYs), 15 with yearlings, and 4 with two-year-olds (2yr). Twenty-three subadults (12 females, 11 males) were tracked (**Table 1**). Overall, Gen IV collars performed superior to Gen III collars. Gen III collars worn by bears that met the requirement for being included in monthly analysis provided an average of 113 locations per month (95% CI = 110-115); Gen IV collars that met the requirement for being included in analysis provided an average of 145 locations/r month (95% CI=142-148). The sample size varied over time due to variation in collar design, deployment, and both planned and unplanned collar retention times (**Table 2**). One lone adult female (X32690) collared in April 2009 emigrated to the Chukchi Sea near Wrangel Island, Russia (**Figure 5**) and was excluded from analyses.

## Kernel Density Estimation

Monthly kernel densities (n=559) were calculated between June 2007 and May 2011 (**Table 2**). Mean number of locations per bear per month for kernel densities was 133 (95% CI=131-136, range 47-186; for details see Appendices 1-5). A total of 74,527 polar bear locations were used to calculate kernel densities (see **Tables 3-8**); 9537 locations from 2007, 9507 from 2008, 23700 from 2009, 24389 from 2010, and 7394 from 2011 (**Figure 12**). A low number of bears contributed to kernel densities in February – April of 2008 (3, 3, and 2 bears, respectively), and March and April of 2009 (5 and 4 bears, respectively).

In overview, the bears caught in the Canadian portion of the Southern Beaufort Sea did not conform well to the population boundaries formally recognized by the IUCN/SSC Polar Bear Specialist Group (i.e., **Figure 1**). Based on minimum convex polygon analysis, substantial overlap between the adjacent populations in the Chukchi Sea, Northern Beaufort Sea, and Arctic Basin was evident and further eastward some overlap was noted with the Viscount Melville population (**Figure 13**). On a seasonal basis, the bears most closely conformed to the Southern Beaufort boundaries in winter and spring and the least in summer and autumn. Lack of conformation with the recognized boundaries is likely due to shifting sea ice conditions. Analyses are ongoing and will investigate the role of age-specific distribution on population structure.

In summer 2007, 6035 bear locations over 55 bear months were used to calculate kernel densities. The highest intensity of use was along Barter Island and the Barrier Islands from Kaktovik to Prudhoe Bay in Alaska and in the near shore regions to east and west (**Figure 14**). Intensity of use along the continental shelf north of Alaska was largely between the 200 m isobath and the coastline (**Figure 15**). Intensity of use from bears that used the pack ice appears greatest along the pack ice edge through the northward ice retreat between July and September. There was also an area of higher intensity of use near northwest Banks Island. The probabilities of use contours reveal a gap between use near shore and use on pack ice with continuum located north of Kaktovik that connects the two regions.

## Summer

A total of 4152 bear locations over 37 bear months were used to calculate kernel densities for summer 2008. Although fewer bears were used to calculate the kernel density for this season, the 95% intensity of use contour covers a larger area than summer 2007. The highest intensity of use during summer 2008 occurred on Barter Island, along the Barrier Islands between Kaktovik and Prudhoe Bay (**Figure 16** and **Figure 17**), and along the spits east of Barrow (**Figure 18**). There was also a high intensity of use west of Banks Island, just beyond the continental shelf and north towards Prince Patrick Island. In comparison to the other summers examined, summer 2008 displays less intensity of use over the continental shelf along the Alaskan coast. Intensity of use contours extend in a north then west direction from north of Barrow towards the northern Chukchi Sea. A notable gap between use near shore and on pack ice is evident.

Summer 2009 kernel densities (n=10890 bear locations, n=80 bear months) revealed that 95% intensity of use contour covered the smallest area relative to the other summers examined despite a larger number of locations. Highest intensity of use occurred along the south edge of the sea ice extent, west of Banks Island and near shore along the Alaskan and Yukon coasts between Kaktovik and Hershel Island (**Figure 19** and **Figure 20**). The 95% intensity of use area did not extend as far north as in the previous two summers. The continental shelf between Prudhoe Bay and Kaktovik highlights a continuum between the near shore regions and the contours over the deeper waters of the Arctic Ocean Basin.

Kernel densities for summer 2010 (n=7893 bear locations, n=62 bear months) indicated the highest intensity of use occurred along the Alaskan coast between the Canadian/Alaskan border to just west of Prudhoe Bay, and between the coastline and the 200 m isobath (**Figure 21**). Unlike previous summers, the highest intensity of use within this region occurred just north of and not over the Barrier Islands (**Figure 22**). There was also high concentration of use west of Banks Island. The notable gap depicted between near shore and pack-ice regions in previous summers was absent in summer 2010. There was low intensity of use over the continental shelf of mainland Northwest Territories.

Overall, the southern perimeter of the intensity of use contours over the pack ice during summer seasons more or less overlies the edge of the ice pack in each year.

## Autumn

In autumn 2007, a total of 2572 bear locations over 23 bear months were used to calculate kernel densities. The highest intensity of use occurred along the continental shelf between Kaktovik and Barrow, with a distinct hotspot on Barter Island (**Figure 23** and **Figure 24**). High intensity of use also occurred west of Banks Island and in the central Beaufort Sea just beyond the continental shelf. Few vertical reaches of 95% intensity of use extend in a north-south direction over the deeper basin waters of the Beaufort Sea.

A total of 1821 bear locations over 14 bear months were used to calculate kernel densities for autumn 2008. High intensity of use occurred along the continental shelf of both Alaska and Canada. Vertical reaches of intensity of use contours extend in a north-south direction in the center of the Beaufort Sea, to the east of Banks Island and in the Chukchi Sea west of Barrow (**Figure 25**). Near shore use was focused on Barter Island and to a lesser extent, Barrow Point and associated islands to the east (**Figure 26**).

In autumn 2009 a total of 4303 bear locations over 29 bear months were used to calculate kernel densities. High intensity of use occurred along the Alaskan coast near Kaktovik and west of northwest Banks Island (**Figure 27** and **Figure 28**). Intensity of use contours formed a band just beyond the continental shelf from Banks Island west to Barrow. The gap between near shore and pack-ice regions was more distinct in the western Beaufort than in the eastern Beaufort. There were some small unconnected contours (circles) extending between the near shore region east of Kaktovik to the pack-ice.

A total of 3775 bear locations over 26 bear months were used to calculate kernel densities for autumn 2010. High intensity of use occurred west of Banks Island and along the near shore region between Prudhoe Bay to Shingle Point (**Figure 29** and **Figure 30**). Overall, the area covered by contours of 95% intensity of use was greater in the eastern Beaufort than the western Beaufort during autumn 2010.

## Winter

A total of 1881 bear locations over 17 bear months were used to calculate kernel densities for winter 2007/08. Intensity of use was highest along the center of the continental shelf from north of Tuktoyaktuk Peninsula west to north of Barrow. The majority of the 95% intensity of use contours were contained between the 200 m isobath and the coastline (**Figure 31**).

A total of 2225 bear locations over 19 bear months were used to calculate kernel densities for winter 2008/09. Intensity of use was highest along the Yukon north coast stretching east to north of Cape Bathurst. 95% intensity of use contours also stretched east along the coast from Pearce Point northeast of Paulatuk, NWT (**Figure 32**).

A total of 5936 bear locations over 40 bear months were used to calculate kernel densities for winter 2009/10. Intensity of use was highest along the continental shelf from

Kaktovik to Cape Bathurst (**Figure 33**). Beyond the continental shelf use occurred in areas west of Banks Island, north of Barrow, and northwest of Cape Parry, and to a minimal extent in Amundsen Gulf.

A total of 4182 bear locations over 28 bear months were used to calculate the kernel density for winter 2010/11. Intensity of use was highest along the continental shelf from the Barrier Islands between Prudhoe Bay to mid-way across the Yukon coast and from northwest of Tuktoyaktuk to Clinton Point (**Figure 34**). As in previous years the intensity of use is contained primarily between the 200 m isobath and land. There was some use over the deeper basin waters north of Kaktovik and from north of Tuktoyaktuk Peninsula to west of Banks Island.

## Spring

A total of 1770 bear locations over 16 bear months were used to calculate the kernel density for spring 2008. The small sample size yielded relatively fragmented intensity of use contours that ranged primarily over the continental shelf from Prudhoe Bay, Alaska to north of Cape Bathurst, with an outlier to this region occurring in the Chukchi Sea northwest of Barrow (**Figure 35**).

A total of 5161 bear locations over 34 bear months were used to calculate the kernel density for spring 2009. Other than the minimal intensity of use in the central Amundsen Gulf, the intensity of use is concentrated between the 200 m isobath and land along the Yukon coast east to Cape Bathurst (**Figure 36**).

A total of 7249 bear locations over 50 bear months were used to calculate the kernel density for spring 2010. The highest intensity of use was along the center of the continental shelf off the shore of Yukon and the Northwest Territories east to Cape Bathurst (**Figure 37**). There was also some use in the near shore around Barrow, north of Prudhoe Bay, and in Amundsen

Gulf. Overall, the 95% intensity of use contours extended further north beyond the continental shelf in spring 2010 than in other years examined.

A total of 4682 bear locations over 29 bear months were used to calculate the kernel density for spring 2011. The highest intensity of use remains along the center of the continental shelf from the Alaska/Canadian border to east of Bathurst Peninsula (**Figure 38**). Intensity of use in spring 2011 shows greater use of the Amundsen Gulf area and near shore regions south of Banks Island in comparison to previous years examined.

### Use as it relates to summer ice cover and ocean depth

Summer refugia were located in three different areas: the Alaskan coast, central northern Beaufort Sea, and the northeastern Beaufort Sea near Banks Island (**Figure 39**). The volume of kernel density is greatest over water between 1-99 m deep (defined *a priori* to represent the majority of the continental shelf) in all seasons, with this region being used most intensively in winter and spring of all years (Summer: **Figure 40**, Fall: **Figure 41**, Winter: **Figure 42** and Spring: **Figure 43**). Deeper waters of the ocean basin have a greater volume of kernel density in summer and autumn than winter and spring. The volume of kernel density over the deepest waters is greatest in summer and autumn of 2007, coinciding with the lowest sea ice extent on record. Land was used to some extent in all seasons, most notably in autumn.

## Discussion

The Southern Beaufort Sea population is estimated to be 1526 bears (95% = 1211-1841) (Regehr et al. 2006) and we assume the 60 adult females and subadults tracked are representative of the Southern Beaufort Sea population. This is important because movement rates and habitat use is thought to differ by sex and female reproductive status (Amstrup et al. 2000; Stirling et al. 1993). However, no adult male bears were tracked. Not all sex-age classes (including female reproductive classes) are equally represented in each season. Collaring effort focused on the area from the Canadian/Alaska border to just west of Cape Bathurst, and was consistent between years; no bears were collared in the regions within the Southern Beaufort Sea population to the east and west of this area. Because polar bears demonstrate high seasonal fidelity in spring (Mauritzen et al. 2001) it is probable that kernel densities of our study best represent this subsection of the Southern Beaufort Sea polar bear population. Future projects should include information from bears collared both within the Canadian and Alaskan portions of the Southern Beaufort Sea.

Polar bear distribution changed seasonally in response to sea ice distribution. Seasonal variation in prey availability play a role in affecting seasonal distribution (Stirling 2002). Adult males, not considered in this study, are thought to distribute themselves according to available females (Ramsay and Stirling 1986). Polar bears are concentrated over the shallower waters of the continental shelf in spring and as the ice melts, they concentrate in three primary areas: near shore along the Alaskan coast, offshore over the deeper waters of the Beaufort Sea, and west of Banks Island. In autumn, polar bear distribution reaches south to shallower waters over the continental shelf as permitted by sea ice extent, and remains there over winter during which distributions gradually move to regions used in spring. Kernel density estimates identified areas of seasonal importance where polar bears spend more time within each season. Though these areas of seasonal importance are similar in most years, there are some noteworthy differences among seasonal use between years that are likely attributable to sea ice conditions and distribution.

In all springs (and winters), two areas of importance were identified: 1) the middle of the continental shelf north of Tuktoyaktuk Peninsula, and 2) the region near shore from Shingle Point to the area around Kaktovik. It should, however, be noted that spring kernel densities must be viewed in light of the fact that few bears were tracked in March and April of 2008 and 2009, limiting the extent to which distributions represent the larger Southern Beaufort Sea population and the ability to compare annual variability across springs. Bear distributions in spring were concentrated in the region collars were deployed for two reasons, firstly, many bears tracked in May were recently collared, and secondly, bears have been noted to display a high degree of seasonal fidelity (Derocher and Stirling 1990a; Mauritzen et al. 2001). Seasonal fidelity was noted to be weaker in spring and higher in summer (Amstrup et al. 2000).

The edge of the landfast ice and areas of open water and active ice are important habitats with adult and subadult males, lone adult females, and adult females with 2yr olds preferring floe edge habitat in spring (Stirling et al. 1993). Floe edge habitat houses the highest densities of ringed seals and bearded seals in the study area (Frost et al. 2004). Ringed seals that are not breeding and bearded seals of all ages are also abundant in moving ice habitat found near the floe edge (Stirling et al. 1993). The current study found the highest volume of kernel densities to be located over shallow depths (1-99m: see **Figures 40-43**) and coincides with the highest ringed seal densities that occur at depths of 50-75m and decline over deeper waters (Stirling et al. 1982). Likewise, ringed seal densities in the Alaskan Beaufort Sea during spring and early summer are highest in shallow waters between 5 and 35 m deep (Frost et al. 2004). From this we infer that the high use of the shallows in spring occurs because seals are found in greater abundance in these areas and hunting success may be higher. The floe edge may furthermore be sought for the high potential to encounter mates during the April and May breeding season (Ramsay and Stirling 1986; Stirling et al. 1993).

Polar bears congregate over the continental shelf to hunt seals not only along open or refrozen leads, but also at seal lairs (Stirling et al. 2008). During late March to early April ringed seals give birth to their pups and suckle them in subnivean liars above their breathing holes

(Smith and Stirling 1975). Such subnivean liars are located in drifting snow accumulated along cracks and pressure ridges where breathing holes may be present (Stirling et al. 1977), such habitat is commonly found in stable fast ice with pressure ridges that have not moved in some time (Stirling et al. 1993). In the study region, such habitat has been documented to occur landward of the moving ice near the shore lead from Cape Bathurst west to Shingle Point (Stirling et al. 1993). Ringed seal pups are a vital food source for females with COYs in particular. Upon emergence from the den, females immediately select ringed seal pupping habitat to replenish depleted fat reserves (Stirling and Lunn 1997). Females with COYs are the only age group to preferentially select such habitat, likely because it avoids exposing their young to the potential hazards of open water and the risk of encountering adult males that may threaten their COYs (Stirling et al. 1993).

In addition to the above noted areas of importance in spring, and in relation to adult female with COY distribution, it should be noted that several land and nearshore areas related to denning were identified. Although locations from bears in dens were not included in creating kernel densities, their locations once they emerged in spring were. Areas used upon emergence from the den by females with COYs include: on land and near shore around the Alaskan/Yukon border, Baillie Island, and the east side of Cape Bathurst. The Pearce Point region was also utilized, however for facultative denning and not maternity denning.

In summer three important areas of use were identified: 1) along the north coastline of Alaska most notably at Barter Island and the Barrier Islands, 2) along the edge of the pack ice, and 3) west of Banks Island. In the autumn these areas were also identified as important in most years. It is noteworthy, however, that the highest intensity of use occurred at Barter Island in summer and autumn of all years with the exception of 2010, where intensity of use was highest just offshore of this area; this general pattern held for use of the Barrier Islands as well.

Summer and autumn kernel densities were consistent with previous studies of polar bear habitat use. Southern Beaufort Sea polar bears follow the southern edge of the pack ice as it retreats north (Amstrup 2000; Stirling 1975), and spend the summer off the northern coast of Banks Island (Stirling 2002). Some bears move between mainland and the pack ice as long as the sea ice is intact (Stirling et al. 1975; Durner et al. 2011; Pagano et al. 2012). High intensity use of land during summer and autumn in all three years along the Alaska coast indicate that this is a refuge habitat, the current study indicates that more bears are on land during the open water period than were previously (Fischbach et al. 2007; Schliebe et al. 2008; Gleason and Rode 2009). An average of 3.7% (maximum of 8%) of bears from the Southern Beaufort Sea population is on land during the autumn (Schliebe et al. 2008).

Bear densities are higher in regions where whales are harvested; Rode and Gleason (2009) noted that a large number of bears monitored during a bowhead whale survey were associated with whale harvests, while (Schliebe et al. 2008) noted 69% of bears sighted on shore in an autumn aerial survey occurred at Barter Island alone. Barter Island houses a bone pile where the remains of harvested bowhead whales are deposited after the autumn bowhead whale harvest (Miller et al. 2006). Bowhead whales compose between 11-26% (mean estimate of 18%) of the diets of polar bears sampled along the Alaskan Beaufort Sea in 2003 (Bentzen et al. 2007). In 2004, this composition changed to 0-14% indicating a high variability in proportion of bowhead whales can be found in the diet of polar bears between individuals and across years. Ringed seals, which compose the majority of diets (53-100%, mean 77%) of Southern Beaufort Sea polar bears along the Alaskan coast (Bentzen et al. 2007) (see also Cherry et al. 2011), may also be drawing bears to the near shore regions. It has been suggested that higher bear densities along the coast may be the result of 1) bears being encouraged to move to land from the sea ice so they have access to seals over the continental shelf or 2) bears being in a prime location to take advantage of hunting opportunities once ice begins to freeze again (Schliebe et al. 2008). Polar bear densities have been noted to increase with increasing ringed seal densities (Schliebe et al. 2008).

The current research noted intensity of use during fall/summer 2010 to be highest just offshore and not on Barter Island and the Barrier Islands as was the case in previous years. MODIS images of the BeaufortEast and BeaufortWest subsets provided by the National Aeronautics and Space Administration Goddard Space Flight Center reveal there was a large amount of broken ice in the near shore region throughout the summer and autumn of 2010. This behavior suggests that when given the opportunity, polar bears that have remained near the mainland during summer/autumn prefer to be on sea ice over the continental shelf where hunting is possible when opportunity to do so exists. Previous research has also noted that polar bears take advantage of the sea ice as soon as it is available (Gleason and Rode 2009; Schliebe et al. 2008).

It has furthermore been suggested that bear densities may be higher near Barter Island because this region often offers the shortest distance from land to pack ice (Schliebe et al. 2008). Monnett and Gleason (2006) noted that bears observed making long distance swims during the autumn annual bowhead whale aerial surveys in the Beaufort Sea were concentrated near the Camden Bay/Barter Island region. Bears from the current research were also observed to swim between the Barter Island region and pack ice offshore. The intensity of use contours for all summers (but most notably 2007 and 2009), as well as fragmented circles of contours of use in the utilization distribution from autumn 2009, support the suggestion that movement occurs between the pack ice and near shore regions near Kaktovik. Miller et al. (2006) additionally noted that most bears observed feeding at the Barter Island feeding site (bone pile) arrived and departed by swimming and that bears that could be recognized fed at the site every one to two days. It may be a viable strategy for bears to move between pack-ice and bone piles at Barter Island and surrounding areas to meet nutritional needs during the fall, however, swimming between pack ice and land may come at a cost (discussed later in expected response of polar bears to projected sea ice conditions).

Our results suggest that the majority of the Southern Beaufort Sea population remains on sea ice during the summer and fall. Utilization distributions viewed in junction with sea ice concentrations during the same period, reveal that bears that remain on the pack ice either make use of the edge of the pack ice or seek refuge west of Banks Island. Several hypotheses may explain why bears may choose to remain near the edge of the pack ice. First, the pack ice edge is nearest to the shallow waters of the continental shelf, which when overlain by annual ice, house the most biologically productive polar bear habitat (Derocher et al. 2004). Second, bears remaining near the pack ice edge minimize the amount of energy required for travel (it would be more energetically demanding to travel further north on the pack ice if a bear was to return south when sea ice advances).

The region west and north of Banks Island may provide a suitable refuge for polar bears because there is often sea ice over the continental shelf in this region during summer. This attribute makes the region potentially suitable for hunting and an attractive alternative to remaining over the deeper ocean waters or on the mainland where food may be more limited. Researchers have observed that bears captured west of Banks Island were in significantly better condition in spring than those captured in the eastern portion of the Alaskan Beaufort Sea, with 47% of independent (not with mother) bears captured east of 150°W considered lean (body condition 1 or 2), and only 26% of bears captured west of Banks Island in similarly poor condition (Amstrup et al. 2006). Furthermore, multiple instances of interspecific cannibalism have also been reported near Pingok Island and Hershel Island in the Beaufort Sea; researchers surmise these killings were nutritionally motivated (Amstrup et al. 2006). No similar incidents near Banks Island have been reported.

The areas of importance during winter were similar to those identified during spring, the middle of the continental shelf north of Tuktoyaktuk Peninsula, and the region near shore from Shingle Point to the area around Kaktovik. Bears captured in this region in spring have been documented to be in better condition that bears captured further east in the Southern Beaufort (Amstrup et al. 2006).

## Response to low sea ice

During summer 2007 and 2008, the two years of the lowest sea ice extent on record (Stroeve et al. 2011b), Southern Beaufort Sea polar bear distributions suggest that bears who did not move to land travelled further north over deeper waters to remain on sea ice in comparison to the summers of 2009 and 2010 when sea ice did not recede as far north. In addition, the kernel densities of bears during autumn of 2007 and 2008 yield several distribution paths oriented north-south, suggesting bears moved south with the ice edge as it advanced during the fall. Overall such movements are energetically demanding. In contrast, the distribution of bears during summer 2009 was concentrated further south than in other years, likely reflective of the abundant extent of sea ice during this summer relative to that in the other years examined. Similarly, movements in autumn 2009 are among the most limited. It is also noteworthy that virtually none of the autumn 2007 utilization distribution overlaid the continental shelf of mainland Canada.

## The state of sea ice and future projections

Sea ice extent (defined as the area of the ocean with a fractional ice cover/concentration of at least 15%) has declined for every month from 1979 through 2006 (Stroeve et al. 2007). The first record breaking sea ice minimum occurred in 2005, and was broken in September 2007, with a sea ice extent 23% smaller than that in 2005 (Stroeve et al. 2008). September 2008-2010 had the second, fourth, and third lowest sea ice extents on record, making the trend of sea ice extent in September a loss of 12.4% per decade (Stroeve et al. 2011b). Multiyear sea ice in March has also decreased in extent in from 75% in mid 80s to 45% in 2011; furthermore, only 10% of the remaining multiyear ice is greater than five years old (Maslanik et al. 2011). On a more regional note, mean survival of multiyear ice extent in the Beaufort declined from 93% to 73% from 1981-2005 to 2006-2010 (Maslanik et al. 2011). The bulk of multiyear sea ice extent reductions are occurring in the Beaufort and the Canadian Basin, with most remaining multiyear sea ice in this region concentrated in the east alongside the arctic islands (Maslanik et al. 2011). Stroeve et al. (2011) provide evidence for three primary linked processes that influence the rapid loss of sea ice. First, extensive open water in autumn produces a domination of thin first year ice in the following spring which is more susceptible to melting during the subsequent summer (Lindsay et al. 2009). Second, an increase in thin ice that is more vulnerable to compression through ridging and rafting results in more open water areas earlier in the summer, enhancing the ice albedo feedback (Maslanik et al. 2007; Perovich et al. 2007). Third, an increase in the light that transmits through the water warms the ocean and increases bottom melting (Perovich et al. 2011). Lastly, the arctic is warming throughout the whole year, hindering the prospect for ice to recover (Stroeve et al. 2011b). Warmer spring temperatures bring about an earlier onset of melt (Markus et al. 2009) and greater amounts of open water absorb solar energy raising the measurable heat content of the ocean, delaying ice formation and increasing and creating positive temperature anomalies in autumn and winter (Serreze et al. 2009).

A discussion of the climatic changes on a regional basis and during the period of the current study (2007 through spring 2011) is relevant to understanding the subsequent analysis.

Scientists surmise that the record low sea ice extent in 2007 was preconditioned by decades of abating sea ice extent and thickness, and would likely not have occurred with abnormal winds and increased temperatures alone (Lindsay et al. 2009; Maslanik et al. 2007; Stroeve et al. 2008). In summer 2007 there was an above normal high pressure system over the western Beaufort Sea, which, along with an abnormally low pressure system over Siberia (termed the Arctic Dipole Anomaly (DA); Wu et al. 2006) resulted in southerly winds that were persistent in the western Beaufort making the ice drift northward and yielding warmer temperatures that lead to increased sea ice melt (Maslanik et al. 2007). There were also abnormally clear skies during this time (Stroeve et al. 2011a). The substantial ice melt in 2007 left spring ice cover to be composed of 72% thin first year ice (Stroeve et al. 2011b), and in the Western Arctic sea ice was 50 cm thinner than the six-year-mean (Giles et al. 2008). September 2008 was the second lowest sea ice extent on record, and set a summer record for the minimum multiyear sea ice coverage (Stroeve et al. 2011a). The DA that was present throughout the entire summer in 2007 was strong in early summer 2008, however, weaker during July and August. In summer 2009 the DA was present in June and July but changed drastically in August and September (Stroeve et al. 2011a), which resulted in a greater sea ice extent in September 2009 relative to 2007 and 2008 (Stroeve et al. 2011a). This may have suggested a temporary recovery in sea ice; however, September 2010 had a lower sea ice extent than expected based on circulation patterns the previous winter, which should have favoured ice retention during summer melt (Stroeve et al. 2011a).

Stroeve et al. (2011b) provide a thorough summary of the sea ice response to climatic conditions in winter 2009/2010. During winter 2009/2010 there was a negative phase of the Arctic Oscillation (AO), characterized by a higher than normal sea level pressure over the arctic resulting in anticyclonic ice motion, which typically promotes a strong Beaufort Gyre that moves ice from west to east pushing it up against the Siberian coast resulting in a thickening of sea ice through ridging and rafting. Substantial old thick multiyear sea ice was transported into the Beaufort and Chukchi seas; and even thought the melt season started with greater multiyear ice than in the previous two years, the sea ice extent was still recorded to be the third lowest on record. In May and June there was a strong high over the Beaufort Sea and low level pressure over northern Europe, similar to that observed in 2007. This facilitated the melting and moving of ice northward, and set a record low sea ice extent for June (2010). Atmospheric conditions changed in July and the sea ice loss rate slowed, although conditions changed back to the DA for August and early September.

In summary there has been an increase in the rate of sea ice loss in the last decade (Comiso et al. 2008; Stroeve et al. 2011b). Scientists predict that sea ice will continue to thin during winter and summer over the next 30 years (Wang and Overland 2009). Projections suggest that the Arctic may be ice-free in September (summer) as early as the late 2020s (Wang and Overland 2009). It is expected that climate change will increase storms, particularly in autumn (Carmack and MacDonald 2002). Overall, the loss of multiyear sea ice in the Beaufort Sea and Canada Basin, coupled with an increase in heat absorption in open waters and the effects of DA may be evidence that a ‘regional tipping point’ may have occurred (Maslanik et al. 2011).

## Expected response of polar bears to projected sea ice conditions

If sea ice continues to recede further from the coast each year and storms increase as is predicted (Serreze et al. 2000), polar bears will be forced to swim further distances through rougher waters between pack ice and land (Monnett and Gleason 2006; Pagano et al. 2012). In September 2004, three bears were observed dead, they were presumed to have drowned during a long distance swim between pack ice and land after a storm with high winds and rough seas (Monnett and Gleason 2006). This observation was made during a bowhead whale survey that covered only

11% of the Alaskan Beaufort Sea, therefore, it is likely that the total number of deaths attributable to drowning in rough seas over long distance swims during this period may have been much greater (Monnett and Gleason 2006). Perhaps the most notable documentation of polar bears making long distance swims is that of an adult female tracked to have made a long distance swim of 678 km over 9 days at the cost of losing 22% of her body mass (Durner et al. 2011). The survival of this bear was likely attributable to the calm seas during the time of travel, however, the fate of her yearling remains unknown, but it has been hypothesized that it likely died during the long distance movement (Durner et al. 2011). Swimming between land and pack ice may have the greatest impact on younger bears because they are more vulnerable to the impacts of increased energy expenditures due to lower fat reserves, greater heat loss and risk of hypothermia, as well as lower stamina while in water than larger bears (Derocher et al. 2004). Furthermore, the risk of swimming may increase if sources of anthropogenic disturbance increase as lack of sea ice leads to increase in shipping and resource development within the Beaufort Sea.

For the portion of the Southern Beaufort Sea population that spends some time on land, research suggests that as the distance between mainland and pack ice increases, so does the density of bears on land (Schliebe et al. 2008). Thus, if sea ice extent continues to decrease as is predicted by climatic models (Zhang and Walsh 2006), and the distance from pack ice to land increases, the amount of time bears spend on land may also increase. Miller et al. (2006) observed a 3-year average of 33.1±15.5 polar bears on Barter Island during autumn [whole island counts between 2002-2004]. Such a large number of bears close to a community has the potential to result in conflict with humans, particularly when the amount of time bears spend on land may increase and the remains of harvested whales on which they depend may not be available in any given year. Earlier break-up of sea ice cover in other polar bear populations such as Southern Hudson Bay (SH) and Western Hudson Bay (WH) have been associated with an increase in bears observed near communities, bears which are likely hungry and in search of food because they have exhausted their reserves (Stirling and Parkinson 2006). There has also been a significant relationship between sea ice break-up and the number of problem bears in the WHB, with early break-up yielding more problem bears (Stirling and Parkinson 2006; Towns et al. 2009). The situation may be somewhat different in the Southern Beaufort Sea because bears may be foraging on bowhead whale remains when on land. Research suggests that in the Southern Beaufort Sea polar bear survival, breeding probability, and cub litter survival has decreased with longer ice free conditions over the continental shelf, likely because bears are nutritionally stressed as a result of having less opportunity to forage over the productive waters of the continental shelf and thus enter winter in poorer condition (Regehr et al. 2010). The proportion of bears fasting in the Southern Beaufort Sea has also increased from 1985-1986 to 2005-2006 (Cherry et al. 2009), and declining sea ice has been associated with reductions in body size and reproduction of Southern Beaufort polar bears due to nutritional limitations (Rode et al. 2010). Furthermore, reproductive output and juvenile survival has been shown to decrease after years with lower availability of favourable sea ice habitat (Rode et al. 2010). The Southern Beaufort Sea polar bear population is projected to decline with less sea ice coverage, largely due to reduced adult female survival and reduced breeding (Hunter et al. 2010).

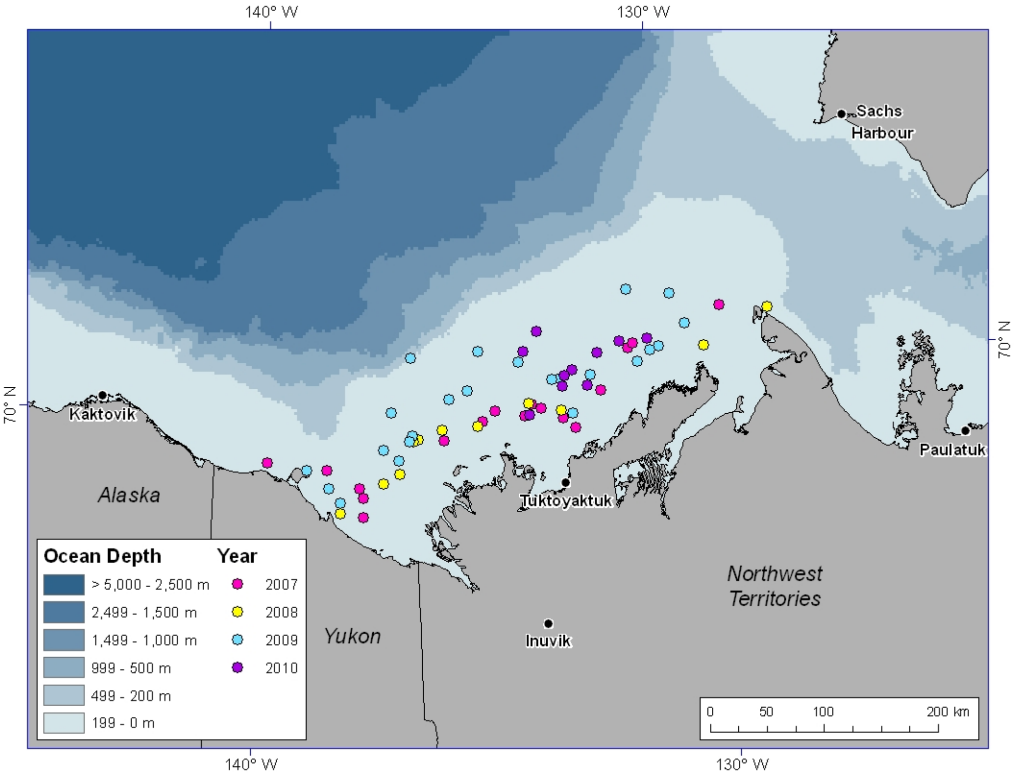

Figure 11 Locations where GPS satellite collars were deployed on polar bears 2007 – 2010.

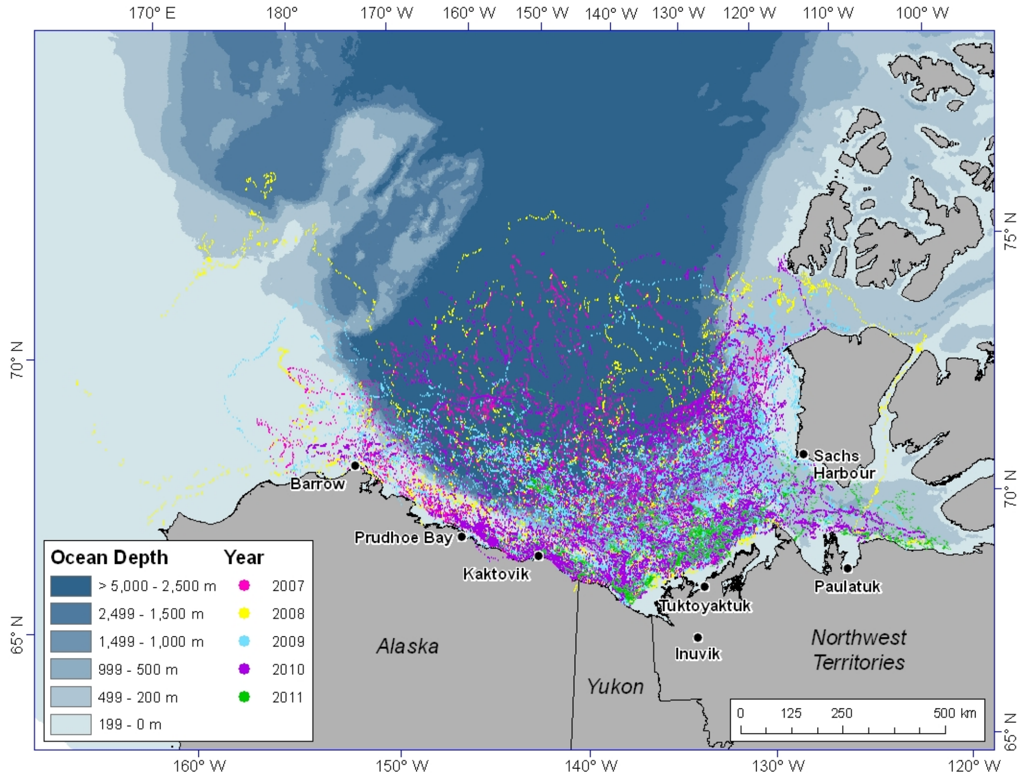

Figure 12 Locations from collared polar bears June 2007 – May 2011 used to build seasonal utilization distributions.

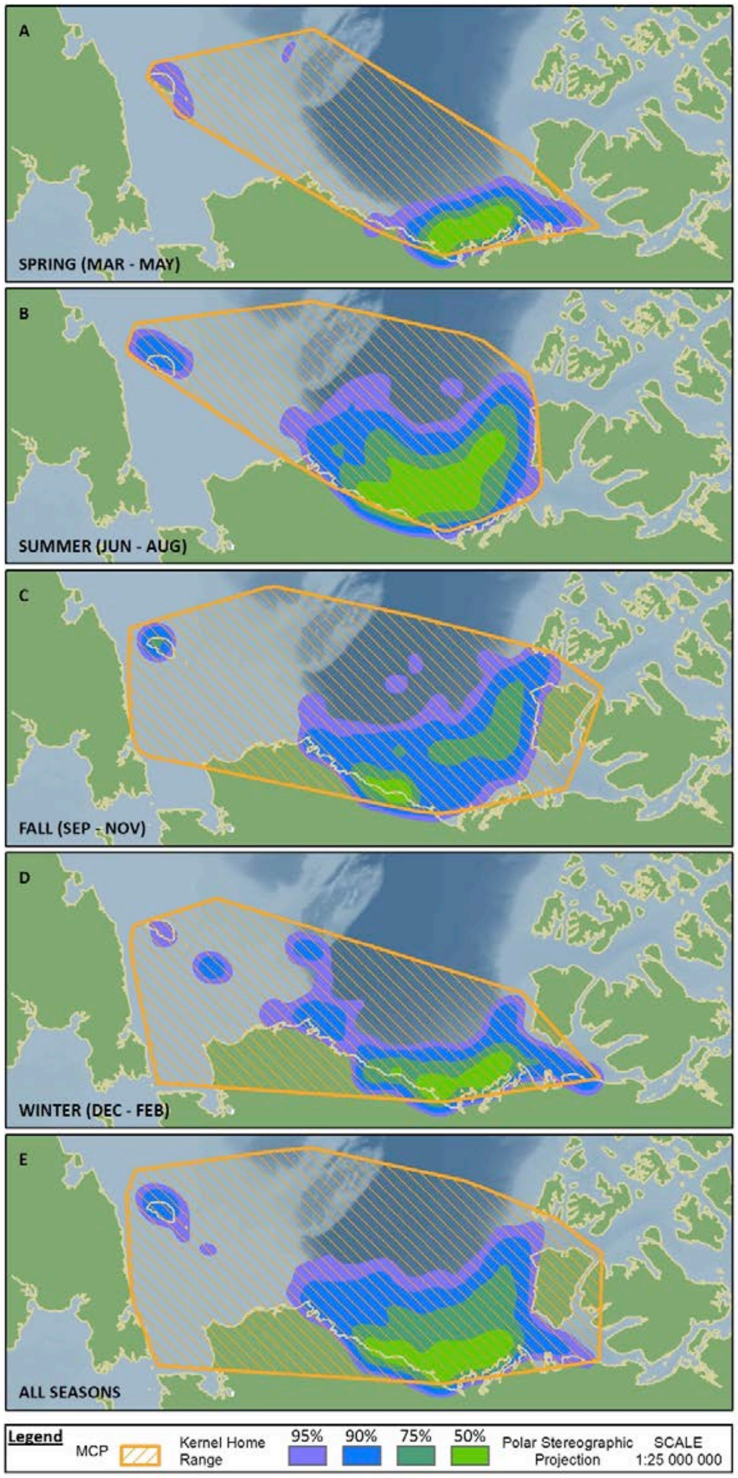

Figure 13 Minimum convex polygon (95%) and seasonal and annual kernel home ranges (95%, 90%, 75%, and 50%) for all polar bears monitored by GPS satellite telemetry 2007-10.

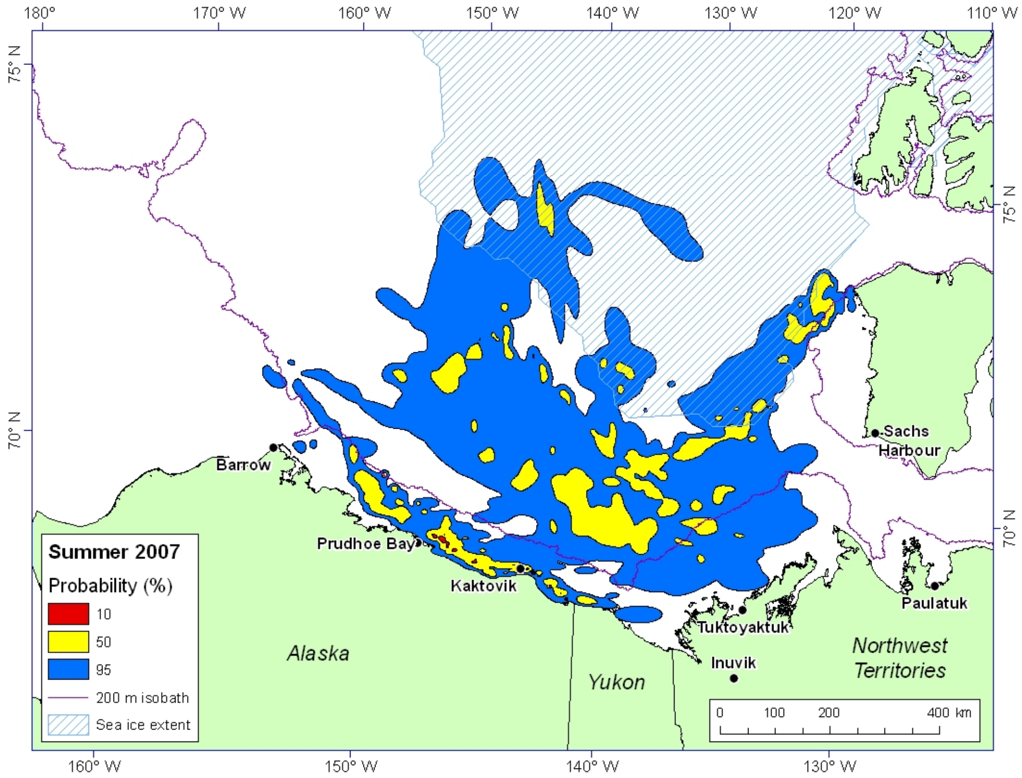

Figure 14 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in summer (June-September) 2007. Monthly sea ice extent for September and 200 m isobath are indicated.

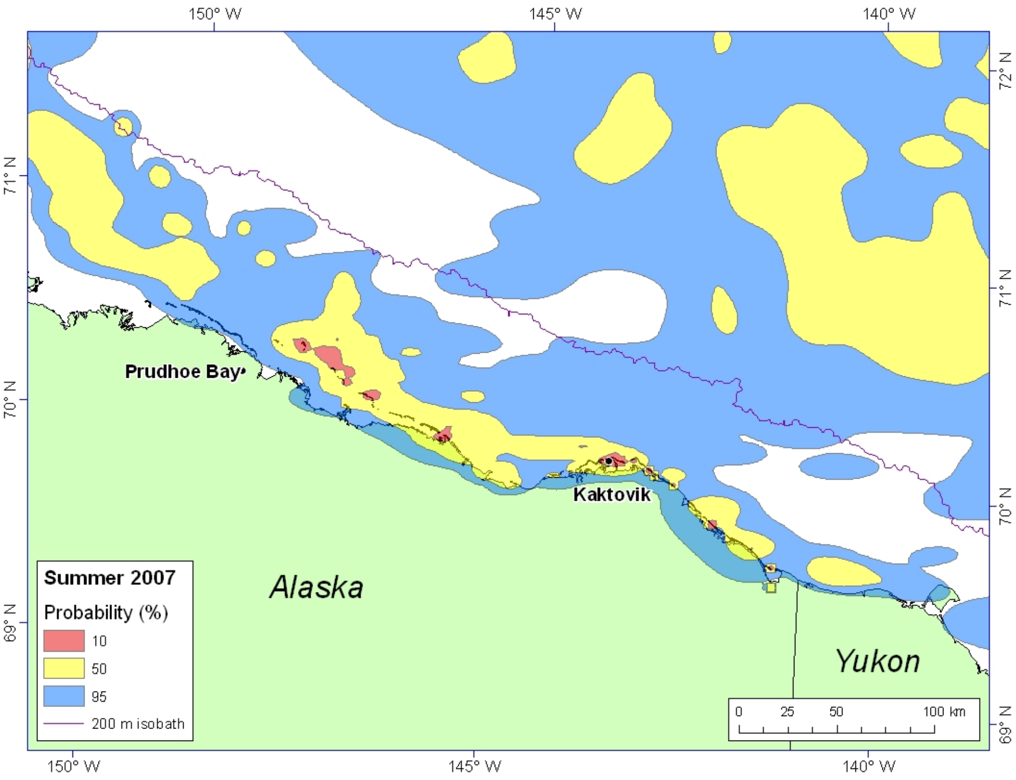

Figure 15 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska and Yukon in summer (June-September) 2007.

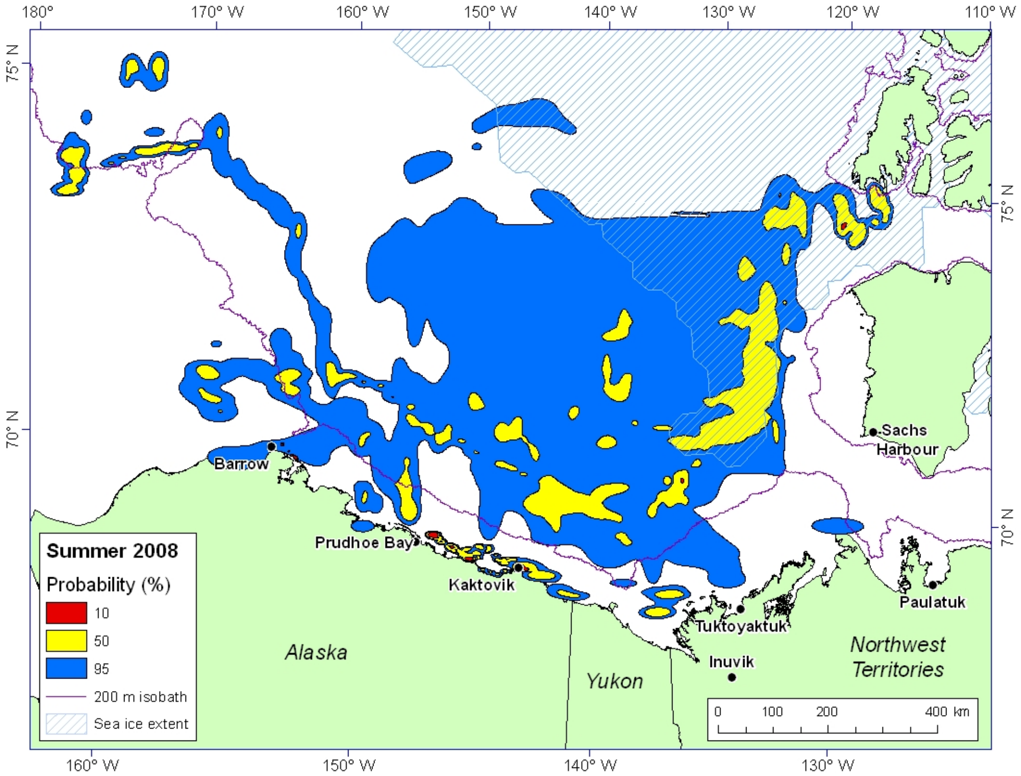

Figure 16 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in summer (June-September) 2008. Monthly sea ice extent for September and 200 m isobath are indicated.

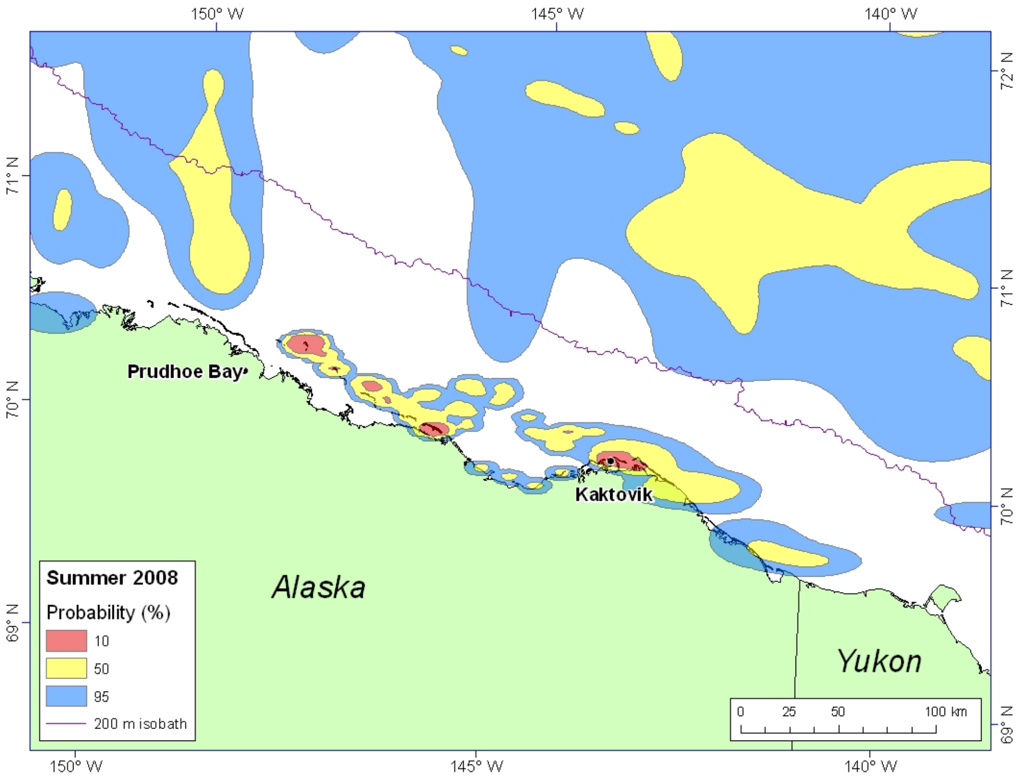

Figure 17 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska in summer (June-September) 2008.

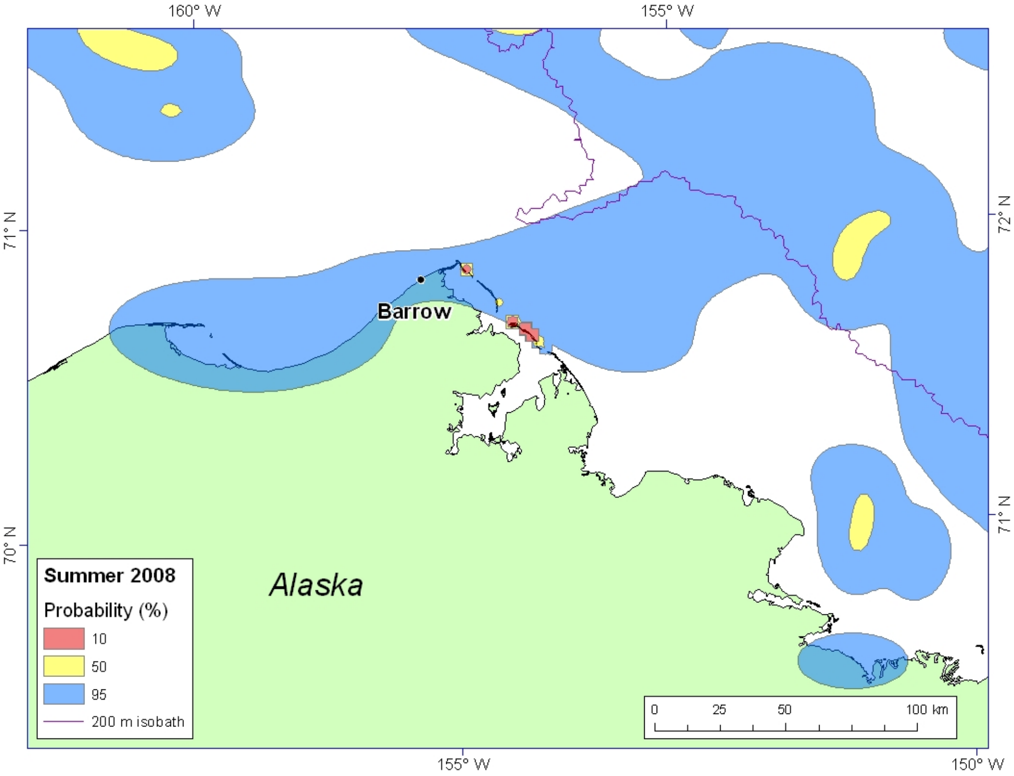

Figure 18 Contours showing the intensity of use (%) by polar bears near Barrow, Alaska in summer (June-September) 2008.

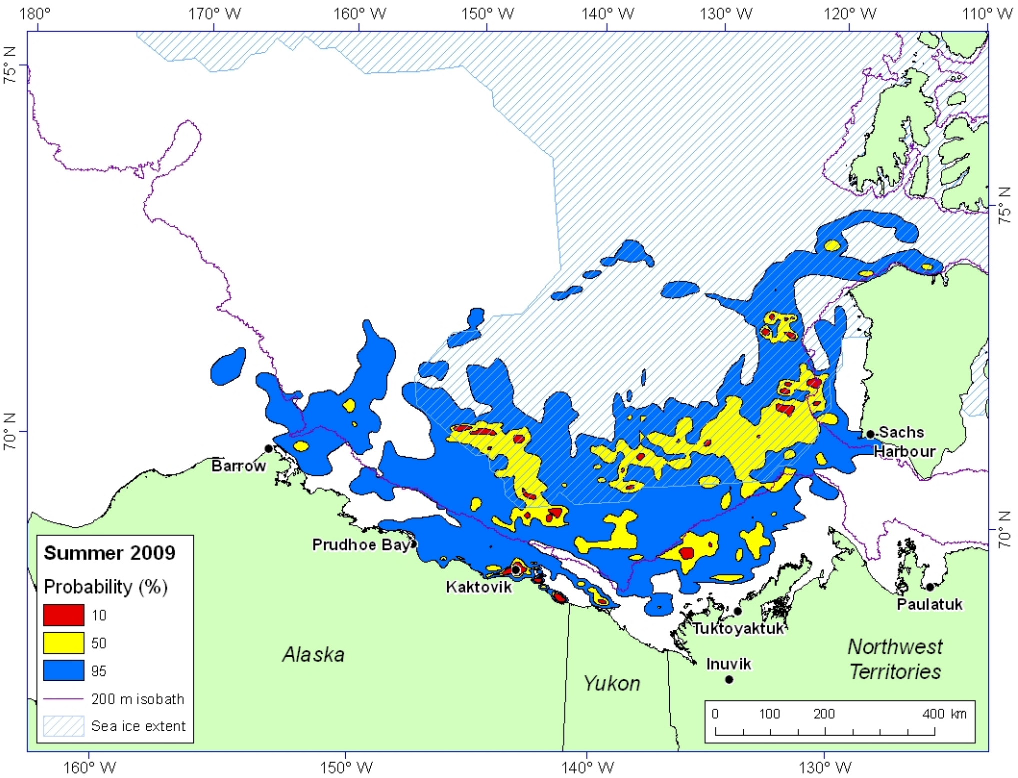

Figure 19 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in summer (June-September) 2009. Monthly sea ice extent for September and 200 m isobath are indicated.

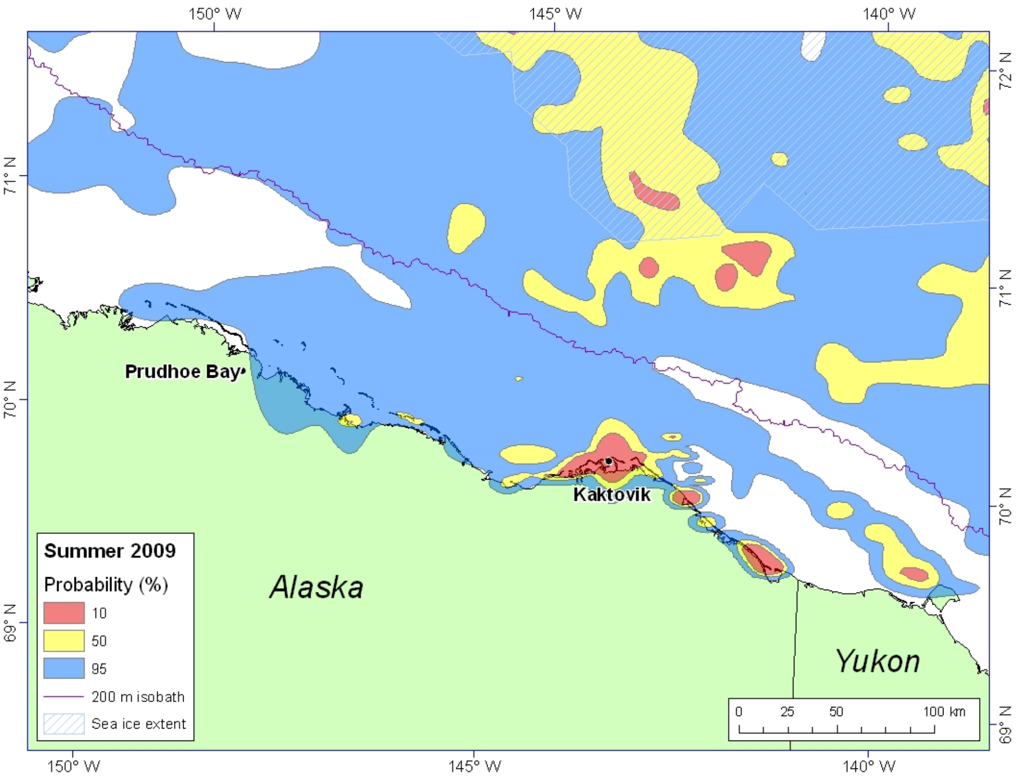

Figure 20 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska and Yukon in summer (June-September) 2009.

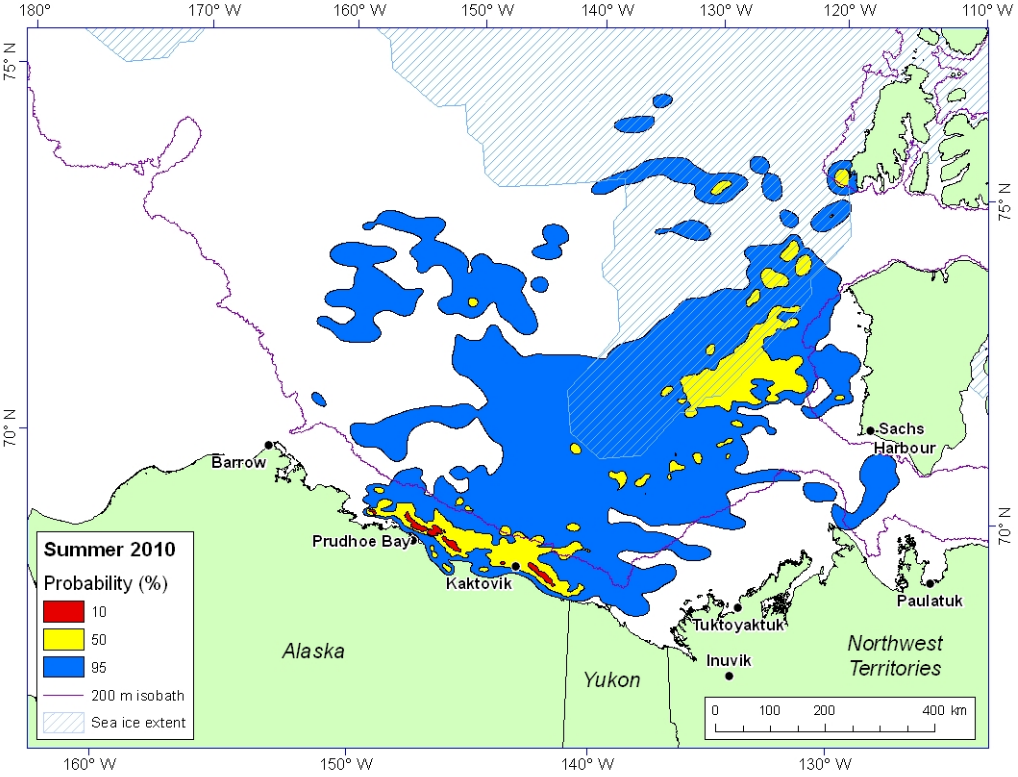

Figure 21 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in summer (June-September) 2010. Monthly sea ice extent for September and 200 m isobath are indicated.

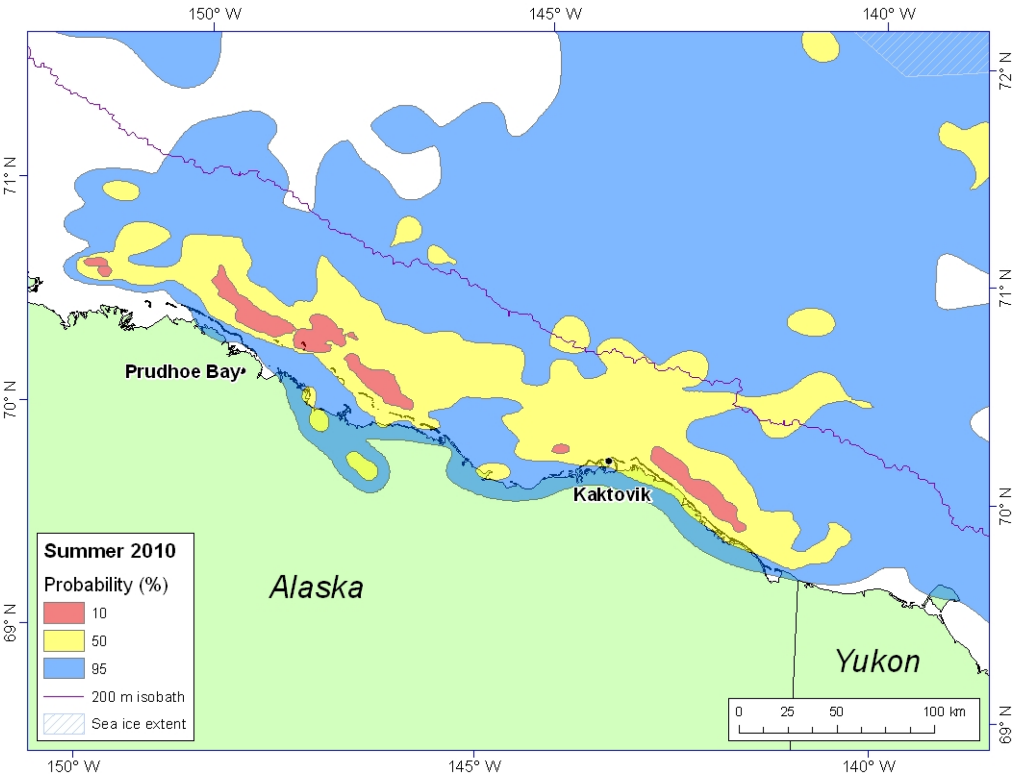

Figure 22 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska and Yukon in summer (June-September) 2010.

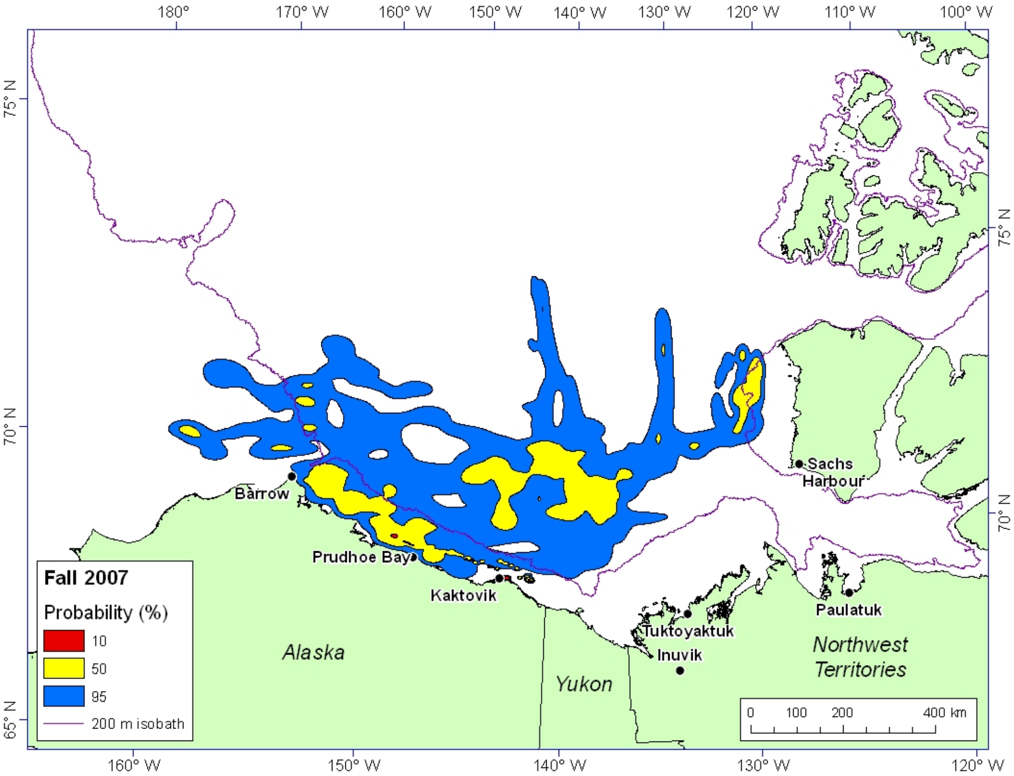

Figure 23 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in autumn (October-November) 2007.

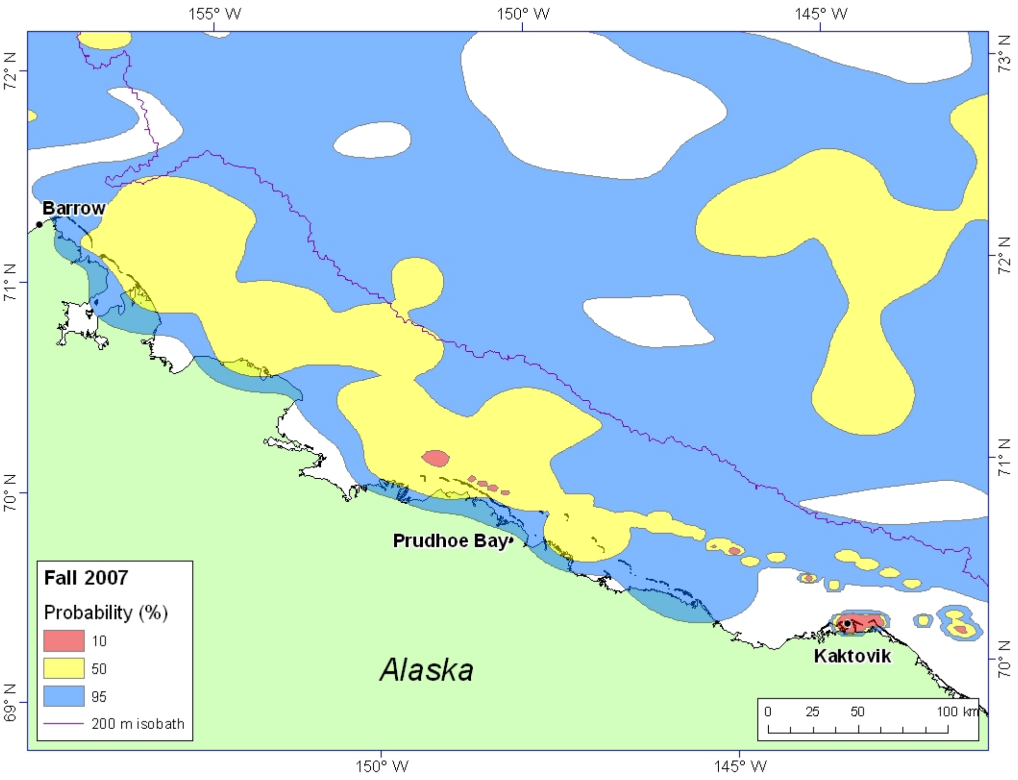

Figure 24 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska in autumn (October-November) 2007.

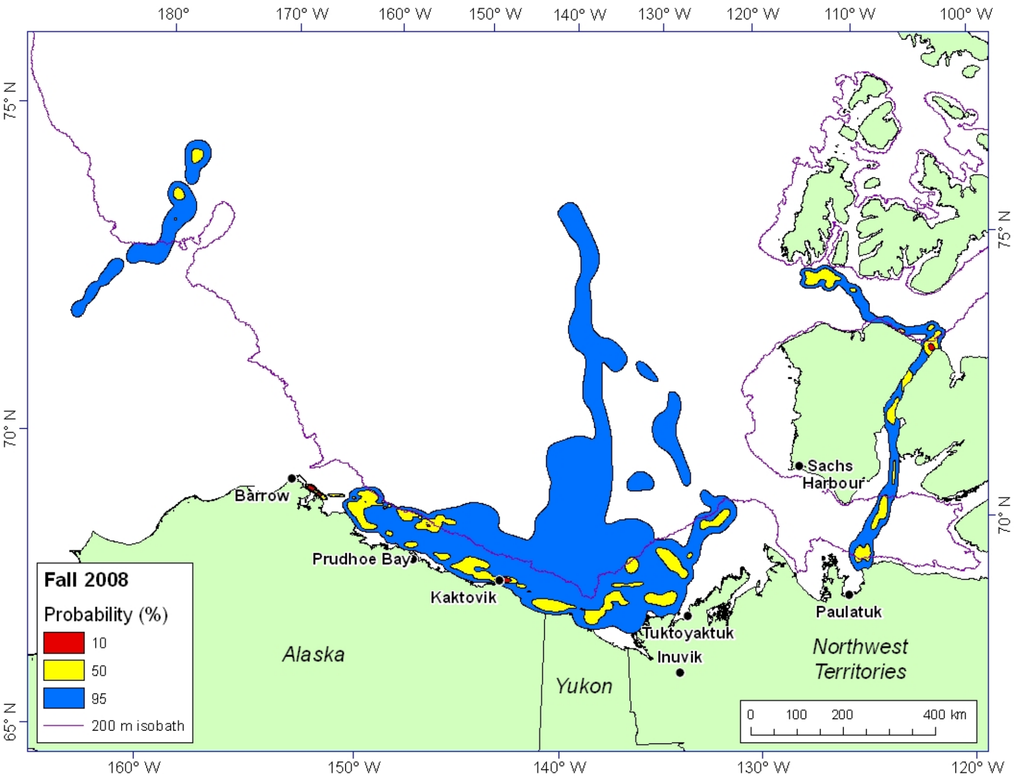

Figure 25 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in autumn (October-November) 2008.

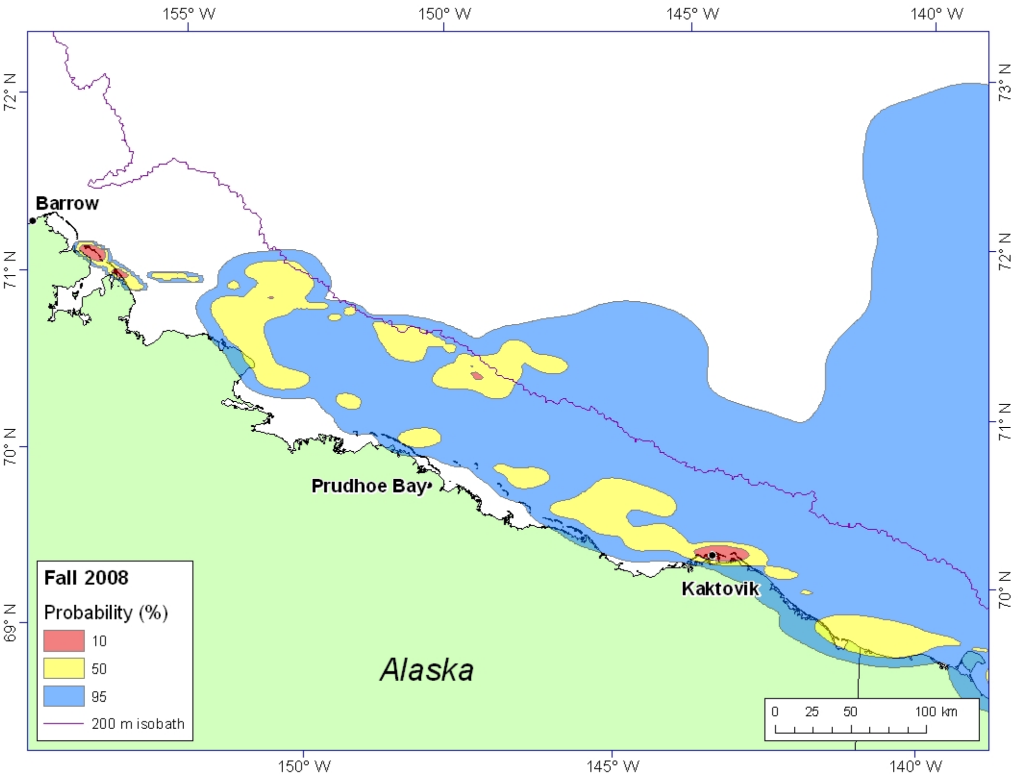

Figure 26 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska and Yukon in autumn (October-November) 2008.

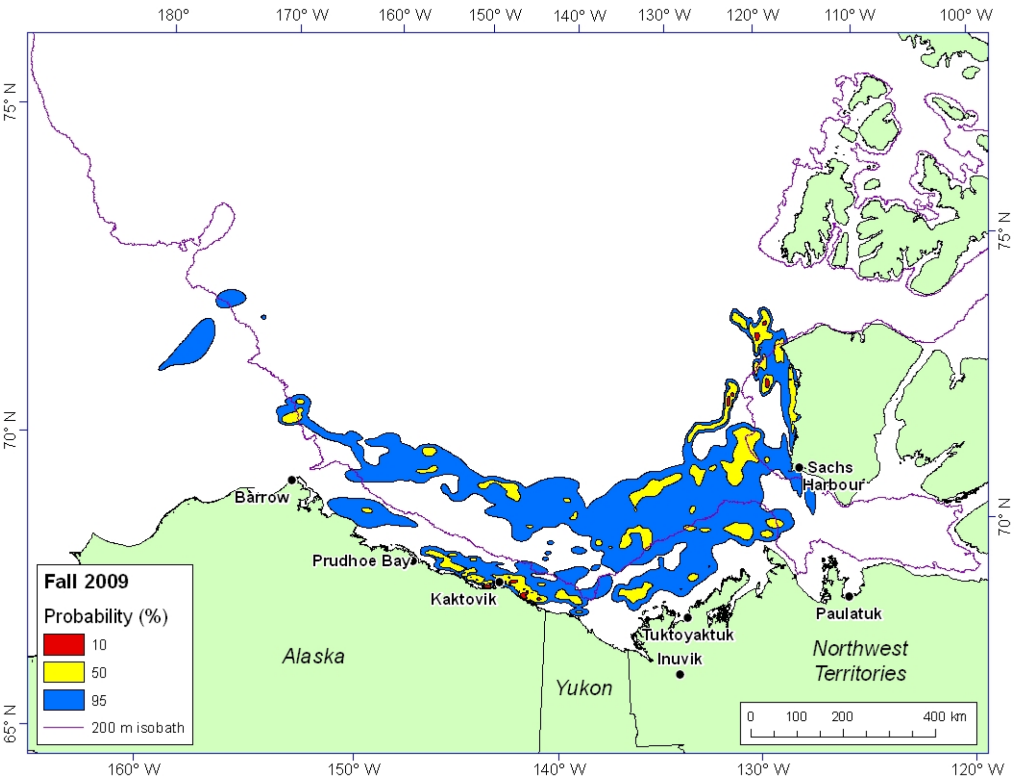

Figure 27 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in autumn (October-November) 2009.

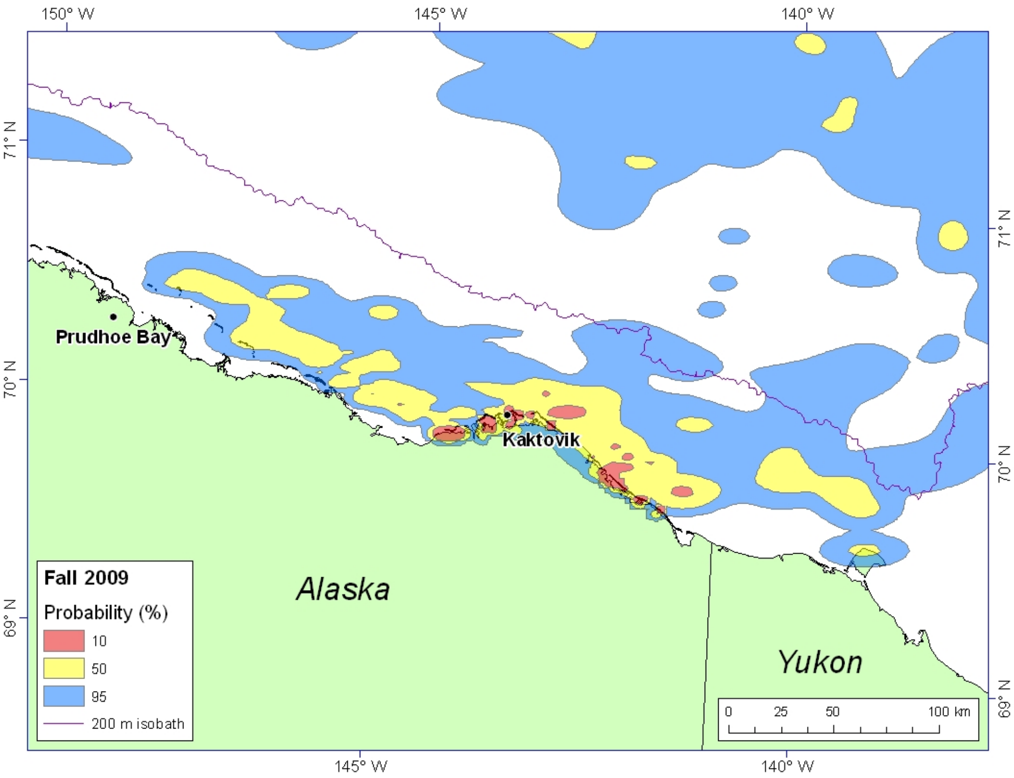

Figure 28 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska and Yukon in autumn (October-November) 2009.

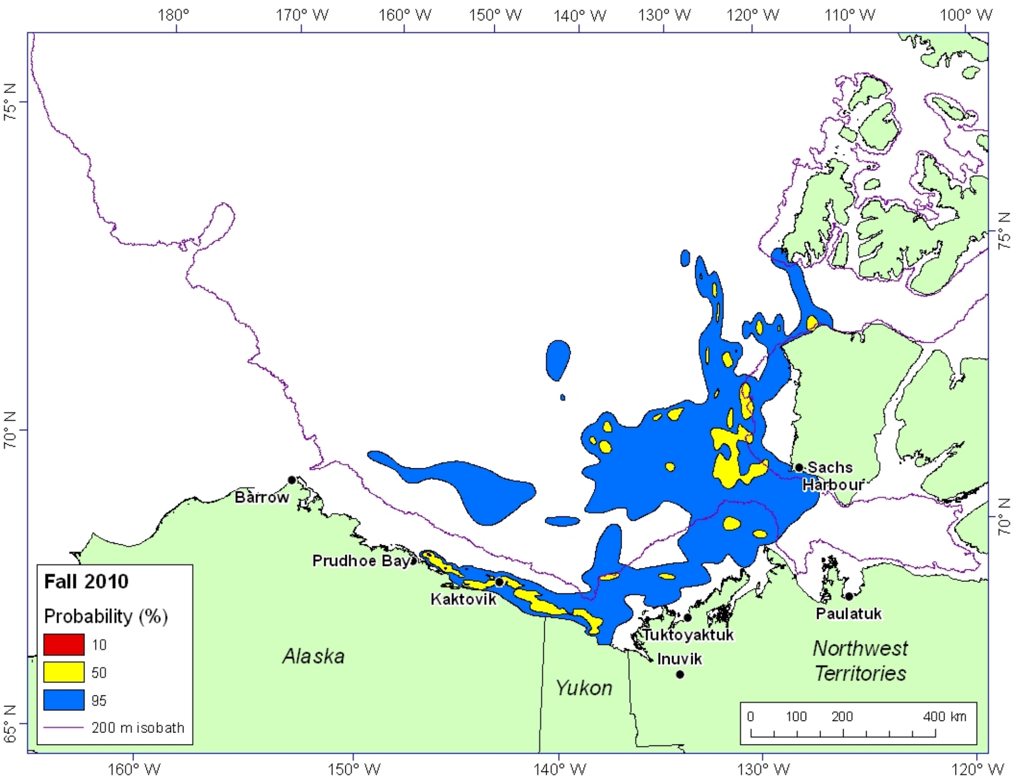

Figure 29 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in autumn (October-November) 2010.

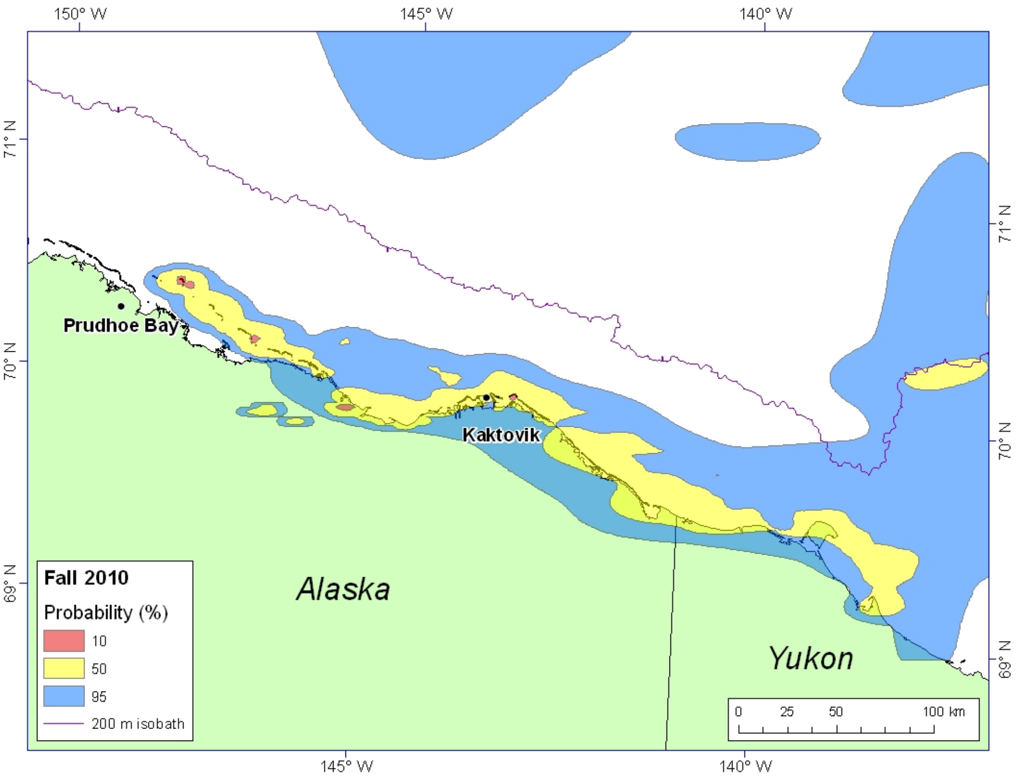

Figure 30 Contours showing the intensity of use (%) by polar bears along the north coastline of Alaska and Yukon in autumn (October-November) 2010.

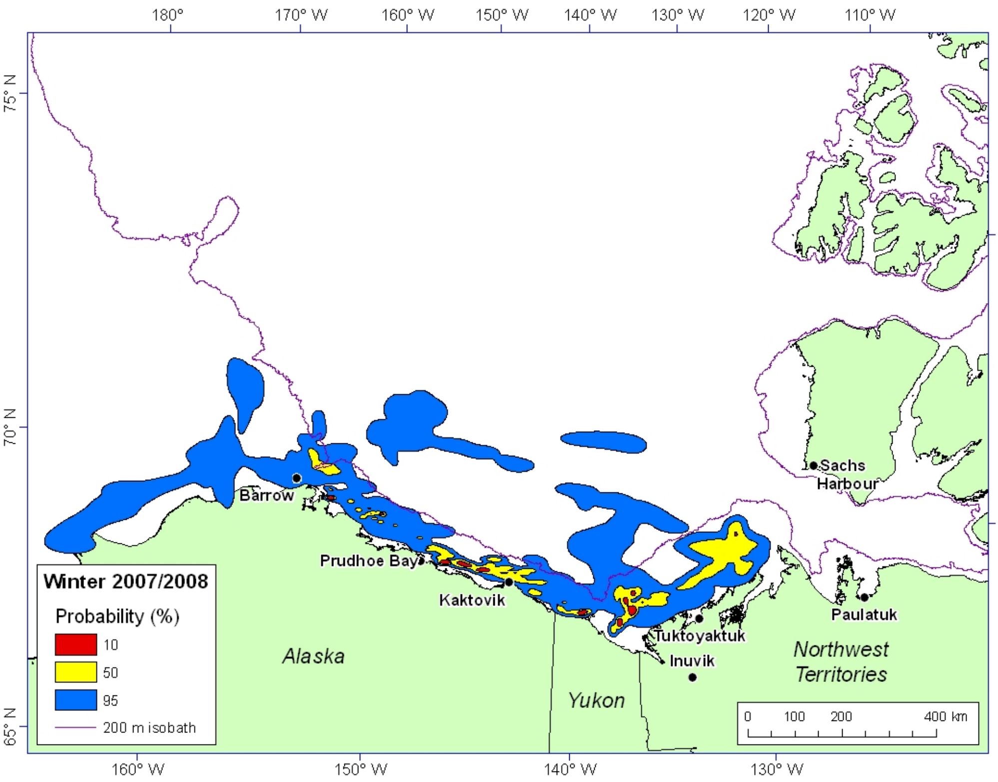

Figure 31 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in winter (December 2007-February 2008).

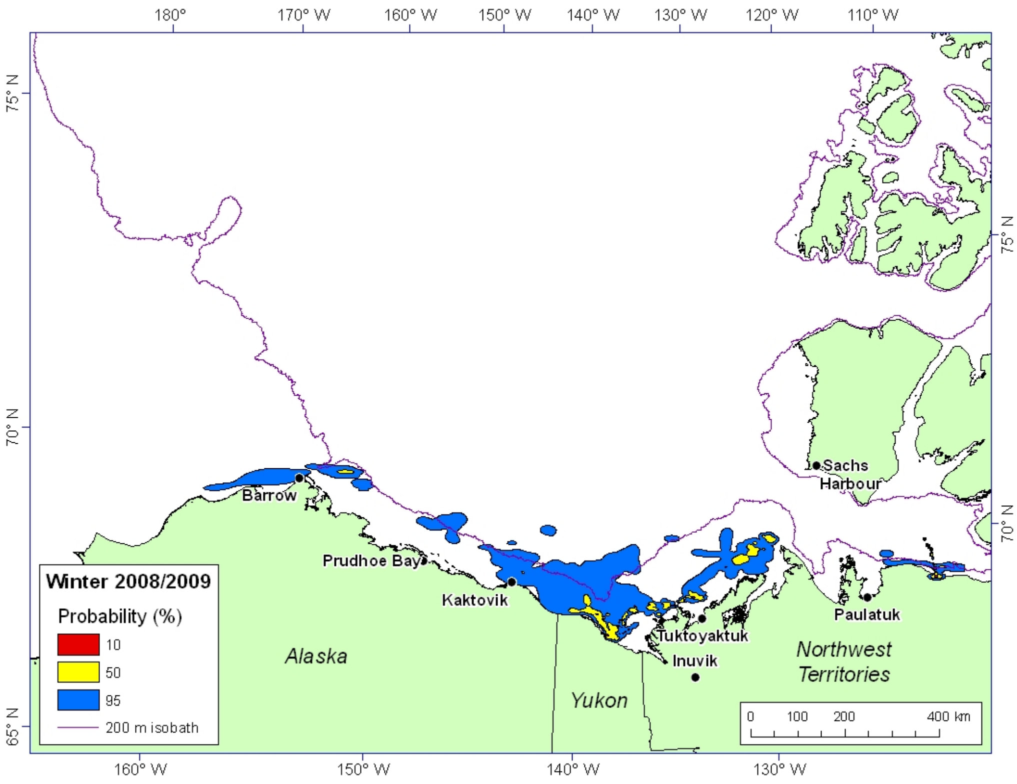

Figure 32 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in winter (December 2008-February 2009).

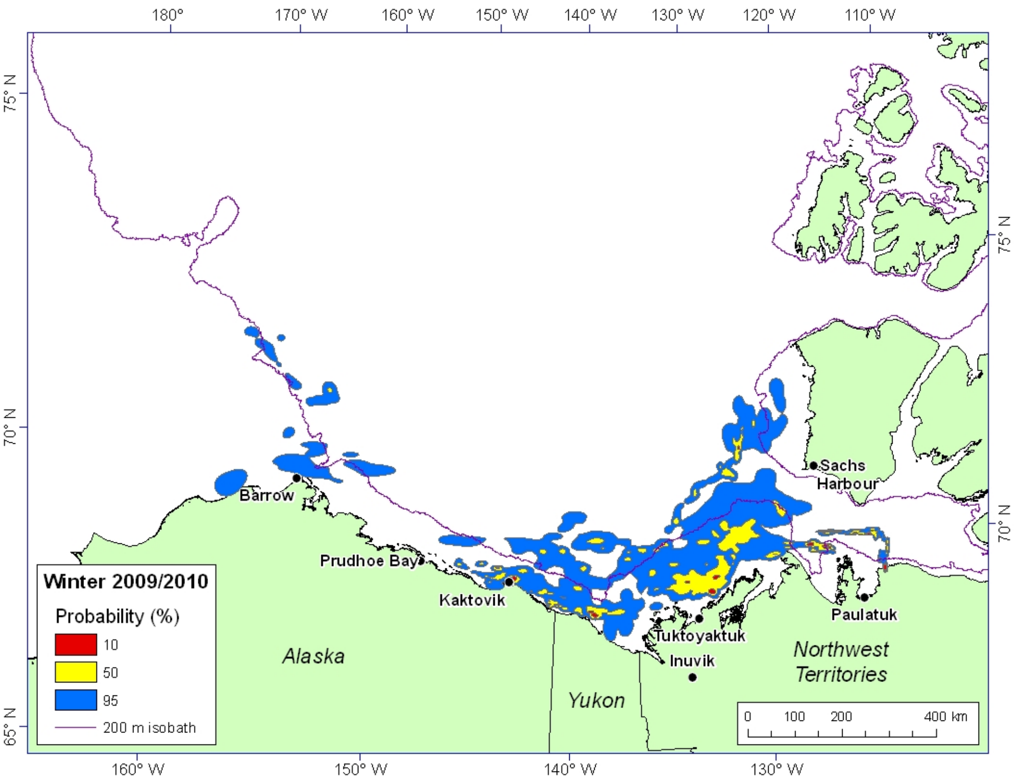

Figure 33 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in winter (December 2009 – February 2010).

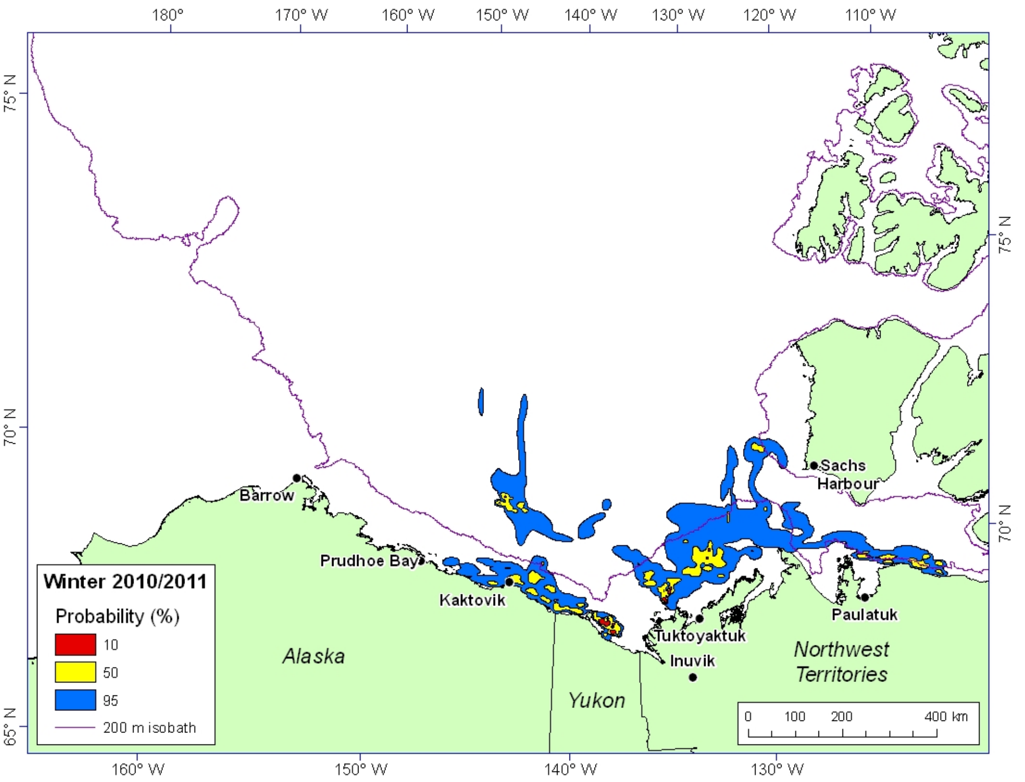

Figure 34 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in winter (December 2010 – February 2011).

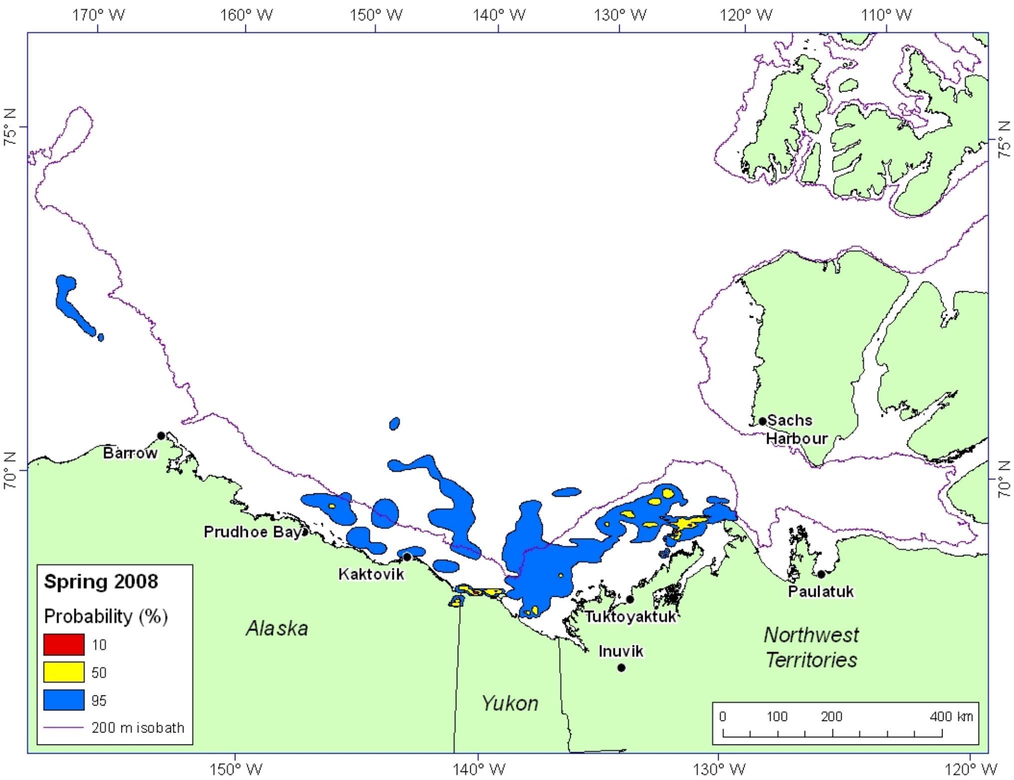

Figure 35 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in spring (March - May) 2008.

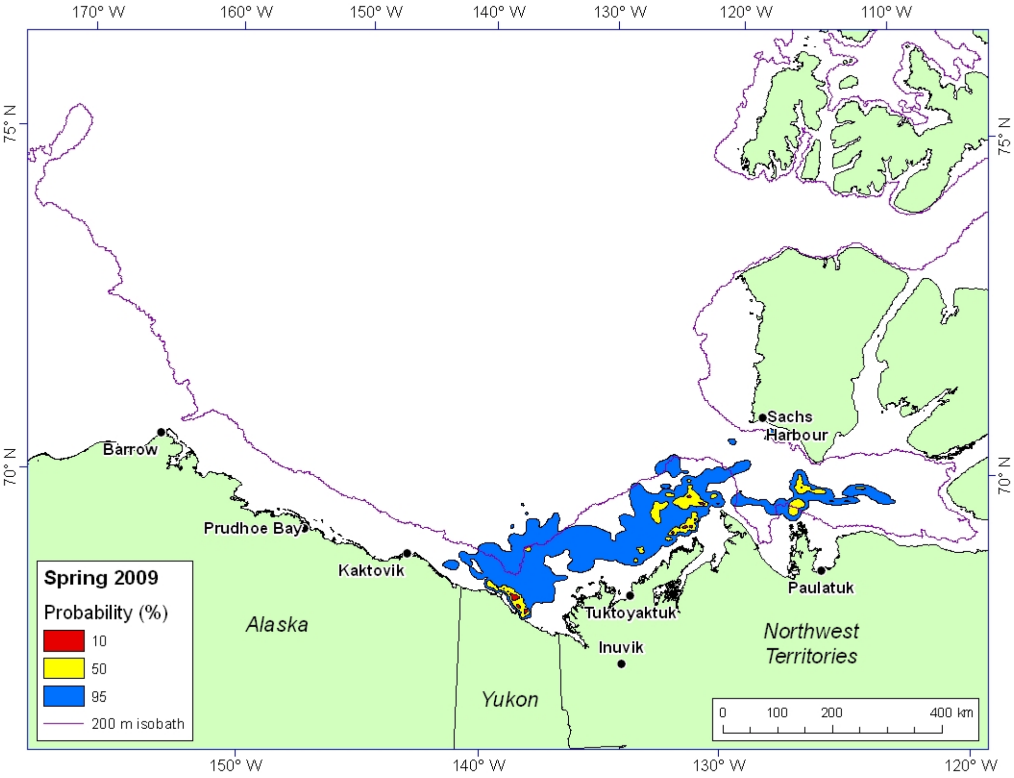

Figure 36 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in spring (March - May) 2009.

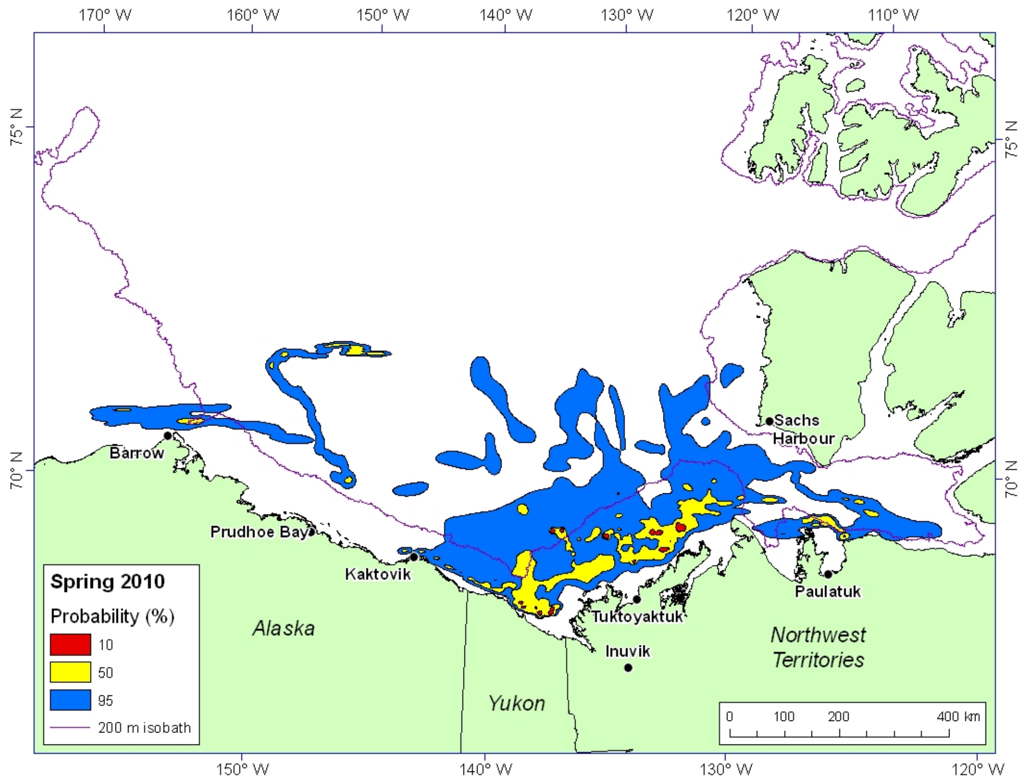

Figure 37 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in spring (March - May) 2010.

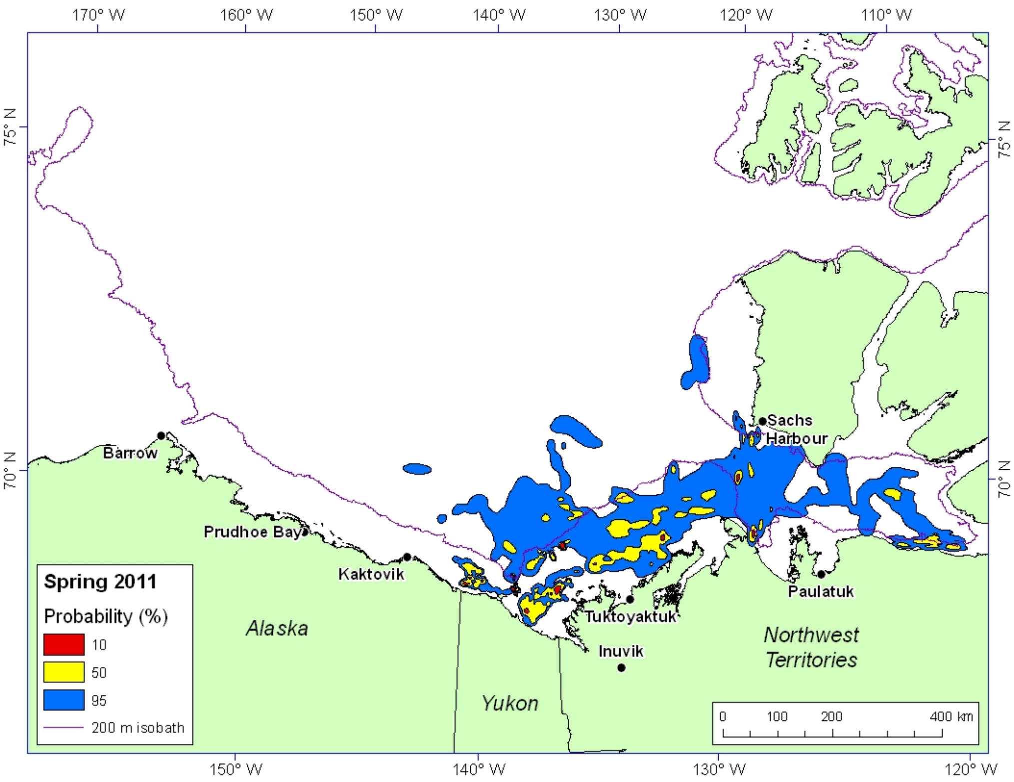

Figure 38 Contours showing the intensity of use (%) by polar bears in the Southern Beaufort Sea in spring (March - May) 2011.

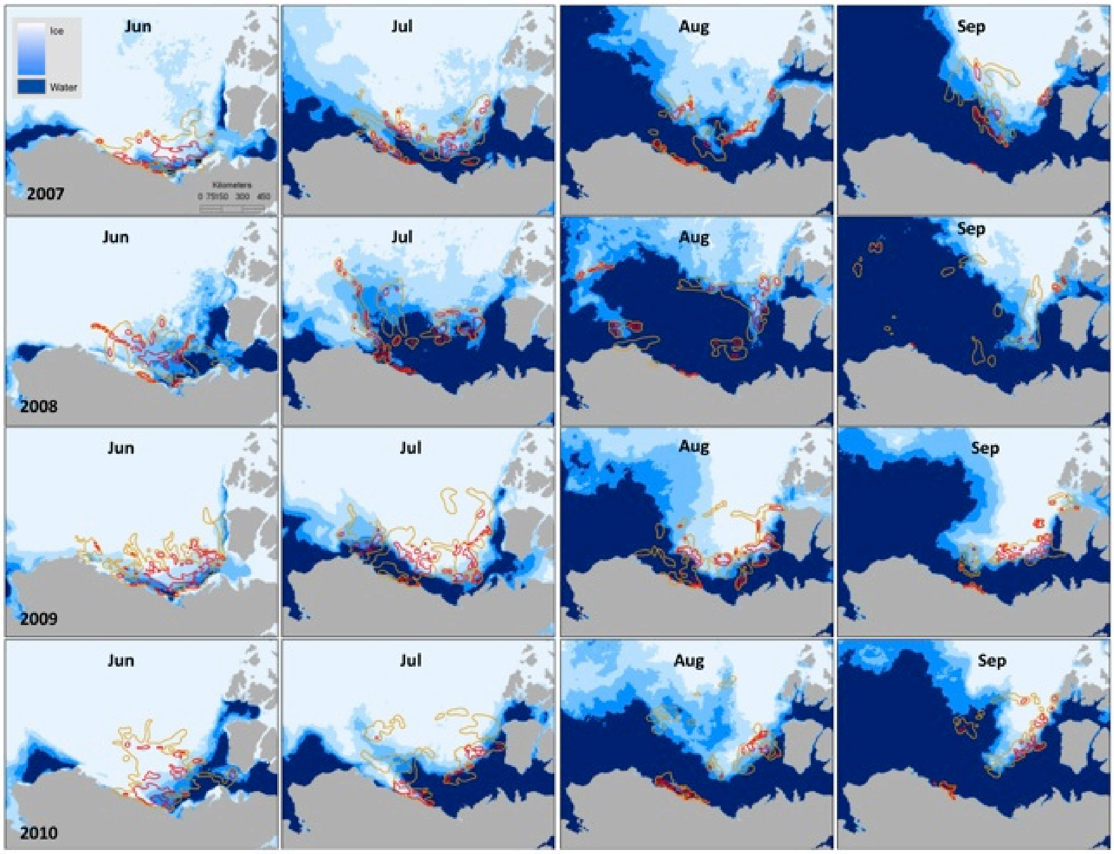

Figure 39 Distribution of summer refugia for polar bears in 2007-2010 relative to the distribution and concentration of sea ice during summer (June-September). Red lines indicate the 50% volume contour of the utilization distributions and the yellow the 95% volume contour of the utilization distribution.

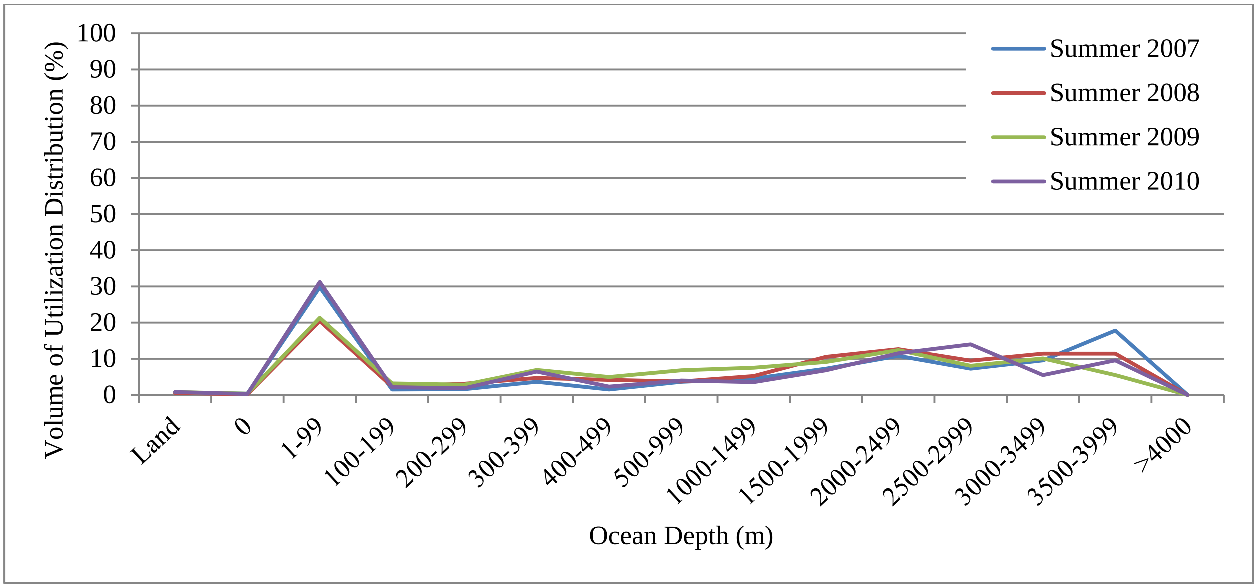

Figure 40 Volume of polar bear utilization distribution during summer 2007-2010 as it relates to ocean depth (m).

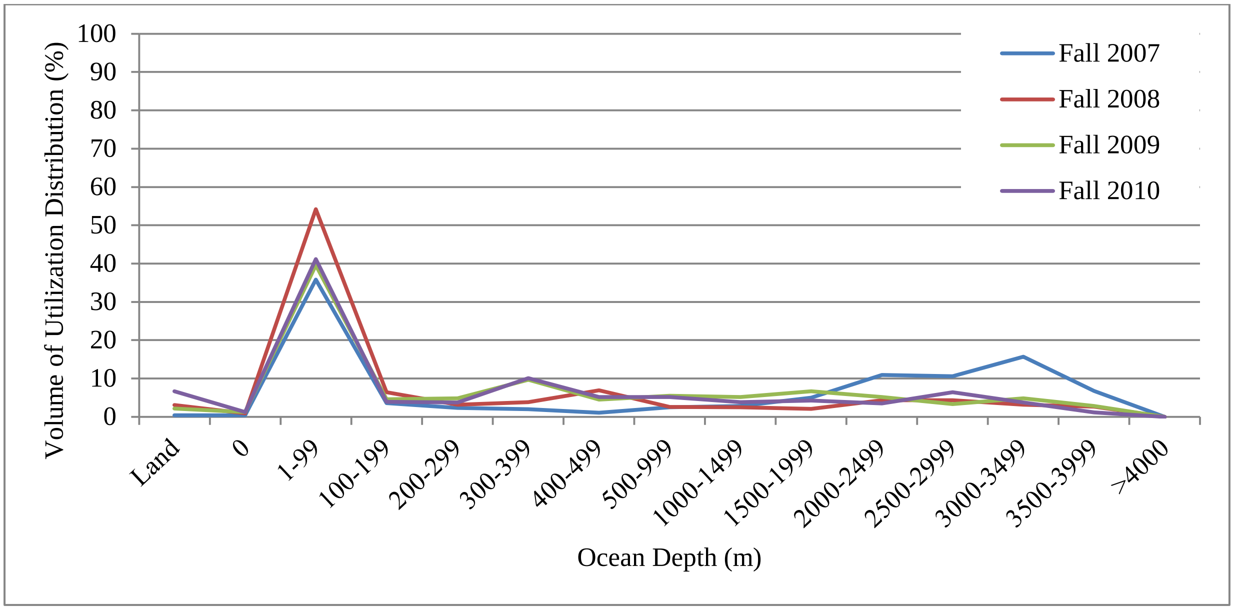

Figure 41 Volume of polar bear utilization distribution during autumn 2007-2010 by ocean depth (m).

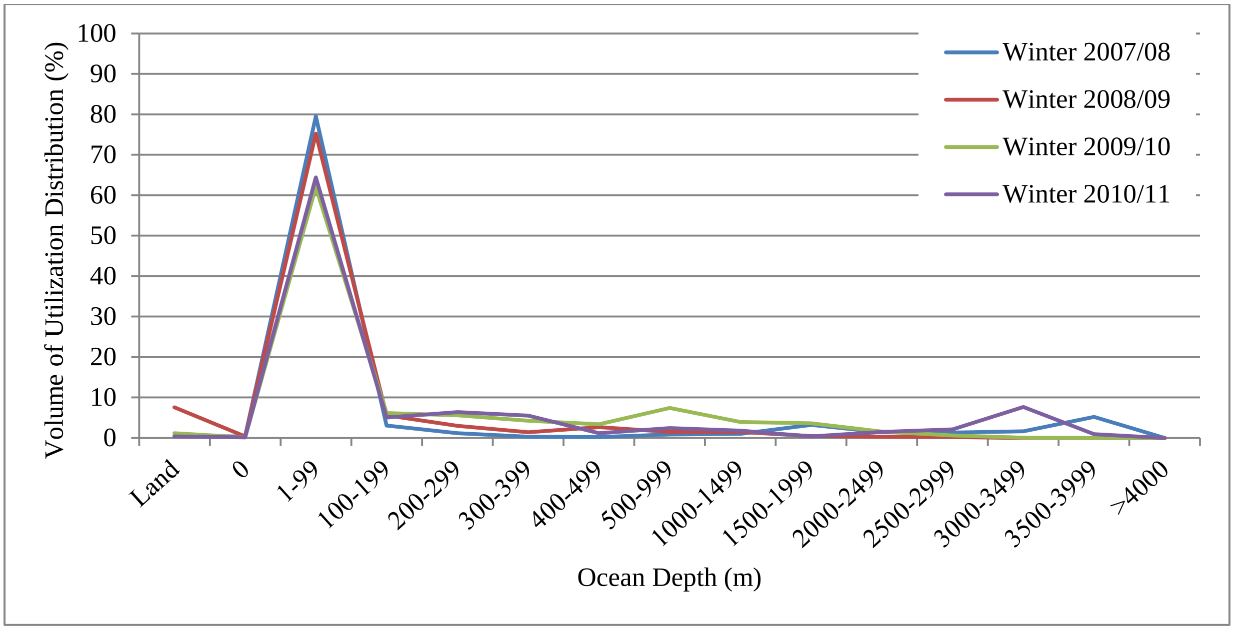

Figure 42 Volume of polar bear utilization distribution during winter 2007-2010 by ocean depth (m).

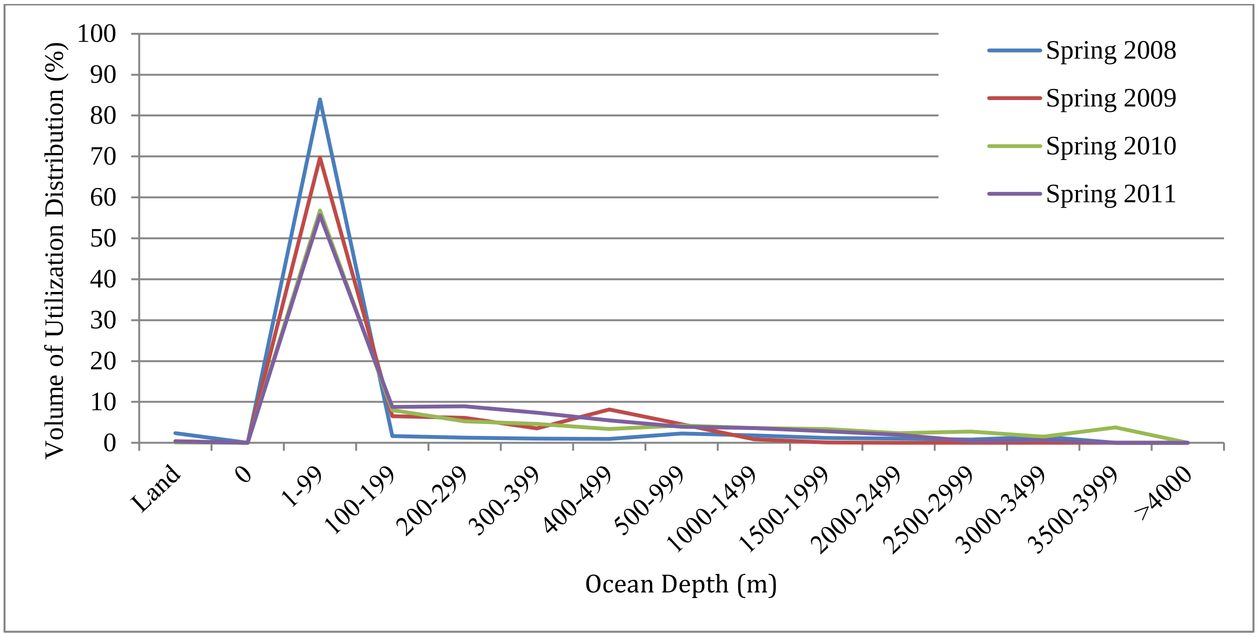

Figure 43 Volume of polar bear utilization distribution during spring 2007-2010 by ocean depth (m).

Table 1 Characteristics for polar bears used in kernel density analysis.

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

| | | | | | | |
|---|---|---|---|---|---|---|
| X32611* | 1-May-09 | M | subadult | no | 413 | Gen IV |
| X32643 | 25-Apr-09 | F | subadult | no | 449 | Gen IV |
| X32644 | 19-Apr-09 | F | adult | yearling (1) | 678 | Gen IV |
| X32647 | 25-Apr-09 | F | subadult | no | 87 | Gen III |
| X32672* | 25-Apr-09 | F | adult | two-year-old (2) | 445 | Gen IV |
| X32673 | 25-Apr-09 | F | subadult | no | 375 | Gen III |
| X32681 | 18-Apr-09 | M | subadult | no | 343 | Gen III |
| X32682 | 18-Apr-09 | F | adult | cub of the year (2) | 771 | Gen IV |
| X32687 | 19-Apr-09 | F | adult | yearling (1) | 365 | Gen IV |
| X32690 | 20-Apr-09 | F | adult | no | 771 | Gen IV |
| X32692 | 25-Apr-09 | M | subadult | no | 691 | Gen IV |
| X32693 | 27-Apr-09 | F | adult | yearling (1) | 570 | Gen IV |
| X32698 | 30-Apr-09 | F | adult | cub of the year (1) | 760 | Gen IV |
| X32700 | 1-May-09 | F | adult | no | 758 | Gen IV |
| X32701 | 1-May-09 | F | adult | cub of the year (1) | 759 | Gen IV |
| X32703 | 1-May-09 | F | adult | no | 392 | Gen IV |
| X32704 | 5-May-09 | M | subadult | no | 57 | Gen IV |
| X32613 | 20-Apr-10 | F | adult | no | 397 | Gen IV |
| X32614 | 21-Apr-10 | F | adult | two-year-old (2) | 397 | Gen IV |
| X32617 | 22-Apr-10 | F | adult | two-year-old (1) | 397 | Gen IV |
| X32645 | 25-Apr-10 | F | adult | yearling (2) | 269 | Gen IV |
| X32649 | 27-Apr-10 | F | adult | no | 396 | Gen IV |
| X32707 | 27-Apr-10 | F | adult | no | 156 | Gen IV |
| X32711 | 25-Apr-10 | F | adult | yearling (2) | 226 | Gen IV |
| X32803 | 22-Apr-10 | F | adult | no | 55 | Gen IV |
| X32804 | 24-Apr-10 | F | adult | yearling (1) | 397 | Gen IV |
| X32808 | 25-Apr-10 | F | adult | no | 335 | Gen IV |

* indicates bears that were relocated and recollared.

Table 2 The number of polar bears that were used to estimate monthly kernel densities for each month during the study.

| Month | 2007 | 2008 | 2009 | 2010 | 2011 | Grand Total |
|---|---|---|---|---|---|---|
| January | | 6 | 6 | 13 | 10 | 35 |
| February | | 3 | 6 | 14 | 8 | 31 |
| March | | 3 | 5 | 14 | 9 | 31 |
| April | | 2 | 4 | 15 | 10 | 31 |
| May | | 11 | 25 | 21 | 10 | 79 |
| June | 17 | 10 | 25 | 19 | | 71 |
| July | 15 | 9 | 22 | 17 | | 63 |
| August | 12 | 9 | 18 | 15 | | 54 |
| September | 11 | 9 | 15 | 11 | | 46 |
| October | 12 | 8 | 14 | 14 | | 48 |
| November | 11 | 6 | 15 | 12 | | 44 |
| December | 8 | 7 | 13 | 10 | | 38 |
| Total | 98 | 83 | 168 | 175 | 47 | 559 |

Table 3 The number of polar bears that were used to estimate seasonal kernel densities displayed by month.

| | Winter | | | Spring | | | Summer | | | | Fall | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Dec | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Total |
| 2007 | | | | | | | 17 | 15 | 12 | 11 | 12 | 11 | 78 |
| 2008 | 8* | 6 | 3 | 3 | 2 | 11 | 10 | 9 | 9 | 9 | 8 | 6 | 84 |
| 2009 | 7* | 6 | 6 | 5 | 4 | 25 | 25 | 22 | 18 | 15 | 14 | 15 | 162 |
| 2010 | 13* | 13 | 14 | 14 | 15 | 21 | 19 | 17 | 15 | 11 | 14 | 12 | 178 |
| 2011 | 10* | 10 | 8 | 9 | 10 | 10 | | | | | | | 57 |
| Total | 38 | 35 | 31 | 31 | 31 | 79 | 71 | 63 | 54 | 46 | 48 | 44 | 559 |

* Refers to the December from the previous year; i.e., winter 2008 includes December 2007 through February 2008.

Table 4 The number of polar bear locations for each bear that were used to estimate monthly kernel densities for June through December, 2007.

| Bear ID | June | July | August | September | October | November | December | Total |
|---|---|---|---|---|---|---|---|---|
| A20163 | 116 | 123 | 117 | 105 | 117 | 124 | 138 | 840 |
| A20434 | 105 | 90 | | | 125 | 106 | 116 | 542 |
| A20716 | 114 | 85 | 82 | 115 | 110 | 105 | | 611 |
| A20760 | 124 | 98 | 98 | 88 | 94 | 100 | | 602 |
| X32253 | 112 | 97 | | | 92 | 103 | 99 | 503 |
| X32373 | 88 | | | | | | | 88 |
| X32381 | 119 | 98 | 103 | 107 | 136 | 124 | 90 | 777 |
| X32606 | 86 | 94 | | | | | | 180 |
| X32608 | 131 | 89 | 79 | 82 | | | | 381 |
| X32620 | 133 | 129 | 84 | 145 | 97 | | | 588 |
| X32628 | 118 | 116 | 101 | 83 | 92 | | | 510 |
| X32650 | 123 | 122 | 139 | | | | | 384 |
| X32651 | 125 | 139 | 127 | 113 | 128 | 119 | 130 | 881 |
| X32654 | 112 | | | | | | | 112 |
| X32655 | 131 | 132 | 135 | 130 | 132 | 126 | 136 | 922 |
| X32658 | | | | | | 115 | | 115 |
| X32660 | 108 | 130 | 111 | 97 | 116 | 118 | 95 | 775 |
| X32665 | 112 | 125 | 86 | 84 | 96 | 97 | 126 | 726 |
| Total | 1957 | 1667 | 1262 | 1149 | 1335 | 1237 | 930 | 9537 |

Table 5 The number of polar bear locations for each bear that were used to estimate monthly kernel densities for January through December, 2008.

| Bear ID | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A20163 | 126 | 118 | 127 | 122 | 119 | 80 | | | | | | | 692 |
| A20434 | 107 | | | | | | | | | | | | 107 |
| A20521 | | | | | 100 | 123 | 130 | 99 | 98 | 130 | | 98 | 778 |
| X32253 | 97 | | | | 104 | | | | | | | | 201 |
| X32381 | 57 | | | | | | | | | | | | 57 |
| X32606 | | | | 150 | 108 | 116 | 108 | 132 | 107 | 134 | 135 | 139 | 1129 |
| X32608 | | | 47 | | | | | | | | | | 47 |
| X32611 | | | | | 124 | 93 | 81 | 64 | 110 | 142 | 112 | 124 | 850 |
| X32651 | 94 | 118 | 87 | | | | | | | | | | 299 |
| X32655 | 140 | | | | | | | | | | | | 140 |
| X32665 | | 94 | | | 104 | 91 | 84 | 96 | 109 | 110 | 88 | 103 | 879 |
| X32670 | | | | | 115 | 120 | 113 | 110 | 129 | | | | 587 |
| X32671 | | | | | 136 | 107 | 129 | 131 | 127 | 134 | 114 | 109 | 987 |
| X32672 | | | | | 110 | | | | | | | | 110 |
| X32675 | | | | | 121 | 119 | 107 | 115 | 74 | 124 | 131 | 127 | 918 |
| X32677 | | | | | 96 | | | | | | | | 96 |
| X32680 | | | | | | 123 | 119 | 103 | 101 | 117 | | | 563 |
| X32685 | | | | | | 98 | 172 | 171 | 163 | 180 | 170 | 113 | 1067 |
| Total | 621 | 330 | 261 | 272 | 1237 | 1070 | 1043 | 1021 | 1018 | 1071 | 750 | 813 | 9507 |

Table 6 The number of polar bear locations for each bear that were used to estimate monthly kernel densities for January through December, 2009.

| Bear ID | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A20415 | | | | | 140 | 124 | 100 | | | | | | 364 |
| A20521 | 94 | | | | | | | | | | | | 94 |
| A20522 | | | | | 177 | 125 | 109 | 105 | 113 | | | | 629 |
| A20667 | | | | | 163 | 171 | 175 | 173 | 162 | 175 | 160 | 96 | 1275 |
| A20854 | | | | | 154 | 135 | 158 | 143 | 150 | 155 | 148 | 172 | 1215 |
| A20961 | | | | | 167 | 155 | 139 | 107 | 97 | 144 | 141 | 157 | 1107 |
| X19450 | | | | | 143 | 107 | 140 | 116 | 85 | | | | 591 |
| X32268 | | | | | 163 | 150 | | | | | | | 313 |
| X32606 | 132 | 122 | 146 | 130 | 148 | 124 | 69 | 90 | | | 103 | | 1064 |
| X32611 | 135 | 119 | 127 | 143 | 141 | 123 | 69 | | | | | | 857 |
| X32643 | | | | | 150 | 92 | 95 | | | | | | 337 |
| X32644 | | | | | 144 | 103 | 86 | | | 86 | 152 | 77 | 648 |
| X32647 | | | | | 137 | 113 | | | | | | | 250 |
| X32665 | 120 | 91 | 118 | 106 | | | | | | | | | 435 |
| X32671 | 127 | 115 | 123 | | | | | | | | | | 365 |
| X32672 | | | | | 174 | 154 | 145 | 69 | | | | | 542 |
| X32673 | | | | | 127 | 121 | 125 | 138 | 89 | 122 | 127 | 111 | 960 |
| X32675 | 133 | 101 | | | | | | | | | | | 234 |
| X32681 | | | | | 125 | 110 | 116 | 109 | 122 | 123 | 107 | 111 | 923 |
| X32682 | | | | | 179 | 166 | 181 | 181 | 167 | 186 | 180 | 186 | 1426 |
| X32685 | | 123 | 181 | 174 | 175 | 161 | 156 | 165 | 119 | 117 | 175 | | 1546 |
| X32687 | | | | | 180 | 171 | 180 | 183 | 172 | 183 | 178 | 184 | 1431 |
| X32692 | | | | | 177 | 157 | 175 | 152 | 139 | 150 | 164 | 175 | 1289 |
| X32693 | | | | | 171 | 142 | 163 | 141 | 139 | 162 | 151 | 151 | 1220 |
| X32698 | | | | | 172 | 165 | 138 | 113 | 148 | 94 | 135 | 164 | 1129 |
| X32700 | | | | | 154 | 134 | 163 | 140 | | | | | 591 |
| X32701 | | | | | 174 | 156 | 180 | 182 | 176 | 182 | 178 | 174 | 1402 |
| X32703 | | | | | 154 | 143 | 141 | 100 | 149 | 164 | 161 | 176 | 1188 |
| X32704 | | | | | 124 | 151 | | | | | | | 275 |
| Total | 741 | 671 | 695 | 553 | 3913 | 3453 | 3003 | 2407 | 2027 | 2043 | 2260 | 1934 | 23700 |

Table 7 The number of polar bear locations for each bear that were used to estimate monthly kernel densities for January through December, 2010.

| Bear ID | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A20415 | | | | 165 | 140 | 173 | 160 | 129 | 95 | 124 | 118 | 150 | 1254 |
| A20667 | | 107 | 147 | 141 | 75 | 86 | | | | | | | 556 |
| A20854 | 177 | 147 | 131 | 131 | 125 | 105 | 90 | 106 | 98 | 106 | | | 1216 |
| A20961 | 181 | 160 | 178 | 169 | 144 | | | | | | | | 832 |
| X32606 | | 109 | | | | | | | | | | | 109 |
| X32611 | | | 100 | 112 | | | | | | | | | 212 |
| X32613 | | | | | 137 | 142 | 116 | | 108 | 171 | 148 | | 822 |
| X32614 | | | | | 148 | 152 | 113 | 82 | 77 | 128 | 139 | 112 | 951 |
| X32617 | | | | | 88 | | | | | | | | 88 |
| X32644 | 99 | | | | | | | | | | | | 99 |
| X32645 | | | | | 142 | 135 | 136 | 94 | 110 | 170 | | | 787 |
| X32649 | | | | | 130 | 137 | 124 | 71 | 98 | 164 | 125 | 84 | 933 |
| X32672 | | | 161 | 174 | | | | | | | | | 335 |
| X32673 | 128 | 125 | 142 | 124 | | | | | | | | | 519 |
| X32681 | 126 | 105 | | | | | | | | | | | 231 |
| X32682 | 186 | 168 | 186 | 178 | 157 | 157 | 165 | 171 | 152 | 176 | 176 | 179 | 2051 |
| X32685 | 128 | 165 | 178 | 171 | 133 | 115 | 134 | 61 | | | | | 1085 |
| X32687 | 186 | 166 | 175 | 119 | | | | | | | | | 646 |
| X32692 | 180 | 159 | 173 | 174 | 138 | 149 | 166 | 147 | 103 | 111 | 153 | 146 | 1799 |
| X32693 | 164 | 152 | 144 | 146 | 118 | 105 | 109 | | | | | | 938 |
| X32698 | 153 | 130 | 163 | 156 | 117 | 113 | 101 | 113 | | 83 | 79 | 75 | 1283 |
| X32700 | | | | | | 131 | 144 | 139 | | 113 | 165 | 175 | 867 |
| X32701 | 181 | 153 | 177 | 171 | 136 | 152 | 152 | 153 | 150 | 175 | 179 | 186 | 1965 |
| X32703 | 156 | 111 | 166 | 152 | 91 | | | | | | | | 676 |
| X32707 | | | | | 139 | 109 | 153 | 80 | | | | | 481 |
| X32711 | | | | | 145 | 131 | 129 | 91 | | 106 | 150 | | 752 |
| X32803 | | | | | 126 | 82 | | | | | | | 208 |
| X32804 | | | | | 147 | 161 | 186 | 176 | 156 | 180 | 175 | 183 | 1364 |
| X32808 | | | | | 169 | 168 | 169 | 148 | 135 | 185 | 176 | 180 | 1330 |
| Total | 2045 | 1957 | 2221 | 2283 | 2745 | 2503 | 2347 | 1761 | 1282 | 1992 | 1783 | 1470 | 24389 |

Table 8 The number of polar bear locations for each bear that were used to estimate monthly kernel densities for January and February, 2011.

| Bear ID | January | February | March | April | May | Total |
|---|---|---|---|---|---|---|
| A20415 | 159 | 157 | 183 | 169 | 180 | 848 |
| X32613 |  |  |  | 176 | 184 | 360 |
| X32614 | 147 | 128 | 169 | 131 | 152 | 727 |
| X32644 |  |  |  | 180 | 159 | 339 |
| X32649 | 101 |  | 127 | 158 | 140 | 526 |
| X32682 | 184 | 167 | 176 | 170 | 179 | 876 |
| X32692 | 118 |  |  |  |  | 118 |
| X32698 | 115 | 66 | 90 | 105 | 159 | 535 |
| X32700 | 184 | 164 | 185 | 171 | 178 | 882 |
| X32701 | 179 | 166 | 182 | 164 | 155 | 846 |
| X32804 | 177 | 163 | 186 | 170 | 176 | 872 |
| X32808 | 173 | 164 | 128 |  |  | 465 |
| Total | 1537 | 1175 | 1426 | 1594 | 1662 | 7394 |

# Long-term changes in the movement patterns of polar bears[3]

The movements and space use patterns of animals are affected by a variety of intrinsic and extrinsic factors. Environmental predictability and heterogeneity (Norbury et al. 1994; Saïd et al. 2005), food supply (Loveridge et al. 2009), reproductive success (Switzer 1993), body size (Baker and Mewaldt 1979), age (Saïd et al. 2009), and sex (Relyea et al. 2000) have all been shown to influence the spatial distribution of free-ranging animals. Despite the varied and complex forces that determine where and how animals move, the availability of resources is a key determinant of how much space an animal needs to fulfill its life processes. Specifically, where resources are scarce or patchily distributed, an animal will require more space to meet its energetic requirements than in a habitat where resources are abundant or homogeneous (Harestad and Bunnell 1979; Switzer 1993).

At high latitudes, resources may be both scarce and unpredictably distributed (Oksanen et al. 1981; Ferguson and Messier 1996). Polar environments are generally highly seasonal, with short pulses of productivity separated by extended periods of limited resource availability. Animals inhabiting these environments have evolved a number of mechanisms to exploit periods of abundance and cope with periods of scarcity, including migration, food caching, metabolic depression and seasonal fasting. However, these mechanisms generally rely on seasonally predictable resources. Where climate change is disrupting the temporal and spatial links between animal populations and their resources, extreme environmental variability may exceed the

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[3] A version of this work is in preparation for publication as Thiemann, G.W., Eriksen, A., Derocher, A.E., Stirling, I., Durner, G., Branigan, M., Cherry, S.G., Pongracz, J., S. Hamilton, and Richardson, E.S. in prep. Long-term changes in the movement patterns of polar bears in the Southern Beaufort Sea.

resilience of populations (e.g., Martin and Wiebe 2004; Post and Forchhammer 2008; Post et al. 2009).

The primary habitat of polar bears is the annual sea ice that forms along the coastline of the circumpolar Arctic. The distribution and characteristics of this habitat have driven the evolution of polar bears and largely define the spatial arrangement of the world's 19 polar bear populations (Ferguson et al. 1998; IUCN/SSC Polar Bear Specialist Group 2010: **Figure 1**). In addition to serving as a substrate for bears to hunt, travel, and mate, the distribution of annual ice determines the availability of polar bear prey and, to a large extent, controls the structure and functioning of the Arctic marine ecosystem (e.g., Spindler 1994). However, this sea ice habitat is declining rapidly in many parts of the Arctic (Holland et al. 2010 and references therein).

One of the most severely affected areas in terms of sea ice loss is the Beaufort-Chukchi Sea area, where the melt season has increased at a rate of more than 10 days/decade (Markus et al. 2009). The record sea ice minima observed in 2007 and 2008 included a substantial loss of ice from the Beaufort and Chukchi Seas. Historically, polar bears in the Southern Beaufort Sea population remain on the ice year-round, following the ice pack as it recedes north in the summer and returning to more productive coastal waters in the fall. Increasing the distance between the summer ice pack and the shoreline could severely impact this life history cycle and recent population data suggest the Southern Beaufort Sea population is in the early stages of decline. Ice loss appears to have contributed to decreased survival (Regehr et al. 2010) and body condition (Rode et al. 2010), increased nutritional stress (Stirling et al. 2008; Cherry et al. 2009), altered denning behavior (Fischbach et al. 2007), and changes in the coastal distribution of polar bears (Schliebe et al. 2008; Gleason and Rode 2009). The effects of habitat conditions on the movements and distribution of polar bears on the sea ice are unknown.

Ferguson et al. (1999) concluded that the annual range size of polar bears is determined by the proportional amount of land (relative to sea ice) in the area, seasonal variation in ice cover, and the amount of coastline habitat (with biological productivity increasing with coastal area). We used satellite telemetry information collected for polar bears in the Southern Beaufort Sea over a 25-year span to examine trends in movement rates and distribution. We hypothesized that because of the limited amount of land cover and coastline and the highly seasonal distribution of sea ice (Ferguson et al. 1999), polar bears in this region should have among the largest annual ranges in the circumpolar region. We further hypothesized that recent declines in the availability of sea ice would represent a decline in habitat quality (i.e., sea ice cover) and resource availability that should further increase the size of annual ranges and the distance and rates of polar bear movements. Determining the relationship between sea ice habitat quality and polar bear movement is key to developing predictive models (see Molnár et al. 2011) that can quantitatively link habitat availability with polar bear energy budgets and population processes.

### Methods and study area

## Capture and handling

Adult female polar bears (> 4 years; n = 31) were located on the sea ice of the southeastern Beaufort Sea (**Figure 44**) and immobilized via remote drug delivery using standard immobilization protocols (Stirling et al. 1989; see also Amstrup et al. 2000, Stirling 2002, and references therein). To assess the effects of handling on polar bear movements, movement data is being analyzed to determine the recovery period after immobilization (Thiemann et al. in prep., Appendix I). The study suggests that movement rates returned to baseline levels after approximately 48 hours after immobilization (Thiemann et al. in prep.). Bears were captured in early spring (April-May) or autumn (Oct-Nov) during population surveys or collaring programs carried out by the Canadian Wildlife Service (1985-03; Stirling 2002), US Geological Survey (1985-93; Amstrup et al. 2000), the Northwest Territories Department of Environment and Natural Resources (2000-03), and the University of Alberta (2007-09).

Each bear was fitted with a satellite-tracking collar that recorded the bear's position at regular intervals. Collars deployed between 1985 and 2003 determined the bear's location by interpreting frequency-shift patterns caused by changes in the collar's position relative to tracking satellites (Amstrup et al. 2000). Data quality control for ARGOS collars follows Amstrup et al. (2000). From 2007 onwards, bears were fitted with Telonics® Gen-III and Gen-IV collars that utilized global positioning system (GPS) satellites to determine position. Data quality control for GPS collars is outlined in the previous section. These collars were also equipped with Telonics CR-2A mechanisms that released the collar on a pre-programmed date. Telemetry data from all collars were processed by the Argos Data Collection and Location System. All capture and handling procedures were reviewed annually and approved by our institutional animal care and use committees.

## Movement analyses and sea ice conditions

We examined net monthly direction of travel, monthly and annual distance traveled, and monthly and annual home range size (minimum convex polygon). We also calculated 95% kernel estimates of annual home ranges using the least-square cross-validation method for determining the smoothing parameter. For comparisons of annual movement patterns, only those bears with >291 tracking days (i.e., 80% of a 365-day year; Amstrup *et al.* 2000) and at least 25 locations were used in analyses. For monthly comparisons, we used only those collars that provided ≥ 4 locations and ≥ 19 tracking days within a calendar month. Because the GPS collars deployed in 2007-09 recorded locations more frequently than collars in earlier years, the GPS location data were subsampled to match the frequency of the older satellite data. The analysis of movement and home range size is sensitive to the number of points used (Andersen et al. 2008) but to harmonize the analyses over time, subsampling to the ARGOS data frequency was necessary.

Monthly and annual distances traveled were calculated by summing the linear distance between each recorded location in the given month or year. Movement rates were calculated by dividing total distance by the number of tracking days. Because each polar bear provided multiple months, and in some cases multiple years, of telemetry data, we used linear mixed models (SPSS Statistics 17.0, SPSS Inc., Chicago, Il) to account for repeated samples across individuals. We tested for effects of month, year, and reproductive status (solitary females *vs*. females with cubs) on polar bear home range size, movement rate and distance travelled.

To examine directional trends in polar bear movements, we determined the net linear distance between the first and last locations recorded for each month. Net direction moved between these points (mean angle) was determined by converting angles to trigonometric functions following methods in Zar (1999). We tested for significant directional tendencies by comparing azimuths of net movements for each month with Rayleigh's Z test for uniformity of distribution. All spatial analyses were performed using ArcMap 9.2 and the Albers equal area conic projection (ESRI, Redlands, California).

We examined temporal changes in sea ice concentration in the area of the Beaufort Sea occupied by collared bears. Sea ice data for 25 x 25 km grid cells were obtained from the National Snow and Ice Data Centre (Boulder, CO; Cavalieri et al. 2008, Meier et al. 2009). Summary sea ice statistics were calculated using ArcMap 9.2. We used analysis of variance (ANOVA) to test for temporal changes in sea ice concentration and linear mixed models to examine the relationship between sea ice (fixed factor) and monthly home range size.

## Results

The polar bears collared in this study utilized an expansive area of the Beaufort and Chukchi Seas, ranging from Wrangel Island in the west to eastern Banks Island in the east. Of the 31 adult female polar bears captured during this study, 24 provided at least one full year of movement data. One bear collared in spring 2007 entered a maternity den in the autumn whereas 6 other collars malfunctioned less than one year after deployment. Among those collars that transmitted for ≥ 1 year, frequency-shift collars (1985-2003) provided a location on average every 8.7 days. For the monthly dataset, locations were recorded from frequency-shift collars every 6.3 days. To allow comparisons across all years, data from the GPS collars (programmed to record locations every 4 hours) were subsampled at the rates observed in the older collars (every 8.7 days and every 6.3 days for annual and monthly comparisons, respectively). Monthly and annual movement data were normally distributed (Kolmogorov-Smirnov test, $P > 0.05$).

## Annual movement

Mean (± SEM) annual home range size more than tripled over the course of this study, increasing from 133,769 ± 44,827 km$^2$ in 1985-93 to 145,307 ± 19,310 km$^2$ in 2000-03 to 454,263 ± 72,869 km$^2$ in 2007-09 (linear mixed model: $P < 0.001$). Post-hoc Bonferroni comparisons showed that home range size in the two earlier periods did not differ from each other ($P = 1.00$) but both differed significantly from 2007-09 ($P = 0.001$). Although there was substantial individual variability in home range size within each timeframe, the recent increase in space use was consistent across polar bears (**Figure 45**). The smallest annual home range observed in 2007-09 (180,936 km$^2$) was substantially larger than the mean for both earlier timeframes. Identical long-term trends were observed whether annual home range size was calculated using minimum convex polygons or 95% kernel estimates (**Figure 46**).

In contrast to the large increase in home range size over time, annual movement rates and distances travelled did not change significantly over time (rate: $P = 0.172$; distance: $P = 0.133$), however, all movement characteristics generally increased over time (**Figure 46**). Reproductive status did not affect any annual movement characteristics ($P > 0.300$), nor were there any significant temporal-reproductive interactions ($P > 0.500$).

## Monthly Movements

In contrast to the annual data, month-to-month trends in movement characteristics were consistent across home range size, distance travelled and movement rate (**Figure 47**). For all three characteristics, movement patterns differed significantly across months ($P < 0.001$) and years ($P < 0.005$). There was no significant effect of reproductive status ($P > 0.300$) and no temporal-reproductive interaction ($P > 0.100$). In 2000-03 and in 2007-09, polar bear movements peaked in June and November (**Figure 47**). Across all years, movements were lowest in February and March.

From 1985-1993, monthly directional movements were uniformly distributed, whereas in 2000-03 bears moved east in February, northwest in July, and south in October (Table 9). In 2007-2009, bears moved west in June and November, north in July, northeast in August and south in October.

## Effects of sea ice

In addition to monthly changes in sea ice (2-way ANOVA: $F_{11,35} = 204$, $P < 0.001$), ice concentration in the area occupied by all collared bears declined significantly over the course of this study (2-way ANOVA: $F_{2,35} = 67.2$, $P < 0.001$). Across the three periods of time, August and September sea ice concentrations declined dramatically and there were trends towards earlier breakup in the spring and later freeze-up in the autumn (**Figure 48**).

Sea ice concentration appeared to drive the monthly movement patterns of polar bears. Linear mixed models showed a significant inverse relationship between June sea ice concentration and monthly home range size ($P < 0.001$; **Figure 49**). Monthly sea ice concentration had similar effects on June distance travelled ($P = 0.004$) and movement rate ($P = 0.007$). Although trends were not significant ($P > 0.080$), there appeared to be a similar inverse relationship between sea ice concentration and polar bear movements in the autumn (Sep-Nov).

## Discussion

The long-term data presented here, although limited in statistical power by small sample sizes, span 25 years of satellite tracking and capture some of the ecological impacts of profound environmental change. Our most recent data (2007-09) reflect the movements of polar bears during years of record sea ice minima and our results collectively suggest that declining sea ice concentration has been the key driver behind observed changes in polar bear movements and spatial distribution.

## Annual movements

The annual area occupied by individual polar bears in the Southern Beaufort Sea has increased in recent years. Our results indicate that although polar bear movement rates and annual distances travelled have not increased significantly over time, annual home ranges have increased by an average of 240% between 1985-93 and 2007-09. These trends suggest that rather than increasing movement rates or distances, polar bears now spread their movements over larger annual areas.

The previously recorded maximum annual range (minimum convex polygon) of an individual polar bear in the Southern Beaufort Sea was 616,800 km$^2$ (Amstrup et al. 2000). Our maximum observed value during 2007-09 was slightly larger than this at 658,826 km$^2$, but the mean value we observed for this period was more than 2.7 times larger than Amstrup et al.'s mean of 166,694 km$^2$. Amstrup et al.'s (2000) value was similar to our mean size for 1985-93 (133,769 km$^2$) and this similarity in part reflects the fact that both studies used some of the same bears collared in the 1980s and 1990s. Collectively however, the congruence of results suggests that the observed shifts in polar bear movements reflect a real ecological trend and not a methodological artefact.

Annual range size for polar bears varies greatly among populations. Ferguson et al. (1999) analyzed movement data from several areas in the Canadian Arctic and found mean annual ranges from 19,400 km$^2$ in Kane Basin to 228,300 km$^2$ in Davis Strait. Across the circumpolar region, observed mean home ranges have varied from 69,468 km$^2$ in the Barents Sea (Wiig 1995) to 244,463 km$^2$ in the Chukchi Sea (Garner et al. 1990). However, these mean values mask substantial individual variation in home range size, which can differ by more than two orders of magnitude within a population (Wiig 1995).

Ferguson et al. (1999) found that polar bears have larger annual home ranges than predicted from allometric regressions and concluded that annual range size in polar bears is affected by (1) the ratio of land: sea area within a given region, (2) seasonal variability in sea ice cover, and (3) the amount of coastline habitat. Home ranges are generally small in the Canadian High Arctic Archipelago, where land:sea ratios are high, sea ice persists through the summer, and numerous deep bays and inlets make coastlines relatively long. In contrast, polar bear home ranges are large in Davis Strait and Baffin Bay, where the sea ice melts completely in summer and home ranges contain relatively little land area and coastline. Based on these environmental factors, polar bears in the Beaufort Sea should have predictably large home ranges as there is substantial seasonal variation in sea ice cover and very little land area and coastline.

In contrast to the increase in annual range size, movement rates and distances traveled did not change significantly over the course of the study, although the trend was generally increasing over time. This may reflect an upper limit to polar bear movement rates as individual polar bears will have a limited sustainable top speed. Our mean movement rates – 8.6 to 11.8 km/d (0.36-0.49 km/h) – are within the range of values reported by Wiig et al. (2003) and slightly higher than those reported by Born et al. (1997) for East Greenland bears. However they are less than half of some of the rates recorded by Amstrup et al. (2000). These earlier rates from the Southern Beaufort Sea utilized shorter location intervals than our current study and there is a significant inverse relationship between calculated movement rate and the interval between locations. Using consecutive locations separated by >100 hours, Amstrup et al. (2000) calculated a mean movement rate of 0.41 km/h, which is within the range of our observed values. The relatively minor shift in mean movement rates from the mid-1980s to the late 2000s, despite dramatic environmental change, suggests polar bears in the Southern Beaufort Sea are traveling at close to their maximum sustainable rate.

We found no difference in the movement rates or home range size of solitary female polar bears vs. those with dependent offspring. Females encumbered with cubs may be forced to move more slowly (Amstrup et al. 2000) and occupy smaller annual ranges (Mauritzen et al. 2001) than solitary females, although this pattern is not consistent across populations (Parks et al. 2006). Small sample sizes precluded testing for differences between females with cubs-of-the-year and those with yearling or two-year-old cubs. Pregnant polar bears entering maternity dens will necessarily have smaller home ranges than non-denning bears (Messier et al. 1992, Mauritzen et al. 2001) and the exclusion of denning bears in our analysis may have reduced that source of variability. Although females with cubs may focus their foraging efforts on the nearshore landfast ice and thereby reduce encounters with potentially infanticidal adult males farther offshore (Stirling et al. 1993), there is exceptionally large individual variability in space use among bears of all reproductive classes (Wiig 1995, Mauritzen et al. 2001, Parks et al. 2006).

## Monthly movements

Shorter-term trends in polar bear movements were consistent with seasonal changes in sea ice. Seasonal peaks in movement rate and distance were associated with spring breakup (June) and autumn freeze-up (November). Messier et al. (1992) observed a similar spring peak in the mobility of female polar bears in the Canadian archipelago, a pattern that is consistent with increased feeding on newly-weaned pups as well as rapid changes in the spatial distribution of sea ice. Nevertheless, seasonal patterns in polar bear movements are regionally variable and among the populations for which there are data, only bears in the Beaufort and Chukchi Seas appear to show a peak in movement rates in the autumn (Garner et al. 1990, Amstrup et al. 2000, this study). For Beaufort Sea polar bears that have spent the summer on offshore pack ice, the autumn movement peak may reflect an increase in feeding activity associated with the return of the ice to more productive coastal waters. In winter, seal availability may be low and polar bears utilize temporary dens during inclement weather. Reduced foraging activity likely accounts for the limited mobility of polar bears from January to April (Ferguson et al. 2001).

The relatively steady movements of polar bears in 1985-93 may have been a consequence of less seasonal variability in ice conditions during that period. The link between sea ice conditions and monthly movement patterns was strongest during breakup in June and in years of exceptionally low June ice availability, polar bears appeared to have been forced to range more widely to find suitable habitat. Early breakup of the sea ice in the Beaufort Sea may have increased the distance between foraging patches and may adversely impact the abundance of prey if ringed seal pups are weaned prematurely.

The small number of observations available for 1985-93 probably limited our ability to detect directional trends in polar bear movements. However, the significant directional trends that were seen were consistent with seasonal shifts in sea ice. In general, bears moved north with the receding ice pack in the spring/summer and returned south with the ice in autumn.

## Effects of sea ice

Coincident with the recent increase in polar bear home ranges was a dramatic shift in their Beaufort Sea habitat. The record sea ice minimum occurred in September 2007 and was nearly matched in September 2008 (Perovich et al. 2011). Between 1985 and 2003, the mean September ice pack was approximately 185 km north of the Alaska coast at the Yukon border. In contrast, the ice in September 2007 and 2008 was 650 km and 400 km north of the Alaska-Yukon border, respectively. As bears follow the sea ice over these increasing northern migrations, annual ranges will necessarily increase as a function of the distance between the summer ice pack and the bears' preferred coastal foraging area.

An inverse relationship between habitat productivity and animal home range size has been observed in a variety of taxa including ursids (Moyer et al. 2007, Edwards et al. 2009), felids (Loveridge *et* al. 2009), canids (Gompper and Gittleman 1991), ungulates (Relyea et al. 2000, Saïd et al. 2009), rodents (Bowers et al. 1990), macropodids (Norbury et al. 1994), and birds (Hurteau et al. 2010). The relationship is generally a consequence of individuals having to utilize more space to meet their energy requirements in resource-poor habitats (Harestad and Bunnell 1979, Switzer 1993). For polar bears, the increase in annual range size observed in the Beaufort Sea is consistent with a decline in habitat quality. Optimal polar bear habitat appears to be an intermediate concentration of sea ice (Stirling et al. 1993, Durner et al. 2009) that provides a substrate for traveling and foraging and abundant ice edge habitat favored by marine mammal prey (Ferguson et al. 2000). Below ca. 50% ice coverage, polar bears may have difficulty traveling and as open water has become both spatially and temporally more abundant in recent years, the quality of polar bear habitat in the Southern Beaufort Sea has clearly declined.

Polar bears with spatially consistent access to seals, particularly during the spring pupping season, will likely have the smallest home ranges (Ferguson et al. 1999), as these bears can meet their nutritional requirements without having to search for widely dispersed prey. In contrast, polar bears with the largest home ranges are likely those bears that are having difficulty locating food or those that have accepted a higher degree of risk to exploit potentially rich patches of food farther offshore. The frequency distribution of these alternative strategies appears to have changed over time in the Southern Beaufort Sea. Before 2007, most bears utilized relatively small home ranges with only 2 bears having exceptionally large home ranges consistent with the riskier offshore foraging strategy. Since 2007, however, the use of small home ranges and the associated exploitation of predictable food patches appear to be a less viable strategy for polar bears.

Recent evidence suggests that an increasing proportion of polar bears in the Southern Beaufort Sea population are electing to remain on land during the increasingly ice-free summer months (Fischbach et al. 2007, Schliebe et al. 2008, Gleason and Rode 2009). Part of this shift may be associated with anthropogenic sources of food available in the form of bowhead whale carcasses left on shore after local subsistence harvests in autumn. The use of land-based refugia during the ice-free season may contribute to large annual ranges as polar bears tend to remain on the ice as long as possible and thereby increase the distance between winter and summer habitats (Ferguson et al. 1999). Bowhead whale carcasses could also attract bears from across the region and stimulate directed migrations. Only 2 bears in this study visited bowhead harvesting sites: one a solitary female and the other with an associated yearling cub. Both bears spent the ice-free season on shore (the solitary female entered a maternity den) in 2007 and visited the bowhead harvesting village of Kaktovik, AK that autumn.

On the sea ice, the main distributional shift of bears in recent years was to the north and west of the area occupied in the 1980s and 1990s. Of the 18 polar bears collared before 2007, only 4 moved beyond the northern boundary of the Southern Beaufort Sea population zone (**Figure 1**) and no bear moved more than 125 km north of the line. In contrast, the majority of bears (7/13) collared in 2007 moved beyond the population area, utilizing ice more than 600 km north of the boundary (*ca*. 900 km offshore) and as far west as Wrangel Island in the Russian Chukchi Sea (**Figure 1**). These trends could be indicative of weakening population boundaries in response to rapid habitat change (Derocher et al. 2004) and could have significant impacts on mark-recapture population estimates and sustainable harvest management. We recommend that the established borders of the Southern Beaufort Sea management unit or “population” be re-evaluated in light of ongoing environmental change. There is substantial overlap between the Southern Beaufort Sea and Northern Beaufort Sea populations (**Figures 7-10**). Qualitative review of the distribution of the three groups of bears (adult females, subadult females, and subadult males) revealed greater overlap between the Southern Beaufort Sea population and the Northern Beaufort Sea population for adult females than subadults of either sex. Overlap for all three groups of bears from the Southern Beaufort Sea with the Chukchi Sea was qualitatively similar although possibly less for subadult males. Ongoing research in the North Beaufort and in the Viscount Melville Sound area will provide new data that will facilitate refinement of population boundaries. Linkage between the eastern parts of the Southern Beaufort Sea population and the Chukchi Sea population were less evident but warrant a full and extensive analysis. To further management of polar bears in the greater Beaufort Sea region (including adjoining waters), it is recommended that an international cooperative working group be struck to facilitate a full analysis of both contemporary and historic movement data. Until such an analysis is undertaken, it is recommended that population boundaries should not be moved.

This study suggests a profound change in the patterns of space use of polar bears in an area undergoing dramatic environmental change. Although our analysis could not separate the walking movements of polar bears from the movement of their floating sea ice habitat, passive transport of polar bears on the ice will be significant (see Mauritzen et al. 2003). To develop predictive models that quantitatively measure the relationship of polar bear energetics to habitat (e.g., Molnár et al. 2011), it will be essential to separate the physical effects of habitat change (i.e., increased dynamism of sea ice) from the behavioral impacts on polar bear movements (i.e., increased energetic costs of locomotion). At present, it is clear that habitat loss in the Beaufort Sea has severely impacted the way polar bears make their living on the sea ice yet quantification of these effects remain only partially documented.

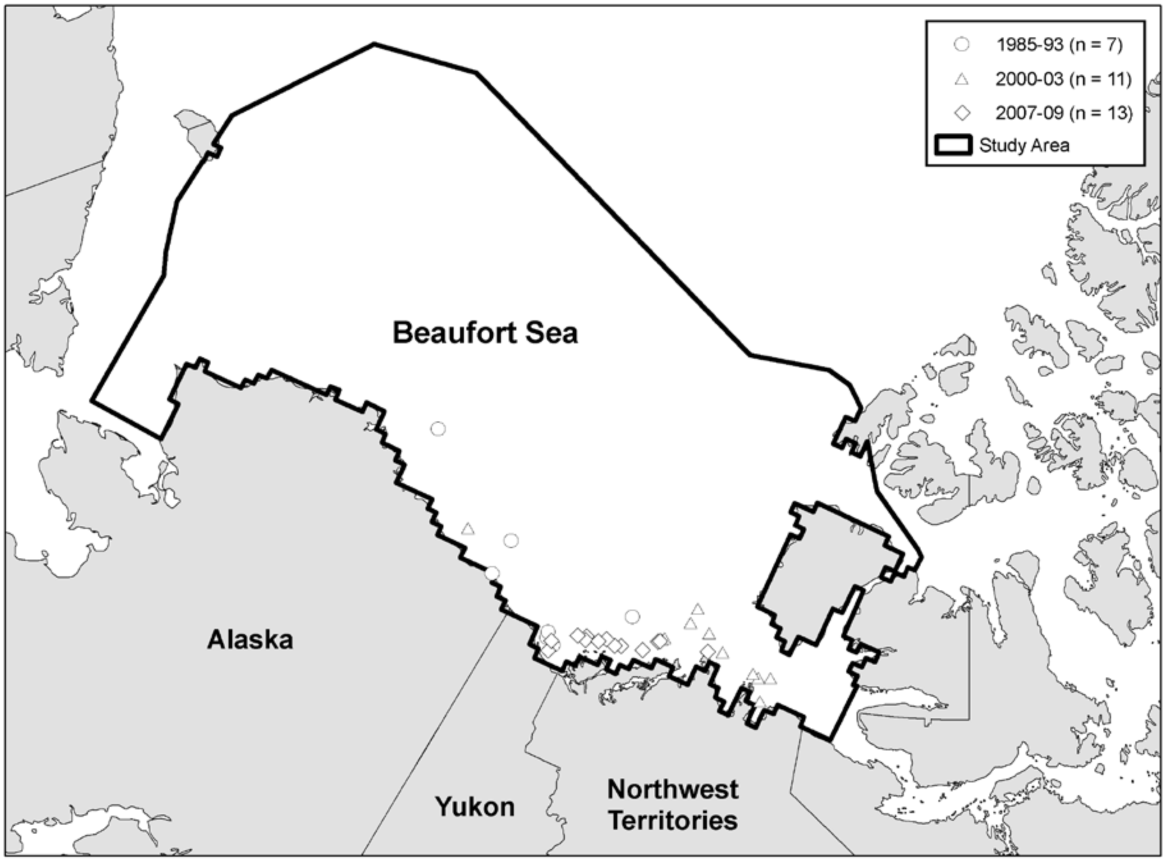

Figure 44 Locations of satellite collars deployed on adult female polar bears between 1985 and 2009. The dark line indicates the minimum convex polygon around all observed polar bear locations and was used to examine trends in sea ice conditions.

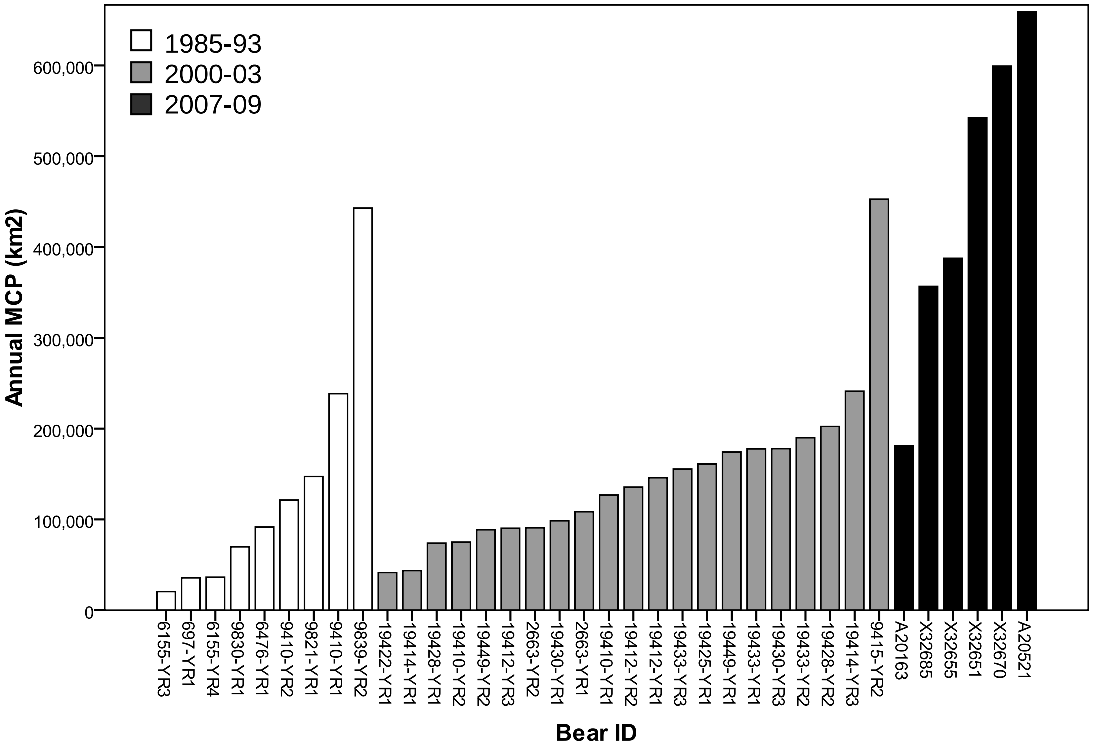

Figure 45 Home range size ($km^2$, minimum convex polygon) of individual polar bears captured in the Southern Beaufort Sea. X-axis labels indicate the identity of collared bears and the year of collar operation.

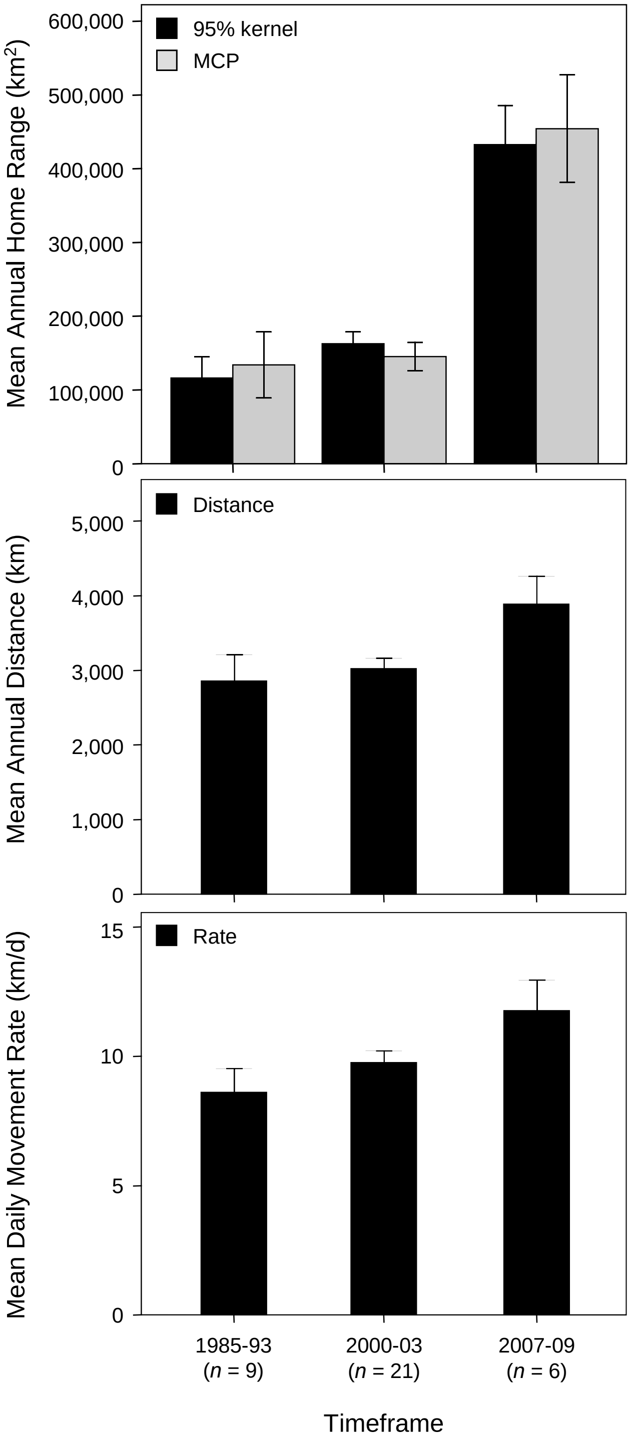

Figure 46 Mean annual home range size (minimum convex polygon and 95% kernel), distance traveled, and movement rate of polar bears captured in the Southern Beaufort Sea. There were no differences between minimum convex polygon and 95% kernel estimates of individual home ranges (paired t-test: *t*(35) = -0.167, *P* = 0.869). Error bars indicate ± 1 SEM.

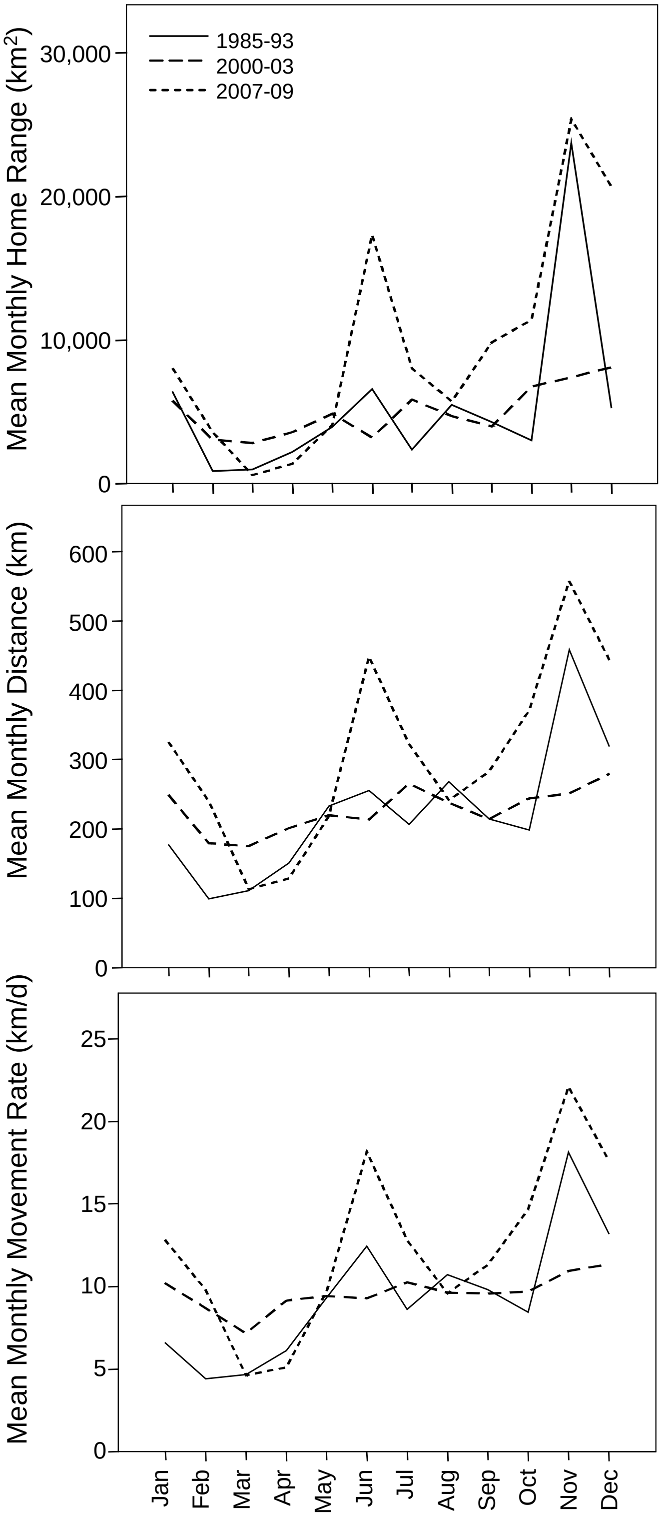

Figure 47 Mean monthly home range size (minimum convex polygon), distance traveled, and movement rate of polar bears captured in the Southern Beaufort Sea.

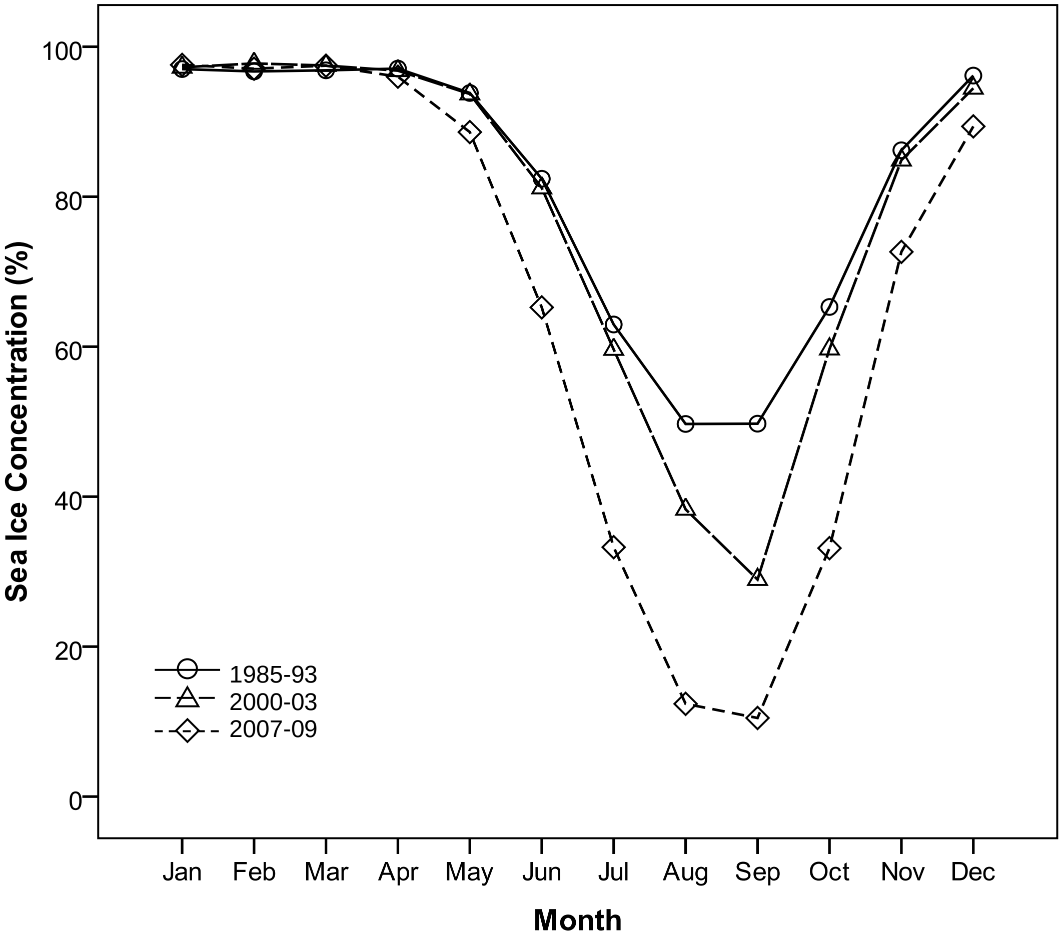

Figure 48 Temporal changes in sea ice concentration in the Southern Beaufort Sea. Monthly mean sea ice concentration was calculated for the area occupied by all collared bears (see Fig. 1) using data available from the National Snow and Ice Data Center, Boulder, CO (Cavalieri *et al.* 2009, Meier *et al.* 2009).

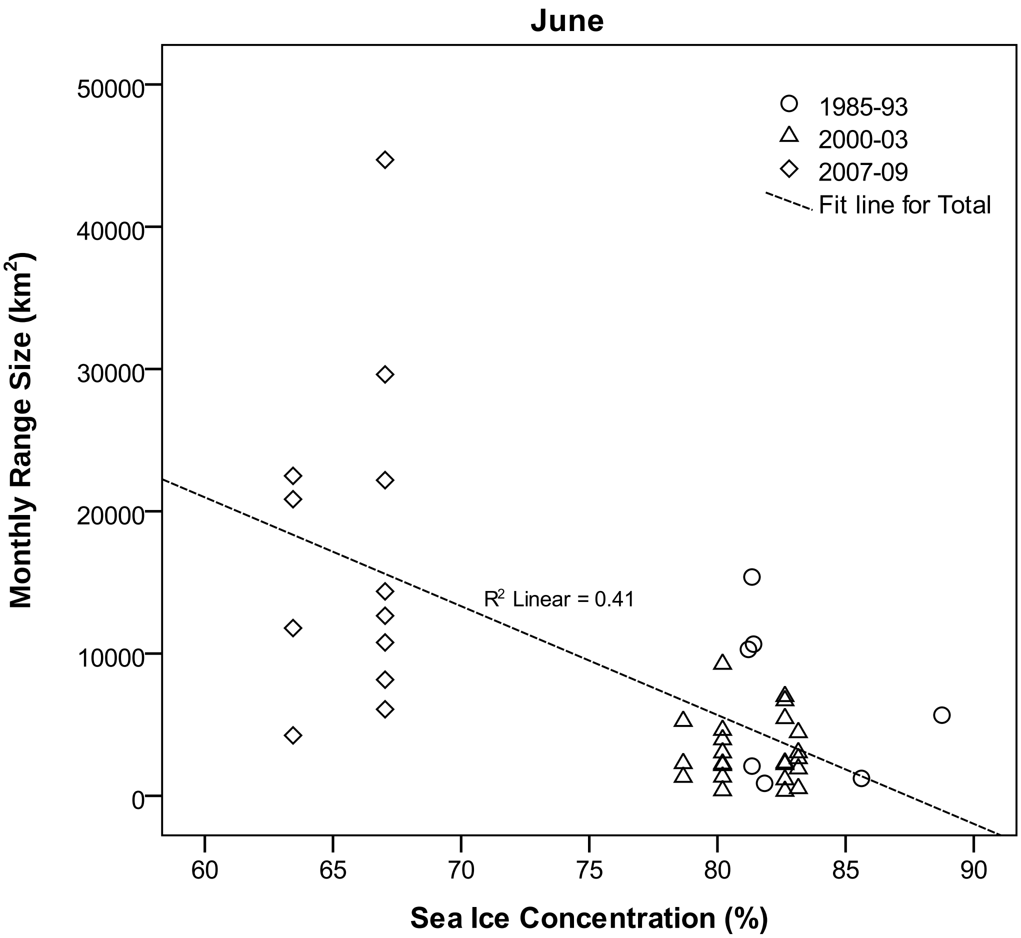

Figure 49 Linear regression of monthly home range size (MCP, km$^2$) and monthly mean sea ice concentration in the study area. Only the relationship for June was significant (linear mixed model: $P < 0.001$), but the same directional trend was seen throughout the autumn months (Sep-Nov).

Table 9 Mean angles and angular deviations of monthly net movements for satellite-collared female polar bears in the Southern Beaufort Sea.

| Timeframe | Month | Mean angle | Angular deviation | *Z* | *P* | No. of bears |
|---|---|---|---|---|---|---|
| 1985-93 | January | 79 | 43.4 | 2.54 | 0.070 | 5 |
| | February | 208 | 66.9 | 0.30 | 0.770 | 3 |
| | March | 78 | 27.6 | 3.90 | 0.010 | 5 |
| | April | 285 | 55.5 | 1.69 | 0.190 | 6 |
| | May | 247 | 73.1 | 0.45 | 0.640 | 13 |
| | June | 298 | 66.5 | 0.74 | 0.490 | 7 |
| | July | 278 | 69.1 | 0.44 | 0.660 | 6 |
| | August | 300 | 30.8 | 3.66 | 0.020 | 5 |
| | September | 117 | 60.4 | 0.99 | 0.390 | 5 |
| | October | 330 | 71.5 | 0.24 | 0.800 | 5 |
| | November | 157 | 72.2 | 0.17 | 0.860 | 4 |
| | December | 131 | 75.8 | 0.06 | 0.950 | 4 |
| 2000-03 | January | 261 | 71.1 | 0.74 | 0.490 | 14 |
| | February | 78 | 50.5 | 4.87 | 0.010 | 13 |
| | March | 135 | 67.5 | 0.93 | 0.400 | 10 |
| | April | 96 | 76.4 | 0.25 | 0.780 | 21 |
| | May | 81 | 76.6 | 0.27 | 0.770 | 24 |
| | June | 219 | 72.7 | 0.87 | 0.420 | 23 |
| | July | 328 | 57.2 | 4.27 | 0.010 | 17 |
| | August | 83 | 63.1 | 2.48 | 0.080 | 16 |
| | September | 25 | 66.0 | 1.69 | 0.190 | 15 |
| | October | 161 | 43.8 | 8.02 | 0.000 | 16 |
| | November | 210 | 65.9 | 1.61 | 0.200 | 14 |
| | December | 261 | 59.1 | 2.62 | 0.070 | 12 |
| 2007-09 | January | 86 | 47.5 | 2.59 | 0.070 | 6 |
| | February | 17 | 61.7 | 0.70 | 0.520 | 4 |
| | March | 262 | 23.1 | 3.38 | 0.020 | 4 |
| | April | 62 | 65.6 | 0.47 | 0.650 | 4 |
| | May | 9 | 72.9 | 0.40 | 0.680 | 11 |
| | June | 282 | 26.2 | 9.63 | 0.000 | 12 |
| | July | 344 | 53.6 | 3.80 | 0.020 | 12 |
| | August | 27 | 56.0 | 2.73 | 0.060 | 10 |
| | September | 23 | 67.3 | 0.96 | 0.390 | 10 |
| | October | 205 | 42.4 | 5.28 | 0.000 | 10 |
| | November | 264 | 34.2 | 6.75 | 0.000 | 10 |
| | December | 17 | 78.2 | 0.04 | 0.960 | 9 |

# Effect of unequal competition and unequal access on the distribution of polar bears[4]

The ideal free distribution (IFD; Fretwell and Lucas 1969) states that a species should distribute itself optimally across a landscape if: all individuals have absolute knowledge of and equal access to high quality patches; and all individuals are competitively equal. For apex mammalian predators, IFD is often violated by territorial behavior, resulting in an ideal despotic distribution (Fretwell 1972). Polar bears however, do not exhibit territoriality, in part due to the labile nature of sea ice (Amstrup 2003; Ramsay and Stirling 1986). Without territoriality, polar bears may distribute themselves across the sea ice landscape in an ideal and free manner.

Habitat suitability is equivalent to a measure of fitness: individuals living in more suitable habitat will raise more young to the age of reproduction. Polar bear reproductive output and cub survival is dependent on the ability of the adult female to gain and store fat (Watts and Hansen 1987; Derocher and Stirling 1996). Additionally, the productivity of polar bear populations correlates with the productivity of their primary prey, across both spatial and temporal scales (Stirling 2002; Stirling and Øritsland 1995). Therefore, one can assert that habitat suitability for polar bears is based upon the availability of prey resources.

Polar bears of the Beaufort Sea hunt ringed seals and bearded seals using the sea ice substrate (Stirling and Archibald 1977; Thiemann et al. 2008). In spring, polar bears enter a hyperphagic-feeding phase, where gains in mass provide the energetic reserves to fast through

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[4] A version of this report section is in peer-review for publication as Pilfold, N.W., Derocher, A.E., Richardson, E. in prep. Influence of intraspecific competition on the distribution of a wide-ranging, non-territorial carnivore.

periods of low prey availability (Ramsay and Stirling 1988). During the spring period, it is expected that polar bear habitat selection will be based on maximizing energy intake, by selecting habitat with the most probable energetic reward (high quality patches). Under an IFD, we would predict polar bears of all demographic classes distribute themselves in equal proportions throughout high quality patches. However, although polar bears are non-territorial, spring habitat selection and distribution by different demographics of polar bears may be influenced by two despotic mechanisms: unequal competitive ability and unequal access.

When individual competitors from the same population are unequal, an important IFD assumption is violated. Phenomenological and mechanistic spatial distribution models of unequal competitors predict one of two general distributions: a (semi)truncated distribution, where competitively superior individuals dominate high quality patches and subordinates are either mixed between high and low or relegated to low quality patches (Holmgren, 1995); or an ideal and free distribution, where distribution is no different than if all individuals were competitively equal (Smallegange and van der Meer 2009; van der Meer 1997).

Polar bears demonstrate unequal predatory abilities between sex and age-class. Due to strong sexual selection, adult male polar bears are at least twice the mass of other demographics of bears (Derocher and Wiig 2002). Adult male's increased mass allows them to handle and kill the highest reward prey items, such as adult bearded seals that can weigh 300kg or more, generally unattainable for other demographics of bears (Thiemann and Iverson 2007; Thiemann et al. 2011a). Polar bear size may also determine hierarchal social dominance (Derocher and Stirling 1990b), pertinent for retaining a mate or a seal kill. Adult male polar bears have been observed to harass and force subadult bears off of fresh kills (Stirling 1974b), and, as a possible response to kleptoparasitism, polar bears will sometimes drag seal kills anywhere from hundreds of meters (Derocher, unpublished obs.) to a few kilometres before consumption (Stirling 1974b).

Therefore, it may be hypothesized that polar bear distribution in spring reflects a (semi)truncated distribution, with adults dominating the highest quality patches, and subadults distributed in lower quality patches to reduce interference competition.

Conspecific predation risk has been shown to drive differentiated habitat selection within species in many systems. In polar bears, adult females with cubs-of-the-year (COYs; <1 year old) and yearlings (< 2 years old) will spatially segregate from adult males (Derocher and Stirling 1990a; Ferguson et al. 1997; Freitas et al. 2012; Stirling et al. 1993) to reduce the risk of infanticide, or potentially being preyed upon themselves (Derocher and Wiig 1999; Taylor et al. 1985). Additionally, some sea ice habitat types pose an increased survival risk to young cubs, and a mother with COYs may avoid them (Freitas et al. 2012; Mauritzen et al. 2003). As predation and cub survival risk for adult females with COYs prevents equal access to all habitat types, it can be hypothesized that adult females with COYs use lower quality patches relative to the rest of the polar bear population.

We employed a novel approach to resource selection functions (RSF; Manly et al. 2002 to quantify patch quality from locations of seals killed by polar bears in spring. We applied the patch quality model to analyse the distribution of seven different demographics of polar bears at a landscape scale. We tested the effects of unequal predatory competition and unequal access on the observed distribution of polar bears relative to patch quality. If unequal competition results in a (semi)truncated distribution, a lower proportion of subadult bears than adult bears should be observed in high quality habitat. If unequal access is a despotic mechanism in determining polar bear distribution, adult females with COYs should be found in lower quality habitat than the rest of the population.

## Materials and methods

Observations of seals killed by polar bears, and polar bear captures, were collected between early-April and mid-May (range April 3 – May 17) in 2003-2011. The study area was the Beaufort Sea east of 141° W and south of 75° N, as well as Amundsen Gulf (**Figure 50a**). Helicopter flights originated from Tuktoyaktuk, Sachs Harbour, Ulukhaktok (Holman), Cape Parry, and Norway Island and were limited to within 150 km of the coast. The study area is composed mainly of annual shorefast ice and pack ice. In spring, a characteristic feature of the region is the formation of a large flaw lead near the shorefast ice boundary (**Figure 50b**). The sea ice conditions near the lead are active in the spring, as changing wind patterns can close the lead, and changing temperatures can refreeze the open water. Comparatively, the sea ice conditions in the near shore areas of Amundsen Gulf and north of the Tuktoyaktuk peninsula are stable, promoted by their attachment to land.

Seal kill sites were identified from helicopter by the presence of blood, carcass, scavengers, or bears. Kills were located during non-selective searching for polar bears to be caught as part of a mark and recapture study. Duplication of kill sites was avoided by logging of kill locations and many sites were sampled thus removing the possibility of resampling. When possible, sites with remains present were investigated by landing, and tissue, jaw, and claw samples from kills were collected. Species and age class were determined through a combination of field observation, tooth histology and DNA analysis (Pilfold *et al*. 2012). In some cases where only blood spots remained, if the amount of blood was minimal, and it was found near a pressure ridge with a dug out maternal seal lairs (Furgal et al. 1996), it was assumed to be a ringed seal pup kill (Derocher et al. 2002). The presence of white lanugo at the kill site also helped confirm ringed seal pup kills when few remains were present. Seal kills by Arctic fox (*Vulpes lagopus*) were excluded based on the presence of fox tracks and the absence of polar bear tracks. Locations of kills were recorded with a handheld GPS.

Polar bears were captured non-selectively as part of long-term inventory and ecology research. Polar bears were immobilized from the air using Telazol (Stirling et al. 1989). Gender was identified in the field, while age was identified by tooth histology from a vestigial premolar (Calvert and Ramsay 1998). All field methods were in accordance with the Canadian Council of Animal Care guidelines. For the purpose of this study, polar bears were categorized into seven demographics: adult males (≥ 5 years), adult females (≥ 5 years), subadult males (< 5 years), subadult females (< 5 years), adult females with COYs (< 1 year), adult females with yearling cubs (1 year), and adult females with second year cubs (2 years).

Sea ice habitat was described using nine covariates including: distance from land (km), bathymetry (m), distance to shorefast ice boundary (km), sea ice concentration locally (%), sea ice concentration of the study area (%), floe edge, and ice type classified as new ice, pack ice, and fast ice (**Table 10**). Bathymetry was measured using the International Bathymetric Chart of the Arctic Ocean (IBCAO) produced on a 2 km grid (Jakobsson et al. 2008). The shorefast ice boundary was determined using Canadian Ice Service (CIS) charts as the intersection between shorefast ice and pack ice. Sea ice concentration locally was determined using Advanced Microwave Scanning Radiometer-EOS (AMSR-E) satellite data, produced on a 6.25 km grid (Spreen et al. 2008; Spreen and Kaleschke 2008). Sea ice concentration values were also averaged over the study area each day, to account for sea ice reduction in the spring. The IBCAO bathymetry grid was resampled to match the AMSR-E grid, and bathymetry values were averaged within each AMSR-E pixel in the study area. Floe edge was determined daily as a two pixel (12.5 km) buffer around any open water pixels as determined by AMSR-E. The floe edge covariate was categorized as a fixed distance binary instead of a continuous distance from open water, as open water is not a consistent feature day-to-day. Sea ice type categories were determined from bimonthly CIS regional ice charts. Fast ice was categorized as thick (>120 cm) annual shorefast ice. Pack ice was categorized as big to vast (500m to 10km) floes of thick (>120cm) annual pack ice. New ice was categorized as small to big (20m to 500m) floes of thin (10cm to 30cm) newly formed ice. These three ice categories accounted for 90% of the sea ice types surveyed, while the remaining 10% of ice surveyed could not be categorized into a single group. Each ice type was dummy coded, with the uncategorized ice types acting as the reference category. Covariates were screened for collinearity using a Pearson's correlation matrix. Covariates displaying a correlation coefficient of |rs| > 0.6, were not retained in the same model. Fast ice and pack ice were correlated ( |rs| = 0.78), and pack ice was removed due to its lack of fit. Patch quality was modelled using weighted binary logistic regression, in a "used" versus "available" framework (Manly et al. 2002). Used locations were sites where seals had been killed by polar bears. Species and age class was determined for each seal kill (n = 219). Prey selection in the spring can range from a newly born 6 kg ringed seal pup to a 300 kg bearded seal adult (Andersen et al. 1999; Smith 1987). Deriving patch quality from seal kill locations, in which each kill is assumed to be equal, could potentially underestimate high quality patches. To account for the energetic value of the kill, each used location was weighted by the estimated biomass of the kill. Kill biomass was determined from literature for each species and age class, and then converted to a weight for the regression (**Table 11**).

As sea ice conditions change on a daily basis, available locations were generated for each flight day. Available points were randomly generated locations, constrained to the helicopter flight path at a rate of one point per 50km travelled. A total of 96,660 km were flown over the study area in 2003-2011, generating 1934 points. Points falling in open water, or in non-negative bathymetry, were removed, resulting in 1736 available points used for modelling. Detection bias along the flight path was limited, as the majority of flight time was spent following recent polar bear tracks, and kills were easily identifiable by the contrast of blood on snow.

Akaike's Information Criterion for small samples ($AIC_c$; Burnham and Anderson 2002) was employed to select the most parsimonious model. Overdispersion ($\hat{c}$) and lack-of-fit was tested by dividing the Pearson $\chi^2$ by the degrees of freedom. Covariates were tested for nonlinearity using quadratic and natural log transformations. Natural log transformation of distance from land, bathymetry, and distance to shorefast ice boundary all provided a better model fit according to $AIC_c$. Sea ice concentration of the study area was transformed as a quadratic for model fit, which is similar to other polar bear studies using sea ice concentration data (Durner et al. 2009). All models were analysed using GLM in SPSS 18.0 (IBM, Chicago, Illinois).

The resulting top model was used to create daily habitat quality maps for each flight day between 2003-2011. RSF values were standardized so the maximum value was 1.0 for each day. Patch quality was determined by the RSF output, with each pixel (6.25 $km^2$) defining a single possible patch. The habitat quality model assumes that polar bears forage in an optimal manner, and therefore trade-offs between prey abundance and vulnerability, and energetic profitability, are inherent to the model. We defined "high quality patches" as: habitat patches within the top 10% of the RSF valued study area each day (RSF quantile > 90%).

Polar bear distribution was evaluated using polar bear locations from capture data collected over the same period as kills ($n = 622$). To ensure independence, capture records were screened with kill locations for each flight day. Any captures that occurred at the same location or on the same pixel (patch) as a seal kill were removed. After screening, 531 polar bear locations remained. Capture locations were intersected with daily patch quality maps, and the pixel value for each polar bear location was compared to the mean pixel value of the study area for the same day using a paired *t*-test. Differences between polar bear demographic classes were tested using a Kruskal-Wallis test, as variances between classes were not homoscedastic (Koenker test; $\chi^2 = 8.4$, $df = 1$, $P < 0.01$; Koenker 1981). *Post-hoc* tests between demographic classes were conducted using the Dunn-Bonferroni method (Dunn 1964). Chi-square tests were used to compare proportions of demographic classes of polar bears in the high quality patches. All tests were completed in SPSS 18.0 (IBM, Chicago, Illinois). For all significance tests, alpha was set to 0.05.

## Results

Between 2003-2011, 204 flight days were flown over the study area. Flights were predominately flown between Herschel Island to the west and the edge of the Amundsen Gulf to the east, resulting in 69.9% of the seal kills and 63.9% of the available locations. Of the 219 kills identified by species and age class, 16 were bearded seal and 203 were ringed seal. Bearded seal kills composed of: 7 adults, 3 juveniles and 6 pups. Ringed seal kills composed of: 78 adults, 10 juveniles and 115 pups. The 531 polar bear captures composed of: 137 adult females, 157 adult males, 48 subadult females, 51 subadult males, 53 adult females with COYs, 61 adult females with yearling cubs, and 24 adult females with second year cubs.

Model selection using $AIC_c$ did not result in a single top model ($w_i \geq 0.90$, **Table 12**), therefore model averaging was employed (Burnham and Anderson 2002). The top three models were used ($w_i = 0.95$), and parameter values were averaged accordingly (**Table 13**). All covariates were included in the final model except ice concentration locally (AMSR), which showed no selection. The model showed no signs of overdispersion or lack of fit ($\hat{c} = 1.36$).

Three recurrent covariates were distance to shorefast ice boundary (ln_I_DIST), distance from land (ln_L_DIST), and bathymetry (ln_DEPTH). Selection for sea ice habitat peaked close to the shorefast ice boundary (**Figure 51a**), near floe edges (OW_Edge), and in areas of newly formed ice (New_Ice). Similarly, there was negative selection close to shorelines (**Figures 51b**, **47c**) and in fast ice areas (Fast_Ice), indicating a preference for active ice areas. Selection for active ice was also present at the scale of the entire study area (Z_AMSR), with relative selection probability peaking at 85% sea ice concentration (**Figure 51d**). Averaging the daily habitat quality maps over all the days flown ($n = 204$) indicated a recurrent high quality habitat near the flaw lead and Cape Bathurst polynya system (**Figure 52**).

Polar bear captures were located in above average kill habitat according to the patch quality model ($t = 10.4$, $df = 530$, $P < 0.001$). All demographics of bears were captured in above average kill habitat, with the exception of females with COYs ($t = -0.33$, $df = 52$, $P = 0.74$, **Figure 53**) and females with second year cubs ($t = 0.60$, $df = 23$, $P = 0.55$, **Figure 53**). Demographic groups of polar bears were not all observed in equal quality habitat ($H = 21.4$, $df = 6$, $P < 0.01$). Females with COYs were observed in significantly lower quality habitat than adult females, adult males, subadult females and subadult males.

Proportions of the seven demographics of polar bears were not equally represented in the high quality patches ($\chi^2 = 13.8$, $df = 6$, $P = 0.03$, **Figure 54**). Proportions of adult males, adult females, subadult males and subadult females in high quality patches did not significantly differ (**Figure 54**). However, relative to adults and subadults pooled across gender, a lower proportion of females with COYs were found in the high quality patches ($\chi^2 = 8.8$, $df = 2$, $P = 0.01$).

## Discussion

The patch quality model was determined using an RSF framework of comparing locations in which we observed seals killed by polar bears, versus locations where we did not. However, instead of developing the model with used sites treated equally, as would be traditional to the modelling approach, we weighted each used point *a priori* by the energetic value of the prey item. To our knowledge, this is a novel approach, and it shifted the focus of the model to weight the landscape by the biological importance of each used location. The success of this tactic relied on the fact that we could confidently quantify the biological importance of used sites by modelling only one behavior directly, instead of trying to infer behavior secondarily (Hebblewhite and Haydon 2010). We see potential in using this approach to evaluate the biological importance of particular habitat types in resource selection studies.

The patch quality model corroborated previous hypotheses on habitat selection by polar bears hunting seals. Patch quality was highest in active areas of sea ice, including edges of large leads, in newly formed ice, and at the shorefast ice boundary. Previous assessments of habitat selection based on polar bear movement and track data indicated similar selection patterns (Ferguson et al. 2000; Hansen 2004; Ramsay and Stirling 1986; Stirling et al. 1993). The patch quality model also agreed with observations of hunting polar bears using active ice areas (Smith 1980; Stirling and McEwan 1975).

The patch quality model forecasted that hunting conditions peaked in the study area at an 85% regional sea ice concentration, while becoming generally unproductive at sea ice concentrations below 50%. Durner et al. (2009) found a similar result from movement data, as polar bears across the polar basin were most likely to be found in areas of 80% sea ice concentration in spring. Mauritzen et al. (2003) found polar bears avoided areas with sea ice concentrations <60%. In seasonal ice environments, polar bears have been observed to migrate from the sea ice to land in association with regional sea ice concentrations of 50% in spring (Stirling et al. 1999). The patch quality model suggests migration from the sea ice, and avoidance of areas with low ice concentrations, is likely due to unproductive hunting conditions.

Additionally, this finding offers biological pragmatism for the use of 50% sea ice cover as the threshold for identifying “ice-free” days in Beaufort Sea ecosystem (Gleason and Rode 2009; Regehr et al. 2010).

Polar bear preference for hunting in active ice areas is reflective of prey habitat choice. Ringed seals are attracted to the shorefast ice boundary where fast ice and pack ice meet (Frost et al. 2004; Moulton et al. 2002). The shorefast ice boundary is generally where large flaw leads open, and biological productivity is high (Perrette et al. 2011). The flaw lead system of the eastern Beaufort Sea is part of a network of polynyas throughout the Arctic, well known for their productivity in supporting Arctic life (Stirling 1980; Stirling and Lunn 1997). Recurrence of high quality patches in the study area overlapped the same general region as the Cape Bathurst polynya. Ringed seals have been observed in high abundance near the polynya (Harwood and Stirling 1992; Stirling et al. 1982), most likely attracted to the productivity of the area (Arrigo and van Dijken 2004; Makabe et al. 2010). Bearded seals also use active ice areas in the spring, as they give birth to their young on floes of drifting pack ice (Kovacs et al. 1996). Bearded seals stay close to lead edges, and prefer areas with medium to smaller floes of pack ice (Simpkins et al. 2003). Polar bears have identified strategies to successfully hunt ringed seals and bearded seals in an active ice environment, including still-hunting around newly formed cracks, and using lead channels for aquatic stalks (Stirling 1988).

Polar bears of unequal competitive ability (adults vs. subadults) did not segregate by patch quality. Instead, we found support that the distribution of unequal competitors may not be (semi)truncated (Smallegange and van der Meer 2009; van der Meer 1997). Although subadult polar bears likely suffer from kleptoparasitism from larger bears (Stirling 1974b; Stirling and Archibald 1977), and are unable to successfully hunt the largest prey items (Thiemann and Iverson 2007; Thiemann et al. 2011a), they are found in equal proportion to adult bears in the highest quality habitat. This outcome may be thought of in two ways: 1) adult polar bears do not perceive any risk or lower encounter rates in allowing subadult polar bears into high quality habitat; and 2) subadult polar bears are able to scavenge enough from carrion to outweigh the cost of potentially losing a fresh kill to an adult bear.

Adult polar bears may not show direct aggression to the presence of subadult polar bears in high quality habitat, allowing for an ideal and free distribution between unequal competitors. An IFD might result if dominant competitors have an increased prey encounter rate relative to subordinates across patches (van der Meer 1997). As subadult polar bears are inexperienced hunters, and smaller in size, their presence may not negatively affect the prey encounter rate of adult polar bears. Instead, subadults may actually act as a competition buffer between dominant individuals (van der Meer 1997), while providing kleptoparasitic opportunities for adult male and female polar bears. Polar bears live in an environment where prey is spread over a large spatial scale and at low density (Stirling et al. 1982). Dominant adult polar bears may benefit by stealing prey caught by subadult polar bears, as is expected for unequal competitors living in environments with low prey density (Broom and Ruxton 2003; Hamilton 2002). While the benefits of an IFD for adult polar bears are clear, the benefits for subadults are more intriguing.

Subadult polar bears may benefit from entering high quality habitat by scavenging from carrion, as well as learning from more experienced polar bears. Subadults are inexperienced hunters (Stirling and Latour 1978), and may need to meet their energy and growth requirements by scavenging. Polar bears can be surplus killers (Amstrup 2003; Stirling and Derocher 1990; Stirling and Øritsland 1995), and given the size of their prey, a single prey item can satiate a polar bear before consumption of the available biomass is complete (Best 1977), leaving substantial biomass as carrion for other polar bears (Smith and Stirling 1975; Stirling 1974a; Stirling and Archibald 1977). On larger kills, polar bears have been observed to share consumption simultaneously with unrelated and subordinate individuals (Miller et al. 2006; Stirling 1974a). The benefit of scavenging opportunities for subadults likely outweighs the cost of potentially losing a fresh kill to a dominant individual in high quality patches. A secondary, longer-term benefit for subadult polar bears may be knowledge transfer. By staying near more experienced polar bears, subadult polar bears may learn new hunting techniques and as well as profitable hunting locations.

Predator satiation is an important regulator of interference competition, and can potentially be an underlying mechanism for an IFD. However, in modelling IFDs from standing stock systems, little attention has been paid to the regulating effects of satiation on interference competition and kleptoparasitism. Satiation has been identified as a factor affecting the functional response of individual predators, as most predators are digestion limited (Jeschke et al. 2002). Dominance at kill sites within social groups is also recognised to be affected by satiation when prey items are large, as dominant individuals will forage first until satiation, while subordinate individuals wait in the periphery. A dominant but satiated predator is less likely to risk competing over a food resource, or defend carrion from scavenging. We suggest that subadult polar bears stay in close proximity to adult bears to take advantage of scavenging opportunities, which is why, although competitive abilities clearly differ, adult and subadult polar bears distribute themselves in an ideal and free manner on a landscape scale.

Female polar bears with COYs were found in lower quality patches compared to other demographics of polar bears. We found support for our hypothesis that unequal access to all habitat types for females with COYs results in the use of lower quality patches. We suggest that females with COYs may trade-off energetic gains for cub protection.

Female polar bears with COYs spatially segregate from the rest of the polar bear population (Derocher and Stirling 1990a; Ferguson et al. 1997; Freitas et al. 2012; Stirling et al.

1993), possibly to avoid conspecific predation (Derocher and Wiig 1999; Taylor et al. 1985) and habitats with open water and rough ice that are challenging for young cubs (Freitas et al. 2012; Mauritzen et al. 2003). However, the consequences of this habitat selection are unknown. Our study suggests that spatial segregation by females with COYs results in the use of lower quality foraging patches, indicating a possible trade-off between cub protection and energetic intake. A similar result was found in Alaskan brown bears inhabiting salmon streams during hyperphagia in autumn (Ben-David et al. 2004).

Female polar bears with COYs may focus their foraging efforts on ringed seal pupping habitat in stable ice areas (Stirling et al. 1993). Although the prey source may be more predictable (Freitas et al. 2012), indirect evidence suggests hunting ringed seal pups in early spring may not be very profitable. Ringed seal pups are born in subnivean lairs (Furgal et al. 1996), and hunting success rates by polar bears at lair sites is estimated to be less than 10% (Stirling and Archibald 1977). Ringed seal pup kills are sometimes found unconsumed (Stirling and McEwan 1975), indicating little usable biomass in early spring. Likely due to the low biomass available in the kills, prime ringed seal pupping habitat in stable ice areas was not identified as a high quality patch in this study. As cub survival and growth is directly related to milk production, and therefore access to high quality prey for the mother (Derocher 1996), we can infer that use of lower quality foraging habitat by females with COYs is not simply a poor behavioral choice (Delibes et al. 2001). The behavioral decision by females with COYs to use lower quality patches likely reflects the fitness trade-off between energetic profitability and exposing cubs to habitat or conspecific predation risks.

Direct evidence of nutritional consequences for habitat segregation in females with COYs is absent. In the two studies where nutritional condition was directly assessed on different demographic classes of polar bears on the sea ice in spring, females with offspring were pooled together (Cherry et al. 2009; Ramsay et al. 1991. This potentially masks the energetic consequence of habitat segregation, as females with yearling or second year cubs do not segregate from the rest of the population (Stirling et al. 1993). We suggest a more rigorous assessment of the impacts of unequal access to high quality patches will be to compare urea/creatinine ratios of females with COYs to different demographics of polar bears in spring.

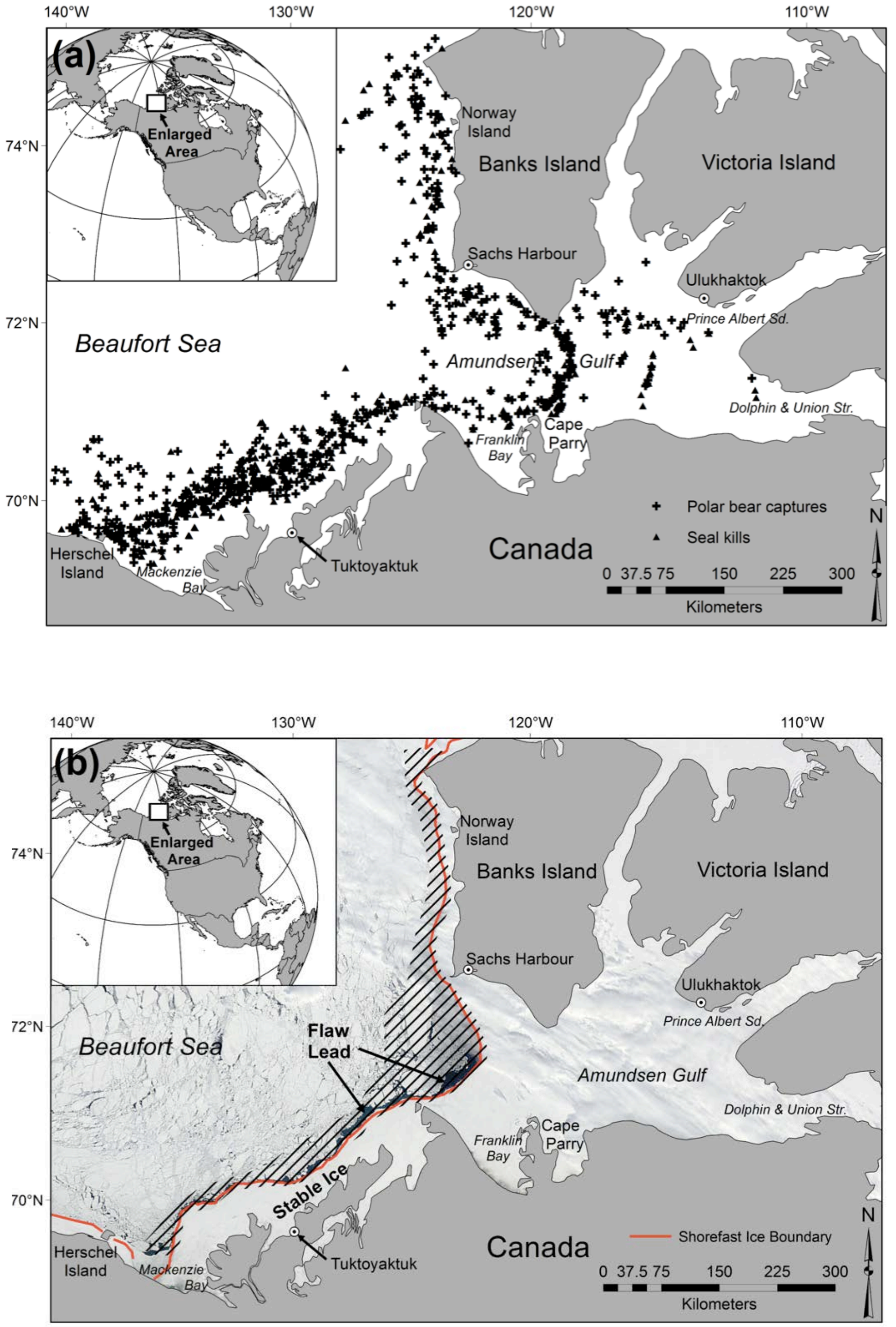

Figure 50 Study area. (a) Locations of seals killed by polar bears (▲) and polar bear captures (✚). (b) NASA/GSFC Rapid Response image for April 30, 2009, with shorefast ice boundary from Canadian Ice Service. Hatched area indicates active ice zone.

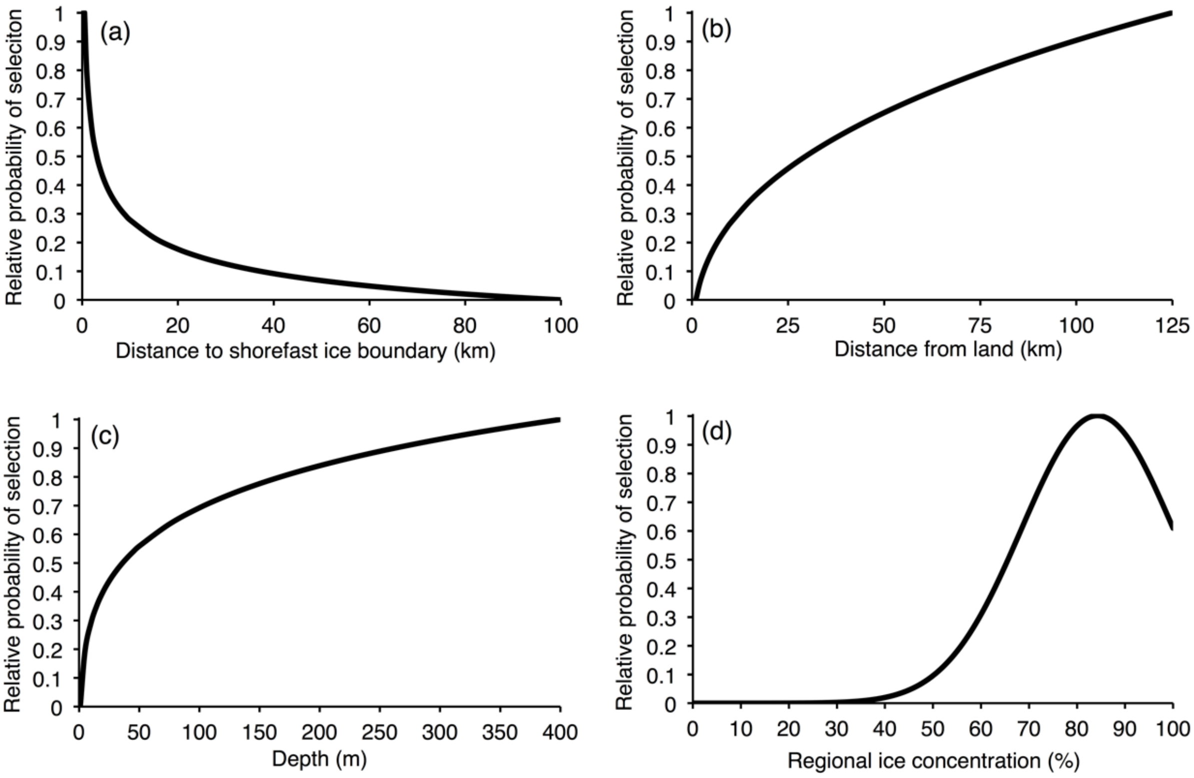

Figure 51 Scaled univariate response for the four continuous habitat covariates. All other covariates were held to their median values when computing the response curve.

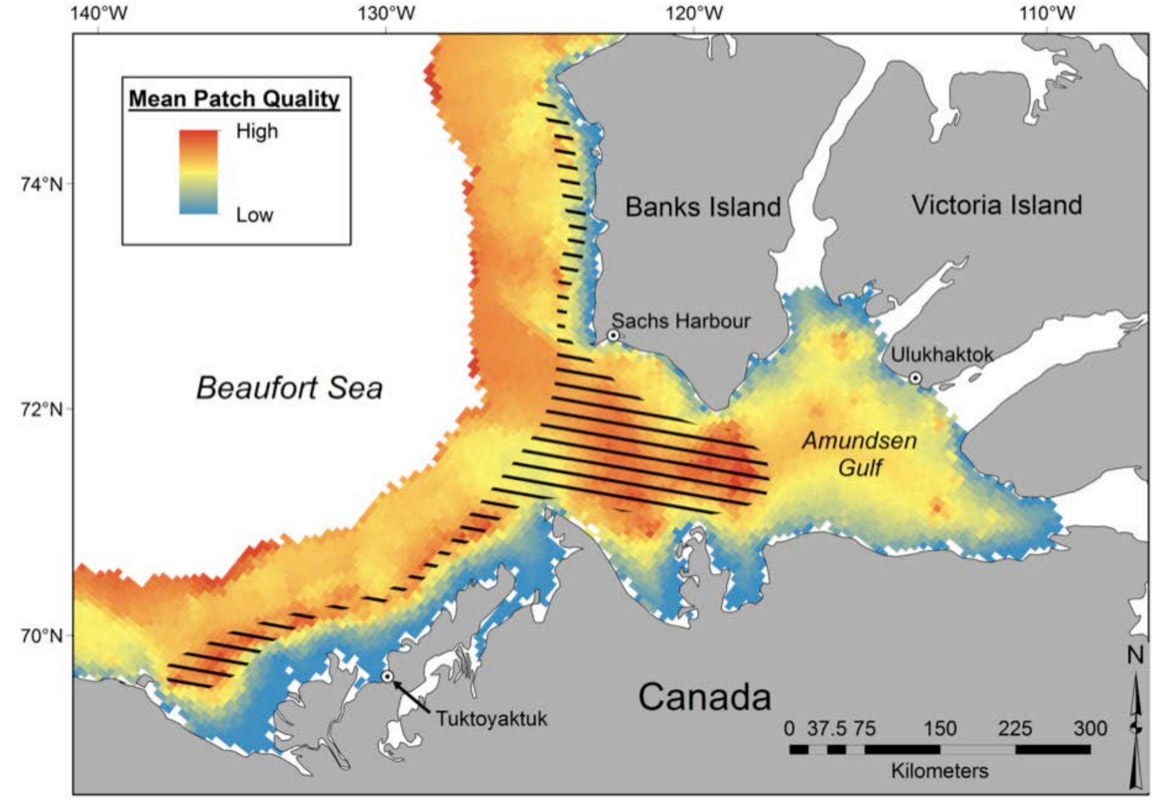

Figure 52 Mean patch quality relative to recurrence for each flight day (*n* = 204). Hatched area represents the Cape Bathurst polynya (Arrigo and van Dijken 2004) and related flaw lead system.

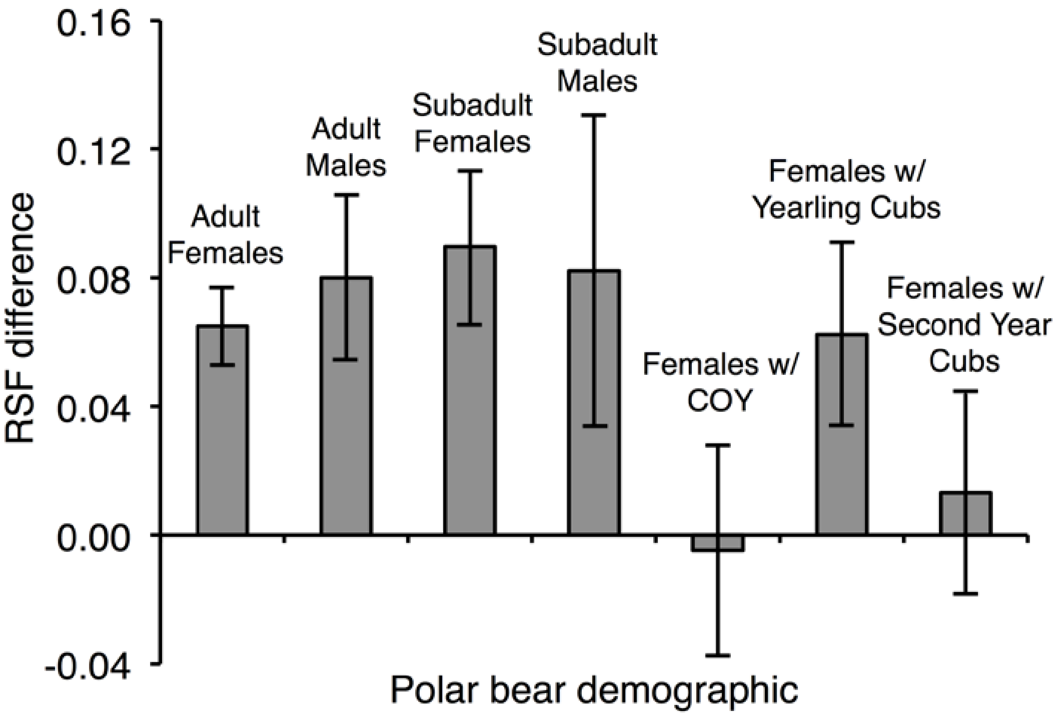

Figure 53 Mean difference in scaled RSF values between capture location and overall study area for seven demographics of polar bears.

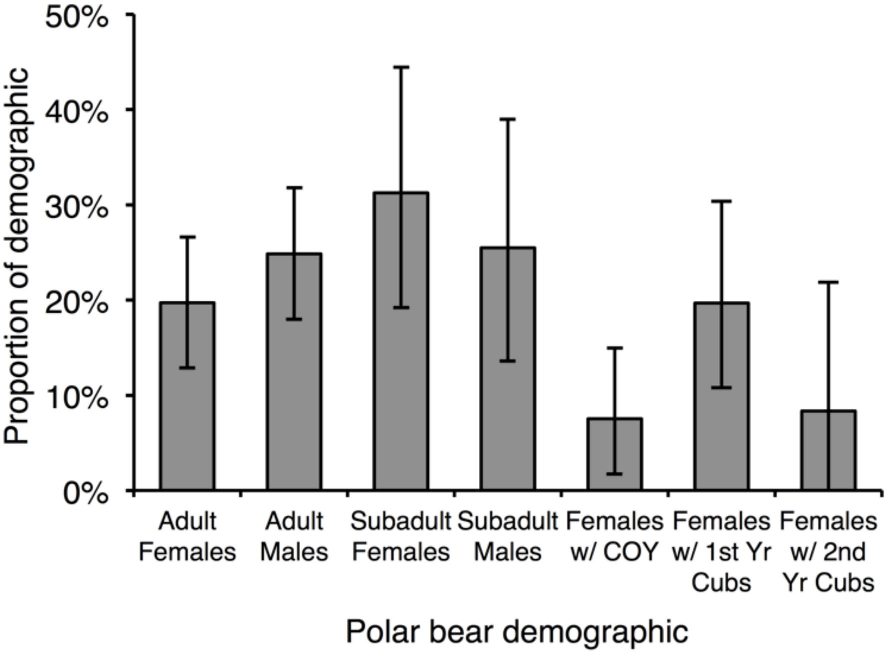

Figure 54 Proportion of polar bear demographics found in high quality patches (top 10% RSF valued area each day).

Table 10 Patch quality model covariates.

| Covariate | Acronym | Range* | Source |
|---|---|---|---|
| Distance to shorefast ice boundary | ln_I_DIST | 0.0 - 174.9 km | Canadian Ice Service regional charts (intersection between pack ice and fast ice) |
| Distance from land | ln_L_DIST | 1.1 - 116.2 km | |
| Bathymetry | ln_DEPTH | 5.2 - 1450.8 (m) | IBCAO Bathymetry charts Jakobsson et al. 2008 |
| Local sea ice concentration | AMSR | 3 - 100 % | AMSR-E satellite data Spreen et al. 2008; Spreen and Kaleschke 2008 |
| Regional sea ice concentration | Z_AMSR + Z_AMSR2 | 70.6 - 99.7 % | AMSR-E satellite data Spreen et al. 2008; Spreen and Kaleschke 2008 |
| Flow edge | OW_Edge | | AMSR-E satellite data Spreen et al. 2008; Spreen and Kaleschke 2008 |
| Thick annual shorefast ice | Fast_Ice† | | Canadian Ice Service regional charts (polygons coded: 10/4•/8) |
| Big to vast floes of very close annual pack ice | Pack_Ice† | | Canadian Ice Service regional charts (polygons coded: 9+/4•/5 to 6) |
| Small to big floes of very close new pack ice | New_Ice | | Canadian Ice Service regional charts (polygons coded: 9 to 9+/1 to 5/3 to 5) |

*Untransformed †Correlated ( $|r_s|$ = 0.78), Pack_Ice removed from analysis

Table 11 Estimated biomass of species and age class of kills used a regression weights.

| Species | Age-Class | Est. Biomass (kg) | Regression Weight |
|---|---|---|---|
| Ringed seal | Pup | 11 | 1 |
| | Juvenile | 57 | 6 |
| | Adult | 57 | 6 |
| Bearded seal | Pup | 62 | 6 |
| | Juvenile | 273 | 27 |
| | Adult | 273 | 27 |

Source: Derocher, Wiig and Andersen 2002

Table 12 Top ranking patch quality models according to $AIC_c$. Top three models used for model averaging ($w_i$ = 0.95).

| Model | $AIC_C$ | $AIC_C$ | $w_i$ | Rank |
|---|---|---|---|---|
| ln_I_DIST + ln_L_DIST + ln_DEPTH + Z_AMSR + ZAMSR2 + OW_Edge + New_Ice + Fast_Ice | 3279.48 | 0.00 | 0.59 | 1 |
| ln_I_DIST + ln_L_DIST + ln_DEPTH + Z_AMSR + ZAMSR2 + AMSR + OW_Edge + New_Ice + Fast_Ice | 3281.48 | 2.01 | 0.21 | 2 |
| ln_I_DIST + ln_L_DIST + ln_DEPTH + Z_AMSR + ZAMSR2 + OW_Edge + Fast_Ice | 3282.16 | 2.68 | 0.15 | 3 |
| ln_I_DIST + ln_L_DIST + ln_DEPTH + Z_AMSR + ZAMSR2 + New_Ice + Fast_Ice | 3284.26 | 4.78 | 0.05 | 4 |

Table 13 Model averaging for top three models. Average (β) used to construct daily patch quality maps. Selection ratio for each covariate is indicated by exp (β), where values that are greater than 1 indicate selection and values less than 1 indicate avoidance.

| Covariate | ln_L_DIST | ln_I_DIST | ln_DEPTH | AMSR | Z_AMSR | Z_AMSR2 | OW_Edge | Fast_Ice | New_Ice |
|---|---|---|---|---|---|---|---|---|---|
| β (Model 1) | 0.378 | -0.255 | 0.134 | | 0.337 | -0.002 | 0.411 | -0.207 | 0.498 |
| β (Model 2) | 0.378 | -0.254 | 0.134 | 0.000 | 0.335 | -0.002 | 0.409 | -0.207 | 0.498 |
| β (Model 3) | 0.364 | -0.267 | 0.138 | | 0.341 | -0.002 | 0.409 | -0.249 | |
| Average (β) | 0.376 | -0.257 | 0.135 | 0.000 | 0.337 | -0.002 | 0.410 | -0.214 | 0.498 |
| Upper CI (β) | 0.496 | -0.200 | 0.205 | 0.005 | 0.552 | -0.001 | 0.718 | -0.032 | 0.950 |
| Lower CI (β) | 0.255 | -0.313 | 0.065 | -0.005 | 0.122 | -0.003 | 0.102 | -0.396 | 0.046 |
| exp (β) | $1.456^{***}$ | $0.774^{***}$ | $1.144^{***}$ | 1.000 | $1.401^{**}$ | $0.998^{**}$ | $1.507^{**}$ | $0.808^{*}$ | $1.645^{*}$ |

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

# Preliminary analysis of polar bear movements and habitat use

Identifying polar bear habitat use requires the availability of both the observations of polar bear locations and the conditions of the habitat at the time of the observations. Polar bear location data were collected from GPS collared bears between 2007 and 2010 in the Southern Beaufort Sea. Data were analysed for step lengths (distance between consecutive positions), and habitat use. Furthermore, the National Snow and Ice Data Centre (NSIDC, University of Colorado, United States) publicly provide sea-ice concentration map data on a daily basis over the same period. Combining these elements, along with bathymetric data provided by Environment Canada, we have summarized seasonal polar bear movements and habitat use for each individual bear, as well as by age- and sex-class.

## Materials and methods

Polar bear data were available for 65 bears (41 adult females, 12 sub-adult females, and 12 sub-adult males) in the Southern Beaufort Sea region between 2007 and 2010 (Appendix 2). A total of 78,720 positions were acquired from GPS telemetry using Telonics GPS collars, and are provided in geographic coordinates (decimal degree, WGS84). A location was logged by the collar at a maximum rate of once every 4 hours, along with the date and time of the location.

For each individual bear, we created GIS point locations in the geographic coordinate system, and then re-projected them into a polar stereographic projection for ease of use, and to be compatible with the sea-ice concentration data.

## Movement Analysis

To determine movement rates, each location was compared to the previous location and assigned a step-length based on the distance travelled and the time between locational fixes. We used the time-sequential location data to create a vector layer for movement paths for each bear, with each line segment representing the distance travelled from location to location. We summarized monthly movement rates for each bear, and provided them in individual data tables. We further summarized monthly movement rates by age- and sex-class (**Figure 55**). In most months, sub-adult males had a larger mean step-length than females of both age-classes, though not always significantly so. January was the only month where sub-adult females moved significantly more than sub-adult males. In all cases, adult females moved the least, which is likely due to denning behavior and the fact they may have been accompanied by cubs-of-the-year. Because there were substantially more adult female locations than the sub-adult males and females combined, the mean movement rate of all bears reflects a bias towards adult female behavior.

## Habitat Use

Sea-ice concentration was available from passive microwave sensor satellite imagery (SSM/I) courtesy of the NSIDC (http://nsidc.org/data/nsidc-0081.html). SSM/I imagery is obtainable in 8-bit raster format with pixel values representing estimated sea-ice concentration values over a 2km x 2km area. Bathymetry is often considered an analogue of ocean productivity, with shallower depths typically being associated with more productive waters. We summarized the seasonal use of habitat for each bear from the mean values of sea-ice concentration and the corresponding location's bathymetric depth. Values were interpolated directly from the data for both ice concentration and bathymetry, and no re-projection of either raster layer was performed. All points which did not intersect with one or both raster were withheld from their respective analyses. We further summarized the habitat use results by age- and sex- class (**Figure 56**). Seasons were classified as: spring (March – May), summer (June – August), autumn (September – November), and winter (December – February).

Habitat use in terms of sea-ice concentration seems to be constant between age- and sex-classes, with the only notable exception being males during the summer months. Nevertheless, except in winter, male sub-adults tend to use areas with slightly less concentration of sea-ice than females of all ages. The change to lower mean concentration habitats in summer and autumn is likely an artefact of the general reduction of sea ice during these periods.

In terms of bathymetry, however, there seem to be a number of identifiable differences in habitat use. Firstly, as corroborated by the home range maps, all bears tend to use areas of deeper water in the summer and autumn. This is likely because the only remaining sea ice during the warmer months is further from shore than in spring and winter. Male sub-adults tend to remain in areas with less depth than females, with the exception of adult females in the autumn months. In summer and autumn, sub-adult females were using habitats with the greatest depths, whereas adult females took on that role in the winter and spring. As was the case with movement rates, the sample size of adult females was proportionally large enough to drive the means of habitat use when all bears were lumped together.

Analyses of movement rates indicate that sub-adult polar bears tended to move more than adult females, and to occupy areas of shallower depths and lower sea-ice concentrations. In general, adult females moved the least, probably due to denning and cub-rearing behavior, while sub-adult females remained in areas with higher ice concentration and deeper water

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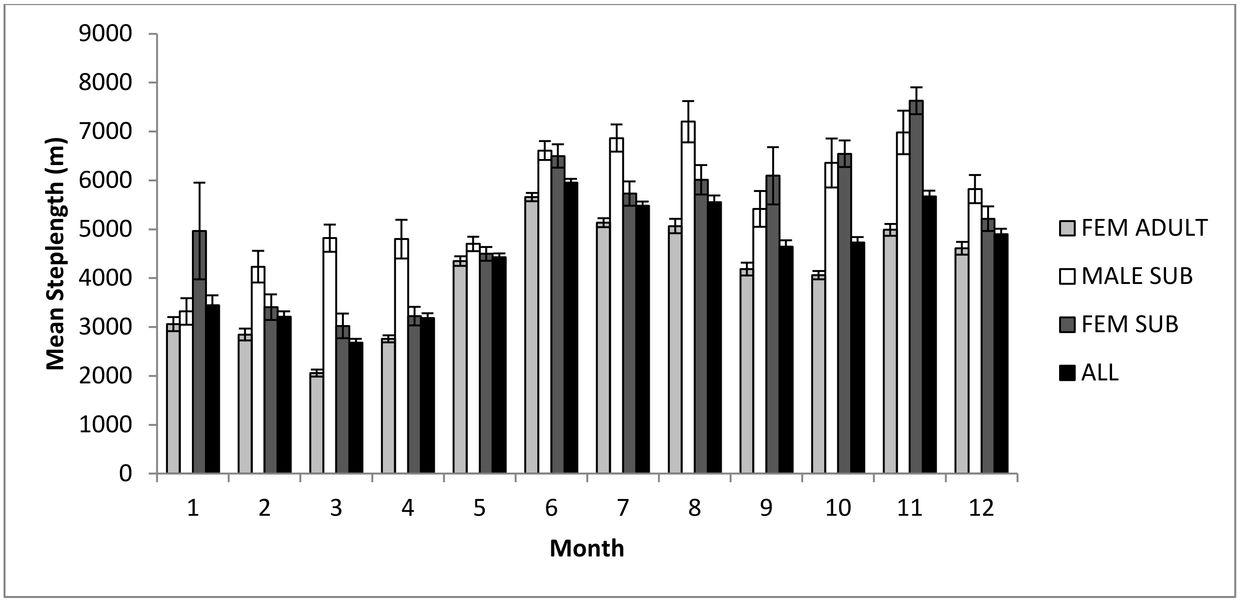

Figure 55 The mean (+/- SE) step-length for polar bears in the Southern Beaufort Sea by age- and sex-class.

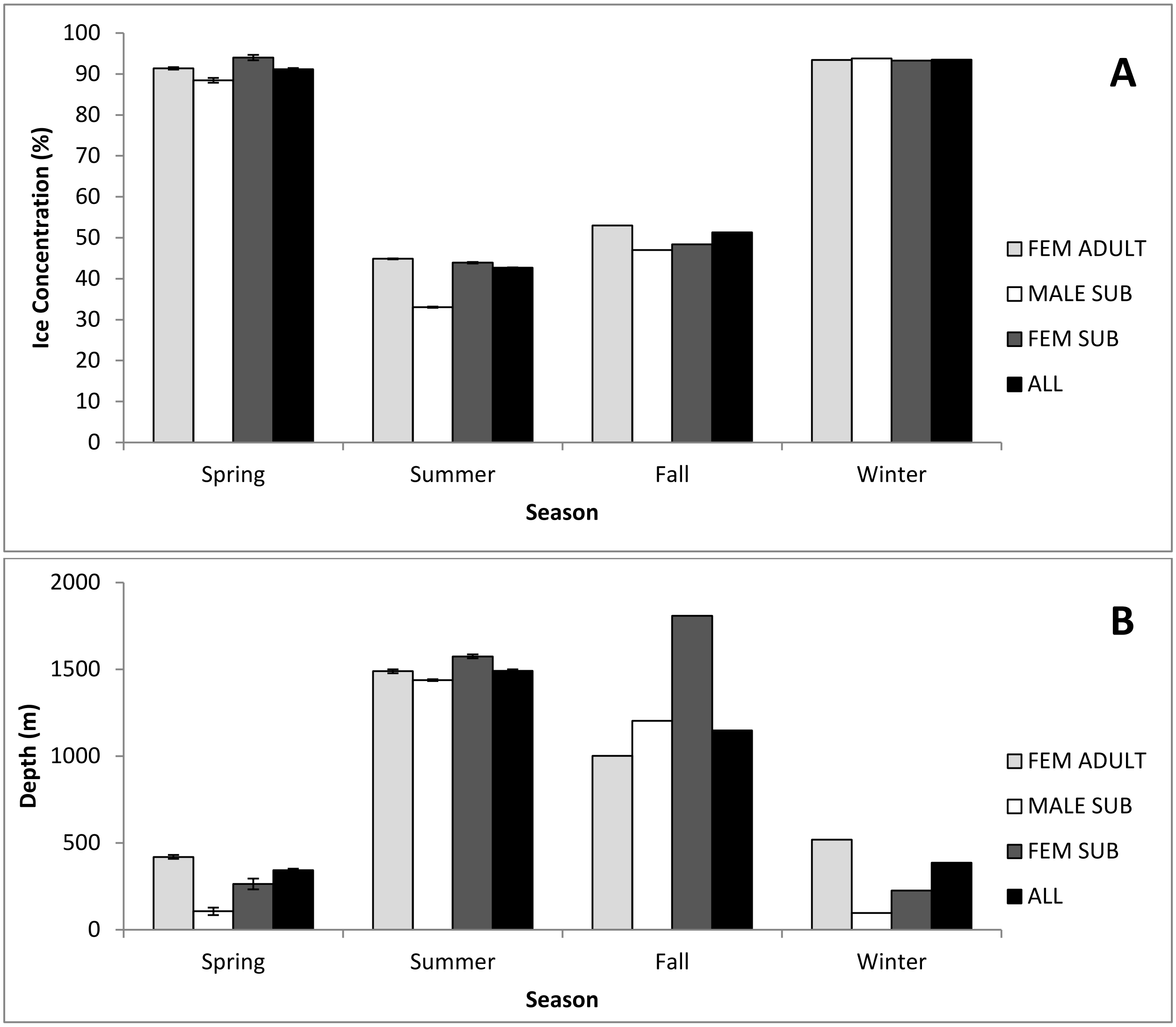

Figure 56. Habitat use by age- and sex-class for polar bears in the Southern Beaufort Sea with given by (A) the mean concentration of sea-ice (% +/- SE) and (B) mean bathymetry (m +/- SE).

Table 14 Summary list of the bears used in the analysis.

| Bear ID | Sex | Age-class | Bear ID | Sex | Age-class | Bear ID | Sex | Age-class |
|---|---|---|---|---|---|---|---|---|
| A20163 | F | adult | X32620 | F | subadult | X32680 | M | subadult |
| A20415 | F | adult | X32628 | F | adult | X32681 | M | subadult |
| A20434 | F | adult | X32643 | F | subadult | X32682 | F | adult |
| A20521 | F | adult | X32644 | F | adult | X32685 | F | adult |
| A20522 | F | adult | X32645 | F | adult | X32687 | F | adult |
| A20667 | F | adult | X32647 | F | subadult | X32690 | F | adult |
| A20716 | F | subadult | X32649 | F | adult | X32692 | M | subadult |
| A20760 | F | adult | X32650 | F | subadult | X32693 | F | adult |
| A20854 | M | subadult | X32651 | F | subadult | X32698 | F | adult |
| X19450 | F | adult | X32654 | M | subadult | X32700 | F | adult |
| X32253 | F | subadult | X32655 | F | adult | X32701 | F | adult |
| X32268 | F | adult | X32655b | F | adult | X32703 | F | adult |
| X32373 | F | subadult | X32658 | F | adult | X32704 | M | subadult |
| X32381 | F | subadult | X32660 | F | adult | X32704b | M | subadult |
| X32606 | F | adult | X32665 | F | subadult | X32707 | F | adult |
| X32606b | F | adult | X32670 | F | adult | X32711 | F | adult |
| X32608 | M | subadult | X32671 | M | subadult | X32803 | F | adult |
| X32611 | M | subadult | X32672 | F | adult | X32804 | F | adult |
| X32611b | M | subadult | X32672b | F | adult | X32808 | F | adult |
| X32613 | F | adult | X32673 | F | subadult | A20961 | F | adult |
| X32614 | F | adult | X32675 | F | subadult | X32282 | F | adult |
| X32617 | F | adult | X32677 | M | subadult |  |  |  |

# Appendix I Effects of chemical immobilization on the movement rates of free-ranging polar bears - Abstract[5]

The capture and handling of free-ranging animals is essential for many wildlife conservation and management applications. However, live capture may expose individual animals to risk of injury, impairment, or mortality. For species of conservation concern, these risks must be clearly understood and weighed against the benefits of capture-based research or management activities. The polar bear is a species of conservation concern throughout its range and physical mark-release-recapture techniques have formed the basis of polar bear research and harvest management for decades. We used the telemetry data from adult female (n = 61) and subadult (n = 13) polar bears in three Canadian subpopulations that had been captured for other studies and examined the movement patterns of individuals post-capture to measure their recovery from chemical immobilization. These bears had been previously fitted with satellite-linked global positioning system collars and we used three individual-based metrics to assess their recovery: (1) time to move 50 m; (2) time to move 100 m; and (3) time to reach a baseline movement rate threshold (km/d) derived from each individual's movements in a fully recovered state (i.e., 30-60 days post capture). There were no differences in recovery rate metrics across years or age classes. When compared across subpopulations, only the time to 50 m differed, being shortest in the Southern Beaufort Sea. Bears captured on land during the ice-free period in western Hudson Bay and Foxe Basin appeared to be more variable in their response to capture than were those

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[5] A full version of this work is in press as Thiemann, G.W., Derocher, A.E., Cherry, S.G., Lunn, N.J., Peacock, E., and Sahanatien, V. 2013. Effects of chemical immobilization on the movement rates of free-ranging polar bears. *Journal of Mammalogy* 94: 386-397.

handled on the sea ice of the Southern Beaufort Sea, but in all three areas, bears showed gradual acceleration in movement. Rates indicative of recovery were reached 48 hours after capture. Sixty-nine percent (51/74) of bears appeared to be fully recovered in ≤ 3 d. Consistent with earlier work on chemical immobilization of polar bears, there was no relationship between dosage and rate of recovery. Our results indicated that polar bears captured in different locations, seasons, and life history stages resumed normal movement rates within 2-3 days of capture.

Table 15 Administration of immobilizing drugs and recovery rates for polar bears captured and outfitted with GPS tracking collars. Values are means (SEM). From Thiemann et al. in prep.*.

| | n | Total drug (mg) | No. inject. | Mass (kg)[a] | Dose (mg/kg) | Structural | | Time to | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | mass (kg)[b] | dose (mg/kg) | 50 m (d) | 100 m (d) | 30-60 d mean rate (d) |
| All ages | 25 | 1792 (74) | 1.6 (0.1) | 178 (6) | 10.3 (0.6) | 107 (3.4) | 17.0 (0.8) | 0.4 (0.0) | 0.5 (0.1) | 2.7 (0.6) |
| Adult females | 12 | 1817 (109) | 1.7 (0.1) | 200 (5) | 9.1 (0.5) | 120.6 (3.0) | 15.1 (0.8) | 0.3 (0.0) | 0.4 (0.1) | 2.3 (0.9) |
| Subadults | 13 | 1769 (103) | 1.6 (0.1) | 157 (6) | 11.5 (0.9) | 94.7 (3.1) | 18.9 (1.2) | 0.4 (0.1) | 0.6 (0.1) | 3.1 (0.7) |

* includes bears only from 2007 and 2008 because the manuscript in preparation required a balanced sample and 2 other populations are used for comparison.

[a] $M = 0.00006039 \times AXG^{1.762} \times SLEN^{1.249}$ (where AXG = axillary girth (cm), and SLEN = straight-line length (cm); (Thiemann et al. 2011b)

[b] $M_{str} = 14.93 \times (SLEN/100)^3$ (Molnár et al. 2009)

# Appendix II Peer reviewed papers published in association with this contract

Cherry, S.G., Derocher, A.E., Stirling, I., and Richardson, E.S. 2009. Fasting physiology of polar bears in relation to environmental change and breeding behavior in the Beaufort Sea. *Polar Biology* 32:383-391.

**Abstract**

We examined the use of the ratio of serum urea to serum creatinine as a physiological biomarker of fasting to monitor temporal patterns in the feeding ecology of polar bears (*Ursus maritimus*). Blood was collected from 436 polar bears in the eastern Beaufort Sea during April and May of 1985-1986 and 2005-2006. The proportions of polar bears fasting were 9.6% in 1985, 10.5% in 1986, 21.4% in 2005, and 29.3% in 2006. We used stepwise logistic regression analysis to evaluate factors that could influence the binary response variable of fasting or not fasting. Significant predictor variables of fasting were: the 2005 and 2006 capture years, solitary adult male bears, and adult male bears that were accompanying an estrous female. The increased number of polar bears in a physiological fasting state from all sex, age, and reproductive classes in 2005 and 2006 corresponded with broad scale changes in Arctic sea ice composition, which may have affected prey availability. The higher proportion of adult males fasting from all years was attributed to spring breeding behavior.

Cherry, S.G., Derocher, A.E., Hobson, K.A., Stirling, I., and Thiemann, G.W. 2011. Quantifying dietary pathways of proteins and lipids to tissues of a marine predator. *Journal of Applied Ecology* 48:373-381.

**Abstract**

1. Using measurements of naturally occurring stable isotopes in animal tissues is useful for

monitoring diets of wide-ranging species that would otherwise be logistically difficult to evaluate. However, differential metabolic routing of macromolecules within a consumer can be problematic when using stable isotope analysis of bulk tissues to trace dietary input.

2. We used stable isotope (delta 13C, delta 15N) analysis to examine polar bear *Ursus maritimus* diet, which includes both lipid-rich blubber and the proteinaceous tissues of their marine mammal prey. Because the proportion of proteins and lipids consumed may depend on prey type and size, it was necessary to consider metabolic routing of these macromolecules separately in isotope mixing models.

3. Bayesian mixing models (MixSIR, version 1.04) were used to separately estimate protein (delta 13C, delta 15N) and lipid (delta 13C) dietary inputs. We used existing knowledge of the relative lipid and protein intake for polar bears and isotopic information from both macromolecules to estimate overall diet composition.

4. The results for both male and female polar bears indicated that smaller prey (e.g. ringed seal *Pusa hispida*) contributed the largest proportion to the protein-metabolic pathway. In contrast, the largest proportion of the lipid-metabolic pathway for both sexes tended to consist of larger prey (e.g. bearded seal *Erignathus barbatus*).

5. The diet composition of male polar bears consisted of more large than small prey. Diet estimates for females overlapped to some degree with males but tended to consist of less large prey.

6. Synthesis and applications. Monitoring polar bear diet may help determine the effects of climate-induced environmental changes in Arctic marine ecosystems including shifts in prey composition. Additionally, tracing origins of anthropogenic pollutants is currently a priority for wildlife managers concerned with the health of marine mammals. However, our results indicate using stable isotopes to infer dietary inputs when proportions of macromolecules fluctuate

amongst food sources requires the sampling and analysis of multiple tissues representing distinct macromolecular metabolic pathways. In such cases, utilizing only proteinaceous tissues for analysis will result in erroneous dietary source estimates and inaccuracies when examining trophic-level transfer of contaminants, especially those that are lipophylic.

Pilfold, N.W., Derocher, A.E., Stirling, I., Richardson, E., and Andriashek, D. 2012. Age and sex composition of seals killed by polar bears in the eastern Beaufort Sea. *Plos One*. 7:e41429 doi: 10.1371/journal.pone.0041429.

**Abstract**

Background: Polar bears (*Ursus maritimus*) of the Beaufort Sea enter hyperphagia in spring and gain fat reserves to survive periods of low prey availability. We collected information on seals killed by polar bears (n = 650) and hunting attempts on ringed seal (*Pusa hispida*) lairs (n = 1396) observed from a helicopter during polar bear mark-recapture studies in the Beaufort Sea in spring in 1985-2011. We investigated how temporal shifts in ringed seal reproduction affect kill composition and the intraspecific vulnerabilities of ringed seals to polar bear predation.

**Principal Findings:** Polar bears primarily preyed on ringed seals (90.2%) while bearded seals (*Erignathus barbatus*) only comprised 9.8% of the kills, but 33% of the biomass. Adults comprised 43.6% (150/344) of the ringed seals killed, while their pups comprised 38.4% (132/344). Juvenile ringed seals were killed at the lowest proportion, only comprising 18.0% (62/344) of the ringed seal kills. The proportion of ringed seal pups was highest between 2007-2011, in association with high ringed seal productivity. Half of the adult ringed seal kills were ≥21 years (60/121), and kill rates of adults increased following the peak of parturition. Determination of sex from DNA revealed that polar bears killed adult male and adult female ringed seals equally (0.50, $n = 78$). The number of hunting attempts at ringed seal subnivean lair sites was positively correlated with the number of pup kills ($r^2 = 0.30$, $P = 0.04$), but was not correlated with the number of adult kills ($P = 0.37$).

**Conclusions/Significance**: Results are consistent with decadal trends in ringed seal productivity, with low numbers of pups killed by polar bears in spring in years of low pup productivity, and conversely when pup productivity was high. Vulnerability of adult ringed seals to predation increased in relation to reproductive activities and age, but not gender.

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