Polar Bear Conservation in a Period of Arctic Warming

by

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Abstract

Polar bear conservation faces significant challenges under Arctic warming, especially with respect to habitat loss and the resulting impacts on their seasonal energetic uptake and maintenance. Polar bears rely on sea ice for hunting, mating, denning, and rearing of offspring, and the availability of ice, both spatially and temporally, influences their fitness and survival. The research collected in this thesis includes an assessment of the global polar bear population, identifying gaps in the knowledge, and presenting a model linking polar bear density to prey diversity, providing estimates for missing subpopulations. The majority of subpopulations are found to be vulnerable to continued Arctic warming based on decadal-scale changes to sea ice and population size. A sea ice projection model for the Canadian Arctic Archipelago provided the means to estimate how sea ice degradation and loss may affect polar bears through the 21st century. Projections suggest that, without curbing greenhouse gas emissions, ice conditions in the Archipelago will shift away from a multi-year sea ice regime, and lengthening ice-free conditions will harm polar bear reproductive success and increase starvation rates. An analysis of movement patterns of adult and subadult, males and female polar bears, in the southern Beaufort Sea suggests that the ice-free season is associated with higher movement rates, thus greater demands on energy stores during a season that is expected to get longer with future warming. An assessment of time and space use of harvest risk areas derived from historical harvest locations found that subadult males were more often in risk areas than other age and sex classes, although they avoided the highest risk areas. Landfast ice in the low-risk areas was decreasing faster over time, with the possibility to concentrate polar bears into areas of higher risk to harvest under continued Arctic warming.

Preface

The research collected in this thesis represents collaborative work between S. G. Hamilton and his co-authors. Animal capture and handling procedures were approved by the University of Alberta BioSciences Animal Care and Use Committee (Protocols 409705, 600804, 600904, 6001004) in accordance with Canadian Council on Animal Care wildlife guidelines (www.ccac.ca/Documents/Standards/Guidelines/Wildlife.pdf). Research was conducted under Government of Northwest Territories Department of Environment and Natural Resources permits (WL003322, WL005372, WL005596, WL007376).

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Chapters 4 and 5 of this thesis relied on data collected as part of a multi-year polar bear telemetry program in the southern Beaufort Sea headed by A. E. Derocher. Data management was performed by S. G. Hamilton with assistance from E. M. Henderson. Analysis in Chapter 4 by S. G. Hamilton and A. Eriksen. Analysis in Chapter 5 by S. G. Hamilton and E. M. Henderson. Chapters written by S. G. Hamilton. A. Eriksen and E. M. Henderson contributed to edits for Chapter 4 and 5, respectively. A. E. Derocher was the supervisory author and contributed to edits of both chapters.

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CHAPTER 1

General Introduction

To ascertain the distribution and density of plants and animals is one of the fundamental questions in ecology (Anderwartha and Birch 1954). Changes to these distributions are typically associated with changes in habitat via expansion, fragmentation, or outright loss due to a combination of physical (e.g., erosion, climate, pollutants) and biological forces (e.g., inter-species competition, disturbance-related alterations in vegetation, changes in microbial communities). Over large time-scales, these habitat changes can affect the species therein, by segregating populations or favouring adaptive traits, and even in some cases lead to the emergence of new species (Darwin 1859, Macarthur and Wilson 1963, MacColl 2011). If these changes are rapid, occurring over only a few generations, species may be unable to adapt, resulting in changes to their distribution or density (Walther et al. 2002, Root et al. 2003). In the absence of sufficient habitat, extirpation or extinction can occur (Pimm et al. 1988, Brooks et al. 2002, Halley et al. 2014).

Studies in ecology often lack the benefit of controlled experiments, so ecologists must rely on identifying patterns and extrapolating principles therein (Hilborn and Mangel 1997). When applied to conservation, ecological principles can inform us regarding habitat use and change, and to the impacts for the resident population of a given species. The scale at which habitat change occurs has significant implications on the number of individuals within a species, and the number of species in total (Arrhenius 1921, Mills 2013). With the Earth in a period of climate warming, changes are being detected globally and all species are likely to be affected in some form (Walther et al. 2002, Thomas et al. 2004). While ecosystem change is normal, the rate of present-day global warming may bring ecosystem changes more rapidly than evolutionary processes can adapt to them (Deutsch et al. 2008, Bennett et al. 2021).

Half the world's land and marine mammals are in a state of decline, and one in four species is threatened with extinction due primarily to habitat loss (Schipper et al. 2008). In the Arctic, climate change is responsible for lessening the average Arctic sea ice cover, thickness, and age, affecting a wide variety of Arctic marine species (Maslanik et al. 2007, Serreze et al. 2007, Wassmann et al. 2011, Comiso 2012). Polar bears (*Ursus maritimus*) are among those marine mammals affected by climate change (Stirling and Derocher 1993, Derocher et al. 2004, Laidre et al. 2008, Hunter et al. 2010) as Arctic Ocean temperatures increase (Zhang 2005) and sea ice cover decreases (Serreze et al. 2007). Polar bears require sea ice cover as a hunting platform, and some rely on multi-year ice for denning (Stirling and Derocher 1993), making this species particularly sensitive to Arctic climate change (Derocher et al. 2004, Wiig et al. 2008, Stirling and Derocher 2012). Habitat loss due to climate change is predicted to result in an overall reduction in the global polar bear population (Durner et al. 2009, Amstrup et al. 2010, Regehr et al. 2016).

This thesis involves topics in polar bear conservation with respect to Arctic warming, including the status and vulnerability of the global population, how projected changes to sea ice affects polar bear survival in the Canadian Arctic Archipelago, how polar bear movement patterns, and subsequent implications to energetic demands, differ by age and sex, and how changes to the timing and availability of sea ice can affect polar bear exposure to harvest risks. In order to place the research collected in this thesis into the broader context of global systems and ecology, I briefly discuss the Arctic sea ice system, how it shapes polar bear evolution and ecology, and the effects of Arctic warming on polar bears.

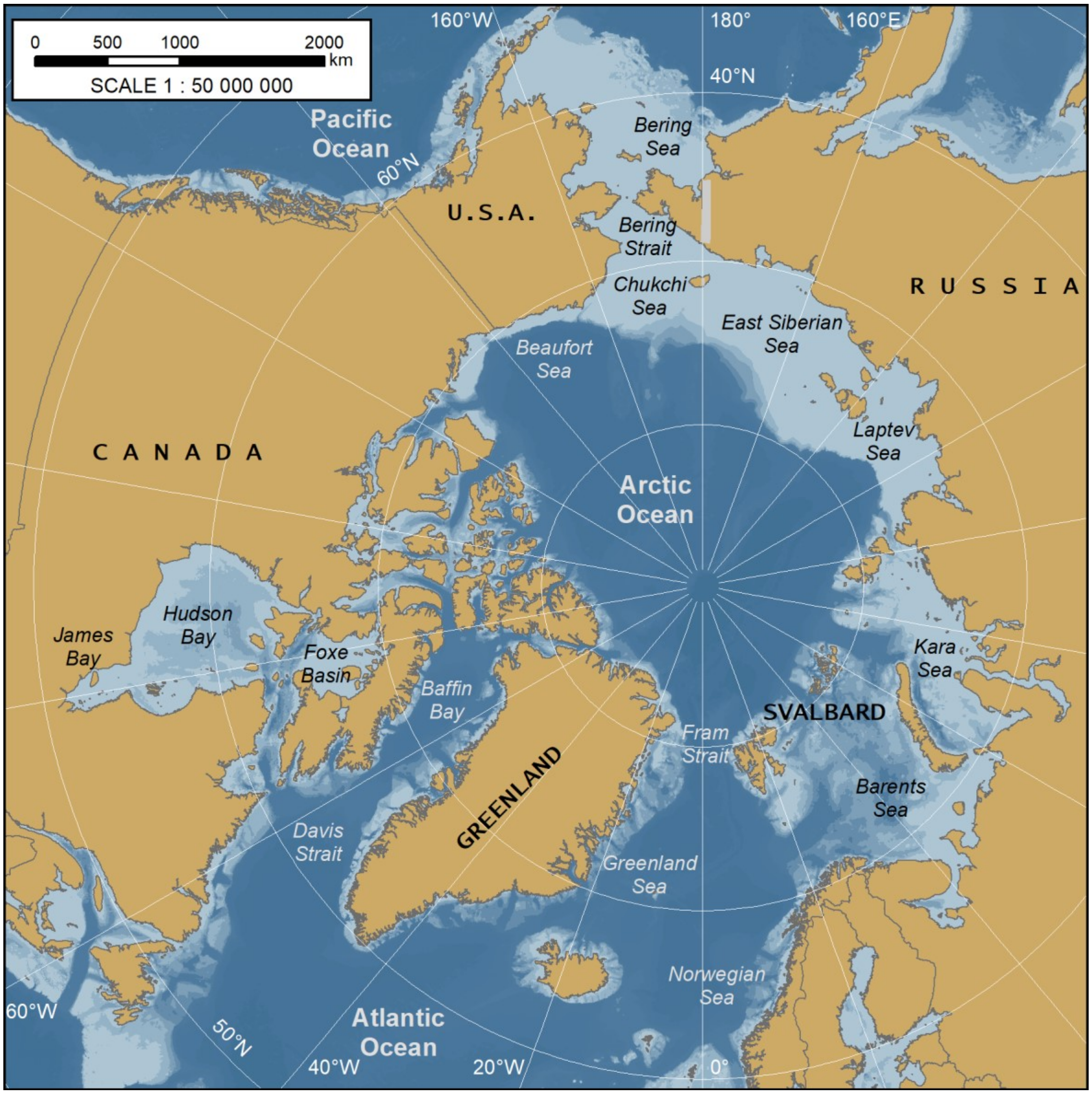

Figure 1-1. Map of the Arctic Ocean and its marginal seas.

On the Arctic Seas, Ice, and Ecosystem Productivity

The Arctic Ocean is surrounded by the North American and Eurasian continents, connecting to the Pacific Ocean through the Bering Strait, and the Atlantic Ocean through the Fram Strait, and East Greenland and Norwegian seas, but also through Baffin Bay, Davis Strait, and other parts of the Canadian Arctic Archipelago (Fig. 1-1). Taken together, this marine region encompasses ~20 million km^2 (AMAP 1998). The Arctic Ocean and surrounding waters are largely covered in sea ice in winter, although the sea ice surface historically shrinks to less than half its size in summer (Comiso and Nishio 2008, Cavalieri and Parkinson 2012, Meier et al. 2012). The 1981-2010 average maximum sea ice extent covers ~15.64 million km^2 of the Arctic waters, and the minimum averages ~6.22 million km^2 (NSIDC 2015), though these values have been in decline, and are projected to decline further into the future (Maslanik et al. 2007, Arrigo et al. 2008).

Warm waters flow into the Arctic Basin from the Atlantic via the Fram Strait and Barents Sea, and the Pacific via the Bering Strait, while cold waters flow out of the Arctic into the North Atlantic via the Canadian Arctic Archipelago (CAA) and the Fram Strait (Macdonald and Bewers 1996). The majority of the water in the Arctic Ocean began as Atlantic water, with less than 20% originating in the Pacific, while three quarters of outgoing water leaves the Arctic via the East Greenland Current (Sugden 1982). Changes in the density of seawater, due in part to sea ice formation and the subsequent salt rejection, are what drive much of the sub-surface movement of water masses (Pond and Pickard 1986, Seidov and Haupt 2003). The change in density generates a thermohaline circulation in the upper layers of the ocean, where cold, salt-heavy waters sink, and warmer, fresher waters rise to the surface (Moline et al. 2008, Worster and Rees Jones 2015). Upwelling waters bring nutrients to the upper water column, especially when circulation occurs over the shallow continental shelf and at the termini of glaciers, resulting in areas of high biological productivity (Greisman 1979, Frey et al. 2014, Van Oostende et al. 2015).

While pack ice circulates off-shore with wind and ocean currents, and land-fast ice forms and remains in contact with shore, marginal ice is found in regions where the pack ice meets ice-free waters, and moves seasonally with ice advance and retreat. Marginal ice is often associated with high biological productivity, representing the melting edge where primary producers thrive, forming the basis of the Arctic food web (Futsaeter et al. 1991, Gradinger 1995, Moline et al. 2008, von Quillfeldt et al. 2009). Polynyas, regions of semi-permanent or permanently open water in the midst of sea ice, are similarly associated with high primary productivity (Smith and Rigby 1981, von Quillfeldt 1997, von Quillfeldt et al. 2009). They are areas of intense ice production where newly formed ice is pushed away briskly from its site of formation, leaving open water, which quickly freezes only to be pushed away by wind again (von Quillfeldt et al. 2009).

Although the oceans account for half of global net annual photosynthesis, with coastal waters over continental shelves representing a disproportionately high fraction of this production (Muller-Karger et al. 2005, Van Oostende et al. 2015), the Arctic Ocean is possibly the least productive of the world's oceans (Pomeroy 1997). Photosynthetic primary producers are reliant on sunlight, which is restricted by sea ice, meaning primary production in the Arctic is highly seasonal (von Quillfeldt et al. 2009, Arrigo et al. 2010, Frey et al. 2011). The timing of the Arctic bloom of ice algae and phytoplankton is directly associated with the seasonal dynamics of sea ice and solar insolation, and thus the production of lipids which form the basis of a food web where polar bears reside as a top predator (Falk-Petersen et al. 1990, Wiig et al. 2008).

On the Ecology and Evolution of Polar Bears

The polar bear (*Ursus maritimus* Phipps 1774) is an Arctic marine mammal inhabiting the ice-covered waters of the Arctic Ocean and its marginal seas, and coastal regions where sea ice persists for enough of the year to provide sufficient foraging opportunities (Stirling and

Derocher 1993, Wiig et al. 2008, Amstrup et al. 2010). Polar bears are especially attracted to the highly productive marine areas over the continental shelves where their prey – primarily ringed seals (*Pusa hispida*) and bearded seals (*Erignatus barbatus*) – are found in abundance (Stirling and Archibald 1977, Thiemann et al. 2008, Wiig et al. 2008). Polar bears rely on sea ice for access to their prey, but also for mating, resting, and sometimes denning (Stirling and Derocher 1993, Derocher et al. 2004, Amstrup et al. 2010). When the sea ice melts in summer, the bears must either follow the retreat of ice to the multi-year pack ice, or move on land where they will not have access to substantial food again until the following freeze-up season (Derocher et al. 2004, Wiig et al. 2008, Molnár et al. 2010, Cherry et al. 2013). While polar bears can be found as far South as James Bay (51^{o}N) and as far North as the North Pole, they are not evenly distributed throughout their range. There are 19 recognized subpopulations of polar bears in the world with boundaries based on telemetry and mark-recapture as well as local knowledge and, while permeable, represent tendencies of bears to adhere to certain broad regions (IUCN/SSC Polar Bear Specialist Group 2021).

Polar bear physiology is highly adapted to life in a sea ice environment as marine mammal predators, and they are distinct from other bears due to these key adaptations (Stirling and Derocher 1990, Shields et al. 2000, Derocher et al. 2004). That polar bears evolved from brown bears (*U. arctos*) is well-established (Kurten 1964, DeMaster and Stirling 1981, Shields et al. 2000), though where and when is the subject of some debate (Kurten 1964, Edwards et al. 2011, Miller et al. 2012, Cahill et al. 2013, Kutschera et al. 2014), but likely more than 530 000 years ago (Hassanin 2015).

Polar bears are a *K*-selected species: long-lived, maturing slowly with few offspring, and investing substantial energy into raising their young (Pianka 1970, Bunnell and Tait 1981, Derocher et al. 2004). They are the largest of the extant ursids (males: 2 – 2.5m, 300 – 800kg; females: 1.8 – 2m, 150 – 300kg), permitting a varied selection of prey species (DeMaster and Stirling 1981, Thiemann et al. 2008). Morphological deviations from brown bears include a skull morphology and dentition adapted to an almost entirely carnivorous diet of marine mammal flesh and blubber (Howell 1930, DeMaster and Stirling 1981, Figueirido et al. 2009, Slater et al. 2010). Concordantly, polar bear livers are adapted to prey very high in Vitamin A content (Rodahl and Moore 1943, Ewer 1973, Bechshoft et al. 2011). Polar bear legs and feet are adapted to swimming, but also for distributing their weight when traversing thin ice (DeMaster and Stirling 1981, Wall 1983). Furthermore, polar bears are covered in dense underfur with coarser guard hairs lacking pigment, resulting in an outwardly, characteristically white appearance (DeMaster and Stirling 1981).

Adaptations are behavioural as well, especially with respect to movement in a dynamic sea ice environment (Ramsay and Stirling 1986). Polar bears persist on a drifting environment that can move rapidly (Hakkinen et al. 2008), necessitating energy expenditure to remain in areas of higher quality habitat (Mauritzen et al. 2003, Auger-Méthé et al. 2015). Male and female movement and space-use can differ, especially during the mating season, and depending on the presence of offspring (Amstrup et al. 2000, Laidre et al. 2013, Pilfold et al. 2014). Polar bears are typically solitary and do not cooperate to hunt or raise young (Derocher and Stirling 1990), though they do aggregate on occasion, for example during the ice-free season when hunting opportunities are limited (Latour 1981, Derocher and Stirling 1990, Ovsyanikov 2005, Kochnev 2006).

Mating occurs between March and May (DeMaster and Stirling 1981). During the spring mating season, the distribution of breeding females is highly variable from year to year so there is little pressure for males to defend a breeding territory (Ramsay and Stirling 1986). Pregnancy follows delayed implantation such that females will select a den site in September (Messier et al. 1994), either on shore or stable pack ice (Amstrup and Gardner 1994, Wiig et al. 2008). Females will emerge from dens with offspring in March, when milk reserves are low and seal hunting opportunities are at their peak, and remain with their young for up to two years, after which they become available for breeding again (Ramsay and Stirling 1986, Wiig et al. 2008).

The physical and behavioural adaptations described reflect a life history that involves storing as much of an energy reserve (fat) as possible when prey is abundant and hunting opportunities are good, then using these stores as efficiently as possible during the rest of the year (Ramsay and Stirling 1988, Wiig et al. 2008, Robbins et al. 2012). While these pressures exist at all latitudes, Arctic marine ecosystems have particularly strenuous thermal demands and seasonally limited access to food (Brown et al. 2004). Changes associated with Arctic warming have the potential to affect all aspects of polar bear ecology, with implications on species survival (Derocher et al. 2004, Wiig et al. 2008).

On Arctic Climate Change and Polar Bears

Earth’s cryosphere is especially sensitive to climate change because of the potential for feedbacks, in particular the change in surface reflectance (i.e., albedo) due to ice and snow loss (Hwang et al. 2011, England et al. 2021). In the case of Arctic sea ice, warming can encourage a loss-of-albedo feedback, where disappearing ice and snow cede incoming sunlight to the less reflective ocean surface below. Furthermore, sea ice insulates heat loss from the seawater beneath it, and snow insulates ice from early melting, meaning their disappearance allows for greater heat exchange between atmosphere and ocean (Vaughan et al. 2013).

The Arctic is warming at twice the rate of lower latitudes (Jeffries et al. 2015), and may be warmer than the last four centuries (Overpeck et al. 1997). Arctic sea ice is in decline, both in surface area and total volume (Rothrock et al. 1999, Wadhams and Davis 2000, Serreze et al. 2007, Lindsay and Schweiger 2015), and has likely been declining from before satellite observations were available (Walsh and Chapman 2001). Multiyear ice is thinning or disappearing from the Arctic ice pack entirely (Johannessen et al. 1999, Maslanik et al. 2007, Comiso 2012), and the loss of Arctic sea ice is occurring more rapidly than originally predicted (Zhang 2005, Stroeve et al. 2007). Record low minimum Arctic sea ice extents have been observed repeatedly since the beginning of the 21st century (Comiso et al. 2008, Parkinson and Comiso 2013), and some projections suggest the Arctic waters could become seasonally ice-free before the end of the 21st century (Johannessen et al. 2004, Serreze et al. 2007). Moreover, snow cover on sea ice has decreased (Armstrong and Brodzik 2001, Brown and Robinson 2011) and precipitation has increased (Groves and Francis 2002), both of which encourage greater melting of sea ice.

Changes in global climate and its effects on the Arctic sea ice are the primary threat faced by polar bears (Stirling and Derocher 1993, Derocher et al. 2004, Laidre et al. 2008, Durner et al. 2009, Amstrup et al. 2010, Hunter et al. 2010, Molnár et al. 2011, Stirling and Derocher 2012). Sea ice loss to a polar bear is synonymous with habitat loss, restricting hunting, mating, migrating, resting, and sometimes denning opportunities (Wiig et al. 2008, Robbins et al. 2012, Rode et al. 2013). An increasing ice-free period in the Arctic limits the energy uptake and expands the energy losses incurred by the polar bear's life cycle, especially to those bears forced to retreat to land in the summer with little access to energy-rich foods like seals and other marine mammals (Cherry et al. 2013, Pagano et al. 2018, Galicia et al. 2021). While some bears supplement their diets with alternate foods (Russell 1975, Derocher et al. 1993, Gormezano and Rockwell 2013), the resulting contribution is of little consequence (Rode et al. 2010b, Rode et al. 2015), meaning bears must ultimately rely on body fat stored before leaving the ice (Derocher and Stirling 1995, Thiemann et al. 2008).

Adult polar bears lose body mass daily while fasting on land (Derocher and Stirling 1995, Polischuk et al. 2002, Pilfold et al. 2016). A widening ice-free period means both less time for the polar bears to build fat reserves on the ice, and more time fasting off the ice, with negative impacts on body size and condition, litter size, cub survival, and ultimately numbers (Atkinson and Ramsay 1995, Stirling et al. 1999, Regehr et al. 2007, Amstrup et al. 2010, Rode et al. 2010a, Rode et al. 2013, Lunn et al. 2014, Bromaghin et al. 2015). Pregnant females attempt to maximize their energy stores prior to ice breakup when they must either look for den sites on stable multi-year ice (Amstrup and Gardner 1994) or on land (Stirling and Derocher 2012). Early breakup in some areas, such as the Western Hudson Bay, means females must begin fasting earlier, and reduces their chances for successful reproduction (Derocher et al. 2004, Molnár et al. 2011). In other areas, females can follow the pack ice North, but will have to swim farther to den on land (Stirling and Derocher 1993, 2012).

Thinning ice can become more fractured and thus more susceptible to drifting, which may produce more necessary swimming events for polar bears (Derocher et al. 2004). Polar bears are powerful swimmers (Stirling 1974), and will swim for great distances on occasion (DeMaster and Stirling 1981, Pagano et al. 2012, Pilfold et al. 2017), but they cannot swim indefinitely and it is an energy-intensive activity to undertake (Durner et al. 2011). Furthermore, greater ice drift can cause polar bears to expend more energy to work against the flow of ice and remain in quality habitat (Mauritzen et al. 2003, Auger-Méthé et al. 2015). Warmer winters can bring more precipitation as rain (Hezel et al. 2012), which may cause maternity dens to collapse (Stirling and Derocher 1993). Furthermore, rain could impact the snow cover in a way that impedes seal denning (Wiig et al. 2008).

As bears become more food-stressed, intraspecific predation, infanticide, and cannibalism may be expected to increase (Wiig et al. 2008). Pollutants stored in fat are more likely to cause problems to polar bear survival as food-stress increases and pollutants are released into the blood, with potential negative impacts on mortality and reproductive success (Jenssen 2006, Sonne et al. 2006). Furthermore, human-bear interactions may become more common as bears become more willing to approach human settlements, resulting in a higher number of mortalities in defence of life and property (Stirling and Derocher 1993, Wiig et al. 2008).

On Harvest of Polar Bears

Large mammalian carnivore populations are sensitive to mortality because they are often found at low densities, with low reproductive rates, and low population growth rates (Belovsky 1987, Wielgus et al. 2001). Polar bears fit this profile, being long-lived, slow reproducers, with high adult survival rates (Wielgus et al. 2001, Derocher et al. 2004) and harvest mortality is likely additive rather than compensatory (Derocher and Taylor 1994, McLellan 1994).

The potential for overharvest became the chief concern in terms of polar bear conservation efforts in the mid-twentieth century (Prestrud and Stirling 1994, Stirling 2002). Currently, harvest of polar bears is permitted under the International Agreement in Canada, USA (Alaska), Greenland, and parts of eastern Russia, while polar bears are protected from harvest excepting problem or defence kills in the Norwegian Arctic (Svalbard) and western Russia (Vongraven et al. 2022). Harvest tends to focus on males, most of which are subadults, while females with young are protected by the International Agreement (Derocher et al. 1997, Lunn et al. 2014, Vongraven et al. 2022). Sport hunting is permitted only in Canada, and only within existing quotas (Wenzel 2011, Vongraven et al. 2022). Despite the substantial management agreements surrounding polar bear harvest and supporting research, there is a lack of understanding on the how mechanisms of Arctic warming can impact the future of the legal harvest.

Preamble to the Thesis

Chapter 2 of this thesis discusses in-detail the global conservation status of polar bears and regional vulnerabilities to Arctic warming, wherein I summarize the status of scientific research on population and propose a modelling solution to estimate polar bear density in regions as-yet unstudied. In Chapter 3, I discuss the implications for polar bears given continued sea ice decline in the Canadian Arctic Archipelago, with particular focus on the energetic implications of lengthening ice-free seasons. Chapter 4 examines the seasonal movement patterns of GPS-collared polar bears of varying age and sex in the southern Beaufort Sea, and contextualizes the findings in terms of class-differing energetic implications. Chapter 5 investigates how polar bear age and sex influences harvest risk exposure, and how risk may be affected by future changes to landfast ice under continued Arctic warming.

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CHAPTER 2

Assessment of Global Polar Bear Abundance and Vulnerability

Stephen G. Hamilton and Andrew E. Derocher

Introduction

Assessing the conservation status of species is hampered by lack of information on distribution, abundance, and trend. Abundance estimation is a primary element of assessing population status (Thomas 1996), yet estimates commonly lack sufficient resolution to determine trend (Read and Wade 2000, Laidre et al. 2015). The conservation status of a species is usually based on its abundance trend, often within the context of habitat loss and range. For example, the International Union for the Conservation of Nature (IUCN) uses four criteria involving population size and range size and their dynamics to assess Red List status for species (Mace et al. 2008). A fifth criterion acknowledges the importance of robust quantitative analysis, which is vital for providing the basis in understanding observed changes and predicting future changes in population estimates (Caughley and Gunn 1996).

Wide-ranging and low-density species, including marine mammals, have threat levels generally higher than terrestrial species yet information required for conservation is often lacking (Schipper et al. 2008, Laidre et al. 2015). Threats to marine mammals vary widely but centre on habitat degradation or loss, harvest, pollution, and climate change (Pimm et al. 1988, Schipper et al. 2008). Polar bears (*Ursus maritimus*) are threatened by these same causes, but historically were depleted by excess harvest until management mitigated this threat (Prestrud and Stirling 1994, Regehr et al. 2015). More recently, climate change has become the primary threat manifesting as a loss of sea ice habitat and due to extensive research and long-term monitoring in some regions, polar bears have emerged as an iconic species for the effects of climate change (Derocher et al. 2004, Stirling and Derocher 2012, Atwood et al. 2016). Nonetheless, our understanding of their conservation status is challenged by incomplete and inconsistent monitoring across their range (Vongraven et al. 2012).

Polar bears have a circumpolar distribution, and for status assessment the population is defined as the global distribution and abundance of the species (IUCN 2012). Globally, polar bears are listed as "vulnerable" under the IUCN Red List due primarily to sea ice loss (Regehr et al. 2016), but threat levels vary across their range. For management purposes, the global population is divided into 19 subpopulations based on site fidelity, movement patterns, and genetics (Bethke et al. 1996, Paetkau et al. 1999, Mauritzen et al. 2002). Monitoring of abundance occurs at the subpopulation level using mark and recapture or aerial survey methods (Aars et al. 2009, Bromaghin et al. 2015, Lunn et al. 2016), and has been identified as a priority for polar bears (Vongraven et al. 2012). Nevertheless, the global abundance of polar bears is poorly established, being based on subpopulation estimates of varying age and accuracy, despite the growing need for a global estimate given the concerns raised over their vulnerability to climate change (Stirling and Derocher 1993, Derocher et al. 2004, Amstrup et al. 2008).

Mid-20th century estimates for the global polar bear population ranged widely, from 5000 – 19 000 animals (Scott et al. 1959, Harington 1964, Uspensky 1965, Uspensky and Shilnikov 1969, Larsen 1972), but lacked scientific rigour, sometimes relying on educated guesses, as standard methods for polar bear population estimation had not been established. More recently, the global population of polar bears was believed to be between 20 000 – 26 000 animals (IUCN/SSC Polar Bear Specialist Group 2010, Wiig et al. 2015). The global estimate, however, was acknowledged for its lack of precision and accuracy, and was not used for population assessment. Because of widespread interest in polar bears, the global estimate was sometimes referenced to satisfy public curiosity. Nonetheless, these estimates were misapplied by some to create doubt on the effects of anthropogenic climate change on polar bears (Harvey et al. 2018). Noting the challenges and expense of obtaining subpopulation estimates, Vongraven et al. (2012) proposed exploring occupancy models or extrapolation, yet there has been no effort to assess global abundance using such approaches.

Polar bear abundance has been correlated to the abundance of their primary prey: ringed seals (*Pusa hispida*) (Stirling and Oritsland 1995), which may be related to marine productivity, and more specifically nutrient availability (Bluhm and Gradinger 2008). Productivity is, in turn, related to solar insolation, ocean depth, and seawater flow (Greisman 1979, Frost et al. 2002, Muller-Karger et al. 2005, Hunt et al. 2016). Polar bears are a sea ice obligate species, with ice conditions such as concentration, thickness, age, and the period of the year during which ice concentration and thickness is insufficient for foraging (hereafter termed the ‘ice-free season’) affecting their hunting, mating, and mobility (Derocher et al. 2004, Wiig et al. 2008, Cherry et al. 2013). As such, the availability of sea ice is likely correlated to their abundance. Modeling methods may give insight into global population abundance if polar bear densities can be inferred from such ecosystem parameters (Nielsen et al. 2005, Mowat et al. 2013), allowing for extrapolation of density estimates to regions with no abundance data. Furthermore, given the broad latitudinal range of polar bears (ca. 52°N to 90°N) (DeMaster and Stirling 1981), variation in continental shelf under sea ice habitat (Amstrup et al. 2008, Durner et al. 2009), variation in prey diversity (Thiemann et al. 2008), and rates of sea ice change with climate warming (Parkinson 2014, Stern and Laidre 2016), the vulnerability of polar bears to climate change will vary spatially and temporally.

Our objectives were to assess the number of estimates per subpopulation in the literature (peer review and reports), the interval between estimates, the time between the last year of sampling and publication/release of results, and the gaps between estimates. We examine subpopulation density in relation to ecological factors, then extrapolate to subpopulations without estimates to estimate a total population size. We further create a subpopulation vulnerability index based on ecological variables and rates of sea ice change. Finally, we discuss recommendations for population monitoring.

Table 2-1. Summary of studies of polar bear subpopulation estimates for which data exist. No estimates were available for the Arctic Basin, Chukchi Sea, East Greenland Sea, Kara Sea, and Laptev Sea subpopulations. The most current subpopulation estimates (+/- CI) are provided, and the year for each is underlined. The mean interval is taken from the first year to the last in the series, including years where studies took place but results have not yet been released. Notable exceptions are demarcated accordingly.

Subpopulation	Current Estimate	Years with Estimates	Mean Interval (Years)	Source
Baffin Bay	2826 (2059-3593)	1997[1], 2013[2]	16	[1]Taylor *et al.* 2005, [2]SWG 2016
Barents Sea	2644(1899-3592)	1968[1], 2004[2], 2015*	23.5	[1]Larsen 1972, [2]Aars *et al.* 2009
Davis Strait	2158 (1833-2542)	1979[1], 2007[2]	28	[1]Stirling & Kiliaan 1980, [2]Peacock *et* al. 2013
Foxe Basin	2585 (2096-3189)	1994[1], 2010[2]	16	[1]Taylor *et al.* 2006, [2]Stapleton 2016
Gulf of Boothia	1592 (870-2314)	1974-1978[1†], 2000[2], 2017*	7.2	[1]Furnell & Schweinsburg 1984, [2]Taylor *et al.* 2009
Kane Basin	357 (221-493)	1997[1], 2014[2]	17	[1]Taylor *et al.* 2008, [2]SWG 2016
Lancaster Sound	2541 (1759-3323)	1975-1977[1††], 1997[2]	7.3	[1]Stirling *et al.* 1984, [2]Taylor *et al.* 2008
M'Clintock Channel	284 (166-402)	1974-1978[1†], 2000[2], 2017*	7.2	[1]Furnell & Schweinsburg 1984, [2]Taylor *et al.* 2009
Northern Beaufort Sea	980 (825-1135)	1972-1979[1], 1985-1987[1], 1985-1987[2], 1989[1], 2000[1], 2003-2006[1], 2006[1]	2.1**	[1]Stirling *et al.* 2011, [2]Stirling *et al.* 1988
Norwegian Bay	203 (115-291)	1975-1977[1††], 1997[2]	7.3	[1]Stirling *et al.*, 1984, [2]Taylor *et al.* 2008
Southern Beaufort Sea	907 (548-1270)	1972-1983[1], 2006[2], 2002-2010[3]	1.9	[1]Amstrup *et al.*, 1986; [2]Regehr *et al.*, 2006, [3]Bromaghin *et al.*, 2015
Southern Hudson Bay	943 (658-1350)	1986[1], 2005[2], 2012[3], 2016*	10	[1]Kolenosky *et al.*, 1992, [2]Obbard 2008, [3]Obbard *et al.* 2015
Viscount Melville Sound	161 (93-229)	1992[1], 2014*	22	[1]Taylor *et al.*, 2002
Western Hudson Bay	1030 (754-1406)	1978-1992[1], 1995[2], 1985-2011[3,4], 2011[5]	1**	[1]Derocher & Stirling, 1995; [2]Lunn *et al.*, 1997; [3] Regehr et al., 2007; [4]Lunn *et al.*, 2016; [5]Stapleton *et al.*, 2014

*Study unreleased – estimates as-yet unavailable.

**Did not use concurrent years to calculate average re-estimation time.

[†] Study conducted over a wider area. Estimates for GB and MC were later derived for 1978 from the data in Furnell (1984).

[††] Estimates given were inclusive of both LS and NW subpopulations, and cannot be directly compared between studies.

Materials and Methods

Data on the most recent assessment of subpopulation size were retrieved from the IUCN Polar Bear Specialist Group (IUCN/PBSG 2017). Further data were collected from peer-reviewed literature and reports and summarized (Table 2-1) to clarify the timing between estimates and identify gaps in knowledge. In estimating the mean interval between studies, where analyses occurred over multiple years we used the final year of the study as the reference point.

Subpopulation Ecological Analysis

Polar bear subpopulations were assumed to be contained within the 19 regions as utilized by the PBSG (IUCN/SSC Polar Bear Specialist Group 2010). Because some southward-fringing subpopulation boundaries extend past modern sea-ice extents (Fig. 2-1), we cropped these subpopulation areas based on the median sea-ice extent from 1979-2010 (Fetterer et al. 2017). Densities were derived for each subpopulation based on the aforementioned estimates and the modified boundaries (Table 2-2). While these areas may overestimate land habitat in some subpopulations, we had no clear basis to crop them as neither habitat quality nor density of use were being considered.

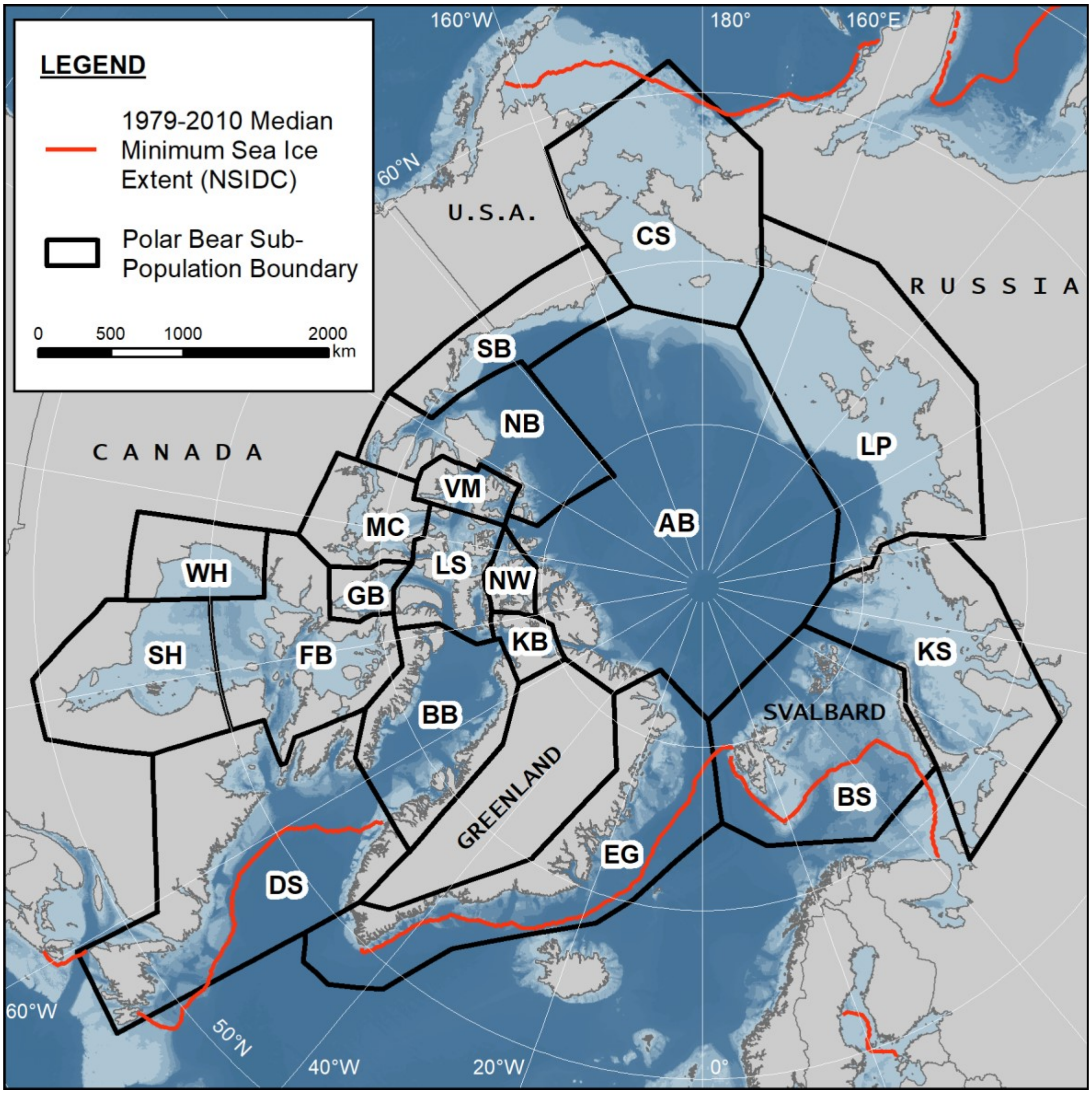

Figure 2-1. Polar bears belong to 19 subpopulations surrounding the Arctic and its marginal seas. The median maximum sea ice extent (1979-2010) is delineated on the map. Subpopulations are abbreviated as follows (in alphabetical order): Arctic Basin (**AB**), Baffin Bay (**BB**), Barents Sea (**BS**), Chukchi Sea (**CS**), Davis Strait (**DS**), East Greenland Sea (**EG**), Foxe Basin (**FB**), Gulf of Boothia (**GB**), Kane Basin (**KB**), Kara Sea (**KS**), Lancaster Sound (**LS**), Laptev Sea (**LP**), M'Clintock Channel (**MC**), Northern Beaufort Sea (**NB**), Norwegian Bay (**NW**), Southern Beaufort Sea (**SB**), Southern Hudson Bay (**SH**), Viscount Melville Sound (**VM**), and Western Hudson Bay (**WH**).

Table 2-2. Summary of key environmental parameters by polar bear subpopulation. Subpopulation densities (+/- CI) were derived from the most recent data available. Area includes land and sea. Continental shelf includes waters up to a depth of 300 m. The minimum sea ice extent is based on the median ice area from 1979-2010. The summer ice period is the 5-year mean number of days between March and September with less ice than the mean (1979-2014) over the same months. The 5-year mean is from the years preceding the most recent subpopulation estimate. The prey diversity is a tally of the number of prey species whose ranges overlap with each subpopulation.

Subpopulation	Current Density (bears/1000km^2)	Area (km^2)	Area Over Shelf (%)	Min. Ice Extent (%)	Summer Ice Period (days)	Prey Diversity
Arctic Basin*	UNK	4 233 530	11	99	111	3
Baffin Bay	2.62 (1.91-3.33)	1 078 840	31	0	160	8
Barents Sea	2.28 (1.64-3.10)	1 158 928	62	22	150	8
Chukchi Sea*	UNK	1 780 602	98	6	214	5
Davis Strait	1.27 (1.08-1.49)	1 703 007	42	0	249	8
East Greenland Sea*	UNK	1 396 254	28	25	168	6
Foxe Basin	2.19 (1.77-2.70)	1 181 019	96	0	171	7
Gulf of Boothia	9.30 (5.08-13.52)	171 136	98	56	87	5
Kane Basin	2.28 (1.41-3.15)	156 514	67	74	155	5
Kara Sea*	UNK	1 763 680	87	23	158	6
Lancaster Sound	5.21 (3.61-6.82)	487 532	70	51	89	6
Laptev Sea*	UNK	2 459 282	85	44	115	5
M'Clintock Channel	0.57 (0.34-0.81)	495 256	99	26	93	2
Northern Beaufort Sea	1.04 (0.87-1.20)	944 667	23	84	118	3
Norwegian Bay	1.38 (0.78-1.98)	147 262	74	100	88	2
Southern Beaufort Sea	1.27 (0.77-1.78)	715 030	60	10	132	4
Southern Hudson Bay	0.83 (0.58-1.19)	1 135 249	100	0	182	5
Viscount Melville Sound	0.77 (0.58-0.96)	209 962	62	100	70	2
Western Hudson Bay	2.05 (1.50-2.80)	502 379	100	0	171	5

* 5-year means for summer ice period were calculated using the most modern 5 years of data for subpopulations with no current density estimate.

We used generalized linear models (R 3.4.2, R Core Team, 2016) to assess the relationship between polar bear densities in subpopulations with estimates and local ecological characteristics (Table 2-2). Densities were derived based on the most recent population counts divided by the aforementioned cropped areas of each subpopulation. Due to the small sample size relative to the ecological variability over these large areas, we restricted our models to three parameters at most, and selected the model with the best fit based on the Akaike Information Criteria adjusted for small sample sizes: AIC$_c$ (Burnham and Anderson 2002). Because the relationships we investigated may be strongest for a subpopulation at carrying capacity, we assumed abundance was at the upper estimate range for each subpopulation.

Due to challenges in estimating productivity in ice-covered waters (Lee et al. 2016), we tested three proxies: the central latitude, continental shelf area, and prey species diversity within the subpopulation boundaries. For latitude, we used the geometric centres of each subpopulation. For continental shelf, we used ETOPO1 topographic maps (Amante and Eakins 2009) to isolate depths ≤300 m. For prey diversity, we considered marine prey species ranges coinciding with subpopulations to be available for consumption (Smith 1985, Calvert and Stirling 1990, Stirling and Oritsland 1995, Thiemann et al. 2008). As we were chiefly concerned with presence/absence, any amount of overlap between a prey species' range and the coinciding subpopulation was included. Prey species included ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), harbor seals (*Pusa vitulina*), harp seals (*Pagophilus groenlandicus*), hooded seals (*Cystophora cristata*), walrus (*Odobenus rosmarus*), narwhals (*Monodon monoceros*), and beluga whales (*Delphinapterus leucas*). Species ranges were obtained from the IUCN Red List database (http://www.iucnredlist.org). Because larger subpopulations were expected to have higher prey diversity than smaller ones, we divided prey diversity by area to create a Prey Diversity Index (species/10^5 km^2), which we used in our analyses. We did not include incidental prey, avian species, or subsistence harvest remains (Rode et al. 2015).

For ice-related parameters, daily sea-ice concentrations were obtained from the National Snow and Ice Data Center (Peng et al. 2013, Meier et al. 2017). We used the area of the minimum median sea ice extent (1979-2010) to represent polar bear habitat at its most limiting. We also used the length of the summer sea-ice conditions defined as the number of days during which the sea-ice area was <50% of mean ice area from March to September, 1974-2014 (Stern and Laidre 2016). Because subpopulation estimates are from different years, we used the ice conditions of a subpopulation for the 5 years preceding the most current subpopulation estimate.

Because our subpopulation abundance estimates were unlikely at carrying capacity in harvested subpopulations, we tested our best model with an additional parameter to account for harvest rates over a 5-year period. Harvest rates were obtained by subpopulation from the IUCN/PBSG (2017).

Using the best linear model of bear density from an environmental covariate, we estimated the number of bears in the previously un-surveyed subpopulations. We established a global estimate by summing the existing subpopulation counts with the counts for un-surveyed subpopulations derived from our model. We provided global estimates with and without the Arctic Basin as it is thought to have a very low density (Lunn et al. 2002) with movement into this area from adjoining subpopulations (Durner and Amstrup 1995).

Vulnerability Index

For estimating the vulnerability of each subpopulation, we summed values of 1 (low vulnerability) to 3 (high vulnerability) over five binned parameters. The parameters investigated for the vulnerability index were binned according to expert knowledge and the criteria for binning is provided for each as follows. We assumed a larger polar bear subpopulation would survive poor conditions better than a smaller subpopulation. Minimum viable population estimates vary across species but abundance >5600 animals has been identified as a meaningful threshold (Reed et al. 2003). Because all polar bear subpopulations are below 5600 animals, we distinguished vulnerability between subpopulations using the number of bears in the most recent estimate, or according to the estimate of our model extrapolation when no estimate was available. We scored subpopulations with respect to the median estimate (~1000 bears), with subpopulations counts >2000, 1000-2000, and <1000 bears scored as 1 to 3, respectively.

Sea ice over the continental shelf is important habitat for polar bears and may contribute to their resilience to climate change (Durner et al. 2009, Rode et al. 2013). We scored subpopulations according to the percent of water area over shelf as a proxy for high-quality habitat, with 67-100%, 34-66%, and <34% scored as 1 to 3, respectively. To further distinguish productivity between subpopulations, especially in the Canadian Arctic Archipelago where shelf area is consistently high, we added a parameter for prey diversity. As climate change has the potential to affect ocean productivity (Arrigo et al. 2008), thus the ranges of Arctic marine species (Hunt et al. 2016), we assume more prey options contributes to the resilience of polar bear subpopulations (Ives et al. 2000). Subpopulations with ≥6, 5-4, and ≤3 species scored as 1 to 3, respectively.

We used two parameters to assess vulnerability to sea ice habitat change (data from Stern and Laidre, 2016; IUCN/PBSG, 2017). Sea ice loss is identified as the greatest threat to polar bears (Amstrup et al. 2010, Stirling and Derocher 2012) and the loss rate in a subpopulation is an indicator of vulnerability. We score the percent change/decade in summer sea ice area (June – October) relative to the mean 1979-1988 summer ice extent, with <5%, 5-10%, and >10% scored as 1 to 3, respectively. The second metric was the ice-free season length, an increase in which results in lost predation opportunities and heightened food-stress (Molnár et al. 2010, Molnár et al. 2014). A seasonal increase of the ice-free period of <7 days/decade, 7-14 days/decade, and >14 days/decade were scored as 1 to 3, respectively.

As a special case, we assessed the vulnerability index for the Last Ice Area (LIA), which is the area believed to retain ice conditions sufficient for polar bear subsistence at the end of the 21st century (Hamilton et al. 2014, Rosen 2017). Because the LIA overlaps several subpopulations, we assigned vulnerability scores based on area-weighted averages. To estimate how many bears may live in the LIA, we assumed the number of bears in the intersecting subpopulations contributed proportionally to the area of overlap with the LIA.

Results

The first polar bear subpopulation estimate was in 1968, with a further 7 subpopulation estimates established before 1980 (Table 2-1). Currently, only 14 of 19 subpopulations have estimates, and of these only 6 are from the past decade. The number of years with estimates for a subpopulation varied from 2 to 34 between 1968-2014. Three subpopulations (i.e., Northern Beaufort Sea, Southern Beaufort Sea, and Western Hudson Bay) were well-studied with 3-6 estimates across 17, 21, and 34 separate years, respectively since the 1970s, though the most recent estimate is from 2011 or older. The remaining subpopulations have a mean re-estimation interval of 10.9 years (range: 1-36 years), with 6 subpopulations having mean intervals >15 years. Publication of a subpopulation estimate took a mean of 5.5 years (range: 0-12 years) after data were collected.

The circumpolar range of polar bears was estimated at 21.7 million km^2. Excepting the Arctic Basin (4.2 million km^2), subpopulations varied in area nearly 17-fold (Table 2-2). Abundances and corresponding densities for the 14 subpopulations of polar bears with estimates ranged from 161 – 2826 bears (0.57 – 9.30 bears/1000 km^2), with a mean density of 2.36 bears/1000 km^2 (median: 1.71 bears/1000 km^2).

Marine habitat of subpopulations is largely over continental shelf (mean 68%, s.d. 29%), ranging from 11 to 100% (Table 2-2). Minimum median ice conditions (1979-2010), which represent the maximum extent of polar bear marine habitat at the end of summer, ranged from 0 to 100% (Table 2-2), and summer sea ice conditions persisted for 70 to 249 days (Table 2-2).

The majority of the subpopulations intersected with 5 or more prey species, but no fewer than 2, one of which was always ringed seals (Table 2-2).

Model Results and Population Estimation

We found what we interpret to be a biologically significant, positive relationship (R^2 = 0.44, p = 0.09) between polar bear density and the prey diversity index despite the small sample size (n = 14, Fig. 2-2). We found a similar relationship between subpopulation counts and prey diversity (number of species, not by area), suggesting the relationship was not area-dependent. We were unable to detect any relationships in our other models because the variance in the parameters was too high for our sample size, and all parameters in all models were non-significant with the exception of the prey diversity index parameter. As such, we did not pursue model averaging between our best-fit model and other models with similar AIC_c (Table 2-3).

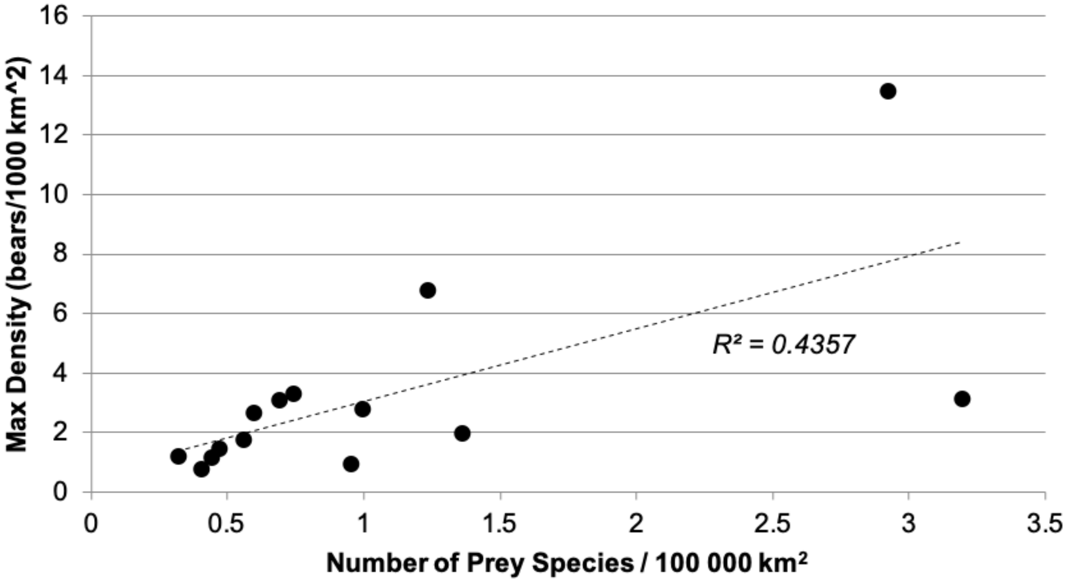

Figure 2-2. The upper CI density of polar bears per subpopulation as a function of prey species diversity normalized by subpopulation area (n = 14, p = 0.09).

Table 2-3. Representation of model hypotheses tested. Significant co-variates are demarcated with ‘O’, while covariates tested but not significant are demarcated with ‘X‘. Null AIC_c = 66.203. Bold indicates the best model.

	Parameter						
Model Hypothesis	Mean Latitude	Shelf	Prey Diversity Index	Minimum Sea Ice Area (5-year mean)	Summer Ice Period (5-year mean)	Harvest Rate (5-year mean)	AIC_c
Productivity		X					67.910
	X	X					70.287
		X	O				63.015
	X						68.212
	X		O				62.980
			O				**60.932**
			O		X		63.008
Habitat		X			X		69.666
					X		67.235
				X			68.255
				X	X		69.174
		X		X	X		71.819
Harvest Modifier			O			X	61.996

Table 2-4. Population counts after extrapolation to the un-surveyed subpopulations based on the modeled relationship between the prey diversity index and density of polar bears. The global population is estimated from the sums of the extrapolated counts with the established counts in previously surveyed subpopulations. Because the Arctic Basin is regarded as poor habitat for polar bears, estimates are also given assuming the Arctic Basin does not contribute to the global population.

Subpopulation	Number of Polar Bears
Arctic Basin	489 (248-725)
Chukchi Sea	823 (416-1220)
East Greenland Sea	991 (501-1469)
Kara Sea	989 (500-1466)
Laptev Sea	812 (411-1203)
Total Bears in Surveyed Subpopulations	19 211 (13 896-25 129)
Estimated Global Population	23 315 (15 972-31 212)
w/o Arctic Basin	22 826 (15 724-30 487)

Extrapolating the results of our model to regions with no estimates, and combined with existing estimates, we estimated the global population to be 23 315 polar bears (range: 15 972 – 31 212 bears) (Table 2-4).

Vulnerability Index

The most vulnerable subpopulations were the Southern and Northern Beaufort Seas and the Arctic Basin (Table 2-5; Fig. 2-3). While the Arctic Basin and Northern Beaufort Sea were among the subpopulations with the lowest shelf area and prey diversity, the Southern Beaufort Sea was vulnerable more due to the worsening of ice conditions. The least vulnerable subpopulation was Lancaster Sound.

Table 2-5. The polar bear vulnerability index is based on rankings from 1-3, with 3 being the most vulnerable. 'Number of Bears' is based on the most modern estimate available. 'Shelf Area' is related to the amount of habitat over the continental shelf. 'Prey Diversity' is the number of polar bear prey species found in the subpopulation. The 'Summer Ice Loss' and 'Ice Free Period (IFP) Increase' parameters are based on decadal scale change. The table is organized from most to least vulnerable. The 'Last Ice Area' values are derived from the area-weighted components of contributing subpopulations (Fig. 2-3).

Subpopulation	Number of Bears	Shelf Area	Prey Diversity	Summer Ice Loss	IFP Increase	Vulnerability Index
Arctic Basin	3*	3	3	2	2	13
Northern Beaufort Sea	3	3	3	2	2	13
Southern Beaufort Sea	3	2	2	3	3	13
Laptev Sea	3*	1	2	3	3	12
Viscount Melville Sound	3	2	3	2	2	12
Chukchi Sea	3*	1	2	3	2	11
East Greenland Sea	3*	3	1	2	2	11
Gulf of Boothia	2	1	2	3	3	11
Kane Basin	3	1	2	3	2	11
Kara Sea	3*	1	1	3	3	11
M'Clintock Channel	3	1	3	2	2	11
Southern Hudson Bay	3	1	2	3	2	11
Barents Sea	1	2	1	3	3	10
Baffin Bay	1	3	1	3	2	10
Western Hudson Bay	2	1	2	3	2	10
Davis Strait	1	2	1	3	3	10
Last Ice Area	*1*	*3*	*1*	*2*	*2*	*9*
Norwegian Bay	3	1	3	1	1	9
Foxe Basin	1	1	1	3	2	8
Lancaster Sound	1	1	1	2	2	7

* Subpopulation size values are based on our model extrapolations (Table 2-4).

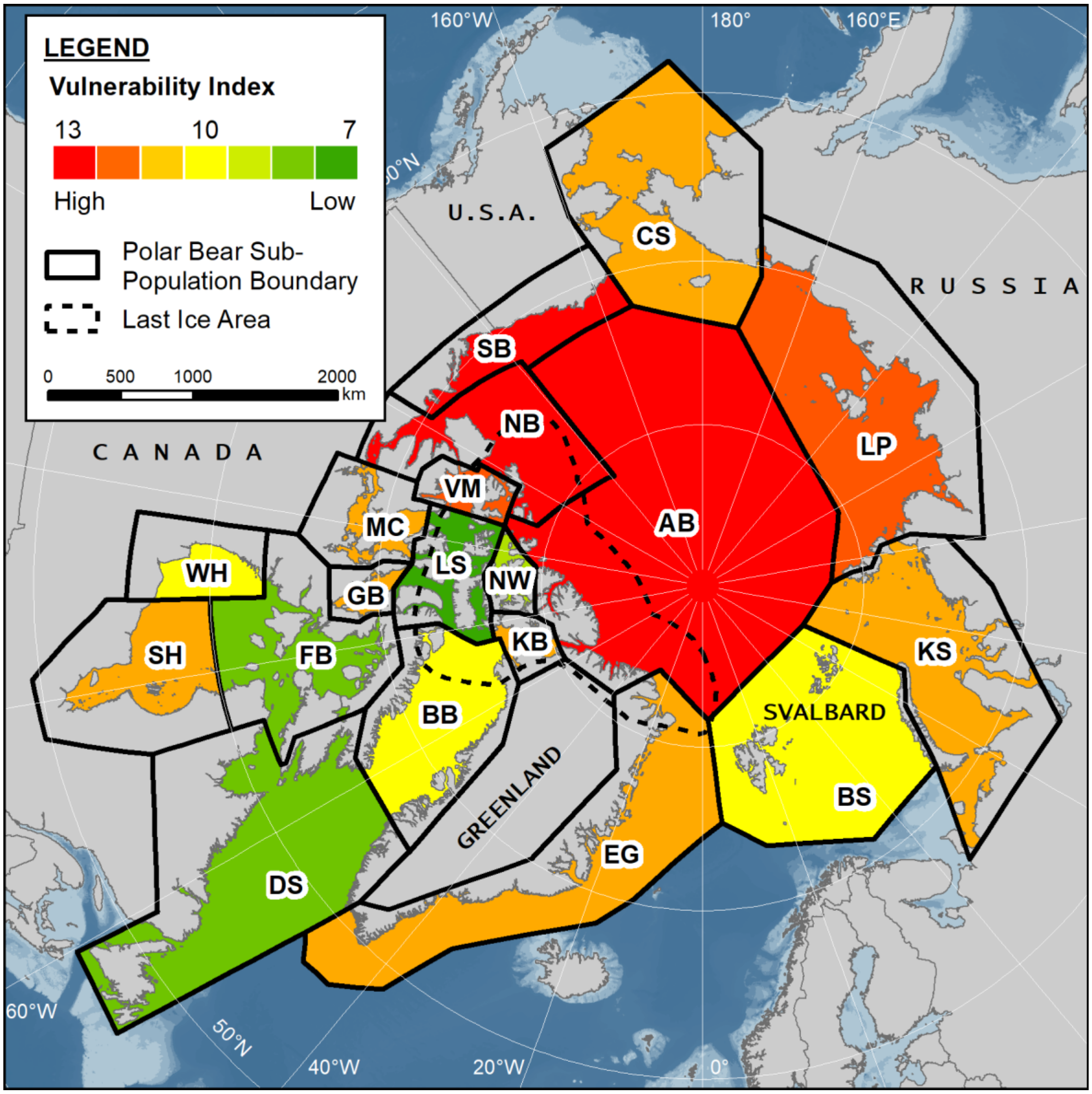

Figure 2-3. Vulnerability of polar bears by subpopulation based on population abundance, prey species diversity, summer ice loss, and increases in the ice-free period. Subpopulations with higher values are more vulnerable to future ecosystem changes. The Last Ice Area (LIA) represents a region which may provide sufficient sea ice for polar bear subsistence by the end of the 21st century.

When examined by parameter, 12 of the 19 subpopulations were high risk due to low population size (<1000 bears). The majority (11/19) of subpopulations had an abundance of shelf-based habitat, and prey diversity was evenly distributed, with 5 high-vulnerability subpopulations scores and 7 with low vulnerability. Only one subpopulation was low-vulnerability with regards to the rate in summer ice loss (Norwegian Bay), while 12 of the remaining 18 subpopulations are currently losing >10% summer sea ice per decade. The lengthening of the ice-free season was >2 weeks/decade in 6 of the 12 subpopulations, and <1 week/decade in Norwegian Bay only. The vulnerability of the LIA was 9, ranking below the median subpopulation vulnerability (11), though it should be noted that the shelf component of the score was high, given the amount of the LIA that expands over the Arctic Basin, which is itself among the most vulnerable subpopulations.

Discussion

The global population status of polar bears is difficult to assess. Some subpopulations have never been estimated, others have out-dated estimates, and estimates often occur over long intervals. Over one-quarter of the subpopulations have no robust estimates. Estimates are inconsistent between, and sometimes within, subpopulations, with 4/19 subpopulations having past estimates that are not directly comparable to modern estimates. Collectively, these issues make trends difficult to establish.

Some polar bear subpopulations have been affected through climate change, exhibiting declines in body condition, cub recruitment, and survival rates (Regehr et al. 2007, Lunn et al. 2016, Obbard et al. 2016). Studies suggest that the Chukchi Sea (Rode et al. 2013), Davis Strait (Peacock et al. 2013), Foxe Basin (Stapleton et al. 2016), and Northern Beaufort Sea (Stirling et al. 2011) subpopulations are stable or productive, although only Foxe Basin has been estimated within the last decade. The Southern Beaufort Sea (Bromaghin et al. 2015) and Western Hudson Bay (Lunn et al. 2016) subpopulations have declined from past levels, perhaps stabilizing at a lower abundance, but show reductions in body condition consistent with altered sea ice pattern.

Our attempts to formalize a statistical relationship between environmental parameters and polar bear densities had limited success, likely due to low sample size (n=14), a problem that is difficult to redress. At most, the sample size could reach 19 if estimates were performed in the remaining subpopulations, but those subpopulations comprise nearly two-thirds of the polar bear range by area (Table 2-2). As such, the variability in ecological parameters within the remaining subpopulations could offset the gains in samples. Furthermore, there is evidence that subpopulation boundaries are permeable to the bears, and boundaries may better represent management areas than ecological units (Peacock et al. 2010).

Our proposed relationship between prey diversity and polar bear density should be used with caution. We do not interpret the prey diversity index as an indication of prey abundance; rather, we suggest it as a proxy for productivity and linkages to marginal ice-covered ecosystems. Similarly, we do not reject studies reporting that polar bear habitat is associated with annual ice over continental shelf because we did not assess habitat use. We believe harvest may further confuse the relationship with ecological covariates. Harvest is likely additive for polar bears (Derocher and Taylor 1994), meaning harvested subpopulations will not be at carrying capacity. Most (16/19) subpopulations experience at least limited numbers of human-caused removals, ranging from <0.1% in the Barents Sea, to 6.2% in the Southern Hudson Bay (IUCN/PBSG, 2017), but in general a harvest rate of approximately 4.5% may be considered sustainable (Regehr et al. 2017). It is notable, however, that the Baffin Bay, Davis Strait, and Southern Beaufort Sea subpopulations experience harvest rates >4.5%. The Chukchi Sea and East Greenland Sea subpopulations may also be above this level based on our modeled subpopulation estimates.

Because the prey diversity index is likely related to productivity, our global estimate accounts for the low-quality habitat in vast areas such as the Arctic Basin. We believe our most meaningful estimate of global polar bear abundance is 23 315 bears (range: 15 972 – 31 212). This estimate is in line with a past estimate of 20 000 – 25 000 bears derived without quantitative analysis (IUCN/SSC Polar Bear Specialist Group, 2010). Nonetheless, our estimate should not be used to compare to previous estimates as an indication of growth or decline in the global polar bear population.

In a multi-species assessment of marine mammal vulnerability to climate change, polar bears were identified as the second most vulnerable species (Laidre et al. 2008), but vulnerability was assessed for the population as a whole. Our vulnerability index ranked the vulnerability to future warming for each subpopulation, with the majority of subpopulations (12/19) in the upper half of the index. Decadal scale changes in sea ice conditions featured strongly in the vulnerability index, with only the Norwegian Bay subpopulation ranking low in both categories. Subpopulation size also contributed strongly to the index, with most of the vulnerable subpopulations (12/19) being small (<1000 bears). The Gulf of Boothia is a notable exception, having twice the density of the next highest-density subpopulation (Lancaster Sound). Even so, the Gulf of Boothia subpopulation scored higher on the vulnerability index than Lancaster Sound due to comparative rates of ice loss.

The LIA was below the median vulnerability of all subpopulations. Rates of ice loss are modest, all prey species are found in the region, and the high-density Lancaster Sound subpopulation overlaps >75% with the LIA. Accordingly, our assessment suggests the LIA could currently contain 3646 polar bears (range: 2508 – 4605 bears), over half of these from Lancaster Sound. However, while population size and prey diversity lend themselves to resilience in the face of warming conditions, the underlying sea ice habitat is only 30% over continental shelf, with the low-quality Arctic Basin subpopulation making up 39% of the LIA by area. Furthermore, ice conditions in the LIA may yet become limiting for polar bears before the end of the 21st century (Hamilton et al. 2014).

Our vulnerability index does not account for all foreseeable changes to polar bear survival. It is possible a shift from multi-year ice to annual ice may improve conditions for polar bears (Derocher et al. 2004) because multi-year ice has low density of seals and thus is poor hunting habitat (Stirling et al. 1993). We do not consider harvest rates in our assessment as these are management-based and can be managed. We also do not consider pollution vulnerability (Jenssen et al. 2015), human-bear conflicts (Wilder et al. 2017), changing disease and parasite issues (Harvell et al. 2002), increasing Arctic shipping (Smith and Stephenson 2013), oil exploration (Stirling 1988), and tourism effects, all of which could negatively affect polar bears.

Recommendations

Arctic warming will not affect each subpopulation of polar bears equally (Amstrup et al. 2010, Rode et al. 2013, Hamilton et al. 2014). Understanding how each subpopulation is affected will require monitoring at regular intervals, and we echo the call to implement a 5-year inventory cycle (Vongraven et al. 2012), as well as the initiation of research for currently un-surveyed subpopulations.

If monitoring is the goal, both the frequency of study and the time to release results are key to keeping managers informed of subpopulation trends. The mean number of years between estimates for all but 3 of the monitored subpopulations was 10.9 years. In the interest of establishing reliable trends, the time between survey and publication should be minimized (of the studies we examined, the mean time to release was 5.5 years after data collection ended). Furthermore, monitoring methods should aim to be consistent both within and between subpopulations to maximize the capacity for comparisons. If research resources are too limiting, more cooperation and sharing of resources between the Arctic nations could improve efforts to meet the needs of regular and robust population monitoring.

Our global estimate of abundance was modeled on a single parameter, the prey diversity index, which is related to the accessibility of prey species. Currently, we have little capacity to relate polar bear densities to sea ice loss, though the development of such a relationship will be critical to understanding long-term abundance as sea ice conditions change.

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CHAPTER 3

Projected Polar Bear Sea Ice Habitat in the Canadian Arctic Archipelago

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Introduction

Observed changes in global climate have influenced Arctic sea ice cover more than most models have predicted (Stroeve et al. 2012), and ongoing sea ice declines indicate loss of maximum ice cover as well as older, thicker multiyear ice (Maslanik et al. 2007, Comiso 2012). These losses are modifying the Arctic marine ecosystems (Arrigo et al. 2008, Bluhm and Gradinger 2008), making Arctic and sub-Arctic marine mammals particularly vulnerable to climate change (Laidre et al. 2008, Schipper et al. 2008). Polar bears (*Ursus maritimus*) are inextricably linked to Arctic sea ice and are sensitive to sea ice loss (Stirling and Derocher 1993, Derocher et al. 2004, Laidre et al. 2008, Schipper et al. 2008, Rode et al. 2010). Polar bears rely on sea ice as a platform for hunting, migrating, and mating, but are forced to move to land in regions where sea ice does not seasonally persist (Stirling 1974, Ramsay and Stirling 1986, Schliebe et al. 2008, Cherry et al. 2013). Energetics modeling and population projections indicate that continued sea ice loss with climate warming will negatively affect polar bear survival and reproduction potentially leading to population declines (Durner et al. 2009, Hunter et al. 2010, Molnár et al. 2010, Molnár et al. 2011). Moreover, of the ice that survives the melt season, insufficient snow cover may limit its viability as habitat for ringed seals (*Pusa hispida*), the primary prey species of polar bears (Hezel et al. 2012).

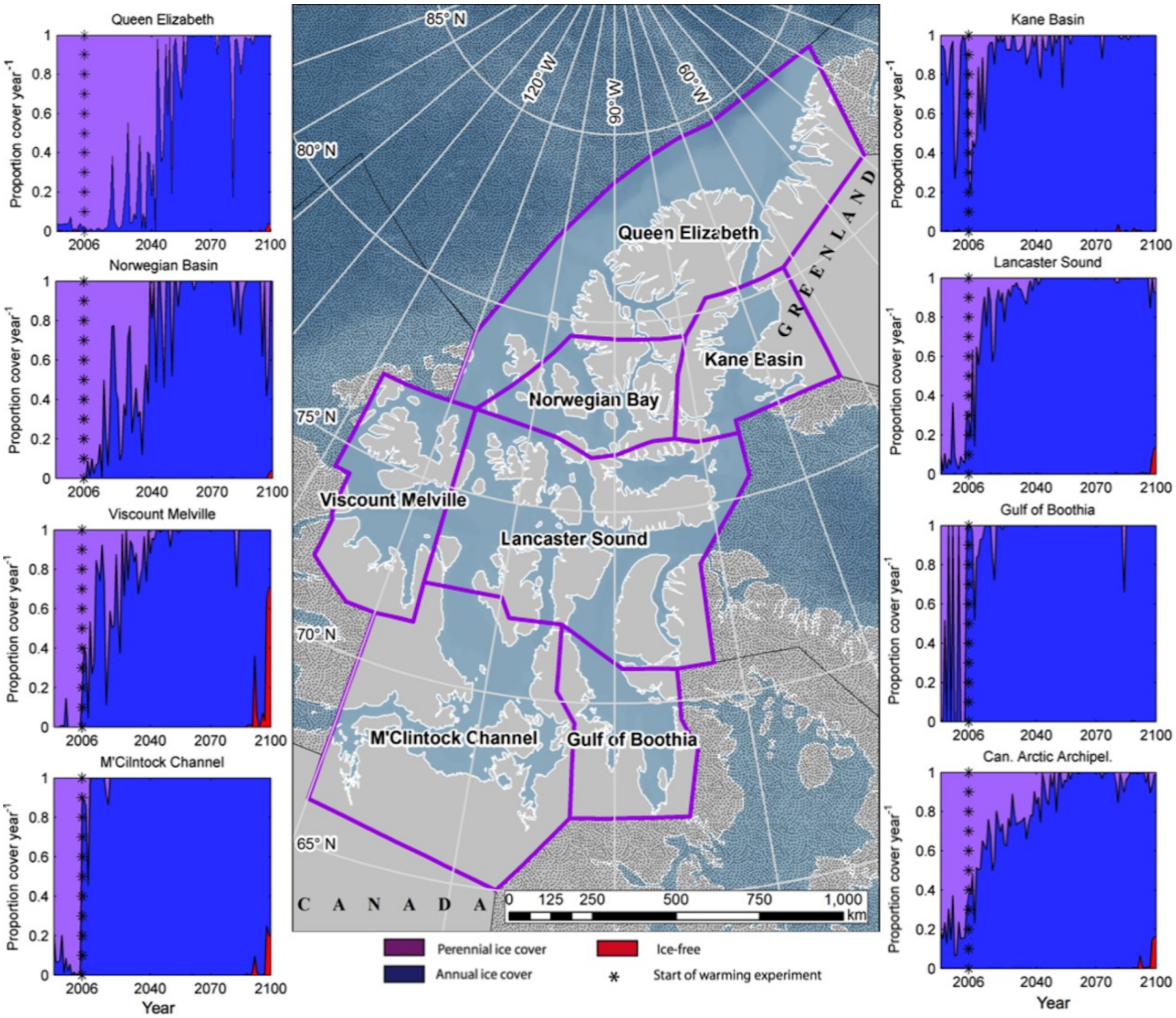

Figure 3-1. Projected dominance of seasonal sea ice in the polar bear populations of the Arctic Archipelago. The seven populations range from 65-85°N in latitude, with significant variation in the length of ice-free seasons. The proportion of multiyear ice, annual ice, and ice-free waters is given by regional means, and averaged over the total area.

Optimal polar bear habitat is predicted to decline in the 21st century, with significant losses in the Hudson Bay and peripheral Arctic seas (Durner et al. 2009, de la Guardia et al. 2013), though greenhouse gas mitigation and geo-engineering strategies could limit some loss (Amstrup et al. 2010, Tilmes et al. 2014). Most sea ice modeling efforts have a crude representation of the geographically complex Canadian Arctic Archipelago (CAA) due to its many narrow channels, which are difficult to resolve. Nevertheless, 7 of the 19 recognized polar bear populations depend on the ice formed within or advected into the CAA (Fig. 3-1). These 7 CAA populations comprise approximately one quarter of the estimated global polar bear population, while covering only 9.1% of the global polar bear range (IUCN/PBSG 2013).

The CAA and Greenland were thought to have the greatest likelihood of sustaining polar bears to the end of the 21st century (Amstrup et al. 2008) although based only on analysis of sea ice conditions in the very northern part of the CAA. Here we investigate the impact of projected warming on polar bears within the CAA from projected monthly mean sea ice concentration (SIC), ice thickness, and snow depth between 2006-2100 in comparison to previously established polar bear energetic needs. Polar bears are well-adapted to prolonged periods without food but lose body mass when fasting (Watts and Hansen 1987, Ramsay and Stirling 1988, Atkinson and Ramsay 1995, Derocher and Stirling 1995, Robbins et al. 2012). Body mass is already declining in some polar bear populations with negative consequences on survival and reproduction (Stirling et al. 1999, Regehr et al. 2007, Hunter et al. 2010). Energy budget models exist in which polar bear survival and reproductive rates can be tied to the availability of access to sea ice (Molnár et al. 2010, Molnár et al. 2011). Such models are based on the basic energy requirements of animals and are useful when predicting population changes under environmental conditions that have yet to be observed (Kooijman 2010). We examine the seasonality of sea ice and determine when the length of the ice-free period in the CAA may become critically limiting to polar bear foraging and thus negatively affect reproduction and survival.

Materials and Methods

Global climate simulations contributed to the Coupled Model Intercomparison Project Phase 5 (CMIP5) are too coarse to effectively resolve the narrow channels of the CAA. Although numerically challenging, one solution is to dynamically downscale a global simulation onto a finer grid using a regional climate model. A comparison between over 30 different CMIP5 models led us to select one simulation from the Geophysical Fluid Dynamics Laboratory Coupled Physical Model (GFDL-CM3) driven by radiative scenario RCP8.5 to pilot the regional model (available from www.gfdl.noaa.gov/coupled-physical-model-cm3). This simulation includes a realistic spatial distribution of sea ice extent and thickness and simulates the trend in observed minimum sea ice extent during the observational record (1979-2013). This pilot simulation was dynamically downscaled using the ice-ocean Massachusetts Institute of Technology General Circulation Model (MITgcm) simulation in regional mode over the Arctic at a resolution of 18km (available from http://mitgcm.org). The 3-hourly atmospheric forcing fields from GFDL-CM3 were bias-corrected at the monthly scale using differences for variables (x,y,z) or ratios for variables (u,t,g) between the Japanese 25 year Reanalysis (JRA25) (Onogi et al. 2007) and GFDL-CM3. These biases were calculated over the 2005-2011 period, arguably too short to compute climatological means, to smooth the transition from the JRA25 driven MITgcm simulation to the GFDL-CM3 driven simulation occurring at the start of 2012. We choose a period of 7 years to calculate the biases between the two forcing datasets because of the transitory nature of the climate in the early 21st century with large trends in many of the Arctic climate forcing fields. MITgcm parameters were provided by Nguyen (Nguyen et al. 2011) and ocean boundary conditions taken from the Estimating the Circulation and Climate Change of the Ocean Phase 2 (ECCO2) experiment (Menemenlis et al. 2008). The MITgcm is run with time steps of 2-hours.

Our model projection is based on the RCP8.5 scenario, which estimates the global average radiative forcing at 8.5 W/m^2 by 2100, and mean global temperature changes of ~3.5°C in 2071-2100 when compared with the historical period of 1961-1990 (Christensen et al. 2011), and represents a worst-case scenario. We compared the seasonal changes in the sea ice cycle between past (1992-2005), near future (2040-2050), and future (2080-2090) by comparing average SIC in each period by month (Fig. 3-2). Population size, survival, and reproduction of polar bears have all been associated with the changes in the seasonal ice cycle, in particular with changes to the ice-free period (Stirling et al. 1999, Regehr et al. 2007, Rode et al. 2010). We assume that effects on polar bears within the CAA will be comparable to those observed in other populations.

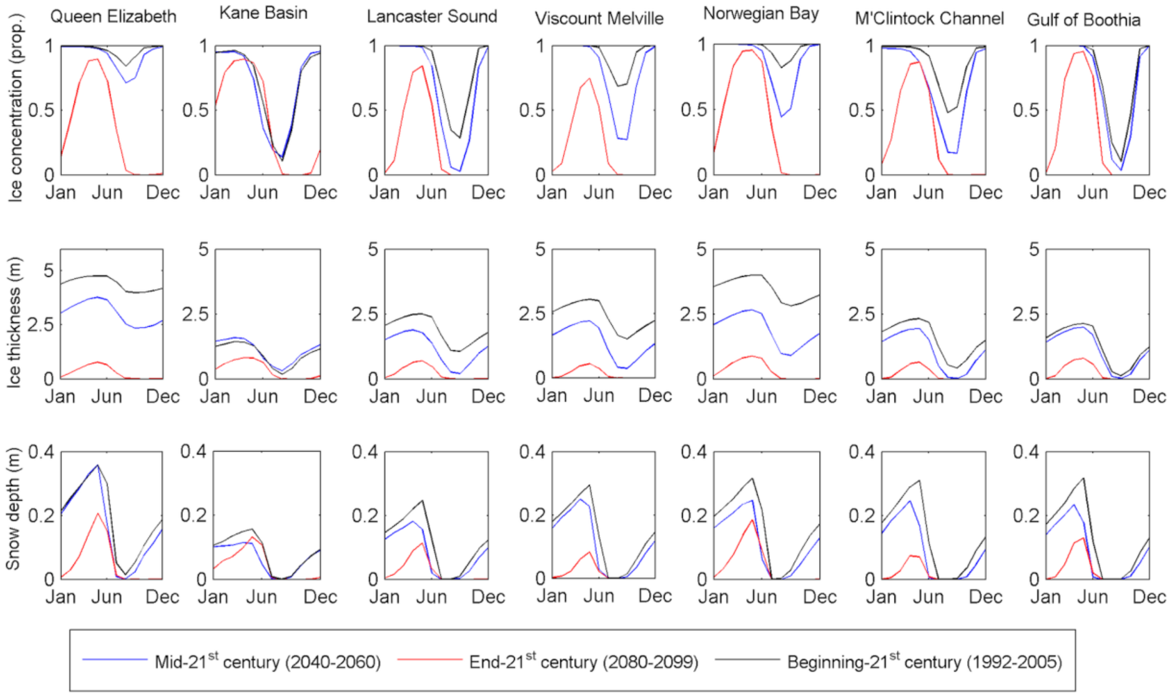

Figure 3-2. Changes in seasonal sea ice concentration (SIC), thickness, and snow depth over time by region. The mean ice-free season length (in months) for each time period is identifiable by segments of zero SIC or zero ice thickness. All values are monthly means over the respective time periods.

To study how habitat could change, we classified each pixel within the CAA as multiyear ice, annual ice, or ice-free. The classification was made based on the SIC of the pixel location over a given year (Comiso 2012). Multiyear ice, which is ice that persists through the height of the melt season (typically March – September), is found when SIC ≥15% year-round. Should SIC dip to <15% before freeze-up begins, but be ≥15% at least once during the year prior, the pixel is classified as annual ice. Ice-free areas are defined as <15% SIC year-round. Polar bears typically avoid or abandon sea ice when concentrations drop below 30-50% although the rate of loss is also important (Stirling et al. 1999, Cherry et al. 2013). The cutoff of 15% we used is conservative because bears will occupy habitat with as little as 15% SIC (Durner et al. 2009), but higher concentrations are more closely associated with habitat use and successful predation (Rode et al. 2013, Pilfold et al. 2014).

We defined a critical ice-free period as one in which sea ice was absent in sufficient concentration for ≥180 days or based on energy budget models (Molnár et al. 2010, Molnár et al. 2011). The ice-free period, with respect to polar bear habitat use, was assessed as the time between break-up (first month in a year with SIC<50%) until freeze-up begins (SIC≥10%). The values of 50% and 10% for break-up and freeze-up, respectively, are correlated with polar bear movements ashore and offshore in regions where there is a seasonal ice cycle (Stirling et al. 1999, Cherry et al. 2013). If all months had a mean SIC<10%, the ice-free season was twelve months. Conversely, if all months had SIC≥10% the ice-free season was zero months, which may be conservative regarding the impacts of low SIC on polar bears. For example, within the CAA polar bears select for habitat with 90% SIC year-round (Ferguson et al. 2000), and in pelagic Arctic regions polar bears tend towards SIC of 75-80% in spring, 65% in summer, 60%

in fall, and 95% in winter (Arthur et al. 1996, Durner et al. 2009). As with the SIC values, we assume that energetic restrictions on polar bears is consistent between populations.

Results and Discussion

All of the CAA exhibits a shift from primarily multiyear ice cover to a primarily seasonally ice-free system by 2100, with the exception of Kane Basin and the Gulf of Boothia, which were largely annually ice-covered regions from the outset (Fig. 3-1). In all cases, the final years of the simulation exhibit some proportion of year-round ice-free areas, where no such areas exist in most of the 21st century.

While multiyear ice is not good hunting habitat due to its low prey abundance (Kingsley et al. 1985, Ferguson et al. 2000), it provides an alternative habitat for polar bears who otherwise must move onto land during summer, and do not have to wait as long for the new ice to form in the autumn (Amstrup et al. 2000). A shift towards annual ice may seem preferable because it is associated with greater hunting opportunities and ringed seals, the primary prey of polar bears (Smith 1980, Thiemann et al. 2008), may increase in abundance if multiyear ice is replaced by thinner annual ice (Schipper et al. 2008). However, sea ice must persist long enough for polar bears to take advantage of potential increases in prey density. With the exception of Kane Basin, all polar bear populations in the CAA reached 100% SIC between October and December in the late 20th century, and a non-zero minimum SIC in August or September (Fig. 3-2). By the late 21st century, our simulation projects the southernmost regions (M'Clintock Channel, Gulf of Boothia) and central regions (Viscount Melville, Lancaster Sound) may be entirely ice-free for 5 months, and may no longer reach 100% SIC at maximum ice extent. In the north (Kane Basin, Norwegian Bay, Queen Elizabeth), the simulation estimates a 2-4 month ice-free season by the end of the 21st century, and maximum concentrations <100% in 2080-2090. Ice thickness and snow depth exhibit similar declines throughout the CAA. Ice thickness in the late 20th century was twice to nearly five times the thickness of the projected thickness in the same month of the late 21st century.

Snow depth declines in part due to the reduction in sea ice surface and dates of formation, but also due to a predicted shift in precipitation from snow to rain (Hezel et al. 2012). Mean snow depth more than halves in the south and central CAA, with the most pronounced changes between the late 20th and late 21st centuries in the western regions (Viscount Melville, M'Clintock Channel). Furthermore, using a conservative estimate of a minimum 20 cm snow depth requirement for seal habitat (Hezel et al. 2012), only the Queen Elizabeth and Norwegian Bay areas may be able to maintain significant ringed seal populations by the end of this century.

Critical Ice-Free Periods

Polar bears fare poorly when sea ice is absent for prolonged periods, losing body mass without the opportunity to hunt (Derocher and Stirling 1995, Polischuk et al. 2002). Energetics modeling predicts that 2-3% of adult polar bear males could starve when the ice-free period reach 120 days and 9-21% could starve at 180 days of ice-free period with other age and sex classes even more vulnerable (Molnár et al. 2010, Molnár et al. 2014, Pilfold et al. 2014). Similarly, early break-up of sea ice could result in reproductive failure in 55-100% of pregnant females (Molnár et al. 2011). The frequency of both events would have significant consequences for population trends in abundance. The thresholds established in these energetics models resulted in four types of critical ice-free periods, with the first two being relevant to male starvation rates, and the second two being relevant to female reproductive failure rates (Fig. 3-3):

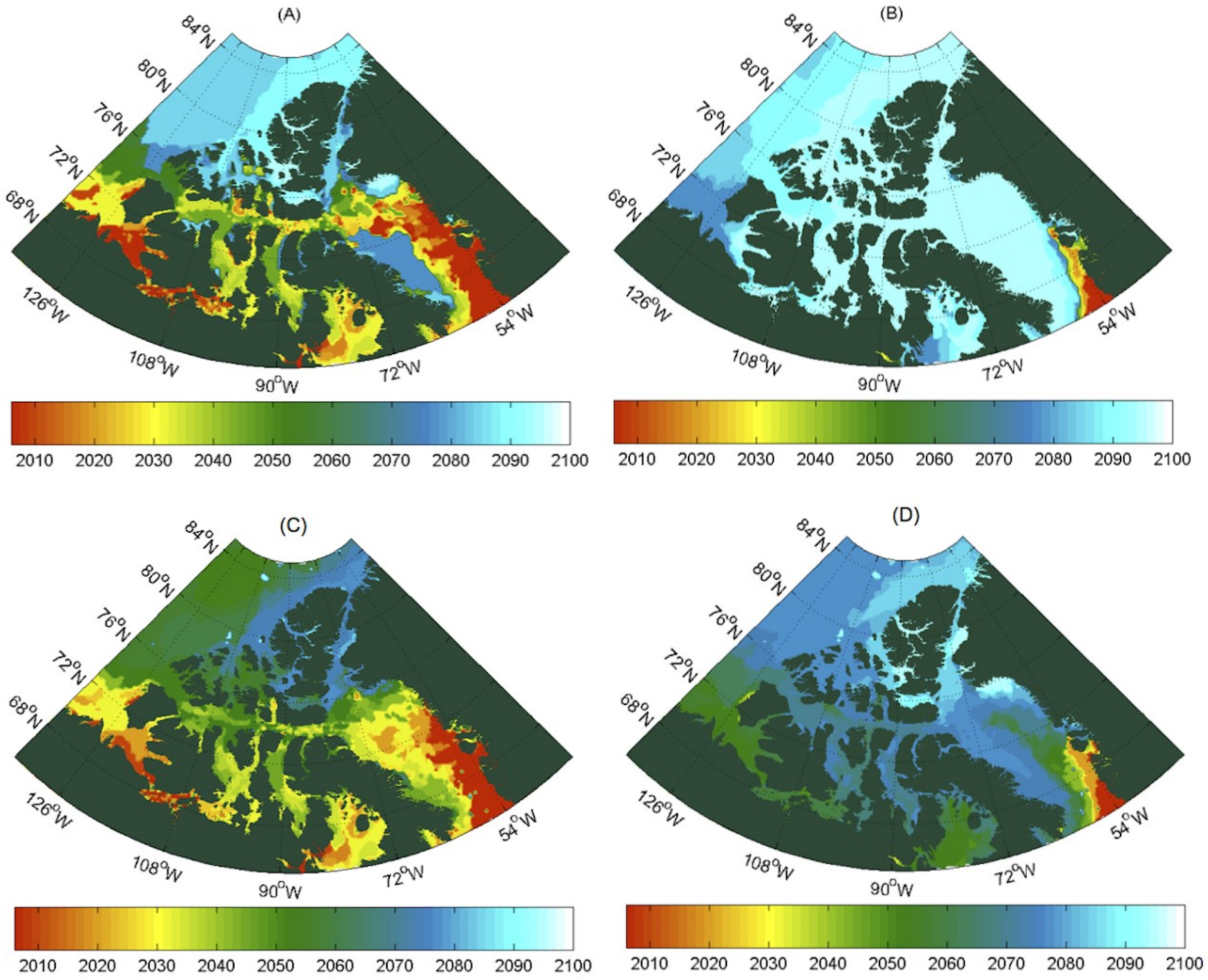

Figure 3-3. Critical ice-free periods for polar bear survival in the Canadian Arctic. The colors represent the year in which critical habitat loss is reached and never improves in subsequent years. Critical states are reached as starvation sets into adult males at (A) ≥120 days ice-free; (B) ≥180 days ice-free; and reproductive failure occurs in females with (C) break-up in July; and (D) break-up June.

(A) ice-free season >120 days; (B) ice-free season >180 days; (C) break-up occurs in July, and; (D) break-up occurs in June.

We find that sea ice conditions may become unsupportive of polar bear population persistence in the CAA and its surroundings by the late 21st century with ice-free seasons reaching critical duration, and early break-ups occurring in parts of all populations we examined. Similarly, to the east of the CAA, the west coast of Greenland and much of Baffin Bay may no

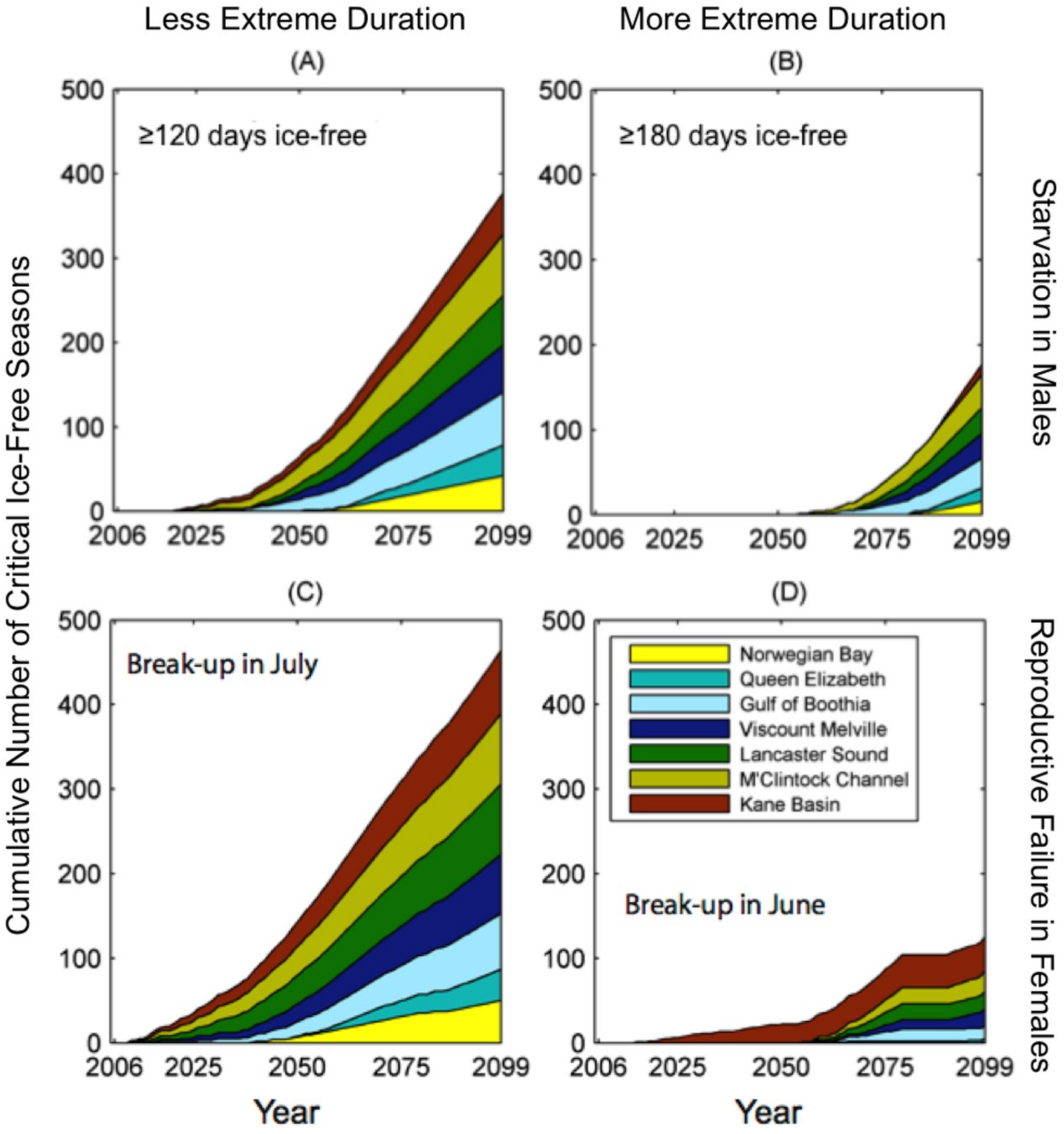

Figure 3-4. Cumulative number of critical ice-free seasons given by individual polar bear populations in the Canadian Arctic Archipelago. Each color represents the contribution of events in each population to the total number of critical seasons in a given year. Starvation in adult males occurs at (A) ≥120 days ice-free; (B) ≥180 days ice-free. Reproductive failure in females occurs when (C) break-up occurs in July; (D) break-up occurs in June.

longer be suitable habitat for polar bears before 2050, though ice should persist along the east coast of Baffin Island until much later. Early break-up in the narrow channels of the central CAA may become critical in 2060-70s, whereas the adjacent coastlines of the open Arctic Ocean remain largely non-critical until near 2100.

It is important to consider that what we deem a critical point-of-no-return occurs once the ice-free period crosses our critical threshold and remains critical for the remainder of the modeled period. Nevertheless, it is feasible that single seasons, or clusters of seasons, may become critically ice-free before that point, with subsequent seasons being non-critical. As such, we examined the cumulative number of critical events for of the aforementioned critical periods (A-D) by population (Fig. 3-4). We found that the less extreme critical durations (categories A and C) occur with lower frequency within the first decades of the simulation, and increase in frequency in later decades. When considering more extreme ice-free durations (categories B and D), critical events do not begin to occur until after 2050, with the exception of Kane Basin, which begins to experience break-up in June before 2020. Nevertheless, the frequency of critical events increases rapidly towards the end of the 21st century.

Implications for Conservation

Without exception, our simulation projects the sea ice habitat in all polar bear populations of the CAA may change from a multiyear to an annual ice system before the end of the century, and the remaining annual ice might not persist sufficiently long each year to allow hunting opportunities for polar bears as we currently understand them. Our model suggests that, by 2070, over 80% of the CAA might experience break-up in July, forcing pregnant females to retreat to land early, with possible negative effects on their reproductive output. Given that our study area comprises approximately one quarter of the world's polar bears, and nearly one-tenth of the total current habitat, our analyses project significant habitat loss and alteration under the business-as-usual model scenario used to estimate sea ice conditions over the coming 21st century.

Conservation efforts to protect polar bear habitat in the Canadian Arctic should focus on regions that are slower to experience change in sea-ice concentration and ice-free period. The Queen Elizabeth and Norwegian Bay populations retain multiyear ice the longest, and their northerly fjords and channels consistently exhibit the fewest critical ice-free events. Nevertheless, by 2100 all regions of the study area may cross the critical point-of-no-return, putting the persistence of the CAA polar bear populations in jeopardy.

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CHAPTER 4

Movement Characteristics of Polar Bears in the Canadian Southern Beaufort Sea

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Introduction

Animal movement reflects habitat use whether for foraging, mating, resting, or security, but it also reflects energy use (Boyce et al. 2016, Wilson et al. 2020), with foraging unique among these factors, providing energy uptake for animals to offset losses. In Arctic ecosystems, productivity is low on land but high off-shore over the continental shelf (Huston and Wolverton 2009). Losses of energy to the thermally challenging Arctic environment can be partially offset by relying on highly energetic prey, but also through energy-conserving behaviours, which may be reflected in movement patterns (Brown et al. 2004). As such, Arctic marine mammals must contend with high energy losses from cold conditions and seasonally limited access to food (Bluhm and Gradinger 2008).

The polar bear (*Ursus maritimus*) subsists primarily on the high-energy prey obtained via sea ice over the continental shelf in the circumpolar Arctic and sub-Arctic seas (Rode et al. 2015, Pagano et al. 2018). The energetic demands on polar bears is met predominantly by the energy-rich fat of other marine mammals, with ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) representing the primary prey (Stirling and McEwan 1975, Thiemann et al. 2008). Hunting is typically enacted from annual sea ice, where the ice thickness is not prohibitive for ringed seals to create and maintain breathing holes from below (Stirling and Archibald 1977, Messier et al. 1992, Stirling 2002). The sea ice system is dynamic, however, with ice sometimes moving kilometers in a day (Hakkinen et al. 2008), driving polar bears to expend energy to remain near sources of prey (Mauritzen et al. 2001, Auger-Méthé et al. 2015, Durner et al. 2017). While hunting itself can entail long periods of stillness, more energy-demanding strategies are also used, and not all encounters result in a kill (Stirling 1974, Pagano et al. 2018).

Aside from hunting, polar bear movement can be substantial when seeking mating opportunities before sea ice breaks up, though differences in strategies may be exhibited by the sexes (Amstrup et al. 2001, Laidre et al. 2013). Pregnant females begin searching for den sites before freeze-up and, once denning, will not emerge again until spring when hunting opportunities peak (Ramsay and Stirling 1988, Messier et al. 1992, Richardson et al. 2005). Depending on the region of the Arctic and the corresponding annual sea ice regime, non-denning bears may move on-shore during the ice minimum season or follow the ice edge to the multi-year ice, both strategies imposing restricted hunting opportunities until the annual ice returns later in the year (Ramsay and Stirling 1988, Derocher et al. 2004). Bears may wander during these periods, with occasional high-energy activity such as swimming (Pilfold et al. 2017, Pagano et al. 2020), though they broadly demonstrate geographic site fidelity (Stirling 2002, Cherry et al. 2013, Lone et al. 2013). Moreover, though they occasionally den for shelter from harsh weather (Ferguson et al. 2000), even low-activity polar bears experience a period of net energy loss between break-up and freeze-up, resulting in reduction in body mass of approximately 1 kg each day (Derocher and Stirling 1995, Polischuk et al. 2002, Pilfold et al. 2016).

With increasing sea ice loss due to climate warming (Stroeve et al. 2014, Stern and Laidre 2016, McCrystall et al. 2021) and a correspondingly longer ice minimum period, polar bears are faced with the prospect of greater energy costs associated with movement, but also reduced hunting opportunities (Pagano et al. 2021). Lessening access to prey may affect female polar bears more than males, with projections suggesting lower cub recruitment and starvation becoming more pronounced with progressive ice loss (Hamilton et al. 2014, Molnár et al. 2020). The southern Beaufort Sea population (SB) of polar bears is among the more well-studied populations, both in terms of population status and ongoing effects of climate warming (Regehr et al. 2010, Vongraven et al. 2018, Hamilton and Derocher 2019). Telemetry-based habitat and movement of adult female polar bears has been documented in SB with evidence of seasonal variation in activity and habitat selection (Amstrup et al. 2000, Amstrup et al. 2005, Johnson and Derocher 2020). Furthermore, an analysis of home range size in SB established the necessity of accounting for drifting ice to accurately assess the amount of habitat polar bears encounter (Auger-Méthé et al. 2015). In addition, a multi-decade analysis of movement patterns reported implications for energy demands when accounting for increased drifting ice speed (Durner et al. 2017). Our study summarizes the findings of a satellite telemetry project undertaken in the southern Beaufort Sea north of the Canadian mainland between 2007 and 2011. Here, we examine seasonal movement and home range characteristics obtained from adult females with and without offspring, and compare them to subadult bears and adult males in the SB.

Study Area and Population

The SB inhabits the waters along the northern coast of the Yukon and Northwest Territories (Canada) and Alaska (US), from the Amundsen Gulf in the east, and Chukchi Sea to the west (Fig. 4-1). It is estimated to be among the lower density populations of polar bears (Hamilton and Derocher 2019) and has experienced a high summer ice loss due to Arctic warming (Stroeve et al. 2014, Stern and Laidre 2016). The SB is located in the divergent ice zone (Durner et al. 2009), characterized by the annual formation of sea ice in winter, followed by breakup and export of unmelted ice toward the Polar Basin in summer. The SB marine ecosystem receives cold, unproductive water from the adjoining Arctic Basin via the Beaufort Gyre, which mixes with west-flowing waters from the Canadian Arctic Archipelago, circulating past Alaska before returning northward toward the Arctic Basin again (Pomeroy 1997, Stirling 2002). Because polar bears either retreat from the ice to land during summer, or follow the multi-year ice over low-productivity Arctic deep waters, their movement patterns can be expected to vary seasonally.

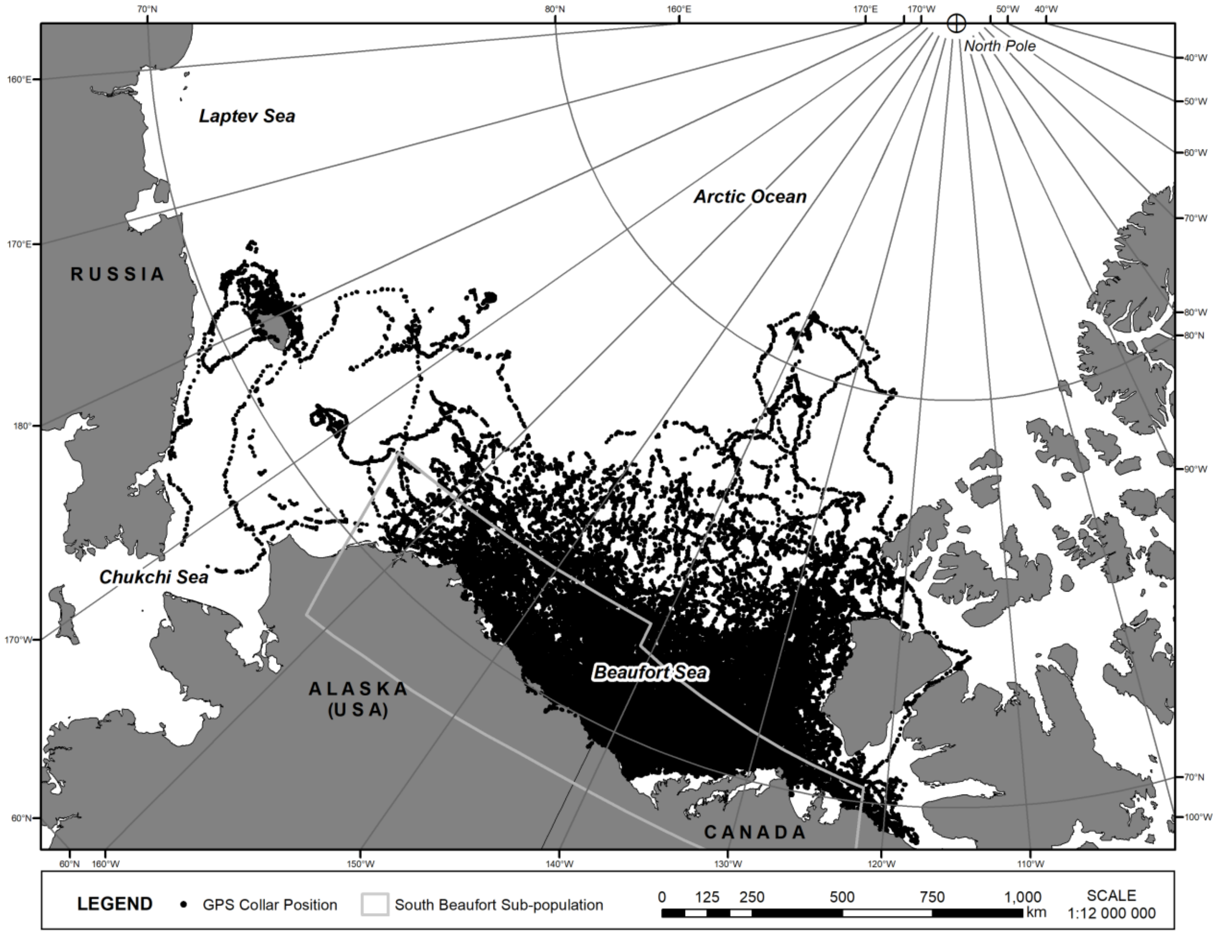

Figure 4-1. Study area map depicting all 82 202 telemetry locations (2007-2012) for all 65 polar bears captured in the Beaufort Sea off the north coast of Canada.

Methods

Wild polar bears of varying age and sex were located by helicopter and chemically immobilized according to standardized methods (Stirling et al. 1989) between 2007 and 2011 in the southern Beaufort Sea in Canada. We deployed GPS collars (Telonics, Mesa, AZ), and recorded the sex of bears as well as the presence/age of accompanying offspring at time of capture. A subset of bears was recaptured in subsequent years and reproductive status was updated to reflect changes. Age was determined from a vestigial premolar extracted for analysis (Calvert and Ramsay 1998), or by tooth eruption patterns for bears <2 years old. Collars had a time-release mechanism set in advance for 1 year on subadult bears or 2 years on adult females, and had corrodible link as a secondary release. Telemetry locations were obtained every 4 hours for up to 4 years. We ignored locations for the first three days after collaring the bears to minimize behavioural effects of capture (Thiemann et al. 2013). Capture and handling procedures were approved by the University of Alberta BioSciences Animal Policy and Welfare Committee and were consistent with the Canadian Council on Animal Care guidelines (www.ccac.ca).

Captured bears were classed as subadults if they were independent and <5 years of age, and as adults if older (Ramsay and Stirling 1986). Adult females accompanied by dependent offspring were further divided by offspring age (0 = cubs-of-the-year, 1 = yearling, 2 = two-year-olds). A mother with offspring <2 years old at capture was assumed to retain them for the remainder of the year, whereas two-year-olds were assumed weaned after the ice maximum season. In the case where a female was captured twice, the age of cubs at the second capture was used to back-cast her reproductive status in the years between captures. Due to the possibility of cub mortality and whole litter loss (Amstrup and Durner 1995), if recapture data were unavailable to confirm the presence of cubs, data after the first year were removed from the analysis to minimize classification errors. Bear classes were categorized as follows: Adult Female with no accompanying offspring (AF), Adult Female with accompanying offspring (AF_{0-2}, where subscript is offspring age), Subadult Female (SF), Subadult Male (SM), and Adult Male (AM).

Maternity denning was identified by either stationary locations on land between November and April (Amstrup and Gardner 1994), or by movements on sea ice that matched drift between November and March (Togunov et al. 2020). Denning bears were classified as solitary for the previous ice melt, minimum, and growth seasons (Ramsay and Stirling 1986). Telemetry locations that were biologically improbable were removed from the data, including a small number of outlier locations hundreds of kilometres inland from the coast, or speeds >15 km/h (N.B., Durner et al. (2017) report a mean drift-corrected daily movement of 14.58 km). Locations from dropped collars were also removed (Togunov et al. 2020). To account for involuntary movement of polar bears due to sea ice drift (Mauritzen et al. 2003, Auger-Méthé et al. 2015), we obtained ice drift data from the Polar Pathfinder Daily 25 km Ease-Grid Sea Ice Motion Vectors (Tschudi et al. 2019). Estimates of ice drift were derived for each bear location following Auger-Méthé et al. (2015).

Positional data were projected in ArcGIS 10.3.1 (ESRI 2015) in the Albers projection. We restricted analysis of movement rates and estimates of path straightness to contiguous sequences of telemetry locations ≤4 h apart. Movement rates were calculated for each segment in terms of the straight-line distance traveled with and without removing ice drift, with the former representing the combination of voluntary movement and ice drift, and the latter representing voluntary movement of the bear, only. Rates were divided by 4 hours (the period between telemetry locations) and reported in km/h. Daily path straightness was calculated by dividing the straight-line distance between first and last points in a 6-location sequence (*i.e.*, 24 hours) by the total sum of distance traveled in that same 6-point sequence. The resulting values were between 0 – 1, where 1 was a straight line. We calculated seasonal and yearly home ranges in ArcGIS 10.3.1 (ESRI 2015) for individual bears using 95% kernel density estimates at a 1-km resolution with a search radius of 120km, representing a liberal estimate of movement over one week, where a daily average speed is >14km/d (Durner et al. 2017).

Seasons were categorized according to the patterns of sea ice melt and growth based on 10-year averages between 1979 and 2008 (Comiso 2012) as follows: Ice Maximum (Dec – May), Ice Melt (Jun – Jul), Ice Minimum (Aug – Sep), and Ice Growth (Oct – Nov). We compared between- and within-season travel speed, path straightness, and seasonal home range size for each bear class using a combination of means, medians, and generalized linear mixed-effects models (GLMM). Comparisons were organized into sets for ease of analysis, comparing all classes of bears within a season to AF, and comparing all seasons within each bear class to the ice maximum season. Because the data were heteroskedastic, we relied on non-parametric Kruskal-Wallis (K-W) tests to identify differences between categories. For the GLMM analysis, we used the *lme4* package in R (Bates et al. 2015) with individual bear and data year as random effects. Travel speed was transformed by sqrt(x+1), straightness by sqrt(1-x), and seasonal home range size by log(x+1). AF was chosen as the reference bear class because it was the most represented in the data, but also because it is a good baseline for comparison with other adult females (i.e., those with accompanying offspring) and with other unaccompanied bears (subadults and males). The ice maximum season was chosen as the reference season because the ice is less dynamic than other seasons, but also because it includes a larger proportion of the year than the other seasons. Lastly, we examined the effects of removing ice drift on median movement rates and home range areas using non-parametric Wilcoxon tests. All statistical analyses were performed in R 3.5.0 (R Core Team 2018). We used $\alpha=0.05$ for the non-parametric tests. For the GLMMs, we considered individual categories to be significantly different from the reference category if the 95% confidence interval (CI) did not overlap with the estimate of the reference.

Results

Telemetry Summary

Polar bear positions used in our analyses were acquired for 65 bears (AF=22, AF_0=5, AF_1=18, AF_2=2, SF=8, SM=9, and AM=1 at capture) in the southern Beaufort Sea between 2007 and 2012 with a total of 82 202 positions. Because bears were categorized by data year and could change class due to reproductive status in years following capture, AF_2 and AM were eventually represented by 4 individuals each. AF contributed the most positions to the dataset (36.3%), while AF_2 contributed the least (1.1%), although AF_2 positions were only available during the ice maximum season (Table 4-1). AM contributed the fewest positions of all classes for which all seasons were represented (6.8%).

Movement Rates

Mean movement rates after removing ice drift and compiled over all seasons (Table 4-2) ranged from $AF_0 = 0.65 \pm 0.0075$ km/h to AM = 0.98 ± 0.012 km/h. The distribution of movement data, however, skewed strongly toward low values with median speeds for all classes being 25-40% lower than means, while a small number of large values filled out the upper 5th

Table 4-1. Number of bears contributing to each age/sex class by season. Seasons correspond to ice maximum (Dec-May), melt (Jun-Jul), minimum (Aug-Sep), and growth (Oct-Nov), with (n) being the number of bears contributing data in that season. "Min/max" values are the smallest/largest numbers of records a particular bear contributes to the total in its respective class, while "Positions" is the total number of records for the category. "Segments" and "Straightness Sequences" represent the number of sets of contiguous positions available for calculating travel speed and path straightness respectively. Class key: Adult/Subadult, Female/Male, (accompanying offspring age: 0 - 2). Note: The AF_2 category is observed only during the ice maximum season.

Class	Season (n)	Min/Max	Positions	Segments	Straightness Sequences
AF	Max (27)	95/1643	13 711	11 983	7 254
	Melt (27)	49/476	6 578	5 465	2 604
	Min (24)	13/413	4 768	4 006	1 976
	Growth (23)	4/361	4 744	4 110	2 345
	Total (27)	263/2747	29 801	25 564	14 179
AF_0	Max (8)	113/860	3 761	3 536	2 804
	Melt (8)	224/347	2 373	2 174	1 546
	Min (8)	234/358	2 265	2 105	1 570
	Growth (8)	229/366	2 355	2 188	1 669
	Total (8)	1061/1673	10 754	10 003	7 589
AF_1	Max (22)	56/1041	7 460	6 741	4 483
	Melt (20)	189/351	5 328	4 692	2 713
	Min (19)	36/335	3 952	3 423	1 848
	Growth (20)	16/364	4 809	4 254	2 592
	Total (22)	131/2056	21 549	19 110	11 636
AF_2	Max (4)	140/300	895	818	583
SF	Max (8)	56/795	1 909	1 537	533
	Melt (8)	88/290	1 766	1 355	267
	Min (6)	29/283	1 084	866	285
	Growth (5)	103/335	1 075	883	360
	Total (8)	144/1517	5 834	4 641	1 445
SM	Max (9)	50/1279	2 940	2 239	689
	Melt (9)	66/395	2 024	1 558	495
	Min (6)	160/347	1 500	1 177	366
	Growth (6)	62/363	1 343	1 072	429
	Total (9)	152/2259	7 807	6 046	1 979
AM	Max (4)	14/1278	2 890	2 609	1885
	Melt (3)	83/483	908	807	515
	Min (3)	108/510	965	848	534
	Growth (3)	7/432	799	748	587
	Total (4)	212/2615	5 562	5 012	3 521

Table 4-2. Travel speed (mean ± SE and percentiles) by age/sex class for all seasons, accounting for ice-drift. "Bears" is the number of individual bears in the class, "n" is the number of movement segments, each of which is a distance traveled over a 4-hour period. Speeds are minimum movement rates assuming a constant pace in a straight line over the 4-hour period. Bears that contributed data for multiple years may appear in more than one class, thus the number of bears in each class does not sum to 65. Class key: Adult/Subadult, Female/Male, (accompanying offspring age: 0 - 2). *AF_2 is listed for summary purposes, but is not directly comparable to other classes because statistics are compiled over one season and not the entire year.

					Travel Speed (km/h)				
Class	Bears	n	Mean	SE	25%	50%	75%	95%	100%
AF	27	25 564	0.76	0.0053	0.14	0.46	1.11	2.54	14.93
AF_0	8	10 003	0.65	0.0078	0.08	0.39	0.90	2.34	6.15
AF_1	22	19 110	0.85	0.0060	0.24	0.59	1.20	2.62	8.73
AF_2*	*4*	*818*	*0.68*	*0.029*	*0.21*	*0.55*	*1.16*	*2.58*	*4.64*
SF	8	4641	0.86	0.013	0.19	0.56	1.26	2.72	5.99
SM	9	6046	0.90	0.010	0.28	0.68	1.31	2.60	5.31
AM	4	5012	0.98	0.013	0.31	0.69	1.41	2.81	5.59
All	65	82 202	0.77	0.0029	0.09	0.42	1.00	2.51	14.93

percentile of the distribution, with maximum speeds approximately 2-6 times >95% of the data. Median AF_0 movement rate retained the lowest rank (0.39 km/h), and AM remained the highest (0.69 km/h), with movement rates between all pairs of classes being significantly different (K-W test, $p < 0.05$) except AF_1-SF, and SM-AM (Table 4-3a). Generalized linear mixed models (Table 4-4), which compared estimated movement rates to the reference class (AF) over all seasons, indicated AF_0 was again lowest (0.30 km/h, 95% CI: 0.28 – 0.33 km/h), but AF_1 was highest (0.68 km/h, 95% CI: 0.65 – 0.72 km/h). In the modeled case, AM did not rank the highest, and was not significantly different from AF.

Estimating seasonal movement rates by class (Table 4-4), AF_0 had the lowest model-estimated speeds of all classes in the ice maximum, melt, and minimum seasons, ranging from 0.17 km/h (95% CI: 0.14 – 0.19 km/h) in the ice maximum season to 0.35 km/h (95% CI: 0.30 – 0.41 km/h) in the ice minimum season. AF_1 had the highest movement speeds of the adult female classes during the same seasons, ranging from 0.59 km/h (95% CI: 0.55 – 0.64 km/h) in the ice maximum to 0.72 km/h (95% CI: 0.67 – 0.78 km/h) in the melt season, though AF_1 melt season rates were not significantly different from the reference class (AF) and the model fit was poor

Table 4-3. Kruskal-Wallis rank sum test results (t-statistic) for movement rate class comparisons in (a) annual, (b) ice maximum season, (c) ice melt season, (d) ice minimum season, and (e) ice growth season. Sign of values denote column class is larger (+) or smaller (-) than row class. Differences are significant (*) at $p < 0.05$. Class key: Adult/Subadult, Female/Male, (accompanying offspring age: 0 - 2). Note: The AF_2 category is found only during the ice maximum season.

(a) All Seasons	AF	AF_0	AF_1	SF	SM
AF_0	13.98*				
AF_1	-18.99*	-28.08*			
SF	-8.59*	-17.01*	2.72		
SM	-19.19*	-26.97*	-6.29*	-7.04*	
AM	-21.38*	-28.61*	-9.37*	-9.48*	-2.92

(b) Ice Max	AF	AF_0	AF_1	AFt	SF	SM
AF_0	25.35*					
AF_1	-10.86*	-31.33*				
AF_2	-1.18	-13.61*	3.31*			
SF	-16.43*	-30.45*	-9.90*	-9.30*		
SM	-13.17*	-29.19*	-5.65*	-6.37*	4.29*	
AM	-16.60*	-32.69*	-8.38*	-7.88*	2.69	-1.93

(c) Ice Melt	AF	AF_0	AF_1	SF	SM
AF_0	9.86*				
AF_1	4.09*	-6.50*			
SF	7.17*	-0.94	4.41*		
SM	-0.83	-8.25*	-3.60*	-6.50*	
AM	-2.46	-8.32*	-4.57*	-6.98*	-1.59

(d) Ice Min	AF	AF_0	AF_1	SF	SM
AF_0	3.24*				
AF_1	-4.77*	-7.16*			
SF	12.74*	9.66*	15.47*		
SM	-5.68*	-7.57*	-2.29	-14.87*	
AM	-7.53*	-9.14*	-4.53*	-15.77*	-2.14*

(e) Ice Growth	AF	AF_0	AF_1	SF	SM
AF_0	-6.34*				
AF_1	-19.09*	-9.49*			
SF	-10.16*	-5.24*	1.10		
SM	-14.20*	-8.56*	-2.03	-2.42	
AM	-18.51*	-13.41*	-8.03*	-7.22*	-5.22*

(R^2=0.08). Comparatively, AF_1 was significantly different from other adult female classes in the K-W tests (Table 4-3c), albeit lower than AF, suggesting that differences between classes during the melt season exist, but class in this season did had low explanatory power for the overall variation.

Table 4-4. Back-transformed model estimates and 95% confidence intervals (CI) for GLMMs comparing movement statistics between polar bears of different age/sex classes (Class key: Adult/Subadult, Female/Male, accompanying offspring age: 0 - 2). Response variables: Speed is a minimum estimate based on distance moved over a 4-hour period, straightness is the total net displacement divided by the sum of six 4-hour steps over a 24-hour period, and area is a 95% kernel density estimate of home range. Seasons correspond to ice maximum (Dec-May), melt (Jun-Jul), min (Aug-Sep), and growth (Oct-Nov). In all models, bear ID and year were included as random effects, and adult females (AF) were used as the reference class. Bold values indicate that the response variable for the given age/sex class was significantly different from the reference class (95% CI not overlapping the estimate of the reference class) in the given season. Superscript numbers denote inter-seasonal significant differences ($p < 0.05$) from Kruskal-Wallis tests. Note: The AF$_2$ category is found only observed the ice maximum season.

			Response variables	
		Speed (km/h)	Straightness	Area (km^2)
		Estimates (95% CI)	Estimates (95% CI)	Estimates (95% CI)
Season	Class	*Pseudo-R^2 (total) = 0.34*	*Pseudo-R^2 (total) = 0.27*	*Pseudo-R^2 (total) = 0.16*
All seasons	^{1}AF (int.)	0.37 (0.20 – 0.59)$^{2-6}$	0.70 (0.63 – 0.76)^{2,4,5}	89 321 (80 016 – 100 709)
	^{2}AF$_0$	**0.30 (0.28 – 0.33)$^{1,3-6}$**	0.69 (0.66 – 0.71)^{1,3,4,6}	93 900 (77 652 – 114 690)
	^{3}AF$_1$	**0.68 (0.65 – 0.72)^{1,2,5,6}**	**0.83 (0.82 – 0.85) ^{2,5}**	102 743 (89 321 – 119 371)
	^{4}SF	**0.50 (0.46 – 0.53)^{1,2,5,6}**	**0.86 (0.84 – 0.87)^{1,2,5,6}**	89 321 (71 681 – 111 301)
	^{5}SM	0.51 (0.36 – 0.70)$^{1-4}$	0.74 (0.65 – 0.82)^{1,3,4,6}	91 125 (73 864 – 111 301)
	^{6}AM	0.51 (0.35 – 0.69)$^{1-4}$	0.72 (0.63 – 0.79)^{2,4,5}	101 721 (76 879 – 113 251)
Season	Class	*Pseudo-R^2 (total) = 0.35*	*Pseudo-R^2 (total) = 0.34*	*Pseudo-R^2 (total) = 0.02*
Max	^{1}AF (int.)	0.31 (0.16 – 0.51)$^{2,3,5-7}$	0.72 (0.65 – 0.79)^{2,4,5}	84 964 (73 864 – 97 733)
	^{2}AF$_0$	**0.17 (0.14 – 0.19)$^{1,3-7}$**	**0.60 (0.58 – 0.64)$^{1,3-7}$**	84 964 (59 277 – 121 782)
	^{3}AF$_1$	**0.59 (0.55 – 0.64)$^{1,2,4-7}$**	**0.84 (0.82 – 0.86)^{2,4,5}**	86 681 (67 507 – 110 193)
	^{4}AF$_2$	**0.38 (0.34 – 0.43)$^{2,3,5-7}$**	0.72 (0.69 – 0.75)$^{1-3,5-7}$	73 864 (45 251 – 120 571)
	^{5}SF	**0.75 (0.68 – 0.83)$^{1-4,6}$**	**0.96 (0.94 – 0.97)$^{1-4,6,7}$**	97 732 (70 262 – 135 943)
	^{6}SM	0.45 (0.30 – 0.62)$^{1-5}$	0.75 (0.64 – 0.85)^{2,4,5}	79 220 (59 277 – 106 937)
	^{7}AM	0.43 (0.28 – 0.60)$^{1-4}$	0.71 (0.58 – 0.81)^{2,4,5}	94 844 (64 860 – 138 689)
Season	Class	*Pseudo-R^2 (total) = 0.08*	*Pseudo-R^2 (total) = 0.14*	*Pseudo-R^2 (total) = 0.11*
Melt	^{1}AF (int.)	0.73 (0.67 – 0.81)$^{2-4}$	0.77 (0.72 – 0.82)^{2,5,6}	112 419 (95 797 – 131 925)
	^{2}AF$_0$	**0.49 (0.45 – 0.54)^{1,3,5,6}**	**0.70 (0.66 – 0.73)^{1,3,4}**	94 844 (70 262 – 129 313)
	^{3}AF$_1$	0.72 (0.67 – 0.78)$^{1,2,4-6}$	0.74 (0.71 – 0.77)^{2,5,6}	128 026 (102 743 – 159 531)
	^{4}SF	0.70 (0.63 – 0.78)^{1,3,5,6}	0.77 (0.73 – 0.81)^{2,5,6}	97 733 (70 968 – 133 251)
	^{5}SM	0.70 (0.60 – 0.81)$^{2-4}$	0.71 (0.64 – 0.77)^{1,3,4}	112 419 (85 818 – 147 266)
	^{6}AM	**0.88 (0.75 – 1.02)$^{2-4}$**	0.73 (0.65 – 0.79)^{1,3,4}	115 843 (76 879 – 174 555)
Season	Class	*Pseudo-R^2 (total) = 0.20*	*Pseudo-R^2 (total) = 0.17*	*Pseudo-R^2 (total) = 0.17*
Min	^{1}AF (int.)	0.54 (0.46 – 0.63)$^{2-6}$	0.69 (0.64 – 0.74)$^{3-6}$	95 797 (81 633 – 113 549)
	^{2}AF$_0$	**0.35 (0.30 – 0.41)$^{1,3-6}$**	**0.74 (0.70 – 0.78)$^{3-5}$**	92 041 (66 170 – 128 026)
	^{3}AF$_1$	**0.66 (0.59 – 0.74)^{1,2,4,6}**	**0.77 (0.73 – 0.80)^{1,2,4}**	90 218 (70 262 – 115 843)
	^{4}SF	**0.39 (0.33 – 0.46)$^{1-3,5,6}$**	**0.59 (0.52 – 0.64)$^{1-3,6}$**	**62 943 (43 044 – 91 125)**
	^{5}SM	0.59 (0.42 – 0.80)^{1,2,4,6}	0.69 (0.59 – 0.78)^{1,2}	102 743 (71 681 – 147 266)
	^{6}AM	0.64 (0.45 – 0.86)$^{1-5}$	0.70 (0.59 – 0.78)^{1,4}	104 819 (66 170 – 166 042)
Season	Class	*Pseudo-R^2 (total) = 0.44*	*Pseudo-R^2 (total) = 0.48*	*Pseudo-R^2 (total) = 0.67*
Growth	^{1}AF (int.)	0.44 (0.26 – 0.67)$^{2-6}$	0.63 (0.50 – 0.74)$^{2-6}$	75 357 (59 277 – 95 797)
	^{2}AF$_0$	**0.96 (0.85 – 1.07)$^{1,3-6}$**	**0.91 (0.88 – 0.94)^{1,6}**	**112 419 (80 821 – 156 372)**
	^{3}AF$_1$	**0.74 (0.63 – 0.85)^{1,2,6}**	**0.87 (0.83 – 0.91)^{1,6}**	**117 007 (89 321 – 153 276)**
	^{4}SF	**1.00 (0.86 – 1.15)^{1,2,6}**	**0.77 (0.71 – 0.82)^{1,6}**	94 844 (61 697 – 145 800)
	^{5}SM	0.85 (0.51 – 1.27)^{1,2,6}	**0.83 (0.70 – 0.93)^{1,6}**	92 041 (59 873 – 141 491)
	^{6}AM	0.70 (0.39 – 1.12)$^{1-5}$	**0.84 (0.70 – 0.94)$^{1-5}$**	115 843 (68 185 – 196 810)

During the growth season (Table 4-4), AF had the lowest movement rates (0.44 km/h, 95% CI: 0.26 – 0.67 km/h), while AF_0 had highest estimated speeds of the adult female classes (0.96 km/h, 95% CI: 0.85 – 1.07 km/h), second highest below SF (1.00 km/h, 95% CI: 0.33 – 0.46 km/h) when considering all classes. Males were not significantly different in model estimates from AF in any season except the melt season, where AM recorded the highest movement rates (0.88 km/h, 95% CI: 0.75 – 1.02 km/h). Male movement rates were significantly higher (K-W tests) than most female classes, with the most notable exception being SF > SM during the ice maximum season (Table 4-3). However, SM and AM were only significantly different from each other during the ice minimum and growth seasons, with SM ranking higher in the former, and AM ranking higher in the latter.

Estimates of class movement rates by season resulted in models of generally poor fit (Table 4-5), however the ice maximum season was associated with the lowest movement rates for AF_0, AF_1, SM, and AM. Estimated AF movement rates were lowest during the growth season (0.34 km/h, 95% CI: 0.32 – 0.35), though not significantly lower (K-W test) than the ice maximum (Table 4-6). Conversely, SF movement rates were highest during the ice maximum season (0.53 km/h, 95% CI: 0.30 – 0.84), though significantly higher only than the ice minimum season in the K-W tests. AF, AF_0, AF_1, and SM all exhibited their highest movement rates during the melt season, while differences for AM between the melt and growth season were not significant.

Table 4-5. Back-transformed model estimates and 95% confidence intervals for GLMMs comparing polar bear movement statistics between seasons corresponding to ice maximum (Dec-May), melt (Jun-Jul), minimum (Aug-Sep), and growth (Oct-Nov). Separate models were run with distance moved (meters between 4-hourly positions), 24-hour straightness index (total net displacement divided by six 4-hour step lengths in a 24-hour period), and seasonal home range area (95% kernel density estimate), as the response variable. Also, separate models were run for different age/sex classes (Class key: Adult/Subadult, Female/Male, accompanying offspring age: 0 - 1). In all models, bear ID and year were included as random effects, and the ice max season was used as the reference season (intercept). Estimate values for all other seasons are relative to the reference season. Bold values indicate that the response variable for the given season was significantly different from the reference season (95% CI not overlapping the estimate for the reference season) in the given season. Superscript numbers denote inter-seasonal significant differences ($p < 0.05$) from Kruskal-Wallis tests.

			Response variables	
		Distance moved (km/h)	Straightness	Area (km^2)
		Estimates (95% CI)	Estimates (95% CI)	Estimates (95% CI)
Class	Season	*Pseudo-R^2 (total) = 0.29*	*Pseudo-R^2 (total) = 0.22*	*Pseudo-R^2 (total) = 0.36*
AF	^{1}Max (int.)	0.40 (0.23 – 0.62)^{2,3}	0.78 (0.71 – 0.85)$^{2-4}$	84 119 (68 185 – 103 776)
	^{2}Melt	**0.71 (0.69 – 0.74)**^{1,3,4}	**0.82 (0.80 – 0.82)**^{1,3,4}	**108 011 (89 321 – 131 925)**
	^{3}Min	**0.49 (0.47 – 0.51)**^{1,2,4}	**0.75 (0.74 – 0.77)**^{1,2}	93 900 (76 114 – 114 690)
	^{4}Growth	**0.34 (0.32 – 0.35)**^{2,3}	**0.73 (0.72 – 0.74)**^{1,2}	74 607 (60 475 – 92 041)
Class	Season	*Pseudo-R^2 (total) = 0.21*	*Pseudo-R^2 (total) = 0.07*	*Pseudo-R^2 (total) = 0.34*
AF$_0$	^{1}Max (int.)	0.24 (0.13 – 0.37)$^{2-4}$	0.66 (0.60 – 0.73)$^{2-4}$	85 818 (60 474 – 123 006)
	^{2}Melt	**0.58 (0.55 – 0.61)**^{1,3,4}	**0.74 (0.72 – 0.76)**^{1,4}	94 844 (66 170 – 135 943)
	^{3}Min	**0.43 (0.41 – 0.46)**^{1,2}	**0.73 (0.71 – 0.75)**^{1,4}	93 900 (65 512 – 133 251)
	^{4}Growth	**0.43 (0.41 – 0.46)**^{1,2}	**0.78 (0.76 – 0.80)**$^{1-3}$	97 733 (68 185 – 140 083)
Class	Season	*Pseudo-R^2 (total) = 0.07*	*Pseudo-R^2 (total) = 0.08*	*Pseudo-R^2 (total) = 0.38*
AF$_1$	^{1}Max (int.)	0.52 (0.46 – 0.58)$^{2-4}$	0.77 (0.72 – 0.81)^{3,4}	86 681 (72 402 – 102 743)^{2}
	^{2}Melt	**0.73 (0.71 – 0.76)**^{1,3,4}	0.78 (0.77 – 0.79)^{3,4}	**128 026 (103 776 – 156 372)**^{1,3}
	^{3}Min	**0.62 (0.60 – 0.65)**^{1,2,4}	**0.72 (0.70 – 0.73)**^{1,2,4}	90 218 (73 864 – 111 301)^{2}
	^{4}Growth	**0.63 (0.61 – 0.66)**$^{1-3}$	**0.80 (0.79 – 0.81)**$^{1-3}$	**109 097 (89 321 – 134 591)**
Class	Season	*Pseudo-R^2 (total) = 0.26*	*Pseudo-R^2 (total) = 0.36*	*Pseudo-R^2 (total) = 0.39*
SF	^{1}Max (int.)	0.53 (0.30 – 0.84)^{3}	0.81 (0.68 – 0.90)$^{2-4}$	95 797 (69 563 – 131 925)
	^{2}Melt	**0.46 (0.41 – 0.50)**^{3}	**0.75 (0.72 – 0.79)**^{1,3}	99 707 (67 507 – 147 266)
	^{3}Min	**0.22 (0.18 – 0.25)**^{1,2,4}	**0.54 (0.50 – 0.59)**^{1,2,4}	**59 873 (39 339 – 92 041)**
	^{4}Growth	**0.47 (0.42 – 0.52)**^{3}	**0.66 (0.63 – 0.70)**^{1,3}	83 282 (52 574 – 130 613)
Class	Season	*Pseudo-R^2 (total) = 0.09*	*Pseudo-R^2 (total) = 0.17*	*Pseudo-R^2 (total) = 0.11*
SM	^{1}Max (int.)	0.58 (0.46 – 0.72)$^{2-4}$	0.75 (0.66 – 0.82)^{3}	79 220 (59 873 – 103 776)
	^{2}Melt	**0.77 (0.72 – 0.82)**^{1,3,4}	0.75 (0.72 – 0.78)^{3}	114 690 (77 652 – 171 098)
	^{3}Min	0.62 (0.57 – 0.66)^{1,2}	**0.69 (0.65 – 0.72)**^{1,2,4}	100 709 (64 215 – 157 944)
	^{4}Growth	**0.64 (0.60 – 0.69)**^{1,2}	0.78 (0.75 – 0.81)^{3}	96 760 (61 697 – 151 751)
Class	Season	*Pseudo-R^2 (total) = 0.05*	*Pseudo-R^2 (total) = 0.04*	*Pseudo-R^2 (total) = 0.06*
AM	^{1}Max (int.)	0.59 (0.50 – 0.68)$^{2-4}$	0.79 (0.76 – 0.81)^{3,4}	94 844 (73 864 – 131 782)
	^{2}Melt	**0.84 (0.78 – 0.90)**^{1,3}	0.77 (0.75 – 0.79)^{3,4}	111 301 (73 129 – 169 396)
	^{3}Min	**0.75 (0.70 – 0.80)**^{1,2,4}	**0.74 (0.72 – 0.76)**^{1,2,4}	108 011 (70 968 – 164 390)
	^{4}Growth	**0.85 (0.79 – 0.91)**^{1,3}	**0.86 (0.83 – 0.87)**$^{1-3}$	118 183 (77 652 – 178 081)
Class	Season			*Pseudo-R^2 (total) = 0.20*
All	^{1}Max (int.)			85 818 (78 432 – 93 900)^{2}
	^{2}Melt			**112 419 (99 707 – 126 753)**^{1}
	^{3}Min			91 125 (80 821 – 103 776)
	^{4}Growth			92 041 (81 633 – 104 819)

Table 4-6. Kruskal-Wallis rank sum test results (t-statistic) for seasonal comparisons of movement rate for (a) AF, (b) AFc, (c) AFy, (d) SF, (e) SM, and (f) AM. Sign of values denote column class is larger (+) or smaller (-) than row class. Differences are significant (*) at $p < 0.05$. Class key: Adult/Subadult, Female/Male, accompanying offspring age: 0 - 1).

(a) AF	Max	Melt	Min
Melt	-39.27*		
Min	-16.48*	16.35*	
Growth	-0.99	30.18*	12.74*

(b) AF_0	Max	Melt	Min
Melt	-33.72*		
Min	-25.19*	7.38*	
Growth	-25.47*	7.48*	0.03

(c) AF_1	Max	Melt	Min
Melt	-22.54*		
Min	-12.18*	7.69*	
Growth	-16.60*	4.89*	-3.02*

(d) SF	Max	Melt	Min
Melt	0.12		
Min	14.43*	13.99*	
Growth	0.64	-0.52	-12.26*

(e) SM	Max	Melt	Min
Melt	-11.69*		
Min	-4.91*	5.41*	
Growth	-7.00*	3.17*	-1.97

(f) AM	Max	Melt	Min
Melt	-9.06*		
Min	-4.77*	3.58*	
Growth	-10.65*	-1.52	-5.04*

Daily Path Straightness

Mean path straightness over a 24-hour period after accounting for ice drift was high for all classes (Table 4-7), ranging from 0.70 for AF_0 (± 0.031) and SM (± 0.053) to 0.74 for AF_1 (± 0.021). Median values were similar, with distributions skewed toward 1.00, but AF_0 and SM still lowest-ranked (0.76) and not significantly different from one-another (Table 4-8a). SF (0.83)

Table 4-7. Mean ± SE and percentile daily path straightness indices (total net displacement over a 24-hour period divided by the sum of six contiguous 4-hourly GPS locations) by age/sex class for all seasons, accounting for ice drift. "Bears" is the number of individual bears in the class, "n" is the sample size for straightness indices. Class key: Adult/Subadult, Female/Male, (accompanying offspring age: 0 - 1).

			Straightness index						
Class	Bears	n	Mean	S.E.	25%	50%	75%	95%	100%
AF	27	14 179	0.72	0.0022	0.55	0.80	0.93	0.99	1.00
AF_0	8	7589	0.70	0.0031	0.47	0.76	0.91	0.99	1.00
AF_1	21	11 636	0.74	0.0021	0.60	0.80	0.92	0.98	1.00
SF	8	1445	0.73	0.0069	0.58	0.83	0.95	0.99	1.00
SM	9	1979	0.70	0.0053	0.56	0.76	0.90	0.98	1.00
AM	4	3521	0.73	0.0038	0.59	0.79	0.91	0.98	1.00

was highest ranked, though not significantly higher than AF_1 (0.80). Estimates from GLMMs also tended toward straighter paths, though differences were less apparent (Table 4-4), with only SF (0.86, 95% CI: 0.84 – 0.87) and AF_1 (0.83, 95% CI: 0.82 – 0.85) being significantly higher than the reference AF (0.70, 95% CI: 0.63 – 0.76).

Class comparisons within seasons (Table 4-4) suggested some variation, with AF_0 paths being less straight than the reference (AF) during the ice maximum and melt seasons, but more-so later in the year, reaching the highest path straightness in the growth season (0.91, 95% CI: 0.88 – 0.94). SF showed particularly high straightness during the ice maximum season (0.96, CI: 0.94 – 0.97%), the highest value of any class in any season, but also a low straightness during the ice minimum season (0.59, 95% CI: 0.52 – 0.64), the lowest estimate of any class in any season. As with movement rates, the GLMM explanatory power during the melt season was poor (R^2 = 0.14), with only AF_0 being significantly different from the reference, although K-W tests identified differences between male and female bears, but not males from each other (Table 4-8). Male bear path straightness was often indistinct from AF, although they were significantly higher during the ice growth season. AM paths were slightly, but significantly, straighter than SM during the growth season.

Table 4-8. Kruskal-Wallis rank sum test results (t statistic) for straightness index class comparisons in (a) all seasons, (b) ice maximum season, (c) ice melt season, (d) ice minimum season, and (e) ice growth season. Sign of values denote column class is larger (+) or smaller (-) than row class. Differences are significant (*) at $p < 0.05$. Class key: Adult/Subadult, Female/Male, accompanying offspring age: 0 - 2).

(a) All Seasons	AF	AF_0	AF_1	SF	SM
AF_0	10.39*				
AF_1	-2.01	-11.73*			
SF	-3.81*	-8.81*	-2.86		
SM	4.50*	-1.57	5.49*	6.16*	
AM	0.54	-6.75*	1.84	3.69*	-3.49*

(b) Ice Max	AF	AF_0	AF_1	AFt	SF	SM
AF_0	18.06*					
AF_1	0.21	-16.51*				
AF_2	-3.99*	12.60*	-3.99*			
SF	-9.38*	17.41*	-9.28*	-4.16*		
SM	1.91	-7.65*	1.77	4.41*	8.62*	
AM	1.87	-11.86*	1.62	4.65*	9.57*	-0.63

(c) Ice Melt	AF	AF_0	AF_1	SF	SM
AF_0	6.13*				
AF_1	2.72	-3.83*			
SF	-0.09	-3.06*	-1.25		
SM	5.88*	1.77	4.37*	3.87*	
AM	4.90*	0.77	3.36*	3.21*	-0.82

(d) Ice Min	AF	AF_0	AF_1	SF	SM
AF_0	0.69				
AF_1	4.13*	3.22*			
SF	6.66*	6.20*	4.54*		
SM	4.39*	3.91*	2.03	-2.18	
AM	3.34*	2.79	0.60	-3.53*	-1.28

(e) Ice Growth	AF	AF_0	AF_1	SF	SM
AF_0	-8.11*				
AF_1	-10.67*	-1.41			
SF	-3.01*	1.54	2.38		
SM	-2.94*	1.94	2.86	0.22	
AM	-9.80*	-4.01*	-3.24*	-4.21*	-4.68*

Models for seasonal variation in path straightness by class (Table 4-5), explanatory power was generally poor, particularly for AF_0, AF_1 and AM, and few regular patterns were found. Nevertheless, AF_0 maintained its pattern of the least straight paths in the ice maximum period and most straight during the ice growth period. Furthermore, SF paths were significantly more tortuous during the ice minimum period, and significantly more straight during the ice maximum period both in the model and the K-W tests (Table 4-9). Seasonal differences in straightness were not clearly detected for SM, although the straightness index was significantly lower during the ice minimum than all other seasons. AM paths were also significantly, though less-strongly, not as straight during the ice minimum season, being straightest during the growth season.

Table 4-9. Kruskal-Wallis rank sum test results (t-statistic) for straightness index seasonal comparisons for (a) AF, (b) AFc, (c) AFy, (d) SF, (e) SM, and (f) AM. Sign of values denote column class is larger (+) or smaller (-) than row class. Differences are significant (*) at $p < 0.05$. Class key: Adult/Subadult, Female/Male, accompanying offspring age: 0 - 2).

(a) AF	Max	Melt	Min
Melt	-4.22*		
Min	4.26*	6.86*	
Growth	7.43*	9.59*	2.24

(b) AF_0	Max	Melt	Min
Melt	-10.69*		
Min	-9.46*	1.13	
Growth	-15.75*	-4.20*	-5.37*

(c) AF_1	Max	Melt	Min
Melt	-1.61		
Min	8.99*	9.53*	
Growth	-5.89*	-3.87*	-12.94*

(d) SF	Max	Melt	Min
Melt	4.21*		
Min	12.36*	6.94*	
Growth	6.21*	1.34	-6.10*

(e) SM	Max	Melt	Min
Melt	1.67		
Min	4.36*	2.66*	
Growth	-1.04	-2.46	-4.86*

(f) AM	Max	Melt	Min
Melt	1.46		
Min	4.90*	2.72*	
Growth	-7.83*	-7.34*	-10.21*

Table 4-10. Mean ± SE and percentile annual home range areas based on kernel density estimates by age/sex class, accounting for sea ice drift. “Bears” is the number of individual bears in the class, “n” is the number of individual home ranges for a given class. Class key: Adult/Subadult, Female/Male, (accompanying offspring age: 0 - 1).

			Area (km^2)							
Class	Bears	n	Mean	SE	0%	25%	50%	75%	95%	100%
AF	27	125	102 724	4475	34 440	62 483	97 941	134 715	184 742	327 779
AF$_0$	8	32	99 164	6802	43 724	61 795	100 430	118 545	165 289	184 048
AF$_1$	22	81	110 336	4978	37 446	74 702	100 220	138 740	181 598	279 983
SF	8	29	101 555	13 069	34 469	59 074	93 552	121 702	158 815	422 919
SM	9	38	107 480	7824	34 449	76 708	109 079	135 769	203 273	223 727
AM	4	19	93 211	7850	77 404	77 404	116 286	134 249	150 035	187 536

Home Range Size

Mean kernel density annual home range sizes (Table 4-10) varied from 93 211 km^2 (± 7850 km^2) for AM to 107 480 km^2 (± 7824 km^2) for SM. Compared to means, the medians were similarly sized, but differently ranked: SF were smallest (93 552 km^2) and AM were largest (116 286 km^2). The smallest home range recorded was an AF bear during the ice growth season (34 440 km^2), similar to a SM bear (34 449 km^2) and a SF bear (34 469 km^2), also during the growth season. The largest home ranged belonged to a SF bear during the ice maximum season (422 919 km^2).

GLMMs exploring home range class variation within season fit poorly with the exception of the growth season ($R^2 = 0.67$), where AF$_0$ and AF$_1$ were both larger than AF (Table 4-4). K-W tests, however, did not identify significant differences between classes during the growth season, nor any other season (Table 4-11). Models exploring seasonal variation by class fit better (Table 4-5), with AF and AF$_1$ having larger home ranges during the melt season than the ice maximum season. AF$_1$ also had larger home ranges during the growth season, while SF had smaller home ranges during the ice minimum season. Of these differences, only the larger melt season home ranges for AF$_1$ were significant in the K-W tests (Table 4-12). Because classes were mostly not significantly different in the models, and not-at-all significant in the K-W tests, we lumped all classes together to assess seasonal differences irrespective of class. In this analysis, we found that estimated home range sizes were significantly larger in the melt season than the reference maximum season (Table 4-5, Table 4-12g).

Table 4-11. Kruskal-Wallis rank sum test results (t-statistic) for home range area class comparisons in (a) annual, (b) ice maximum season, (c) ice melt season, (d) ice minimum season, and (e) ice growth season. Sign of values denote column class is larger (+) or smaller (-) than row class. Differences are significant (*) at $p < 0.05$. Class key: A̲dult/S̲ubadult, F̲emale/M̲ale, (accompanying offspring age: 0 - 2).

(a) Annual	AF	AF$_0$	AF$_1$	SF	SM
AF$_0$	0.06				
AF$_1$	1.41	1.02			
SF	0.78	0.58	1.67		
SM	-0.71	-0.60	0.36	-1.18	
AM	-1.14	-1.01	-0.31	-1.43	-0.53

(b) Ice Max	AF	AF$_0$	AF$_1$	AFt	SF	SM
AF$_0$	0.02					
AF$_1$	0.00	-0.01				
AF$_2$	0.67	0.56	0.64			
SF	-0.27	-0.21	-0.25	-0.75		
SM	0.50	0.34	0.45	-0.33	0.60	
AM	-0.67	-0.54	-0.63	-0.99	-0.36	-0.92

(c) Ice Melt	AF	AF$_0$	AF$_1$	SF	SM
AF$_0$	0.70				
AF$_1$	-1.24	-1.51			
SF	0.80	0.07	1.59		
SM	-0.45	-0.94	0.52	-1.01	
AM	-0.12	-0.56	0.53	-0.61	0.16

(d) Ice Min	AF	AF$_0$	AF$_1$	SF	SM
AF$_0$	0.14				
AF$_1$	0.53	0.25			
SF	2.38	1.90	1.97		
SM	-0.18	-0.26	-0.54	-2.09	
AM	-0.40	-0.44	-0.69	-2.01	-0.22

(e) Ice Growth	AF	AF$_0$	AF$_1$	SF	SM
AF$_0$	-0.74				
AF$_1$	-1.82	-0.59			
SF	-0.25	0.32	0.86		
SM	-0.74	-0.03	0.53	-0.33	
AM	-1.21	-0.57	-0.19	-0.79	-0.54

Table 4-12. Kruskal-Wallis rank sum test results (t-statistic) for home range area seasonal comparisons for (a) AF, (b) AFc, (c) AFy, (d) SF, (e) SM, and (f) AM. Sign of values denote column class is larger (+) or smaller (-) than row class. Differences are significant (*) at $p < 0.05$. Class key: Adult/Subadult, Female/Male, (accompanying offspring age: 0 - 1).

(a) AF	Max	Melt	Min
Melt	-2.18		
Min	-1.20	0.77	
Growth	0.49	2.34	1.49

(b) AF_0	Max	Melt	Min
Melt	-0.64		
Min	-0.69	-0.05	
Growth	-0.61	0.02	0.08

(c) AF_1	Max	Melt	Min
Melt	-3.38*		
Min	-0.48	2.79*	
Growth	-2.22	1.13	-1.68

(d) SF	Max	Melt	Min
Melt	-0.36		
Min	1.74	1.97	
Growth	-0.07	0.23	-1.54

(e) SM	Max	Melt	Min
Melt	-1.62		
Min	-0.89	0.51	
Growth	-0.75	0.64	0.12

(f) AM	Max	Melt	Min
Melt	-0.84		
Min	-0.50	0.30	
Growth	-1.04	-0.18	-0.48

(g) All	Max	Melt	Min
Melt	-4.02*		
Min	-1.15	-1.72	
Growth	2.53	1.98	-0.53

Effects of Accounting for Ice Drift

Differences in median movement rates before and after ice drift was removed were significant ($p < 0.05$) in all class/season comparisons except for AF_0 and SM in the ice maximum season (Table 4-13). Furthermore, the differences were always towards a lower median movement rate after removing ice drift. Differences in median home range area before and after drift was accounted for were significant in only 10 of 40 pairwise comparisons (Table 4-14), only 5 of which were comparing a single class/season grouping. When lumping all classes together, the ice maximum and minimum season home ranges increased in median area after accounting for ice drift, but decreased in the melt and growth seasons. AF_1 was the only class that significantly differed from the aggregated class direction, and only in the melt season where removing ice drift resulted in a larger median home range. AF_1 was the only class where significant differences were found in the aggregated seasons category, decreasing in median size after removing drift.

Table 4-13. Median movement rates (km/h) by season and class based on collar position before (P) and after (D) ice drift was removed. Differences were significant (bold) at $p < 0.05$ based on Wilcoxon signed rank tests.

	Max			Melt			Min			Growth			All Seasons		
	P		D	P		D	P		D	P		D	P		D
AF	**0.40**	>	**0.33**	**0.84**	>	**0.76**	**0.58**	>	**0.53**	**0.49**	>	**0.35**	**0.55**	>	**0.46**
AF_0	0.12		0.13	**0.68**	>	**0.63**	**0.51**	>	**0.49**	**0.52**	>	**0.46**	**0.43**	>	**0.39**
AF_1	**0.54**	>	**0.46**	**0.78**	>	**0.70**	**0.66**	>	**0.59**	**0.83**	>	**0.69**	**0.68**	>	**0.59**
AF_2	**0.45**	>	**0.33**												
SF	**0.68**	>	**0.64**	**0.68**	>	**0.62**	**0.30**	>	**0.28**	**0.82**	>	**0.69**	**0.61**	>	**0.56**
SM	0.57		0.54	**0.89**	>	**0.80**	**0.73**	>	**0.69**	**0.84**	>	**0.73**	**0.74**	>	**0.67**
AM	**0.67**	>	**0.57**	**0.90**	>	**0.83**	**0.78**	>	**0.69**	**1.17**	>	**0.91**	**0.81**	>	**0.69**
All	**0.41**	>	**0.35**	**0.78**	>	**0.72**	**0.60**	>	**0.55**	**0.66**	>	**0.53**	**0.57**	>	**0.49**

Table 4-14. Median home range areas (10^5 km^2) by season and class based on collar position before (P) and after (D) ice drift was removed. Differences were significant (bold) at $p < 0.05$ based on Wilcoxon signed rank tests.

	Max			Melt			Min			Growth			Annual		
	P		D	P		D	P		D	P		D	P		D
AF	0.92		0.85	**1.21**	>	**1.11**	1.02		1.08	0.88		0.74	1.06		0.98
AF_0	0.72		0.92	1.05		1.03	1.01		1.10	0.86		0.92	0.92		1.00
AF_1	0.85		0.87	**1.23**	<	**1.28**	0.88		0.84	**1.33**	>	**1.27**	**1.10**	>	**1.00**
AF_2	6.43		6.47												
SF	**0.77**	<	**0.85**	1.05		1.00	0.56		0.56	1.08		1.04	0.99		0.94
SM	**0.63**	<	**0.77**	1.31		1.21	0.95		1.06	1.03		1.14	1.02		1.09
AM	0.73		1.09	1.20		1.22	0.91		1.14	1.16		1.15	0.83		1.16
All	**0.82**	<	**0.88**	**1.11**	>	**1.06**	**0.84**	<	**0.94**	**1.07**	>	**0.95**	0.98		0.97

Discussion

Variation in movement patterns in large mammals have been noted to differ by age, sex, and reproductive status (Nicholson et al. 1997, van Beest et al. 2013), and energetic costs are not linearly related to time and distance moved, but depend on other factors, for example movement speed or environmental substrate (Taylor et al. 1970, Crete and Lariviere 2003, Klappstein et al. 2022). Movement patterns that appear similar can occur for different reasons related to the demographic of an animal (Penteriani et al. 2022). Previous work in the Beaufort Sea has found that adult females with offspring of any age moved more slowly than unaccompanied adult females (Amstrup et al. 2000). Our analysis suggests a more nuanced variation.

Annually, AF_0 bears in our study had the lowest mean and median movement rates, and the lowest model estimated rates of all classes. Seasonally, however, AF_0 were slowest and had the least straight paths in the ice maximum and melt seasons, when emerging from maternity dens and traveling with very young cubs-of-the-year (COY). As the year progressed into the growth season, their movement rates and path straightness exceeded other adult female classes, when COY are approaching yearling age. Concordantly, AF_1 was the highest among adult females for movement rates and path straightness throughout the ice maximum season. Median movement rates for AF_1 were again higher than AF during the ice minimum and growth seasons, as yearlings approached two years old. Continuing in consistency, the AF_2 class in the ice maximum season had model estimated rates that were slightly – yet significantly – higher than AF. The pattern described suggests that adult female movement rates were affected by the age of accompanying offspring, moving their shortest distances in the early months as offspring are physically small, but increasing as offspring grow, then decreasing again to resemble the movement rates of solitary females during the final months before two-year-old offspring are weaned. This pattern is consistent with Durner et al. (2017), who suggested that females with yearlings travel at greater speeds than females with COY or solitary females. Amstrup et al. (2000) reported a similar pattern in median movement rates, though in their study females with yearlings did not exceed the speeds of solitary females.

Our analysis of polar bear movement patterns in the southern Beaufort Sea focused on class and seasonal comparisons including all periods of the day, differing from some studies which assess daily movement rates relative to an estimated activity period (Amstrup et al. 2000, Durner et al. 2017). When translated to a daily movement speed for comparison purposes, our overall estimate for all classes in all seasons (mean: 18.48 ± 0.07 km/d) was higher than other studies in the same region (Auger-Méthé et al. 2015, Durner et al. 2017), which could partly be explained by our inclusion of subadult and male bears. The most comparable results to our study are the >8h movement rates reported by Amstrup et al. (2000), although these rates did not account for ice drift. Nevertheless, we maintain that using the mean overestimates movement rates as displacements were strongly skewed towards small values. Focusing on the daily active period of polar bears likely improves the reliance on mean estimates by minimizing small displacements, but we instead focused our efforts on mixed effects models and median values which are more appropriate for our day-round data.

While AF_0 had consistently the lowest median movement rates, AM had the highest, although model estimates were not different between AM and AF except during the melt season where AM was highest. AM and SM were rarely statistically different, which could be because, although AM were sexually mature by age, they were still young adults and their behaviours may have been more similar to SM than more mature AM. Further to this point, with one exception AM bears were a subset of SM bears at time-of-capture, meaning the majority of the sample were from the same set of individuals. There may be value in considering all male bears in our study as a single “young male” class, although there is little reason to expect the general relationships we found between female and male bears would be different. Rather, it may obscure the few differences we did detect between males and females as SM and AM were often not statistically different from one-another. Nevertheless, we caution against using our classification system to draw conclusions about the differences – or lack thereof – between subadult and adult male polar bears, especially given the small sample size.

Both male and female subadults had higher movement rates, in terms of medians and model estimates, than AF. The difference was significant in all seasons except SF during the melt and ice minimum seasons. This difference suggests that younger bears may expend more energy on larger displacements than sexually mature adults. Younger bears have been observed spending less time hunting than older bears, perhaps because of less experience and greater curiosity, but also to avoid more mature bears (Stirling 1974, Stirling and Latour 1978). Aside from the aforementioned distinction, SF bears were atypical in a number of ways: they were the only class with their highest movement rates in the ice maximum season, when all other classes were lowest or nearly lowest. Conversely, SF was the only class that had its lowest movement rates during the ice minimum season. Furthermore, SF model-estimated home range area was smaller than AF during the ice minimum season, and they were the only class with significantly smaller home ranges during the ice minimum season. Their small seasonal home range sizes were reflected by their low movement rates and low path straightness during the same seasons, all of which were the lowest values reported for any class in any season. It is unclear if there is a general explanation for these deviations based on a sample of 8 subadult females, but the SF bears in our study may have focused on energy conservation more than other classes by not actively countering ice drift to move them during seasons with greater drift. Nevertheless, our findings highlight that subadult females should not be assumed to follow the behaviours of sexually mature adult females.

Except for SF bears, all classes in our study showed a marked increase in movement rates when transitioning from the ice maximum to the melt season, and home range size increased for AF and AF_1 in particular, and when all bears were considered together. This was followed by a decline in movement rate during the ice minimum season, though still higher than during the ice maximum. The spring months at the end of the ice maximum and beginning of the melt season are vital for polar bears in terms of hunting opportunities and mating activities (Ramsay and Stirling 1986, Pilfold et al. 2014, Galicia et al. 2021). Pagano et al. (2018) highlighted the importance of this transitional period in terms of energy budgets as the melt period begins earlier in the year with increasing Arctic warming. We suggest that not only will a shortening of the ice maximum period reduce foraging opportunities, with strong implications for pre-summer fat storage, but it could decrease the period of low-rate movement in exchange for a lengthening of season associated with the highest median movement rates for all adult females and potentially subadult and male bears as well.

Warming is expected to change the timing of the transitional seasons, with overall decreases to the ice maximum and increases to the ice minimum period (Stern and Laidre 2016). Not only will this diminish foraging opportunities, but the rate of ice drift has increased between 1987 and 2013 (Durner et al. 2017). Polar bears can compensate for increasing ice drift by expending energy to remain in better habitat, or conserve energy and risk drifting into poorer habitat. Auger-Méthé et al. (2015) analyzed a subset of adult females from our study to suggest that area of habitat encountered increased with increasing ice drift, suggesting geographic home range underestimates area they encounter, but we found it may be more nuanced, varying by ice season. When comparing home ranges by bear class, we found accounting for ice drift had little impact on median home range area in most cases. However, when considering all classes together, median home range size was affected seasonally, with home ranges being larger after accounting for drifting ice during the ice minimum and maximum seasons, but smaller during the transitional melt and growth seasons. Similar seasonal variation was also detected by Durner et al. (2017). Our analysis found that voluntary median movement rates, those calculated by removing ice drift, were lower than observed from the raw telemetry in nearly all class and season comparisons, and never higher, but this could be because we used day-round activity, including a high proportion of very small movements: ~15% of our voluntary movement rates were < 100 m/h, and the 25th-percentile movement rate was < ¼ of the median.

The timing of the ice season is crucially connected to the annual energy uptake and loss cycle of polar bears (Messier et al. 1992, Regehr et al. 2007). Spring foraging opportunities are especially timed with the ringed seal pupping period (Pilfold et al. 2012). Females with offspring emerging from maternity dens must regain energy stores after a months-long fast to ensure offspring survival through the summer when prey are less available (Ramsay and Stirling 1988, Regehr et al. 2010). The lack of access to sufficient food resources can affect body size or outright survival (Rode et al. 2010, Stirling and Derocher 2012). Polar bears in the SB population show signs of declining condition (Regehr et al. 2010, Bromaghin et al. 2015), and sea-ice projections suggest cub recruitment and adult bear starvation could become severe before the end of the century (Hamilton et al. 2014). As Arctic warming shifts not only the length and timing of the ice seasons but the rate of drift as well, the increasing demands on energy for polar bears can be made up by additional hunting (Durner et al. 2017). However, with the exception of SF, all classes of bear in our study moved more during the ice melt and ice minimum period than during the ice maximum, and home range size for all bears was largest during the melt season. This transition from low-to-high rates of movement means more emphasis for polar bears on energy conservation during the increasingly shorter ice maximum season, greater foraging success before the ice minimum season, and potentially increasing energy expenditures during the melt and minimum seasons if drift speed increases over time.

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CHAPTER 5

Spatial and Temporal Harvest Risk to Polar Bears in the Canadian Beaufort Sea

Stephen G. Hamilton, Erin M. Henderson, Andrew E. Derocher

Introduction

Understanding factors that influence wildlife harvest is fundamental to management (Caughley 1977), yet the relationship between wildlife harvest and humans is complex due to the dynamics of interacting factors that involve both species ecology and human behaviour (FitzGibbon 1998, Toigo et al. 2008, Brodie et al. 2013). Arctic ecosystems confer particularly stringent challenges in terms of low productivity, stark thermal demands, and seasonal access to food into the ecology of large mammals that are often at low density and have low population growth rates (Pomeroy 1997, Brown et al. 2004, ACIA 2005). Such conditions raise species susceptibility to overharvest, necessitating an understanding of harvest effects on populations, especially in a warming climate (Walther et al. 2002, Schipper et al. 2008, Weinbaum et al. 2013). Hunting is vital to communities in the north, both traditionally and economically, and climate change has resulted in new challenges that are affecting wildlife harvest of many marine species (Hovelsrud et al. 2008, Pearce et al. 2015, Hauser et al. 2021). In the Arctic, rapidly changing sea ice conditions have affected the distribution and abundance of marine species (Tynan and DeMaster 1997, Laidre et al. 2008, Wassmann et al. 2011). Of particular note, polar bears (*Ursus maritimus*) have been negatively affected by the warming climate in parts of their distribution with predicted declines or increased vulnerability across much of their range (Stirling and Derocher 2012, Regehr et al. 2016, Hamilton and Derocher 2019). Such changes are likely to affect aspects of future polar bear harvest.

Polar bears have a long history of harvest back to prehistoric and medieval times (Oleson 1950, Makeyev et al. 1993), and in the 1950s and 1960s concerns arose that unsustainable levels of harvest were threatening the species (Loughrey 1956, Prestrud and Stirling 1994). With the signing of an international agreement in the 1970s, polar bear harvest moved to a science-based management approach (Prestrud and Stirling 1994). Polar bears are hunted across much of their circumpolar range, excluding Norway and most of Russia, with management focusing on a maximum sustainable yield (Vongraven et al. 2012, Vongraven et al. 2018). Several studies have assessed the harvest of polar bears to determine sustainable harvest levels (Taylor et al. 1987, Taylor et al. 2008), the sex and age composition of harvest animals and the population impacts (Derocher et al. 1997, Taylor et al. 2006), and projected demographic impacts (Molnár et al. 2007). Recent analyses have examined the management of harvesting polar bears in a changing climate (Regehr et al. 2017, Regehr et al. 2021, Vongraven et al. 2022). Concerns have also emerged about the sustainability of polar bear harvest in light of declines in population abundance and changes in management regulations (Wiig 2005, Sonne et al. 2019).

Our understanding of polar bears varies across their range and the two populations in the Beaufort Sea (i.e., Southern Beaufort Sea (SB) and Northern Beaufort Sea (NB)) are well-studied compared to others (Hamilton and Derocher 2019, Vongraven et al. 2022). In the Beaufort Sea, north of the Northwest Territories, Canada, and Alaska, USA, polar bears were severely overharvested before 1968 when quotas were introduced in Canada and removal of all but subsistence hunting in Alaska (Schweinsburg 1981, Stirling 2002, Vongraven et al. 2022). The annual harvest in the Canadian Beaufort Sea is undertaken by Inuvialuit and Inupiat hunters under a co-management system with a user-to-user agreement established in 1988 (Brower et al. 2002, Wenzel 2011). Harvest rates target 4.5% of the local population, with bias toward males and regulations protecting females accompanied by offspring (Taylor et al. 2008, Regehr et al. 2017, Vongraven et al. 2022). Despite the variety of studies on polar bear harvest, there is little examination of the mechanisms involved.

Vulnerability to harvest in wildlife is dependent on a variety of biological factors including age, sex, and reproductive status as well as environmental factors including habitat use and proximity to humans (Nielsen et al. 2004, Bischof et al. 2009). The distribution and habitat use of polar bears in the Beaufort Sea is well-understood and varies by age, sex, and reproductive status (Stirling et al. 1993, Johnson and Derocher 2020). Significant changes to the sea ice associated with climate change (Stern and Laidre 2016) coincided with a decline in polar bear abundance in the SB (Bromaghin et al. 2015). The NB has seen less change in sea ice (Stern and Laidre 2016) and the population is thought to be stable (Stirling et al. 2011). Both populations are predicted to decline in abundance due to sea ice loss associated with climate change (Durner et al. 2009) and the SB is predicted to show drastic declines by the end of the 21st century (Hunter et al. 2010). Changes in abundance are of management concern as the maximum sustainable harvest is set at 4.5% of the population size with a 2:1 male to female sex ratio (Taylor et al. 1987). In the Canadian Beaufort Sea, the harvest quota has not been filled in recent years (IUCN/SSC Polar Bear Specialist Group 2018). The causes for the decline in harvest are unknown but we postulate they could be due to changing access to polar bears, the decline in abundance, or social factors affecting hunting effort.

Understanding how polar bear harvest may change over time involves understanding the interactions between the spatial and temporal distribution of both the bears and humans. To examine the risk of harvest of polar bears by sex, age, and reproductive class, we used telemetry locations of satellite-collared individuals to assess their exposure to harvest in the Canadian

Beaufort Sea. We focus our analysis on the variation in polar bear accessibility by mapping historic polar bear harvest areas and spatially defining risk to harvest. We assess use of these areas by polar bears according to age and reproductive status, and examine how climate warming may affect the use of harvest risk areas.

Study Area

The Beaufort Sea encompasses an area along the northern coast of the Yukon and Northwest Territories (Canada) and Alaska (US), stretching eastward towards the Amundsen Gulf, westward toward the Chukchi Sea, and northward past Banks Island toward the Arctic

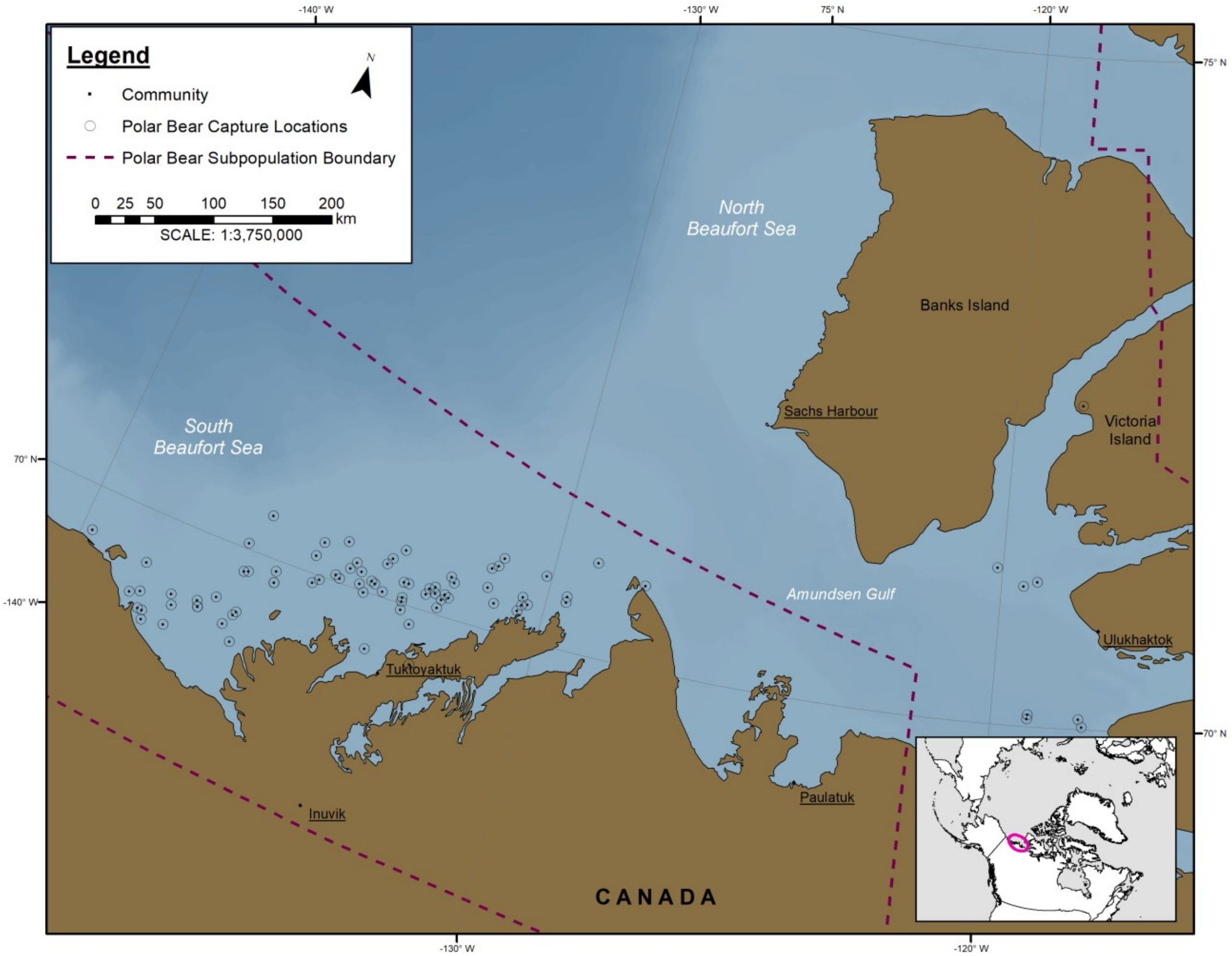

Figure 5-1. Study area map detailing polar bear capture locations. Bears were captured between 2007 and 2012 from the South Beaufort and North Beaufort subpopulations over Canadian waters.

Basin (Fig. 5-1). It is part of the divergent ice ecoregion, where sea ice is driven offshore, most notably in summer when new ice ceases formation and the remaining ice drifts away from the productive continental shelf and over the deep waters of the polar basin (Amstrup et al. 2008). Landfast ice is typically the last ice to leave during the breakup season, providing the last ice platform for polar bears hunting seals before summer, and also providing human hunters access to the polar bears.

Methods

Polar Bear Capture

We deployed GPS satellite-linked collars (Telonics, Mesa, AZ) on 78 wild polar bears in the SB between 2007 and 2012 using standardized methods (Stirling et al. 1989), with the bears being located by helicopter and chemically immobilized. The collars were programmed to register locations every four hours for up to four years. Collars had a time-release mechanism set in advance for 1 year for subadults and 2 years for adult females. Collars had corrodible attachments as a secondary release. Positions returned during the first three days after deployment were removed to account for potential changes in behaviour following capture (Thiemann et al. 2013).

We recorded bear reproductive status (sex and offspring presence/age) at capture with the following classes: subadult male, subadult female, solitary adult female, and adult female accompanied by offspring, along with offspring age. Reproductive status was projected for the tracking period following Johnson and Derocher (2020) and Henderson and Derocher (2022), and based on offspring remaining with their mothers for 2.5 years (Ramsay and Stirling 1986, 1988). Females with cubs-of-the-year (COY) were projected to be with yearlings, and those with yearlings to be with 2-year-olds by March – July of the following year. Mothers with 2-year-olds were projected to be solitary by the following January. Land-denning bears were identified by stationary locations on land from November – April (Amstrup and Gardner 1994), and ice-denning bears were identified by on-ice movements that matched ice drift (Togunov et al. 2020) from November – March. Denning bears were classified as solitary for the previous breeding season (March – July), and with COY for the following year (Ramsay and Stirling 1986).

Telemetry Data Filtering

The study period began in January and lasted until breakup of each year. The start of breakup was defined as the first day the sea ice concentration within the risk area was <50%, and did not increase above this threshold until the following fall (Stirling et al. 1999, Lunn et al. 2016). Sea ice concentration was averaged over the harvest risk area using the ‘raster’ R package in R version 3.6.1 (Hijmans 2019, R Core Team 2019) from Advanced Microwave Scanning Radiometer-Earth Observing System (AMSR-E & AMSR2; resolution 3.125 km) from May 2007 – September 2011 and September 2012 – December 2014, and Special Sensor Microwave Imager/Sounder (SSMIS; resolution 3.125 km) from October 2011 – August 2012 (Spreen et al. 2008). Locations outside of the study period were removed.

Biologically impossible telemetry locations with speeds >10 km/h or turning angles >165° or >155° that were respectively >25 km or >50 km from the previous and subsequent location were removed using the ‘argosfilter’ R package in R version 3.6.1 (Freitas 2012, R Core Team 2019). Telemetry locations from dropped collars were removed (Togunov et al. 2020), as well as locations resulting from presumed ice-denning bears until voluntary movement resumed. If the time between subsequent locations was >4 but ≤24 h, the ‘crawl’ R package (Johnson et al.

2008, Johnson and London 2018) was used to estimate the missing locations using a continuous-time correlated random walk (CRAWL) model with the Kalman-filter.

Harvest Risk Analysis

We used historical harvest positions from the Beaufort Sea and adjoining waters collected between 1985-1987 (Stirling et al. 1988) to generate a pre-climate warming harvest risk area via a kernel density estimation (KDE) at a 2-km resolution using ArcGIS 10.3.1 (ESRI 2015). We classified the KDE output into areas of low, medium, and high risk based on KDE values in the 10-50%, 50-90%, and 90-100% ranges, respectively. To assess the exposure to harvest-risk, each bear location was assigned one of four risk categories ("no", "low", "medium", or "high"). We used the 'raster' R package (Hijmans 2019) to get both a count of the number of locations within each risk category and the length of each continuous track with 4 hours between consecutive locations per risk category. The number of locations and length of the track within each risk category was compared based on reproductive status. We used chi-squared analysis to determine if risk zone usage was statistically greater or lesser than usage expected by chance alone.

Landfast Ice

Landfast ice was extracted from regional Canadian Sea Ice Charts for the Western Arctic (Canadian Ice Service 2005) between 1980 – 2021. The area of usable landfast ice was calculated for each risk area using the 'raster' R package (Hijmans 2019), and linear regression was performed to detect trends over time in available ice area during the harvest season. When ice concentrations reached <50%, we determined the harvest period to have ended as hunter access would become too limited although most harvest is completed before the end of May (Lee and Taylor 1994).

Results

Polar bear risk analysis began after collaring in mid-May 2007 and lasted until breakup in 2014 with a mean breakup date of 21 June (range: 3 – 17 June, 2007-2014). The collars provided 71 258 locations with the majority being adult females with offspring (Table 5-1). Harvest risk areas were generated from 121 historical harvest locations, resulting in total areas of high risk: 4996 km^2, medium risk: 25 420 km^2, low risk: 162 285 km^2, and negligible (no) risk: 1 377 311 km^2 (Fig. 5-2).

Except for solitary adult females, all classes had more positions inside of harvest risk areas than outside of them (Fig. 5-3). Females with offspring were located 50.0% in the low-risk areas, 10.6% in the medium- or high-risk areas, as opposed to unaccompanied females, with only 37.6% of their locations in the low-risk areas, and 7.1% in the medium- or high-risk areas. Subadult females were located in the high-risk areas proportionally the most of all classes, but still not often (0.7%), and more in the medium-risk areas than either category of adult females (11.3%). Subadult males had 70.5% of locations in low- or medium-risk areas, with more positions overall in the harvest risk areas than any other class, although they did not appear in the

Table 5-1. Number of positions by class of polar bear in each harvest risk area. Risk areas were derived from historical harvest locations (1985-1987) and calculated from a kernel density estimate.

	Harvest Risk			
Class	No	Low	Medium	High
Adult F (Solitary)	9116	6193	1141	27
Adult F (Offspring)	15 782	20 059	4001	241
Subadult F	3115	2821	768	49
Subadult M	2336	3504	2105	0

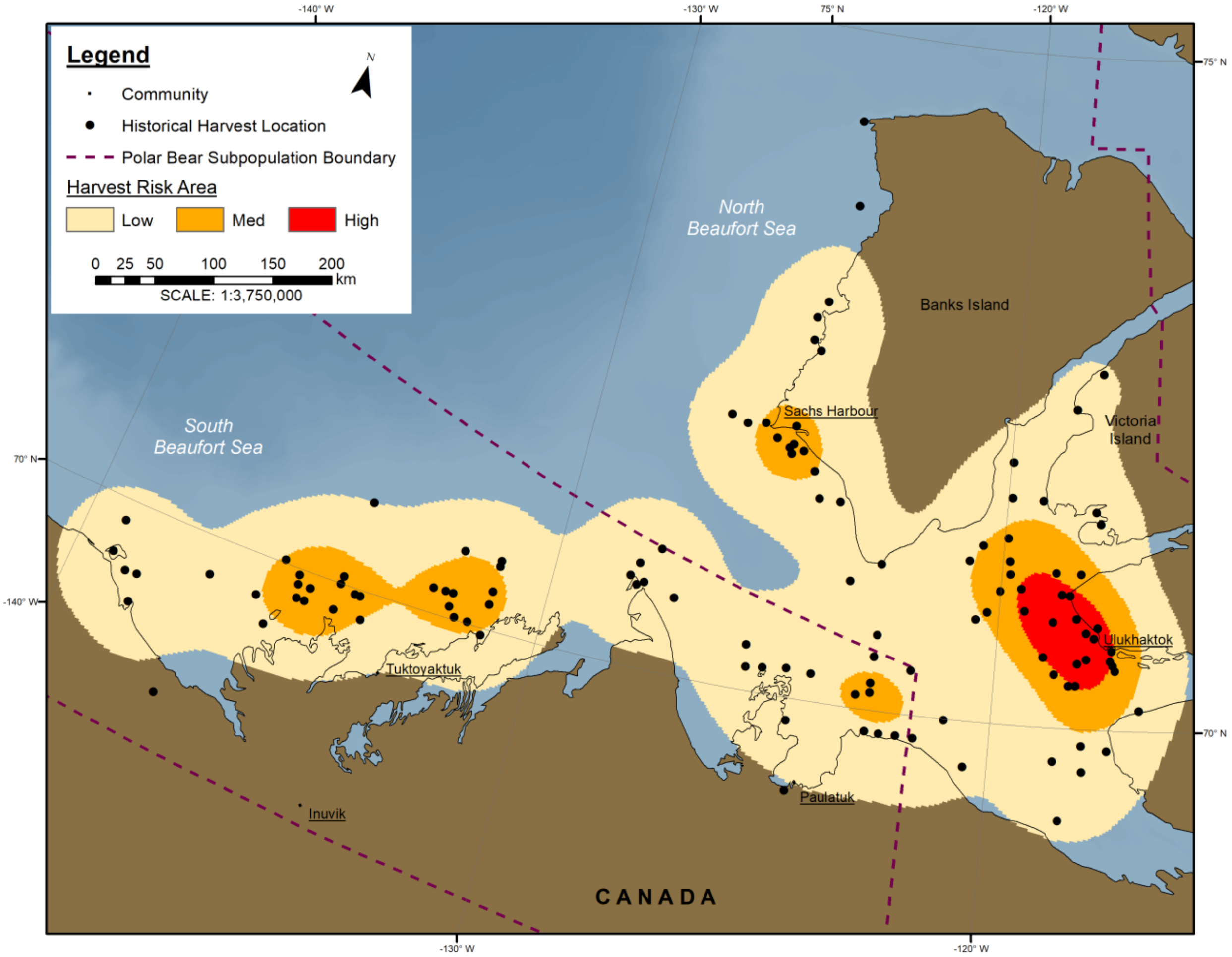

Figure 5-2. Harvest risk area map. Historical harvest locations were collected between 1985-1987 and used to generate risk areas from kernel density estimation, with cells representing relative exposure to harvest (Low: 10-50%, Medium: 50-90%, High: 90-100%).

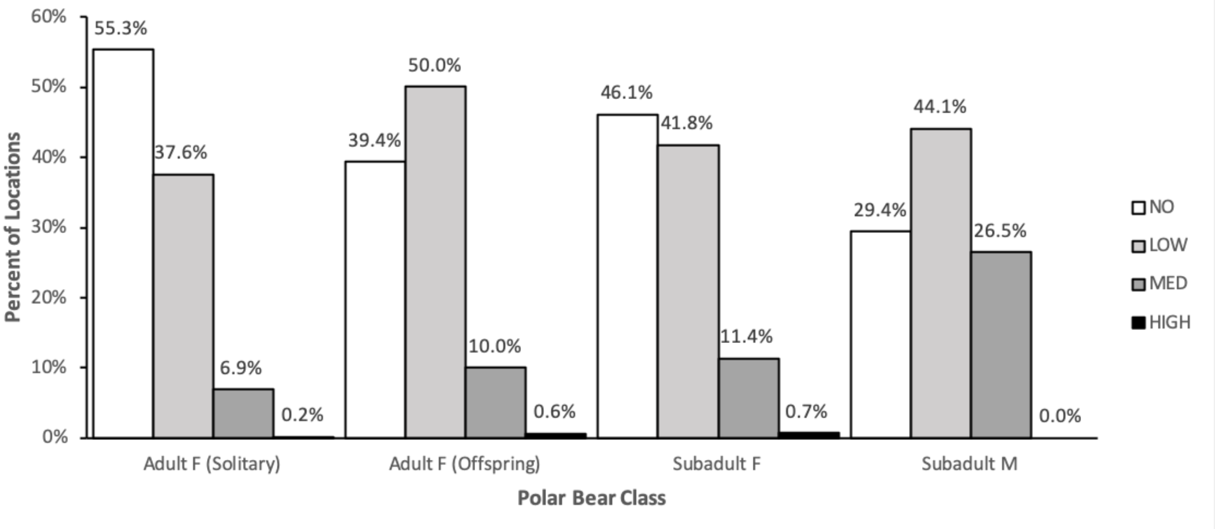

Figure 5-3. Percentage of polar bear telemetry locations (2007-2014) in harvest risk areas of the Beaufort Sea, Canada, by class.

high-risk areas. All bear classes were located less often than expected in the no-risk areas ($p < 0.05$), and more often than expected in the low- to high-risk areas ($p < 0.05$) with the exception of solitary adult females and subadult males in the high-risk areas (Table 5-2).

When considering tracks, which account for contiguous periods of time spent inside risk areas, all bear classes remained outside the harvest risk areas more than expected by chance (Table 5-3), but >50% of the time inside the risk areas (Fig. 5-4). Solitary adult females remained outside the risk areas 40.2% of the time, with a small amount of time (1.0%) in the high-risk area. Adult females with offspring spent less time in the low-risk areas (35.4%) than their solitary counterparts, but more time traversing the medium-risk areas (26.4%), and had more contiguous tracks in the high-risk areas than any other class (4.2%). Subadult female bears were similar in traversal time to unaccompanied adult females in the low- and medium-risk areas (also 58.7%), but spent more time in the high-risk areas (3.9%) and less time outside the harvest

Table 5-2. Chi-square analysis to compare polar bear positions observed relative to expected given the proportion of habitat in each harvest risk zone. Risk zone values are the difference between observed and expected positions, with negative values indicating the risk zone is less-used than expected, and positive values indicating risk zones are more-used than expected. All values are statistically significant at $p < 0.05$.

	Harvest Risk				
Class	No	Low	Medium	High	Chi-square
Adult F (Solitary)	-5339	4490	874	-25	16 685
Adult F (Offspring)	-19 381	15 916	3352	113	89 236
Subadult F	-2809	2123	659	28	11 792
Subadult M	-4634	2683	1976	-25	42 209

Table 5-3. Chi-square analysis to compare polar bear tracks (sets of contiguous 4-hour positions) observed relative to expected given the proportion of habitat in each harvest risk zone. Risk zone values are the difference between observed and expected tracks, with negative values indicating the risk zone is less-used than expected, and positive values indicating risk zones are more-used than expected. All values are statistically significant at $p < 0.05$.

	Harvest Risk				
Class	No	Low	Medium	High	Chi-square
Adult F (Solitary)	-46.1	26.0	19.4	0.7	334
Adult F (Offspring)	-114.0	53.1	52.6	8.3	1106
Subadult F	-25.7	13.7	10.2	1.8	197
Subadult M	-28.0	13.9	14.2	-0.2	311

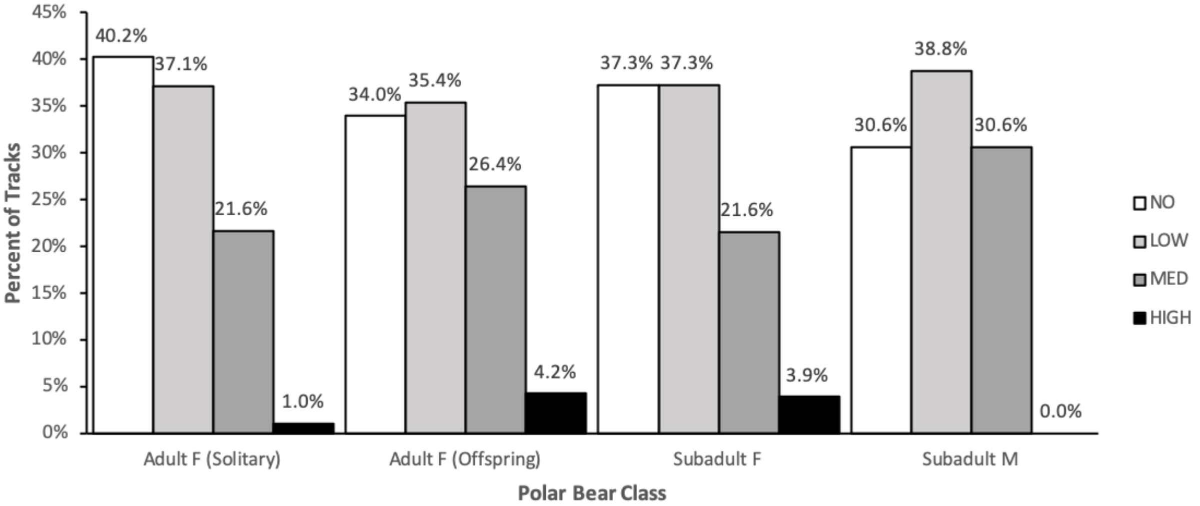

Figure 5-4. Percentage of polar bear tracks (contiguous 4-hour positions) in harvest risk areas of the Beaufort Sea, Canada, by class.

risk areas (37.3%). Subadult males spent the least amount of time outside of the harvest risk areas (30.6%), and more of their time traversing the low-risk areas (38.8%). Because no positions were available for the subadult males in the high-risk areas, we were unable to establish any estimates of time spent there.

Landfast ice area exhibited a statistically significant ($p < 0.05$) decreasing trend over our study area, and in each harvest risk area, with the lower risk areas showing more rapid decreases than the medium- and high-risk areas (Table 5-4). We observed declining landfast ice cover during the pre-melt (Jan-Mar) period of the harvest season between 1980 and 2021, indicating that the maximum area available to human hunters and bears foraging near shore has diminished in recent decades (Fig. 5-5). Furthermore, the areas of landfast ice overall and by risk area toward the end of the harvest season (Jun-Jul) declined over the same years (Fig. 5-6). When looking at proportions of risk zones covered by landfast ice, the high-risk areas were frequently (17 of 41 years) > 85% ice-covered at the end of the harvest season, but nearly as frequently (16 of 41 years) <10% covered, with 10 of those years occurring since 2020 (Fig. 5-7).

Table 5-4. Linear regression analysis for landfast ice area by year in each of the harvest risk areas. All trends were decreasing between 1980 and 2021.

	Pre-Melt (Jan-Mar)			End-of-Harvest (Jun-Jul)		
	Slope (km^2/a)	R^2	p	Slope (km^2/a)	R^2	p
No Risk	-485	0.30	<0.001	-325	0.34	<0.001
Low Risk	-598	0.21	0.002	-351	0.11	0.034
Medium Risk	-169	0.23	0.001	-110	0.11	0.031
High Risk	-57	0.22	0.002	-45	0.14	0.013
Total Area	-1309	0.30	<0.001	-831	0.21	0.002

Discussion

We found that polar bears of varying age and sex were detected near historically successful harvest locations in the Beaufort Sea with greater frequency than by chance alone, and when observing contiguous tracks, more than half of the time. Human hunters, reliant on tracking and scanning techniques, need access to sea ice to successfully approach polar bears, as well as sufficient daylight hours. As landfast ice is the last ice to break up, the harvest season is constrained to the pre-breakup springtime in near-shore areas. Polar bear access to sea ice during the harvest season is vital as it coincides with the prime period in which the bears can store food energy before the ice-free summer, after which foraging opportunities become diminished (Stirling and Derocher 1993, Robbins et al. 2012). While it is difficult to know from our analysis how much of the reason for spatial overlap is due to polar bear willingness to tolerate the risk of harvest (i.e., avoidance of humans), and how much is because experienced hunters can effectively locate polar bears where they are (Freeman and Wenzel 2006, Wenzel 2011), what is clear is that the individuals we tracked were often in proximity to historical harvest areas. It should be noted that none of the collared polar bears in this study were harvested, meaning our sample consists of bears that were exposed to harvest risk and survived. This is not unexpected given our sample size relative to the population, a target harvest rate of 4.5%, and the majority of our sample being females with offspring protected from harvest (Vongraven et al. 2022).

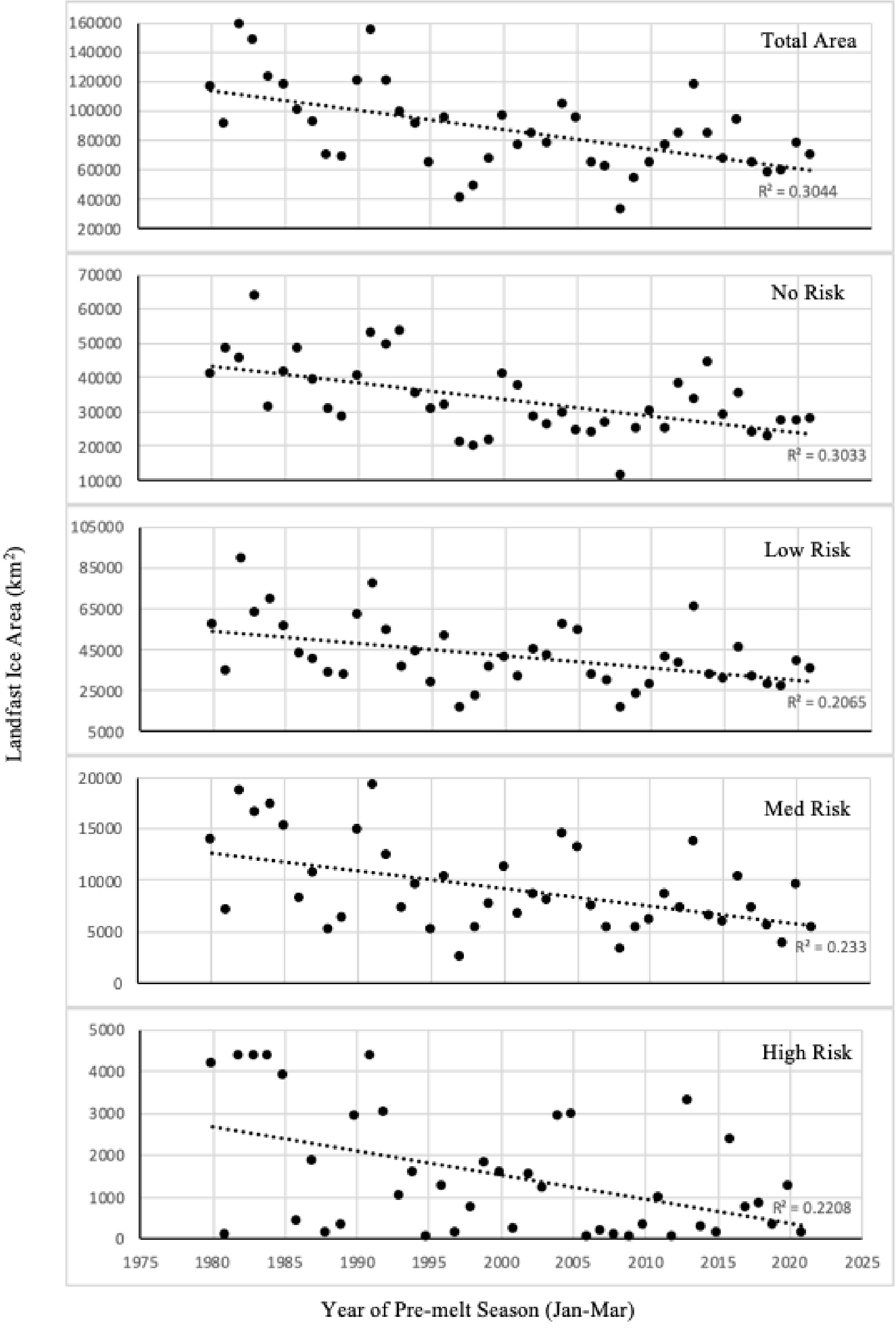

Figure 5-5. Trends in mean landfast ice cover in the pre-melt season (Jan-Mar) between 1980-2021 by polar bear harvest risk area in the Canadian Beaufort Sea. Linear regression trends are significant at $p = 0.05$.

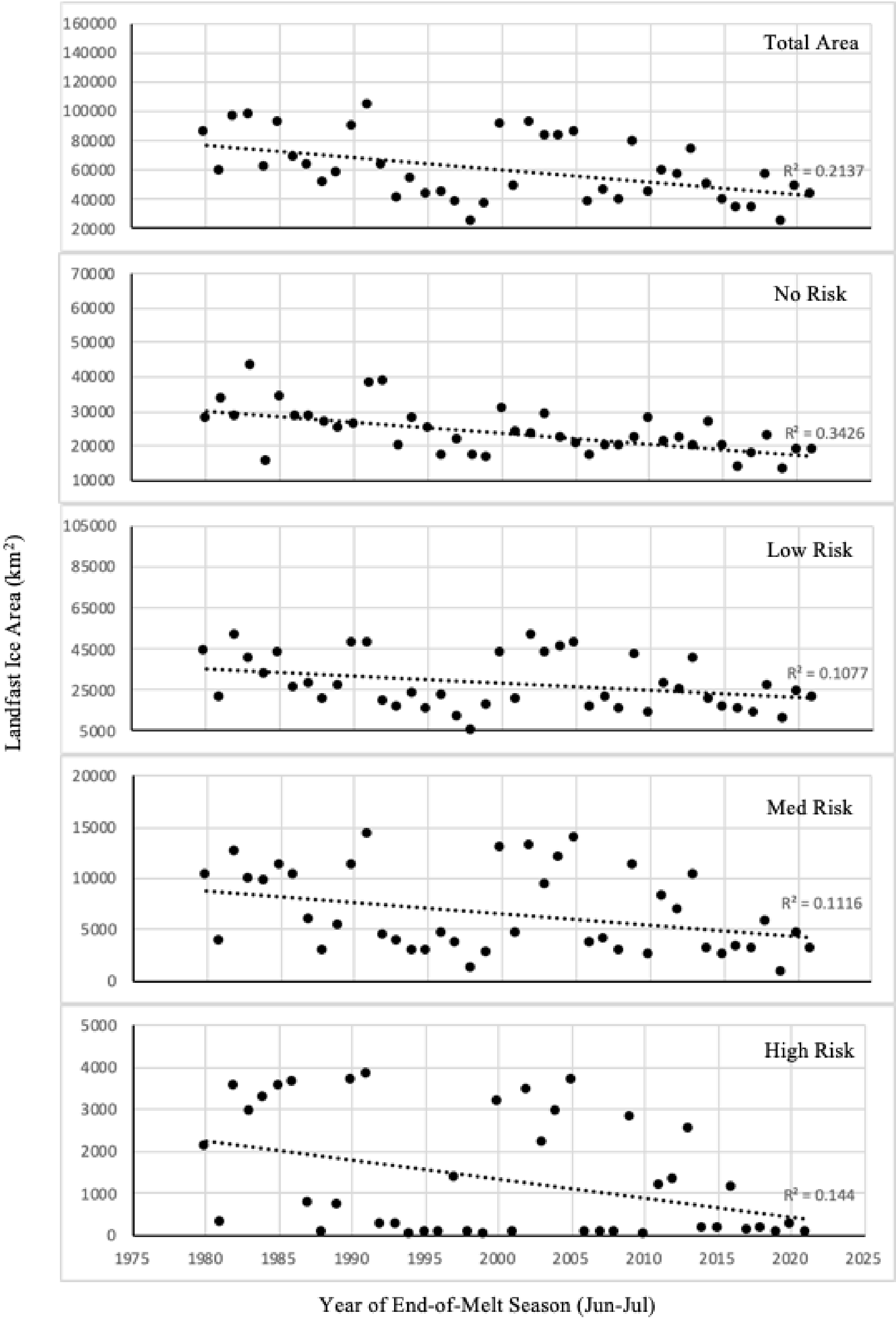

Figure 5-6. Trends in mean landfast ice cover in the end-of-melt season (Jun-Jul) between 1980-2021 by polar bear harvest risk area in the Canadian Beaufort Sea. Linear regression trends are significant at $p = 0.05$.

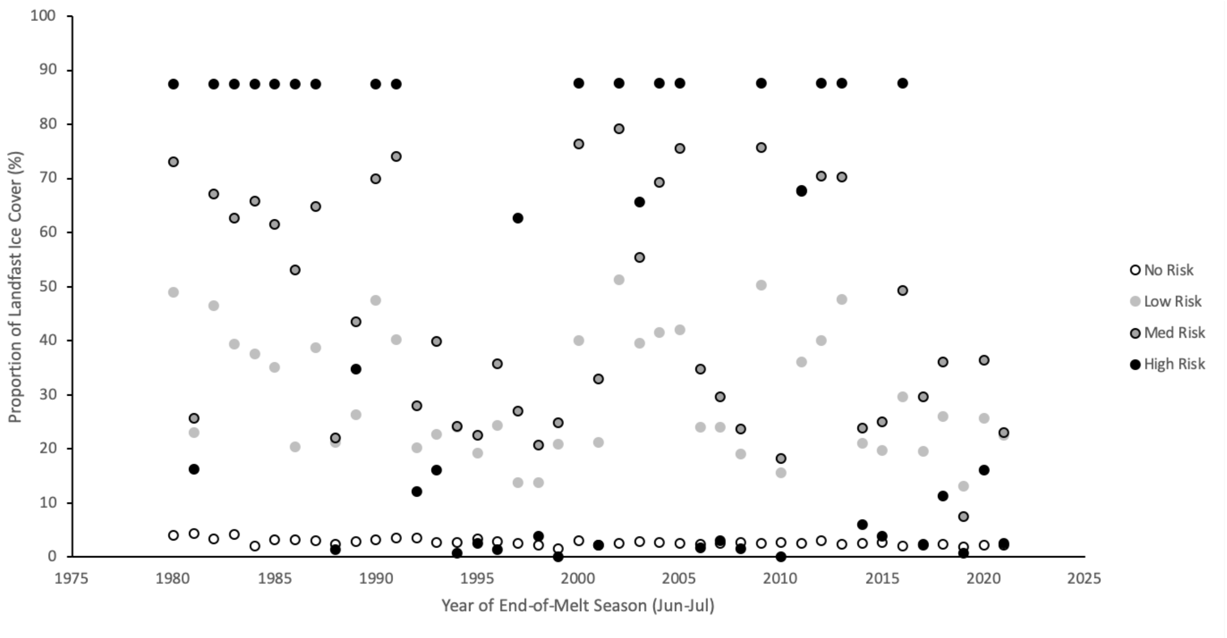

Figure 5-7. The end-of-season (Jun-Jul) proportion of each risk area still covered by landfast ice usable by both polar bears and human hunters (1980-2021).

Nevertheless, it would be of interest to know how much time bears that were successfully harvested had spent in risk areas before death.

Solitary adult females were notable in their comparative absence from harvest risk areas. While their tracks indicated they spent the majority of their time in risk areas, they spent the highest proportion of their time outside of the risk areas relative to the other classes, and were the only class to have fewer than half of their positions within the harvest risk areas. Compared to female with offspring, the time solitary adult females spent in the harvest areas was greater in the lower risk regions, with roughly only a quarter of their time spent in the high-risk regions. It is possible the accompanied females are able to spend more time in higher-risk areas because they are protected from human harvest, but also that accompanied females move more slowly because of the offspring (see Chapter 4), thus upon entering a risk zone they take longer to leave it again. A further possibility is that solitary adult females may be engaged in mating, which is concurrent with the harvest season (Ramsay and Stirling 1986), while females with offspring may tend to preferentially select landfast ice to hunt for seal birth lairs (Johnson and Derocher 2020).

Solitary adult females were similar to subadult females with regards to the track analysis, differing notably in the greater time they spent outside risk areas. The difference in tracks outside risk areas was almost entirely accounted for by the lesser time they spent in the high-risk areas. This may indicate that subadult females are constrained somewhat more to areas with higher likelihood of encountering hunters while actively avoiding other bears, in particular adult males, but it may also be a sign that younger bears are less cautious about avoiding humans. In either case, these findings are consistent with habitat selection models regarding subadult activity close to land (Johnson and Derocher 2020).

Subadult males, interestingly, spent the least amount of time outside of the harvest risk areas, but were not detected at all within the areas of highest risk. The largest proportion of their activity took place in the low-risk areas, both in terms of number of positions and in terms of contiguous tracks. Similar to subadult females, this could indicate that they are constrained somewhat by the space-use of older bears, but may once again be a sign that they have a higher tolerance for human presence. It is difficult to conclude that they actively avoided the high-risk areas as we lack any positional data. However, indications are that young males are pressed to disperse to potentially less-ideal areas, and are generally more vulnerable to harvest (Ramsay and Stirling 1986, Stenhouse et al. 1988, Derocher et al. 1997).

Climate warming in the Arctic has affected communities reliant on harvest, with changes affecting the timing of breakup and introducing challenges and increased costs to travel (Pearce et al. 2010, Wenzel 2011). Our risk areas were derived from harvest locations from the 1980s, when ice conditions were not yet reflective of modern rates of change (Serreze et al. 2007, Stroeve et al. 2007, Stern and Laidre 2016). Arctic warming is expected to lead to earlier breakup of ice, thus reducing the time available for polar bears to capitalize on ideal foraging conditions (Regehr et al. 2007, Stirling and Derocher 2012). Our analysis suggests that landfast ice available to both polar bears and human hunters in the Beaufort Sea is trending downward over time, especially in areas of lower harvest risk, potentially restricting both bears and humans to smaller areas that might result in higher encounter rates. Bears facing more challenging energy balance circumstances due to climate warming may be forced to take on elements of higher risk to offset losses of fitness (Reimer et al. 2019). We note that the higher risk areas have proportionally more landfast ice later in the harvest season than the lower risk areas, which could indicate that polar bears not moving off-shore drifting pack ice may be increasingly concentrated to areas of higher harvest risk. It is difficult to predict climate warming-related harvest risk, however, because hunting conditions may worsen over time, lowering overall harvest pressure.

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CHAPTER 6

Concluding Remarks

The world's climate is warming due to increasing greenhouse gas emissions from the continued burning of fossil fuels, trapping energy in the Earth climate system, and forcing Earth's climate to change (IPCC 2014). The extent of warming is not yet determined, although some warming is unavoidable even if no further emissions were to occur from now (Meehl et al. 2005, Cubasch et al. 2013, Box et al. 2022). Ecosystem changes due to warming are being observed worldwide, threatening a wide variety of species in terms of population reduction, extirpation, or extinction because of warming-induced habitat loss (Hazen et al. 2013, Wessely et al. 2017, Bonan and Doney 2018).

Warming is happening faster in the Arctic than in other regions of the world, primarily due to feedback effects rooted in the loss of ice and snow (Zhang 2005, Serreze and Francis 2006, Hwang et al. 2011, England et al. 2021). Arctic warming encourages permafrost melt and higher rates of deglaciation (Armstrong McKay et al. 2022), more rapid rates of ocean acidification (Qi et al. 2022), increased precipitation as rain rather than snow (McCrystall et al. 2021), reduction of Arctic sea ice extent and thickness (Serreze et al. 2007, Li et al. 2022), and the subsequent timing of algal bloom (Sakshaug et al. 2009), with potential perturbations to the Arctic ecosystem food web (Carmack et al. 2006, Falk-Petersen et al. 2009, Søreide et al. 2010, Frey et al. 2014).

Arctic warming affects a myriad of species, animal and otherwise (Wassmann et al. 2011, Macias-Fauria and Post 2018, Li et al. 2019), though particular concern exists for Arctic marine mammals due to their connections with sea ice (Laidre et al. 2008, Schipper et al. 2008, Laidre et al. 2015). For Arctic marine mammals, warming effects on sea ice are often synonymous with habitat degradation or loss (Post et al. 2013, Chambault et al. 2022). Changes to the Arctic ecosystem may result in state shifts and the invasion of other species, with subsequent changes to ecological niches (Quinlan et al. 2005, Post et al. 2019).

The challenges faced by polar bears due to continued Arctic warming is well-documented (Derocher et al. 2004, Amstrup et al. 2010, Regehr et al. 2016) and discussed at-length throughout this thesis. My research covers topics on the global conservation and vulnerability of polar bears, future projections for polar bear survival in the Canadian Arctic, and, more specifically to the Beaufort Sea region, the age- and sex-related movement patterns of polar bears as well as risk to human harvest. Throughout this work I have raised the common thread of the energetic challenges faced by polar bears associated with the lengthening of the ice-free period, highlighting that habitat loss for polar bears is both spatial and temporal. Temporal habitat loss (i.e., the timing of key habitat availability) in the case of polar bears is exemplified through the increasing length of annual ice-free conditions with direct impacts on the bears' year-to-year energy balance (Regehr et al. 2007, Stirling and Derocher 2012).

Polar bears have historically spent significant time each year in a fasting period, losing body mass daily from the stores they build up when seal-hunting opportunities are most abundant (Ramsay and Stirling 1988, Pilfold et al. 2012), but are able to recover later in the sea ice melt-freeze cycle given sufficient hunting successes (Stirling and McEwan 1975, Robbins et al. 2012, Rode et al. 2015). However, energetics models suggest that when exposed to greater fasting periods, polar bears fare poorly (Rode et al. 2010, Molnár et al. 2020). My research into the effects of an increased ice-free season on polar bears in the Canadian Arctic Archipelago found that elements of reproductive failure as well as starvation could occur, even in areas often considered superior habitat (Amstrup et al. 2010, Hamilton et al. 2014).

Furthermore, sea ice is less motile during the ice maximum season (Kwok et al. 2013), meaning bears can benefit from lower energy expenditures while remaining over good habitat (Mauritzen et al. 2003, Auger-Méthé et al. 2015, Durner et al. 2017). My research noted, based on movement patterns in the southern Beaufort Sea, that an earlier break-up of ice under warming conditions may not only reduce the length and quality of the prime foraging season, but decrease the period when bears can reliably use less energy with day-to-day movement almost regardless of age or sex. Furthermore, my research into harvest risk suggests that landfast ice habitat in the Beaufort Sea may become relatively more constricted to higher-risk areas under continued warming, potentially exposing bears to more human encounters during a season when the bears rely on maximizing energy uptake (Messier et al. 1992, Regehr et al. 2010).

Concerns over polar bear persistence in the face of Arctic warming are widespread, and public interest in polar bear conservation is multi-faceted, with much curiosity around the status of the population and whether it is in decline (Prestrud and Stirling 1994, Harvey et al. 2018, Born 2019). My research into the status of contemporary population research highlighted that it would be difficult to make science-based statements regarding trends on the global population of polar bears, although some subpopulations have been sampled sufficiently to indicate rates of population decline (Hamilton and Derocher 2019). However, with respect to the mechanisms of population decline, insomuch as they revolve around energetic constraints and might require several years to result in an individual's death, it may be more prudent to look first at signs of poorer body condition or lower cub recruitment (Prestrud and Stirling 1994), circumstances for which there is evidence in multiple subpopulations (Regehr et al. 2007, Rode et al. 2010, Lunn et al. 2016, Obbard et al. 2016).

A recent study produced evidence of a genetically distinct subpopulation of polar bears in Southeastern Greenland, which uses marine-terminating glaciers to retain year-round access to prey (Laidre et al. 2022), distinguishing them from other subpopulations and raising questions about the possibility for refugia from climate change (Peacock 2022). In my assessment of polar bear vulnerability by subpopulation, the East Greenland Sea subpopulation (which encompasses the newly proposed subpopulation) was given a score of 11 on a scale of 5-15, where 15 was high vulnerability to the effects of Arctic warming. However, assuming the summer ice loss and ice-free period indices are scored lower due to glacial access to prey, the score could be considered to be 9, which is on par with the proposed "Last Ice Area". Nevertheless, the East Greenland Sea subpopulation was scored among the most vulnerable in terms population size, and the number of bears in the new subpopulation will necessarily be smaller still, along with indications of low birth rates and relatively low adult female body mass (Laidre et al. 2022). Comparatively, the Last Ice Area scored among the best in terms of vulnerability to population size (Hamilton and Derocher 2019). Furthermore, while the discovery of a subpopulation of polar bears that can reliably hunt seals year-round is important to acknowledge, many polar bears globally do not have access to marine-terminal glaciers.

The research collected in this thesis aims to highlight aspects of polar bear conservation that revolve around the loss of habitat (i.e., the area of quality sea ice and the timing relative to energetically vital periods of the year) and the resulting effects that may be felt on bears of differing age and sex. Nevertheless, polar bear conservation encompasses a variety of additional issues, such as effects of pollution or human contact, direct or indirect, through expanding industrial and tourism activities (Prestrud and Stirling 1994). Heavy metals and PCBs have been detected in polar bears (Braathen et al. 2004, Bechshoft et al. 2015, Liu et al. 2018), and microplastics have been detected in regions throughout the Arctic (Strand et al. 2021), with implications not yet fully understood. Meanwhile, warming-induced losses of Arctic sea ice have been commensurate with increased human development in the region (Lam et al. 2021), with implications on, for example, polar bear movement behaviour (Lomac-MacNair et al. 2021) and den-site disturbance (Florko et al. 2020), but also introduction of invasive species (Goldsmit et al. 2020).

Polar bear conservation efforts face significant challenges stemming from, or exacerbated by, ongoing global warming and the resulting changes to the Arctic marine ecosystem. Indications are that greenhouse gas mitigation can prolong wild polar bear populations, though perhaps not as globally widespread nor in the numbers we have today (Amstrup et al. 2010), and global greenhouse gas emissions have continued to rise (IPCC 2022). It is conceivable that a sufficient surface area of sea ice over quality habitat could still not sustain a polar bear population if the amount of time the ice was available were insufficient. Fossil records indicate that polar bears must have lived in regions south of their modern range many thousands of years ago (Kurten 1964, Aaris-Sørensen and Petersen 1984), though it is likely that they were forced North with receding Arctic ice after the last glaciation (Wiig et al. 2008). As modern-day sea ice is projected to continue its Northward retreat, the southernmost polar bear populations will struggle harder to survive, eventually facing extirpation (e.g., de la Guardia et al. 2013), and even areas of historically good habitat, such as in the Canadian Arctic Archipelago, may eventually prove insufficient to support persistent polar bear populations (Hamilton et al. 2014).

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