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Maternal Denning Phenology and Substrate Selection of Polar Bears (*Ursus maritimus*) in the Southern Beaufort and Chukchi Seas

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Maternal Denning Phenology and Substrate Selection of Polar Bears (*Ursus maritimus*)
in the Southern Beaufort and Chukchi Seas

Jay Wesley Olson

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Master of Science

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ABSTRACT

Maternal Denning Phenology and Substrate Selection of Polar Bears (*Ursus maritimus*) in the Southern Beaufort and Chukchi Seas

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Master of Science

Loss of sea ice due to global warming may affect the phenology and distribution of polar bear (*Ursus maritimus*) denning by altering access to denning habitats. We examined trends in the selection of maternal denning substrate (land versus sea-ice denning) in the southern Beaufort Sea (SB), addressing the potential influence of summer land-use and fall sea-ice conditions on substrate selection. We developed an algorithm based on statistical process control methods to remotely identify denning bears and estimate denning phenology from temperature sensor data collected on collars deployed 1985–2013 in the SB and Chukchi Sea (CS). We evaluated cub survival relative to den entrance, emergence, and duration, and examined differences in the phenology of land and sea-ice dens. Land denning in the SB was more common during years when ice retreated farther from the coast and off of the continental shelf in September. All SB bears that occupied land prior to denning subsequently denned on land; however, only 29% of denning bears that summered on sea ice denned on land. Den entrance and duration in the SB and CS were similar, although CS bears emerged later. Land dens were occupied longer than those on ice. Bears later observed with cubs remained in dens 23 days longer and emerged from denning 17 days later on average than bears that denned but were subsequently observed without cubs, suggesting that den exit dates are related to cub survival. The increase in land-based denning in the SB when sea ice retreated farther from shore, along with the positive correlation between fall land-use and land denning, suggest that further sea-ice declines may result in continued increases of onshore denning. Growing numbers of denning females along the coast may increase the potential for human-bear interactions.

Keywords: polar bear, *Ursus maritimus*, den, sea ice, phenology, Alaska, southern Beaufort Sea, Chukchi Sea

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CHAPTER 1

CHANGES IN THE DENNING SUBSTRATE OF POLAR BEARS ASSOCIATED WITH SEA-ICE LOSS IN THE SOUTHERN BEAUFORT SEA

ABSTRACT

In response to a changing climate, many species alter habitat use. Polar bears (*Ursus maritimus*) in the southern Beaufort Sea have increasingly been observed using land for maternal denning as sea ice retreats farther off shore during late summer and fall. We examined trends in denning on land versus pack ice from 1985–2013 and looked at potential relationships between land-based denning and sea-ice conditions. We also assessed if summer land-use was associated with terrestrial rather than ice-based denning. We identified maternal dens remotely and objectively by developing an algorithm that used statistical process control methods to identify denning bears from temperature-sensor data. We found a 3.1 fold increase in the rate of land denning during 1996–2013 relative to 1985–1995. Land denning was more common during years when ice retreated farther from the coast and off of the continental shelf in September. All denning bears that occupied land prior to denning subsequently denned on land; while 29% of denning bears that summered at sea denned on land. Because land-based denning was more common during years when ice retreated further from shore suggests that further sea-ice declines may result in continued increases in land denning. While the effects of this behavior on the nutrition, energetics, and reproduction of polar bears in the southern Beaufort Sea remain unclear, an increase in bears onshore will likely increase human-bear interactions.

INTRODUCTION

Arctic marine mammals are typically resilient to sudden interannual changes in their

environment (Derocher et al. 2004, Harington 2008, Laidre et al. 2008); however, rapid warming in the Arctic may challenge the adaptive capacity of species that have life histories reliant on sea ice (Moore & Huntington 2008). Dramatic changes in the timing, characteristics, and distribution of sea ice can have biological and demographic consequences for ice-dependent animals (Tynan & DeMaster 1997, Laidre et al. 2008, Wassmann et al. 2011). Earlier onset of melt and later freeze up of sea ice in the Arctic has lengthened the seasonal melt at a rate of 5 days decade⁻¹ from 1979 to 2013 (Stroeve et al. 2014). This has led to a decrease in the sea-ice minima (measured in the month September), declining at an estimated -12.4% per decade (Cavalieri & Parkinson 2012, Stroeve et al. 2012). Many species respond to climate change by shifting their range towards the poles or higher altitudes, though such shifts are not possible for species that already occur at geographic extremes (e.g., polar and alpine species) or where constrained by additional limiting factors such as light (Walther et al. 2002, Parmesan 2006). Changes in habitat use due to climate change are likely to be species-specific and vary regionally (Walther et al. 2002, Laidre et al. 2008).

As a sea-ice obligate, polar bears (*Ursus maritimus*) are sensitive to climate-induced habitat changes in the Arctic (Gleason & Rode 2009). Unlike other marine mammals that temporarily haul-out on ice, polar bears rely on sea ice as a primary platform for hunting, breeding, traveling, and resting. Declines in body condition, reproduction, and survival have been linked to reductions in sea ice (Stirling et al. 1999, Regehr et al. 2007, Regehr et al. 2010, Rode et al. 2010a). While these trends have generally been attributed to reduced access to prey, loss of sea ice may also affect polar bear reproduction by altering access to maternal denning habitat (Derocher et al. 2011; Stirling & Derocher 2012).

Maternal denning is a crucial behavior for polar bears in which parturient females give

birth to altricial neonates in the relative warmth and protection of subnivean dens (Lentfer & Hensel 1980, Amstrup 1993). While some bears may den on drifting pack ice (Amstrup & Gardner 1994), throughout most of their range polar bears den primarily on land or landfast ice (Ramsay & Stirling 1990, Durner et al. 2003). For bears that summer on retreating sea ice, access to terrestrial denning habitat requires that ice freezes or drifts in time to either walk or swim to shore (Derocher et al. 2004). Thus, declines in sea ice may affect the ability of bears to reach land-based denning areas (Derocher et al. 2004, Derocher et al. 2011, Stirling & Derocher 2012). As an alternative strategy to adapt to increased open water, some bears may leave the pack ice at break-up to summer and subsequently den on land (Derocher et al. 2004).

Historically, denning on sea ice was assumed to be the result of failure to reach preferred coastal habitats (Lentfer & Hensel 1980), but a later study showed that polar bears of the southern Beaufort Sea subpopulation (SB) denned more frequently on pack ice than land (Amstrup & Gardner 1994). More recently, from 1985 to 2005, maternal dens in the SB shifted away from sea ice in favor of terrestrial habitats, a change that occurred during a period in which sea-ice stability was reduced because of declines in multi-year ice. However, because oil and gas development, infrastructure, and local communities occur along the SB coast of Alaska, bears denning near or on land may have an increased risk of disturbance by humans (Amstrup 1993, Linnell et al. 2000). In addition to increased use of coastal habitats for denning, increases in bear density along the SB coast have been observed in September and October, and have been correlated with reductions in the extent of summer pack-ice (Schliebe et al. 2008). Such increases in land use prior to the denning season may influence the selection of den substrate (land versus sea ice) in autumn.

We developed an algorithm based on temperature sensor data to determine if a bear

denning and examined whether the trend of increased land denning found in Fischbach et al. (2007) continued during an additional 8 years (2006-2013). Specifically, we addressed the following questions: (1) Is the frequency of denning on land continuing to increase? (2) Is the frequency of land-based denning related to sea-ice conditions? (3) Is increased land-use during summer related to increases in terrestrial denning (i.e., do bears that summer on shore also den there)?

METHODS

Study Area

The SB subpopulation of polar bears is comprised of approximately 900 individuals (Bromaghin et al. 2015) and has a range that extends from Icy Cape, Alaska, USA (159° W) to Tuktoyaktuk, Northwest Territories, Canada (133° W), with a northern boundary of approximately 74° (Amstrup et al. 2004a). Bears in the SB generally select for medium to high sea-ice concentrations (>50%) in productive, shallow waters off the continental shelf (Durner et al. 2009). As sea ice over the continental shelf retreats during summer, most bears follow the retreating ice north over the deeper waters of the Beaufort Sea's Canadian Basin (Schliebe et al. 2008). In the autumn or early winter, pregnant polar bears enter maternal dens (Amstrup & Gardner 1994).

Polar bear capture and collaring

Polar bears were instrumented with satellite linked data logging transmitters on the sea ice during spring (mid-March to mid-May) and occasionally during autumn (August to November) in the Alaska portion of the SB by the U.S. Geological Survey (USGS) during most years 1985–2013. Polar bears were located from a helicopter and immobilized with a rapid-injection dart (Palmer Cap-Chur Equipment, Douglasville, Georgia, USA) containing

zolazepam-tiletamine (Telazol[®] or Zoletil[®]) (Stirling et al. 1989) 1987–2013, or Sernylan, M-99, or phencyclidine prior to 1987. Spring captures overlapped with timing of den emergence, but generally lasted beyond the time period when all females would have emerged from dens (i.e., early May; Amstrup and Gardner 1994). Studies were conducted under U.S. Fish and Wildlife Service research permit MA 690038 and followed protocols approved by Animal Care and Use Committees of the USGS (assurance no. 2010-3). Platform-transmittal-terminal (PTT) satellite-radio collars (Telonics, Inc., Mesa, AZ) were deployed on a subset of adult females 1985–2013, except during 1993–1997 and 2010. PTTs transmitted an ultra-high frequency (UHF) signal to polar orbiting satellites through an antenna located lateral to the neck of the bear. Temperature was measured by a thermistor inside the radio collar. Though warmed by the body temperature of a collared bear, these temperatures generally tracked ambient conditions (Fischbach et al. 2007). PTTs were equipped with a very high frequency (VHF) beacon to allow for radiotracking via aircraft by personnel in the field.

Classifying denning behavior using sensor temperature

Because polar bears occupy vast and remote habitats, the use of conventional methods used to monitor ursid dens (e.g., identifying denning via radio telemetry and den observations) is expensive and potentially dangerous (Fischbach et al. 2007). This is particularly true in the SB, where many bears den on drifting pack ice in the Beaufort Sea Canadian basin (Amstrup & Gardner 1994). The drift of sea ice along prevailing wind and ocean currents confounds attempts to identify dens using satellite location data. Fischbach et al. (2007) successfully identified denning attempts using satellite-collar temperature and activity sensor data as well as location frequency and quality. However, this method required that denning signatures be identified by qualitative examination of seasonal sensor and location quality plots. We sought to create an

algorithm that used temperature alone to distinguish between denning and non-denning individuals, with the purpose of providing an objective tool for remotely identifying denning behavior.

We used statistical process control methods (Shewart 1931) to identify maternal denning behavior in polar bears based on sensor temperature data. Commonly used in industrial manufacturing and quality control, control charts quantify the routine variation in a stochastic process so that special causes of variation can be identified. Individual observations of the variable of interest are binned into subgroups and plotted along the y -axis, while the x -axis represents a time scale or sample number (Morrison 2008). The expected mean of the process is summarized by the centerline of the control chart. Upper and lower control limits then provide an expected range of variation. Observations beyond these limits indicate the potential presence of a special cause of variation (Montgomery 2001). The use of specified control limits is equivalent to testing a hypothesis that observations are different from the expected average (Morrison 2008).

We quantified the routine variation in temperatures of non-denning bears in order to identify extended periods of warmth that are indicative of denning animals (Fig. 1-1). The expected mean (centerline) and control limits were derived using a subset of temperature records spanning from 1 July to 30 June (hereafter referred to as a “bear-winter”) in which denning statuses had previously been assigned qualitatively using a combination of activity, temperature and location data (Fischbach et al. 2007). We used a subset of ‘non-denning’ bear-winters ($n = 109$) that exhibited temperature regimes characteristic of non-denning individuals (i.e., warmer temperatures during summer months and cooler temperatures in winter) to establish the routine seasonal variation for our control charts. We smoothed the daily averages of these non-denning

bear-temperatures and used locally-weighted scatterplot smoothing (LOESS; span = 0.35) (Cleveland 1979) to create an expected seasonal mean (centerline) for our control charts. Because individual temperature profiles varied substantially from this expected average, we adjusted the position of the centerline for each bear-winter using the mean of the first five temperature observations in each record as an intercept to adjust the starting position of the centerline. This altered the actual temperature of the centerline but maintained the seasonal variation typical of non-denning bears. If the first recorded temperatures occurred during typical denning months (Oct–Apr), the mean of the final five observations was used rather than the first five observations to adjust the centerline for a bear-winter.

While control charts commonly use a 3-sigma (three standard deviations) distance to define upper and lower control limits, these limits may be adjusted to attain a particular distribution (Morrison 2008). We used an upper control limit of 1.8-sigma and assumed standard deviation of 9° C for all bear-winters because these parameters most accurately distinguished between denning and non-denning bear-winters ($n = 418$) as previously determined in Fischbach et al. (2007). Temperature observations were plotted as daily means in control charts as suggested by Fischbach et al. (2007) in order to reduce the effects of outlying observations.

The number of temperature observations in a given bear-winter varied greatly over time due to variable collar programming and signal degradation. Collar signals degrade during denning due to the surrounding substrate and interference from the bear's body, resulting in gaps in temperature data (Fischbach et al. 2007). As a result, we based den status classifications on the number of days temperatures remained above control parameters and not the number of observations above the upper control limit. Bear temperatures were considered above control limits when >1 consecutive mean daily temperature rose above the upper control limit.

Similarly, a bout of temperatures above control limits ended when >1 consecutive mean daily temperature returned below the upper control limit. This rule prevented a single outlying observation from resetting the number of days counted above control limits. The time cutoff that best replicated known den tenure was used to define denning versus non-denning. Consequently, a bear-winter with >34 consecutive days above the upper control limit was considered a denning event. To minimize the risk of identifying a denning event where none occurred, we excluded bear-winters classified as denning based on <6 mean daily temperature observations above the upper control limit. Since many bear-winters were missing data during the winter months when denning occurs, we also excluded bear-winters in which observations ended before January 1 unless denning status was identified prior to January 1. Bear-winters with apparent bear mortalities or dropped collars were identified using location and activity sensor data and were excluded from the dataset prior to analysis. Each bear-winter was assigned a den year based on the year in spring when den emergence was presumed to have occurred.

Validation of den classification

We validated control chart classifications of denning behavior by comparing them with denning classifications made via VHF radio tracking (either by direct observation of denning or by subsequent observation of females with dependent young during annual capture and den monitoring efforts). Additionally, we measured the performance of our algorithm by comparing our classifications to those made by Fischbach et al. (2007); although this was not an independent comparison since classifications from Fischbach et al. (2007) were used to develop our methodology.

Determining substrate use: sea ice versus terrestrial habitats

Denning substrate was determined by a geographic overlay of modeled locations and a

coastline dataset (Fig. 1-2). Polar bear locations were collected through various satellite data collection systems throughout the course of this study. Prior to 2010, all radio collar locations were determined by the Argos system with accuracy from < 250 m to > 1500 m (see <http://www.argos-system.org/web/en/78-faq.php#faq-theme-55>) with sampling every one to three days. These location data were filtered to remove implausible locations using the Douglas Argos-Filter algorithm (Douglas et al. 2012), which retained all standard quality class locations (classes 3, 2, and 1), rejected all class Z locations, and retained auxiliary class locations (0, A, and B) if they were corroborated by a consecutive location within 10 km, or if movement rates were < 10 km hr⁻¹ and turning angles were not extremely acute. Beginning in 2004 we began collecting locations using transmitters that collected GPS locations every 4 hours. Because the physical properties of polar bear dens often attenuate transmission, location data were frequently unavailable or of low quality during the denning period. If at least one observed location at the start of, during, or at the end of the denning period identified via temperature data occurred on land, it was assumed that the den occurred on land.

Substrate use prior to denning was determined based on the number of days bears spent onshore during the months of August and October. If a bear spent ≥ 25 days onshore, they were classified as having summered on land. Although this threshold may not have spanned the entire open-water period in a given year, we set this threshold to identify bears that spent a relatively long duration on land and to determine if there was any possible relationship between a pregnant bear coming ashore prior to denning and her subsequent denning substrate.

Because location data were collected at varying intervals and with varying location accuracies, we used the R statistical computing (R Development Core Team 2013) package ‘crawl’ (Johnson 2013) to model daily polar bear locations from 1 July through October. This

method allowed consideration of varying location accuracy and generation of daily locations that could be used to determine the number of days a bear spent onshore prior to denning. For more details on the use and validation of CRAWL location estimates in modeling polar bear locations, see Rode et al.(2015).

We classified daily CRAWL-modeled bear locations as on land if they were located within 5 km of land as identified by the Global Self-consistent, Hierarchical, High-resolution, Geographic Database (GSHHG version 2.3.4; <http://www.soest.hawaii.edu/pwessel/gshhg/>). The 5 km buffer was used to encompass small barrier islands that may receive heavy use by polar bears in the summer (Schliebe et al. 2008) but were not depicted as land in the GSHHG, and to account for low accuracy of some locations. Our 5 km buffer might have resulted in some offshore bears being classified as on land, and vice versa, but this was less likely to occur during the focal time period of our analysis (July through October) because landfast ice is largely absent during this period (Mahoney et al. 2012) and the pack ice has generally receded >5 km north of the coast. Bears within 5 km of the coast during this time were likely to be on land. Because the UHF antenna was submerged while bears are in water, transmissions were prevented from reaching satellites. Hence, it is unlikely that locations received within 5 km on shore occurred in water.

Changes over time and relationships with sea ice

We compared the rates of denning on land versus sea ice across three semi-decadal time periods: 1985–1995, 1996–2006, and 2007–2013. These periods were chosen due to their use in previous studies of denning and habitat changes (Fischbach et al. 2007, Durner et al. 2009), and because time as a categorical, rather than continuous, variable allowed for non-linear variation over time. Additionally, these time intervals generally represented a decline of multi-year ice

beginning in the mid-1980s (Maslanik et al. 2011) and a lengthening melt season throughout the Arctic (Stroeve et al. 2014).

We related annual selection of den substrate to minimum sea-ice conditions during the prior autumn. Although most female polar bears do not enter dens until after the September sea-ice minimum, conditions during the minimum are likely to reflect the timing of ice returning to coastal regions and accessibility of land habitats for denning. We used a measure of the mean daily minimum distance (hereafter referred to as “distance”) from the edge of the continental shelf (300 m isobath) to the edge of the pack ice defined as either 15% or 50% sea-ice concentrations and averaged over the month of September (the month of the sea-ice minimum) (Rode et al. 2014). Ice concentrations were determined from 25×25 km resolution passive microwave satellite imagery (Cavalieri et al. 1996). These concentrations were chosen since polar bears often select for ~50% sea-ice concentration during summer (Durner et al. 2009), but have been found to use ice as low as 15% concentration (Durner et al. 2006; Cherry et al. 2013). For more details on the methods used to generate sea-ice metrics, refer to Rode et al. (2014).

Statistical analysis

We used mixed effects, binary, logistic models to test hypotheses involving the effects of distance to pack ice on den substrate (i.e., land versus sea-ice denning) and in comparing den substrate among study periods. We included individual animals as a random effect in mixed models to account for repeated denning observations from individual bears. We used an analysis of variance *F*-test (ANOVA) to examine differences among time periods in the distance from the continental shelf to sea ice at 15% and 50% concentrations. Relationships between summer location and den substrate were analyzed using a chi-squared test. Statistical significance was set at $\alpha \leq 0.05$. We programmed our control chart algorithm using SAS/STAT® software, while

all statistical analyses were performed using program R version 3.0.3 (R Development Core Team 2014).

RESULTS

We applied our denning behavior classification algorithm to 365 bear-winters for which sensor-temperature data were collected from instrumented polar bears in the SB from 1985 to 2013. We culled records from 69 bear-winters due to insufficient data. Of the remaining 296 bear-winter records, we classified 155 as denning and 141 as non-denning based on our algorithm. Our denning behavior classifications agreed with 94.5% of denning events independently confirmed via VHF radio tracking and subsequent family history observations ($n = 73$). Additionally, our denning classifications agreed with the den statuses identified by Fischbach et al. (2007) 96.3% of the time ($n = 218$).

Den substrate trends among study periods

Based on geographic overlay of modeled bear locations, we determined the den substrate for 138 bear-winters. Of these, 73 occurred on pack ice and 61 dens were located on or immediately adjacent to land (Fig. 1-2). The average odds of denning on land was 2.8 times greater during 1996–2006 than during 1985–1995; however, this difference was suggestive but inconclusive at the $p = 0.083$ level after accounting for repeated measures from individuals tracked to more than one denning event (Fig. 1-3; GLM; 95% CI = 0.9 – 9.1). We found no difference in the odds of denning on land between 1996–2006 and 2007–2013 (GLM; $p = 0.669$), but found a marginally significant difference in the rate of land denning between 1985–1995 and 2007–2013 ($p = 0.083$). Because insignificant results could be driven by small sample sizes during the latter two time periods, and because of the apparent similarities in the rate of land denning during these periods, we combined the latter two periods for comparison against the first

period. With this grouping the odds of denning on land was 3.1 times greater in 1996–2013 than in 1985–1995 (GLM; 95% CI = 1.1 – 9.1, $p = 0.039$).

Den substrate in relation to sea-ice availability

During the three time periods, the distance to ice from the continental shelf in September increased significantly (15% concentration sea ice: $F_{2,24} = 11.0$, $p < 0.001$; 50% concentration sea ice: $F_{2,24} = 17.3$, $p < 0.001$). The average daily minimum distance to 50% sea-ice concentration increased by 155 km from between the 1985–1995 period and the 1996–2006 (Tukey–Kramer test; 95% CI = 45.85 – 264.5, $p = 0.005$), and by 162 km between the 1996–2006 period and the 2007–2013 period (Tukey–Kramer test; 95% CI = 23.24 – 299.8, $p = 0.020$), with a total increase of 317 km between the 1985–1995 period and the 2007–2013 period (Tukey–Kramer test; 95% CI = 178.41 – 455.0, $p < 0.001$). Similarly, the distance to 15% sea-ice concentration increased by 108 km from 1985–1995 to 1996–2006 (Tukey–Kramer test; 95% CI = 18.20 – 198.4, $p = 0.016$). We did not find a difference in the average distance to 15% sea-ice concentration between 1996–2006 and 2007–2013 (Tukey–Kramer test; 95% CI = -16.95 – 210.9, $p = 0.106$); however, there was an increase of 205 km between 1985–1995 compared to 2007–2013 (Tukey–Kramer test; 95% CI = 91.33 – 319.2, $p < 0.001$).

The modeled odds of land denning were positively associated with the distance to 50% sea-ice concentration (binary logistic regression; $p = 0.009$) and 15% sea-ice concentration (binary logistic regression; $p = 0.029$) from the continental shelf (Fig. 1-4). For every 100 km increase in the distance to 50% sea-ice concentration, the modeled odds of denning on land increased on average by 31% (95% CI = 10% – 60%). For every 100 km increase in the distance to 15% sea-ice concentration, the predicted odds of denning on land increased by approximately 34% (95% CI = 4% – 66%). However, these modeled odds ratios were unable to account for

repeated individuals due to convergence issues.

Den substrate and summer location

There was a significant relationship between the substrate used by a bear prior to denning and the den substrate ($\chi^2 = 21.4$, $df = 1$, $p < 0.001$). All pregnant bears that spent ≥ 25 days on land prior to den entrance denned on land ($n = 14$). Among pregnant bears that did not spend at least 25 days on land prior to denning only 29 % denned on land ($n = 20$) while 71% remained on sea ice to den ($n = 49$). We were not able to account for repeated individuals by using generalized linear models due to the lack of variation in the den substrate of bears that summered on land (i.e., all bears that summered on land denned on sea ice).

A total of 29 individuals were tracked during more than one denning season. Of these, 21 bears were faithful to their original den substrate while the remaining 8 individuals used a different substrate during at least one denning season. A total of 5 bears transitioned from sea ice to land dens, while 3 bears changed from land to sea ice for maternal denning. Of those individuals that remained faithful to their original denning substrate, 11 were faithful to land and 10 maintained denning on pack ice.

DISCUSSION

The distance between retreating pack ice and coastal denning habitat is an important factor determining den substrate use by pregnant females in the SB. It has been suggested that increasing distances of sea ice from coastal areas, as indicated by the distance of sea-ice retreat off of the continental shelf, could preclude polar bears from reaching land-based denning areas (Stirling & Derocher 2012). However, our results suggest that in the SB, higher occurrences of land-based denning occur with greater distances of sea ice from the coast. This suggests that, thus far, polar bears in this region have not been precluded from reaching land-based dens by

sea-ice conditions and in fact are increasingly using land for denning when distances to the pack ice are greater. Concurrently, we found that bears that spent substantial time (≥ 25 days) on land prior to denning were also highly likely to den on land, whereas only 29% of those that remained on pack ice during the sea-ice minimum returned to coastal areas to den. Thus, substrate use by polar bears during summer and denning appear to be related in the SB. The influence of sea ice in determining summer habitat use is further supported by observations from aerial surveys in which the density of SB polar bears spotted along the coast during September and October was positively correlated with greater distances from the shore to pack-ice (Schliebe et al. 2008).

The lack of an observed increase in land-based denning between the three time periods in our study (1985–1995, 1996–2006, 2007–2013) may be a result of smaller sample sizes in the latter two time periods, reducing the power to detect differences in logistic regression estimates. After combining data collected 1996–2013 and comparing that period to 1985–1995, we found an increase in land-based denning similar to the findings of Fischbach et al. (2007). Low annual sample sizes (e.g., < 3 bears) precluded analyzing annual proportions as a continuous response variable using linear regression. Thus, relatively small increases in the frequency of land-based denning may not have been detectable in our grouped years of data. However, our observation that land-based denning was related to sea-ice conditions and projections for continued reductions in the minimum sea-ice extent (Serreze et al. 2007) suggest that terrestrial denning is likely to continue to increase in the future.

The role of sea-ice dynamics in determining den distribution likely varies by region due to differences in the availability of terrestrial denning habitat and the seasonal distribution of sea ice. In western Hudson Bay, northward shifts in maternal denning may have been in response to changing sea-ice conditions (Ramsay & Stirling 1990). Similarly, at Hopen Island near the

southern portion of the Svalbard archipelago in the Barents Sea, later arrival of sea ice has resulted in a lower density of dens, and in years with very late freeze-up, bears did not reach the island in time for denning (Derocher et al. 2011). However, bears were able to access terrestrial denning habitat at the higher latitudes of Svalbard. In contrast, land habitats in the SB are only available at the southern and eastern edges of their range, which limits denning options spatially.

The nutritional implications of pregnant polar bears summering and denning on land are unclear. Declines in body condition and reproduction have been observed and associated with sea-ice conditions in the SB, but the exact nutritional mechanism causing those declines has not been identified (Cherry et al. 2009, Rode et al. 2010a). In most locations throughout their range, polar bears summering onshore are unable to meet their energetic requirements by foraging on land and lose substantial body mass while onshore (Stirling et al. 2008, Rode et al. 2010b). In the SB, however, an increasing proportion of bears avoid fasting onshore during the open-water period by feeding on bowhead whale carcasses left from subsistence harvests (Schliebe et al. 2008, Rogers et al. 2015). Bears that summer on shore may also have first access to autumn hunting opportunities over the continental shelf due to the earlier formation of landfast ice (Schliebe et al. 2008). In contrast, individuals that remain on ice during late summer and autumn months are thought to have limited access to seals (Whiteman et al. 2015), which become more pelagic as open water increases (Harwood & Stirling 1992, Pomeroy 1997, Schliebe et al. 2008). The unique situation of marine foods being predictably available onshore in the SB means that increased land-based denning may or may not have the negative nutritional consequences for pregnant females that are expected elsewhere where such foods are not predictably available.

An increase in bears summering and denning on land in response to sea-ice declines could have implications for human-bear interactions. In northern Alaska, oil and gas

developments span approximately 200 km of the SB coast and are expected to expand (Amstrup et al. 2004b). Industrial activity typically peaks during winter months, minimizing effects on most wildlife and vegetation; however, these activities coincide with the maternal denning season (Durner et al. 2006). Denning females with altricial cubs are particularly susceptible to human disturbance (Linnell et al. 2000). While anecdotal evidence suggests that many bears can be tolerant of human activity near dens (Smith et al. 2007), avoidance of premature abandonment due to disturbance requires proactive management (Amstrup 1993).

In our study, 29 % of pregnant bears that summered on the sea-ice came to land to den. In years where the distance from the pack ice to the coast is large, travel to maternal denning areas may have substantial energetic costs. A rise in the number of bears attempting long-distance swims between pack ice and coastal areas has been documented in recent years (Durner et al. 2011, Pagano et al. 2012). While considered good swimmers, such attempts may increase risk of drowning due to fatigue or poor weather conditions (Monnett & Gleason 2006). However, even at the maximum distance of 579 km to 50% sea-ice concentration (394 km to 15% sea-ice concentration) which occurred in 2009, three individuals in our study were able to reach land to den after having spent the summer on pack ice. Meanwhile, females that remain on sea ice to den may be exposed to more dynamic movements of pack ice, increasing the chances of premature abandonment and cub mortality (Derocher et al. 2004). The energetic and reproductive tradeoffs between reaching land to den versus remaining on ice in low ice years are not well understood.

Climate change is affecting land and ice habitats differently, and could be a factor affecting den site suitability and the observed increases in land-based denning by SB polar bears. For example, while snowfall is projected to decline on sea ice, it is expected to increase on land

(Martin et al. 2009, Hezel et al. 2012), potentially making land preferable for polar bear denning. In northern Alaska, denning females typically select habitat features that include coastal bluffs and river banks where prevailing winds drift sufficient snow for den construction (Durner et al. 2001). However, recent increases in open water have dramatically increased erosion along shorelines in the SB. This is especially true for steep coastal bluffs where the majority of polar bears den (Jorgenson & Brown 2005, Durner et al. 2006). If reductions in multi-year ice continue, the suitability of terrestrial denning habitat may become increasingly important. Fidelity to denning areas and den substrate has been documented in SB polar bears (Amstrup & Gardner 1994). However, of bears followed for multiple years in our study, 31% changed denning substrate at least once. Such observations of behavioral plasticity may be significant in a warming Arctic. If preferred denning areas become unsuitable or inaccessible, bears are likely to change den substrates between denning attempts, provided that alternative habitat is spatially and temporally available (Zeyl et al. 2010).

We found that control charts using temperature were reliable in identifying denning behavior in polar bears. These charts provided a consistent and automated method to remotely identify denning bears with relatively high accuracy although some limitations exist. Of 75 identified dens confirmed visually via VHF radio tracking, 4 could not be classified using our approach due to insufficient sample sizes. Of these, one appeared to be missing all observations during the denning period, likely due to signal degradation, while another bear-winter had too few observations to effectively fit an intercept for the centerline. Filtering out bear-winters due to such issues is necessary because gaps and sparse observations are not uncommon in our satellite collected telemetry data. The remaining two bear-winters did exhibit consecutive bouts of raised temperatures, but did not meet the minimum duration requirement (>34 d) to be

considered maternal dens in our algorithm. Observations from VHF data indicated that these two bears denned for approximately 44 and 34 days. While positively identified as dens, their short durations suggest they likely aborted denning.

Short denning events can be identified via control charts, but since our classifications were based generally on extended periods of warm temperatures, separate criteria would be needed to generate control limits that allow for shorter denning periods while still distinguishing between normal variation found in non-denning bears. Disagreements between our den classifications and those by Fischbach et al. (2007) were mostly bear-winters they considered non-denning that were classified as denning by our algorithm. Generally these were also shorter duration events, some of which did not have a clear contrast between denning and non-denning temperatures. In such cases, an objective algorithm such as presented here may provide added consistency in identifying denning bouts of short duration, provided that adequate data are available. These shorter duration denning bouts may be of importance in monitoring polar bear reproduction. We are aware of at least one female that denned no longer than 50 days and produced two cubs (USGS unpublished data).

Summer sea-ice cover in the Arctic is projected to continue to decline, and may ultimately lead to a seasonally ice-free Arctic Ocean (Holland et al. 2006, Serreze et al. 2007). As open water between land and the remaining ice increases, more pregnant bears in the SB are likely to move towards the coast in search of suitable habitat for maternal denning. Moreover, these bears may arrive earlier and remain on land longer than has been observed historically, choosing to summer on land rather than on pack ice. The implications of increased denning on land for polar bear survival and reproduction are difficult to predict and should be addressed in future studies. However, an increased potential for human-bear interactions is likely to

accompany increased denning on land. Policies and measures to guard against the disturbance of polar bears will likely become more important as a greater proportion of females rely on terrestrial habitat for maternal denning.

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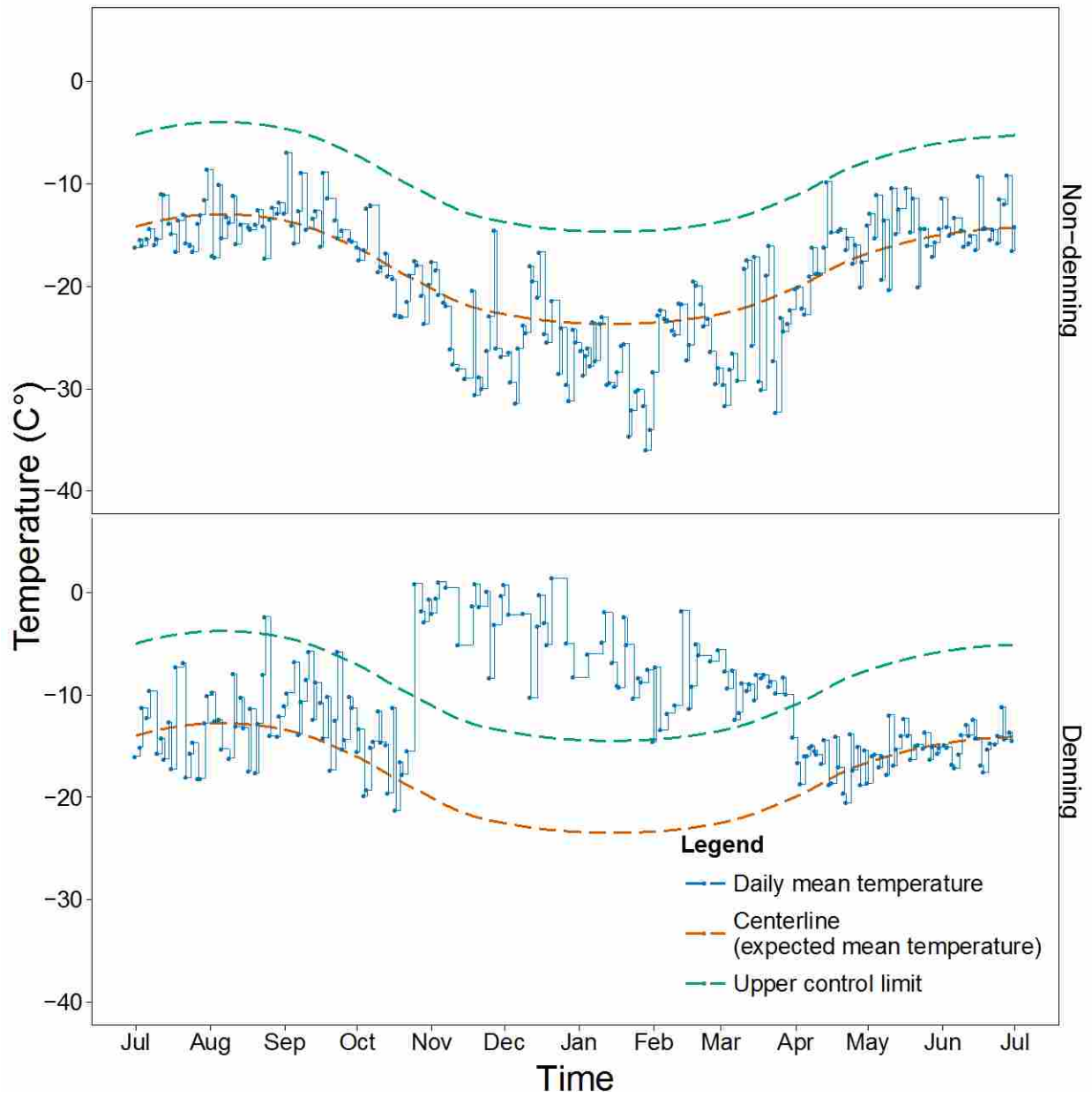


Figure 1-1. Example control charts of temperatures from both denning and non-denning polar bears in the southern Beaufort Sea. Daily mean temperatures were measured by thermistors onboard satellite collars. Expected mean temperatures and upper control limits were calculated using data from 109 non-denning females. Consecutive observations above the upper control line with a duration of >34 days were considered denning events.

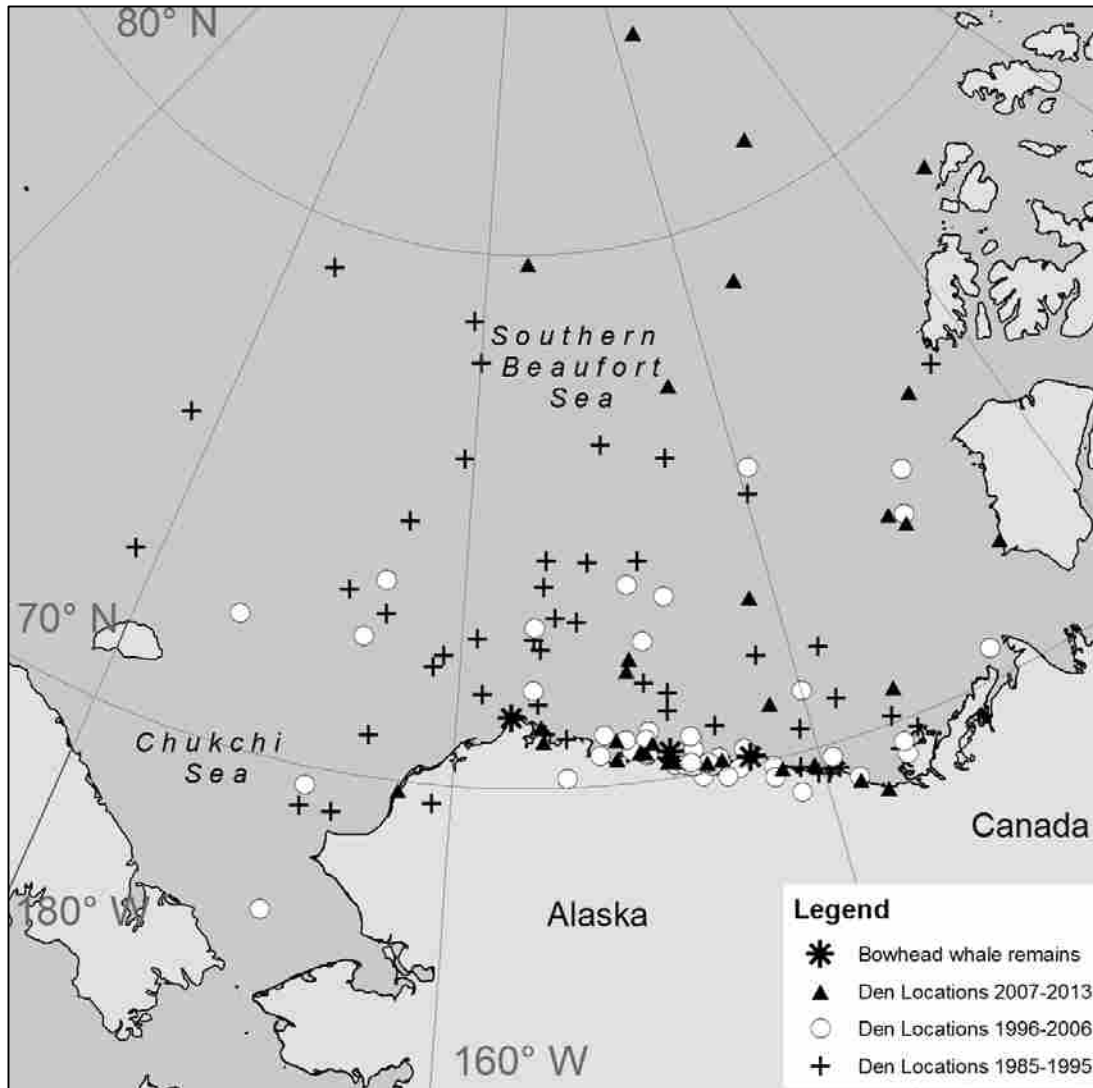


Figure 1-2. Denning locations of female polar bears in the southern Beaufort Sea between 1985 and 2013. Denning was identified based on temperature data from radio collars.

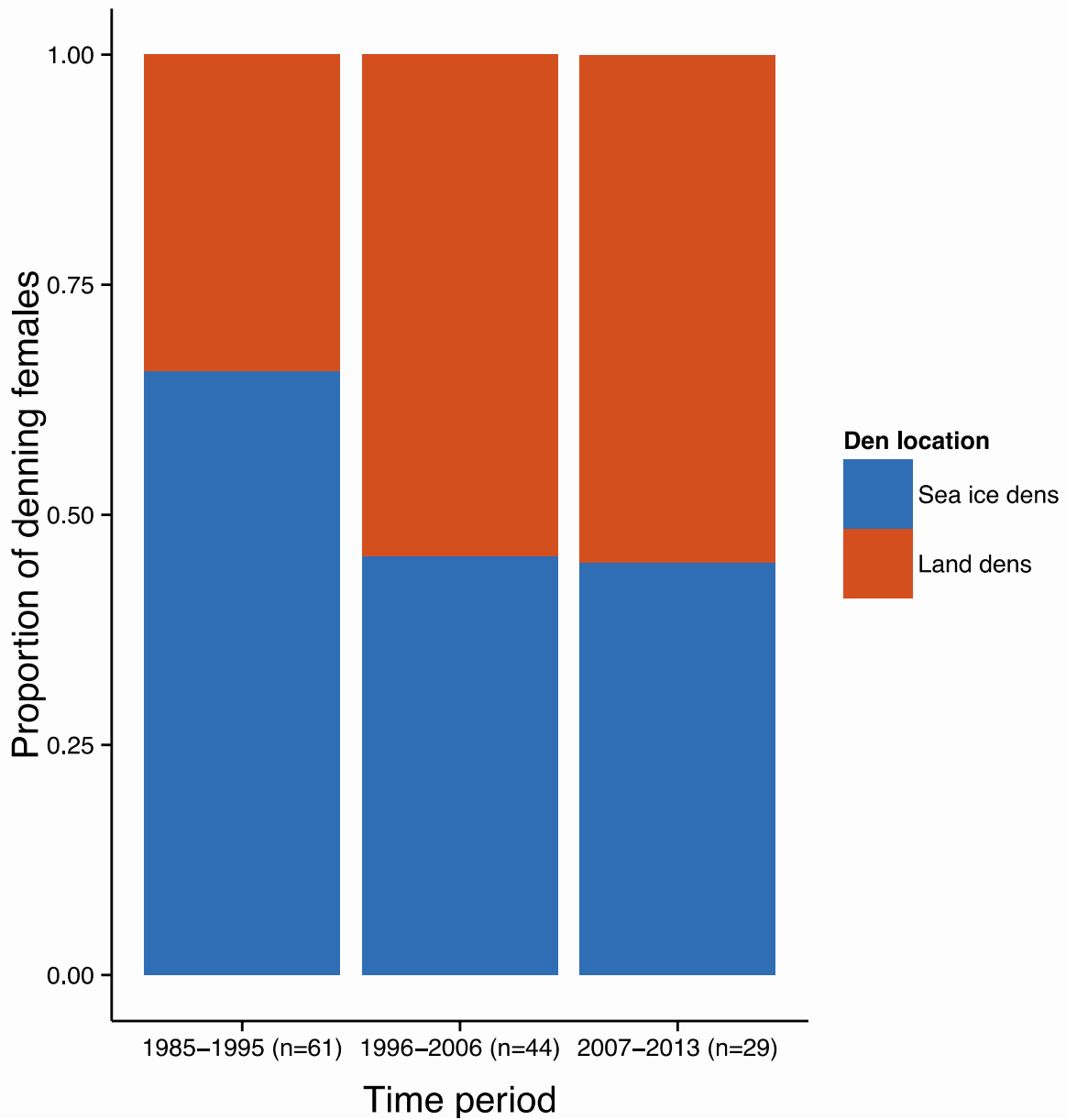


Figure 1-3. Percentage of bears denning on sea ice or land as measured over three time periods.

Substrate use did not differ between the three periods, but did differ between the early time period and the two latter time periods combined.

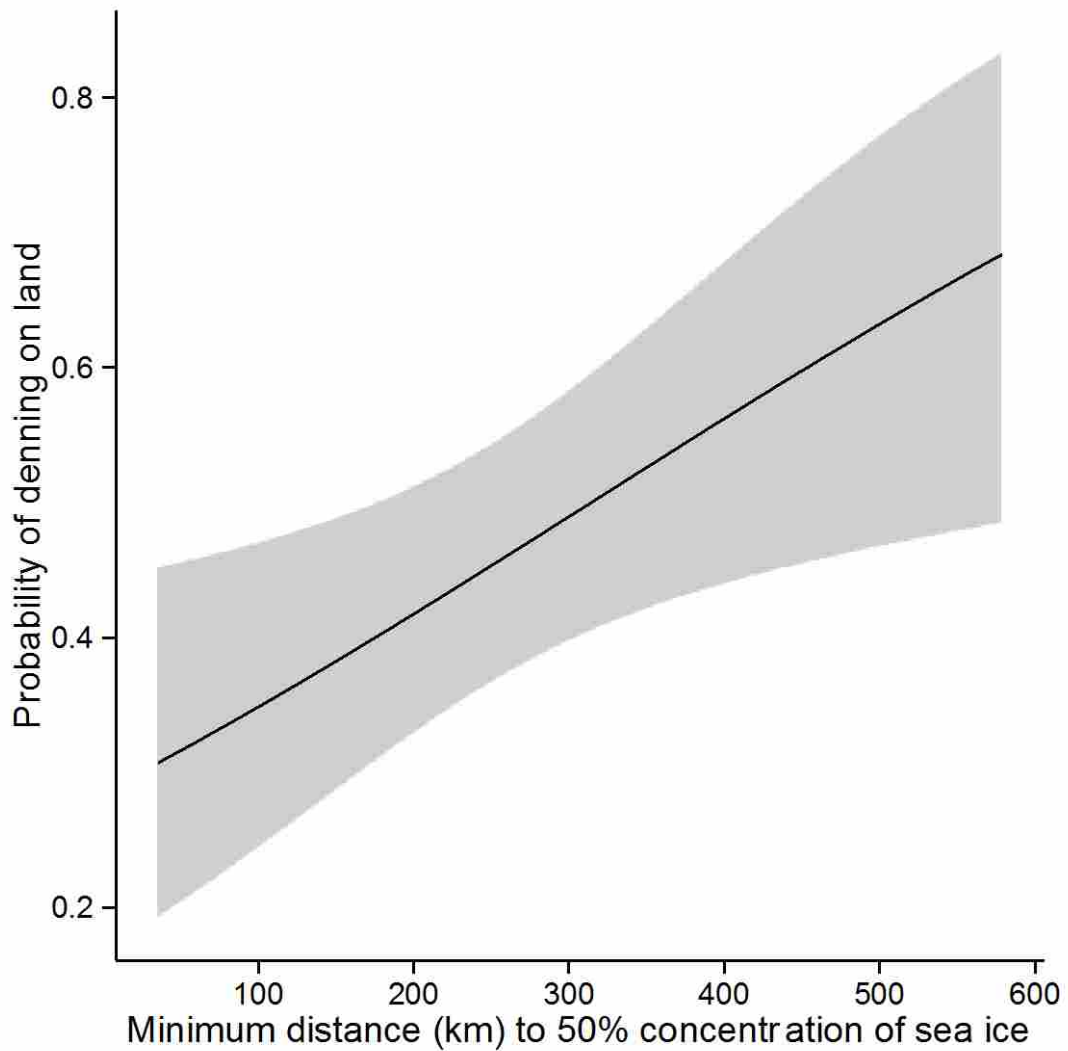


Figure 1-4. Relationship between the probability of denning on land and the minimum distance between the continental shelf break (300m) to sea ice of 50% concentration as determined from a binary, logistic regression.

CHAPTER 2
POLAR BEAR DENNING PHENOLOGY IN THE SOUTHERN BEAUFORT
AND CHUKCHI SEAS

ABSTRACT

Climate change can affect the phenology of important life history traits, especially in the marine Arctic where species respond to the seasonal dynamics of sea ice. For polar bears (*Ursus maritimus*), loss of sea ice may affect the phenology of maternal denning by altering access to denning habitats. While the seasonal timing of denning is considered an important aspect of polar bear reproduction, its relative role in cub survival is not well understood. We developed an algorithm based on statistical process control methods to remotely identify denning bears and estimate denning phenology from temperature sensor data collected on collars deployed 1985–2013 in the southern Beaufort (SB) and Chukchi seas (CS). We evaluated cub survival relative to den entrance, emergence, and duration, and examined differences in the timing of land and sea-ice dens. We then related the timing of denning to minimum sea-ice extent in autumn. Den entrance and duration in the SB and CS were similar, although CS bears emerged later. Land dens were occupied longer than those on ice. Bears later observed with cubs remained in dens 23 days longer and emerged from denning 17 days later on average than bears that denned but were subsequently observed without cubs, suggesting that den exit dates are related to cub survival. However, we found no correlation between denning phenology and changes in minimum sea-ice extent.

INTRODUCTION

Climate change has been associated with changes in the phenology of numerous species (Parmesan & Yohe 2003). Warming temperatures are correlated with advances in spring events,

particularly at higher latitudes, with examples that include earlier bud burst, flowering, breaking hibernation, migrating, and breeding (Parmesan 2006). Changes in phenology can disrupt tight trophic coupling (i.e., mutualistic or feeding interactions) when resources become available at the wrong time or place (Sydeman & Bograd 2009). Such trophic asynchrony can have population level effects by reducing foraging efficiency, ultimately affecting reproductive success (Sydeman & Bograd 2009).

As a marine mammal in the Arctic, the polar bear (*Ursus maritimus*) has experienced dramatic losses in sea-ice habitat due to climate warming (Derocher et al. 2004, Stirling & Derocher 2012). Changes in the distribution, characteristics, and timing of sea ice have been associated with changes in habitat use (Fischbach et al. 2007, Schliebe et al. 2008, Durner et al. 2009), increased fasting, (Cherry et al. 2009), poor body condition (Stirling et al. 1999, Stirling & Parkinson 2006, Regehr et al. 2007, Rode et al. 2012), decreased recruitment and litter mass, (Regehr et al. 2006, Rode et al. 2010), and population reductions (Regehr et al. 2007, Regehr et al. 2010, Bromaghin et al. 2015). However, these effects may vary greatly over the geographic range of the polar bear due to regional differences in environment making it difficult to form predictions about the effects of reduced sea ice that apply generally to populations (Amstrup et al. 2008, Rode et al. 2014). Thus, monitoring the phenology of important life history events between populations may yield greater understanding about proximate effects of reduced sea ice.

For polar bears, maternal denning is a seasonal behavior (Lentfer & Hensel 1980, Blix & Lentfer 1992) in which timing has important reproductive consequences (Messier et al. 1994, Friebe et al. 2014). Den entrance occurs in the fall when many female bears reach peak condition and as seals become less available (Blix & Lentfer 1979, Durner et al. 2009). For bears that use pack ice as refugia during the summer melt, returning sea ice in autumn provides access to

terrestrial denning areas (Derocher et al. 2004). Like other ursids, polar bear cubs are born as altricial neonates (Ramsay & Dunbrack 1986, Messier et al. 1994). Subnivean dens provide relative protection from the harsh Arctic winter while mothers nurse their young until large enough to venture onto the sea ice (Lentfer & Hensel 1980, Ramsay & Dunbrack 1986). Den emergence in the spring is synchronized with the onset of seal pupping, providing the greatest availability of prey for polar bear mothers while meeting the high energetic demands of lactation (Stirling 2002, Molnar et al. 2011).

Like most carnivores, polar bears exhibit embryonic diapause (delayed implantation) in which blastocysts do not immediately attach to the uterine wall but instead remain free in a state of dormancy in the uterus lumen (Sandell 1990). This reproductive strategy uncouples parturition from the mating season, allowing for greater flexibility in the timing of reproduction (Friebe et al. 2014). Studies conducted in captive and wild bears have suggested that the timing of implantation, as well as subsequent denning and parturition, may vary in response to environmental conditions (Robbins et al. 2012a). Changes in denning phenology may indicate a behavioral response to common sources of environmental variation (Linnell 2000) or to dramatic shifts in climate occurring throughout the circumpolar Arctic (Molnar et al. 2011).

In the southern Beaufort (SB) and Chukchi seas (CS), declines in sea-ice extent may be altering the availability of and access to denning habitats. In the CS, increased land-use by pregnant polar bears was related to declines in fall sea-ice extent (Rode et al. 2015), while in the SB declines in multiyear ice has been correlated with a shift away from denning on pack ice towards an increase in land denning (Fischbach et al. 2007). How such changes may affect the timing and duration of maternal denning is unclear.

Although the timing of maternal denning is likely an important aspect in polar bear

reproduction, its relative importance in cub production and survival have not been studied. While it is thought that cubs must spend > 2 months in a den in order to survive on the ice (Amstrup 1993), baseline data on the time required in a den to successfully produce cubs are not available. In this study we developed a method to estimate maternal denning phenology of polar bears using 28 years of available data. Our goals were to 1) examine the role of denning phenology in cub survival, 2) compare denning phenology of two adjacent, yet ecologically distinct populations (i.e., the Southern Beaufort and Chukchi Sea), 3) compare the denning phenology of land and sea-ice dens, and 4) examine the potential influence of retreating sea ice on the timing of denning.

METHODS

Study Area

The SB subpopulation consists of approximately 900 polar bears (Bromaghin et al. 2015). Thought to have been overharvested before coming under the protection of the U.S. Marine Mammals Protection Act in 1972 (Amstrup et al. 1986), the subpopulation increased through the 1990s (Amstrup et al. 2001). Recently, however, population declines have been associated with longer ice-free periods over the continental shelf (Ramsay & Stirling 1990, Regehr et al. 2010). In addition, increased fasting (Cherry et al. 2009), unusual predation attempts (Stirling et al. 2008), reduced body condition, and low cub recruitment (Rode et al. 2010) have been observed in SB polar bears. The SB has a relatively narrow continental shelf that declines steeply into deep waters over the Arctic Ocean (Jakobsson et al. 2008). The region is covered by annual ice from October through June and retreats north towards the polar basin in July through September (Comiso 2006, Hunter et al. 2010). Historically, many females in the SB denned on drifting pack ice while others denned at low concentrations along the coast of Alaska and Canada

(Amstrup & Gardner 1994); however, recent observations suggest denning may be shifting landward (Fischbach et al. 2007). Increasing densities of bears have been spotted along the coast during summer and autumn (Schliebe et al. 2008).

Reliable estimates of population dynamics are not available for bears in the CS (Rode et al. 2014). The region rests almost entirely over an expansive continental shelf of shallow water (<300m) in which sea-ice habitat has historically been available even during the annual sea-ice minimum (Douglas 2010). While the CS has experienced some of the greatest loss in optimal sea-ice habitat (Durner et al. 2009), polar bears have not exhibited reduced body condition or recruitment as seen in the SB (Rode et al. 2014). This may be in part due to high levels of primary productivity, greater prey diversity, or differences in the timing of sea-ice loss (Rode et al. 2014). Most maternal denning in the CS occurs in relatively high density, terrestrial habitats, namely along the Chukotkan coast and Wrangel and Herald Islands (Uspenski & Kistchinski 1972, Rode et al. 2015).

Polar bear capture and collaring

Bears were captured on the sea ice during spring (mid-March to mid-May) and occasionally during autumn (August to November) in the Alaska portion of the SB during most years 1985–2013. Captures occurred in the CS and northern Bering Seas 1986–1995 and 2008–2013 on or near Wrangel Island, Herald Island, the Alaskan mainland coast, St. Lawrence Island, Alaska, and the northeast Chukotkan coast. Bears were located via helicopter and immobilized with a rapid injection dart (Palmer Cap-Chur Equipment, Douglasville, Georgia, USA) containing either zolazepam-tiletamine (Telazol[®] or Zoletil[®]) (Stirling et al. 1989) 1987–2013, or Sernylan, M-99, or phencyclidine prior to 1987. A subset of adult females in the SB were fitted with platform transmittal terminal (PTT) satellite radio collars (Telonics, Inc., Mesa, AZ) 1985–

2013, except during 1993–1997 and 2010. In the CS, adult females were fit with collars 1986–1995 and 2008–2013, except 2012. These PTTs transmitted an ultra-high frequency (UHF) signal to polar orbiting satellites through an antenna located lateral to the neck of the bear. Beginning in 2004 we began collecting locations using transmitters that collected GPS locations every 4 hours. Temperature was measured by a thermistor inside the radio collar. Though warmed by the body temperature of a collared bear, these temperatures generally tracked ambient conditions (Fischbach et al. 2007). PTTs were equipped with a very high frequency (VHF) beacon to allow for radiotracking via aircraft by personnel in the field.

Classifying denning behavior and estimating denning phenology

Because polar bears frequently den in remote areas, the use of conventional den-monitoring techniques (i.e., radiotelemetry or direct observation) to estimate den entrance and emergence is logistically challenging and cost-prohibitive (Fischbach et al. 2007). Additionally, since many bears den on moving pack ice, dens cannot be reliably identified by consecutive, stationary locations. As such, we used statistical process control methods to remotely identify maternal denning behavior in polar bears using temperature sensor data. Annual temperature records (hereafter referred to as a bear-winter) from bears with known denning statuses were used to develop control chart limits of expected variation for non-denning females during winter months. For previously unclassified bear-winters, bouts of warm temperatures that remained above the expected upper limit for an extended period (>34 consecutive days) were considered a maternal denning event. For further details on the classification of denning behavior, see Olson et al. (2015).

Estimates of den entry, emergence, and duration were based on control charts of denning behavior. In bear-winters positively identified as denning, we defined den entrance as the

median between the last temperature observation within control limits and the first observation above control limits. Similarly, den emergence was estimated as the median between the last observation above control limits and the first observation to return within control limits. The total den duration was defined as the number of days between den entrance and emergence (Fig. 2-1). Because these estimates were based on consistent changes in expected temperature, we hypothesized that entrance estimates made using control charts likely represent the point at which a female bear enters a den and remains thermally protected from the elements. Similarly, we expected den emergence to represent the transition at which a bear emerges from a den and is frequently exposed to the elements. While this method did not estimate the arrival at or departure from a den site, it provided a standardized metric in which to compare denning phenology.

Validation of denning phenology estimates

We validated control chart estimates of denning phenology (i.e., den entrance, emergence, and duration) by comparing them to estimates of arrival at and departure from the densite using locational data. Only land-based dens were used to estimate arrival and departure dates because dens on sea ice are continually in motion and difficult to detect using locations. Prior to 2010, all radio collar locations were determined by the Argos system with accuracy from < 250 m to > 1500 m (see <http://www.argos-system.org/web/en/78-faq.php#faq-theme-55>) with sampling every one to three days. These location data were filtered to remove implausible locations using the Douglas Argos-Filter algorithm (Douglas et al. 2012), which retained all standard quality class locations (classes 3, 2, and 1), rejected all class Z locations, and retained auxiliary class locations (0, A, and B) if they were corroborated by a consecutive location within 10 km, or if movement rates were <10 km hr⁻¹ and turning angles were not extremely acute.

Instances of dropped collars were identified based on activity and temperature sensors and data collected post-drop were removed.

We used the “Optimized Hot Spot Analysis” tool in ESRI® ArcToolbox (Version 10.3; ESRI Inc., Redlands, CA, USA) to identify statistically significant clusters of temporally consecutive locations for individual bears. For some bear locations, this tool could not identify clustered locations, in which case we manually identified them. Clusters were considered den sites if they occurred during potential denning months (October–May), the majority of locations fell within a radius of approximately 30 m for GPS locations and 15 km for Argos locations, and the total duration was >34 days. Arrival at the den site was estimated as the median date between the location prior to arrival at the den site and the first location at the den site. Similarly, abandonment of the den was estimated as the median date between the last location at the den site and the first location that moved away from the den site cluster and did not return.

Identifying den substrate: sea ice versus terrestrial habitats

Den substrate was determined using GPS and Argos locations that occurred during denning periods identified by our control chart algorithm. Dens occurring within 5km of land as identified by the Global Self-consistent, Hierarchical, High-resolution, Geographic Database (GSHHG version 2.3.4; <http://www.soest.hawaii.edu/pwessel/gshhg/>) were classified as land dens, while dens beyond this buffer were classified as occurring on sea ice. The 5 km buffer was used to encompass small barrier islands that are frequently used as denning habitats (Schliebe et al. 2008), but were not depicted as land in the GSHHG, and to account for low accuracy of some locations. Because the physical features of dens in snow banks often attenuate transmission, location data were frequently unavailable or of low quality during the denning period. If at least one observed location at the start of, during, or at the end of the denning period occurred on land

or immediately adjacent to land, it was assumed that the den occurred on land.

Assessing reproductive outcomes

Females that attempted denning, as determined using our temperature algorithm, were considered to have emerged with cubs if they were subsequently observed with cubs-of-the-year (COY, <12 months old) or dependent young (2-year olds) within 2 years of a denning attempt. Individuals that denned but were observed without dependent cubs in the 2 years following a denning attempt were assumed to have suffered whole-litter-loss or aborted reproduction. Observations were conducted via VHF radiotracking during ongoing mark-recapture efforts. Time between denning and subsequent observation or recapture may have influenced observations of reproductive outcomes since COY are subject to high mortality rates after den emergence. Thus, we measured the number of days between den initiation and subsequent observation of females to see if this had an effect on the observation of cubs

Identifying subpopulations

Subpopulation classifications were based on the designated boundaries established by the International Union for Conservation of Nature (ICUN) Polar Bear Specialist Group (PBSG). Individuals were assigned to the subpopulation in which the majority of their locations occurred. Bears with <60% of locations within the boundaries of a single subpopulation were give a dual designation, listing the subpopulation with highest proportion of locations first. However, the PBSG's northern boundaries for these subpopulations exclude large portions of the Arctic Basin commonly used by bears in the SB and CS. Therefore, if a majority of a bear's locations occurred in the area identified as the Arctic basin subpopulation boundary, they were assigned to either the SB or CS subpopulation if the remainder of their locations occurred primarily in one of those two subpopulation boundaries. Only bears with a single designation in either the SB or CS

were used in analyses that included subpopulation. Bears with primary designations outside of the SB and CS were excluded from analysis.

Estimating sea-ice metrics

We related denning phenology to minimum sea-ice extent in September prior to denning. While most bears enter dens after September, the degree of sea-ice retreat likely affects the timing of ice return to coastal areas, and may influence access to terrestrial denning habitats. We used two metrics of sea-ice availability developed by Rode et al. (2014) using 25×25 km resolution passive microwave satellite imagery (Cavalieri et al. 1996). First, we used the mean daily minimum distance (hereafter referred to as “distance”) from the edge of the continental shelf (300 m isobath) to the edge of the pack ice during the typical sea-ice minimum (i.e., the month of September). Second, we used the number of reduced ice days per year (number of days where sea ice over the continental shelf was $<6250 \text{ km}^2$) as a measure of habitat availability. Since polar bears often select for $\sim 50\%$ sea-ice concentration during summer (Durner et al. 2009), but have been found to use ice as low as 15% concentration (Durner et al. 2006; Cherry et al. 2013), both distance to pack ice and reduced ice days were measured to these sea-ice concentrations. These metrics were used because they are indicative of likely annual trends in the availability of summer and autumn sea ice for bears and therefore, potential impacts of habitat availability on denning phenology. For more details on the methods used to generate sea-ice metrics, see Rode et al. (2014).

Statistical analysis

Paired *t*-tests were used to compare dates of den arrival and departure at the den site to estimates of den entrance and emergence estimated using temperature data. We used a multiple linear regression model to estimate the effects of subpopulation and substrate on denning

phenology (i.e., den entrance, emergence, and duration). Binary, logistic regression was used to test for an effect of time between den entrance and subsequent observation on reproductive outcomes. We compared estimates of denning phenology for bears observed with and without cubs using two-sample *t*-tests and Welch's two-sample *t*-test. Simple linear regression was used to analyze the relationship between denning phenology and sea-ice metrics. A Bonferroni adjustment was used to account for multiple comparisons. Statistical significance was set at $\alpha \leq 0.05$. The Olson et al. (2015) algorithm for identifying denning behavior utilized SAS/STAT[®] software. All other statistical analyses were performed using program R version 3.0.3 (R Development Core Team 2014).

RESULTS

We applied the Olson et al. (2015) algorithm for den behavior classification to 577 bear-winters for which temperature sensor data was collected from polar bears in the SB and CS. We classified 212 bears to the CS subpopulation and 351 bears to the SB. The remaining 14 individuals split time between these two areas and could not be classified to a single subpopulation. We removed 104 bear-winters from analysis due to insufficient data. Of the remaining 473 records, we classified 218 bear-winters as denning and 255 as non-denning based on the control chart algorithm. We were able to classify den substrate for 193 bear-winters. Of these, 86 dens occurred on pack ice, while 107 bears denned on or immediately adjacent to land. Reproductive outcomes were determined for 93 individuals. Of these, 65% of bears were observed after denning with cubs, while 35% were next observed without cubs. Bears were generally observed or recaptured in the spring following den emergence, on average 196 ± 108 days after den entrance, though this varied significantly (RANGE 51–599). The number of days between den entrance and subsequent observation had no effect on reproductive outcomes

(binary logistic regression; $\beta = -0.002 \pm 0.002$, $p = 0.459$), thus we did not include it in other analyses of reproductive outcomes.

We calculated arrival and departure from den sites for 32 dens occurring on land and compared these dates to paired entrance and emergence estimates from our control chart algorithm. On average, temperature estimates of den entrance were 6.4 days later than estimates of den site arrival made using location data; however, this difference was not statistically significant (paired t -test: 95% CI: -14.3–1.6, $t = -1.6$ days, $df = 33$, $p = 0.113$). Temperature estimates of den emergence were approximately 7.7 days earlier than estimates of den site abandonment generated using location data (paired t -test: 95 CI: 3.1–12.2, $t = 3.4$ days, $df = 33$, $p = 0.002$).

The mean den entrance for all bears was 15 November \pm 28 SD ($n = 215$). On average, bears emerged from dens 1 March \pm 28 SD ($n = 179$), with a total average duration of 105 days \pm 37 SD ($n = 179$). After accounting for the effects of den substrate, we found no difference in the entrance dates between SB and CS bears (multiple linear regression; $\beta = 4.54 \pm 4.49$ SE, $p = 0.313$). However, CS bears emerged from dens on average 10 days later than SB bears (multiple linear regression; $\beta = 9.64 \pm 4.60$ SE, $p = 0.038$). Overall, there was no difference in the total number of days spent in den by SB and CS bears (multiple linear regression; $\beta = 2.86 \pm 6.28$ SE, $p = 0.649$; Table 2-1).

After accounting for the subpopulation effects, comparisons of land and sea-ice dens showed no difference in dates of den entrance (multiple linear regression; $\beta = -5.74 \pm 4.18$, $p = 0.172$) or emergence (multiple linear regression; $\beta = 6.80 \pm 4.15$ SE, $p = 0.104$). However, land denning bears spent an average of 13 days longer in dens than bears denning on ice (multiple linear regression; $\beta = 13.44 \pm 5.68$ SE, $p = 0.019$; Table 2-1).

We observed no difference in den entrance dates between bears that successfully emerged from dens with cubs and those that were observed without cubs (Welch two-sample t -test: $t = 0.39$, $df = 49$, $p = 0.696$). However, bears observed with cubs emerged 17 days (95% CI: 7–28 days) later on average than females without cubs (two-sample t -test: $t = -3.3$, $df = 80$, $p = 0.001$) and had an overall greater denning duration (two-sample t -test: $t = -3.3$, $df = 80$, $p = 0.001$), spending an average of 23 days (95% CI: 9–38 days) longer in den than bears observed without cubs (Table 2-2).

In the SB and CS, the mean distance from the continental shelf to sea ice and the number of reduced ice days per year in September increased between 1985–2013 at 15% and 50% concentrations of ice (Fig. 2-2). However, we found no correlation between reduced ice days and estimates of den entrance, emergence, or duration (simple linear regression; $p > 0.05$ for all tests). Similarly, there was no correlation between denning phenology estimates and the mean daily minimum distance to 15% or 50% sea-ice concentrations (simple linear regression; $p > 0.05$ for all tests).

DISCUSSION

Control charts provided a useful tool for estimating the denning phenology of polar bears. Our temperature estimates of den entrance and emergence followed expected patterns relative to estimates of den arrival and departure made using locations of land-based bears. Though these two methods did not estimate the same behaviors, the close association suggests that estimates of entry and emergence from temperature data were biologically relevant. A few individuals had much greater differences between the two types of estimates (0–52 days). Some of this variation in phenology estimates may be caused by gaps in observations that were more likely to occur during denning due to attenuated Argos/GPS signals. Since we determined entrance and

emergence dates using the median between observations within and above control parameters, large gaps during denning may bias our estimates towards shorter denning durations. In a few cases, very early arrivals suggest that bears may have summered onshore near the future den site. Because of the variability in Argos location accuracy, over-summering events were difficult to distinguish from maternal denning. Given the similarity in estimates using both temperature and satellite location methods, we suspect that these effects were relatively limited in our sample of bear dens.

Our temperature-based estimates of den entry in the SB were similar to observations made by Amstrup and Gardner (1994) via VHF radiotracking and qualitative estimates of den occupation based on temperature and activity, with den entrances occurring mid-November. However, our den emergence dates were substantially earlier (4–33 days) than those reported by Amstrup and Gardner (1994). Differences may be due in part to the distinct classification methods. After initial emergence from the den, family groups may remain at the den for a time before departing to foraging areas (Smith et al. 2007). Emergence, as identified by temperature sensor data, likely represents the opening of the den cavity and increasing exposure to ambient temperatures, while methods based on location data mark the departure from the den site. This distinction is supported by our finding that temperature-based emergence occurred 7 days earlier on average than paired estimates of den site abandonment from location data.

Our study emphasizes the importance of den duration in successful cub production. While pregnant bears generally entered dens on similar dates, longer denning duration and later den emergence was associated with cub production and survival post-emergence while shorter denning was correlated with whole litter loss sometime within the first 2 years. The factors that cause shortened denning events are not well understood, but there are a number of potential

causes.

Maternal condition is an important factor affecting cub production (Robbins et al. 2012a, b) and therefore may similarly be an important factor in determining the length of denning. Females must accrue sufficient fat stores to produce cubs and lactate while fasting for extended periods up to eight months (Ramsay & Dunbrack 1986, Atkinson & Ramsay 1995). Females with inadequate reserves may cease lactation and abandon cubs in dens in order to ensure their own survival (Derocher et al. 1993, Rode et al. 2010, Robbins et al. 2012b). Robbins et al. (2012b) found that female grizzly bears with <20% body fat did not produce cubs. Further, female condition influences cub survival post-birth. In a randomized study that manipulated feeding, Robbins et al. (2012b) found that brown bears with higher maternal fat content gave birth earlier to faster growing cubs than thinner females. Cub litter mass in polar bears is strongly correlated with maternal fat content in summer/autumn; with fatter females producing larger cubs (Atkinson & Ramsay 1995, Robbins et al. 2012a). Additionally, cub mass appears to be the dominant factor influencing COY survival in the spring and autumn as larger cubs have greater fat reserves, are less susceptible to heat loss, and are better equipped to travel long distances to areas with high prey abundance (Derocher & Stirling 1996). Thus, denning phenology may be indicative of a female's condition and ability to fast for the duration required to produce cubs that ultimately are fit enough to survival post-emergence. Other factors that could affect denning phenology such as predation and human disturbance are either rare or not widely reported (Amstrup 1993; Amstrup et al. 2006).

On average, polar bears in our study that were observed without cubs after denning emerged in the latter half of February. Ringed seal pups, born in late March to early April (Smith 1987), are largely not available at this time, creating a potential trophic mismatch for

newly emerged family groups and peak food availability (Molnar et al. 2011). Polar bears are at their lightest in March and depend on successful hunting of seals during the spring pupping season to build fat reserves that will sustain them throughout the year (Stirling & Oritsland 1995). For bears that emerged earlier, relatively poor foraging opportunities may have contributed whole litter loss.

Because longer denning and later den emergence was associated with the presence of cubs post-denning, observed differences in phenology between study populations and den substrates could be associated with differential reproductive success. The later den emergence of CS bears compared to SB bears (approx. 10 days) may influence cub survival, which has been documented to be higher in the CS than in the SB (Rode et al. 2014). Further, land denning, which was also associated with longer den duration compared to ice denning (approx. 13 days), is more common in the CS (Rode et al. 2014) compared to the SB (Olson et al. 2015). This longer duration of land-based dens is interesting in light of observed shifts towards land denning in the SB (Fischbach et al. 2007). While we observed some differences in denning phenology by population and substrate, the large degree of variability in our estimates, partially a result of temporal gaps in observations, may obscure some differences in the timing of denning.

Relatively similar den entrance and emergence dates between subpopulations and substrates suggest the influence of a common factor regulating den phenology such as latitude or photoperiod. Such patterns were reported in the Canadian High Arctic and Greenland, where later den entrance was associated with higher latitudes (Ferguson et al. 2000), and are widely reported for other Holarctic bear species (Linnell 2000). Other sources of variation in the denning phenology may include snow accumulation (Amstrup & Gardner 1994), the consolidation of pack ice sufficiently stable for denning (Amstrup & Gardner 1994, Rozhnov et

al. 2014), food availability (Johnson & Pelton 1980, Linnell 2000), age class (Baldwin & Bender 2010), and maternal condition (Robbins et al. 2012a, Friebe et al. 2014).

We hypothesized that reductions in minimum sea-ice extent over time might lead to changes in denning phenology. However, we found no evidence that polar bears in the SB or CS have responded to longer ice free-periods by changing the timing of denning and reproduction. Rather than alter the timing of maternal denning in response to changes in the seasonal melt of pack ice, polar bears may be more likely to change patterns of habitat use such that timing of denning remains relatively constant. Northward shifts in maternal denning in the western Hudson Bay were thought to be a result of changes in sea ice (Ramsay & Stirling 1990). Similarly, later arrival of sea ice at Hopen Island in the southern portion of the Svalbard archipelago resulted in lower density of maternal dens and sometimes precluded bears from denning altogether (Derocher et al. 2011). In the CS, the distribution of dens has largely shifted northward to coastlines with later dates of sea-ice retreat (Rode et al. 2015). In addition to these northward shifts, bears in several subpopulations have increased land-use during summer and fall months (Schliebe et al. 2008, Olson et al. 2015, Rode et al. 2015). In the SB, bears that summered on land were more likely to den on land (Olson et al. 2015). Such changes in habitat use may compensate for temporal shifts in the availability of or access to historic denning habitat.

Although polar bears have not demonstrated changes in denning phenology related to minimum sea-ice extent, they may yet be sensitive to such changes in the future. Bears that emerge prematurely from maternal dens due to insufficient fat reserves may be subject to poor foraging conditions and are at risk of whole litter loss. While changes in denning distribution and land use may compensate for changes in the timing of access to denning habitat, further sea-

ice retreat may strain maternal fat reserves. Continued shifts towards land-denning habitats farther north are ultimately limited by geography in the SB and CS (Rode et al. 2015). Additionally, as the distance between land and ice increases, accessing terrestrial denning areas from pack ice will become more energetically demanding (Bergen et al. 2007). If maternal condition continues to deteriorate in the SB, we could expect shorter denning durations, or more females forgoing reproduction.

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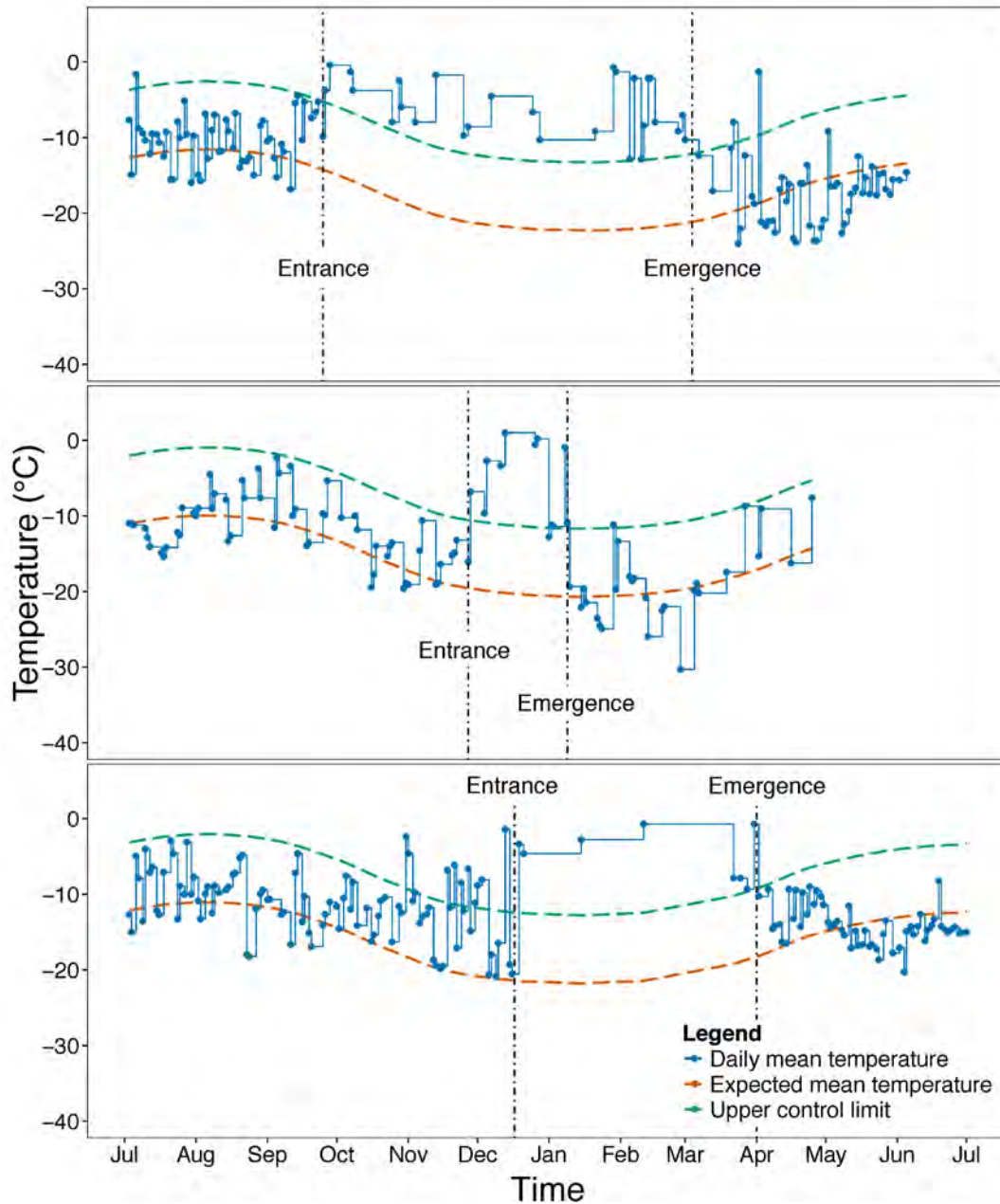
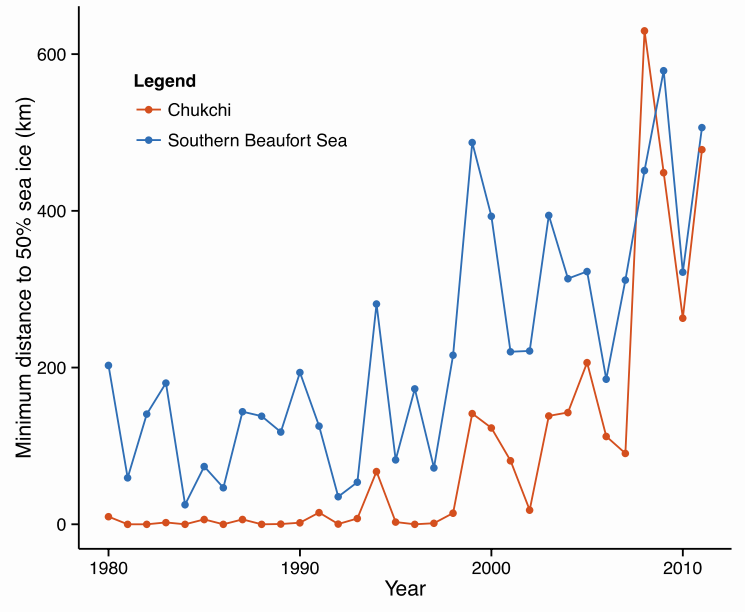


Figure 2-1. Examples of control charts used to identify denning bears and estimate den entrance and emergence using temperature data measured by thermistors onboard satellite collars.

Entrance and emergence dates were calculated as the median between observations within and above control limits at the start and end of a denning event.

a)



b)

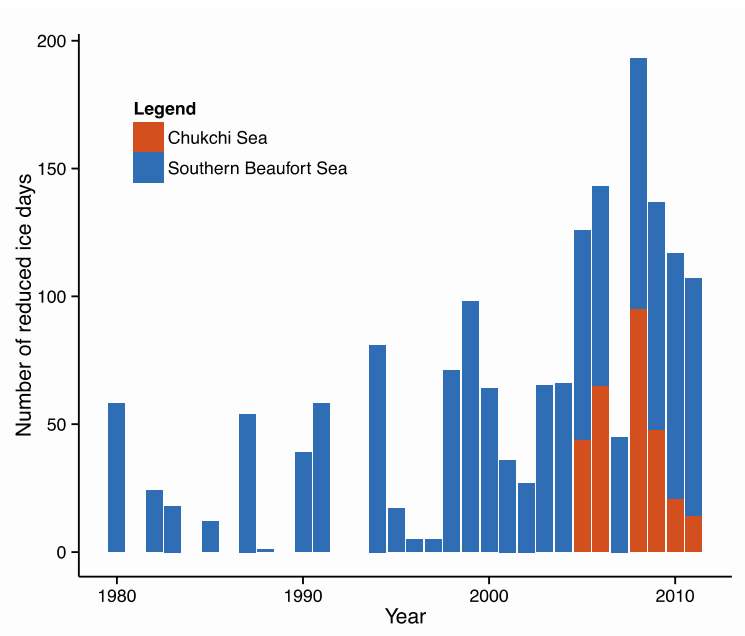


Figure 2-2. Trends in the minimum sea-ice extent averaged during September measured as (a) the minimum distance from pack ice of 50% concentration to the continental shelf, and (b) the number of reduced ice days where there was $<6250 \text{ km}^2$ of sea ice at 50% concentration over the continental shelf.

Table 2-1: Comparisons of den phenology estimates by den substrate in the southern Beaufort and Chukchi seas.

| Population | Den substrate | Entrance | | | Emergence | | | Duration (days) | | |
|-------------------|---------------|----------|-------|------|-----------|-------|------|-----------------|-----|------|
| | | n | x | SD | n | x | SD | n | x | SD |
| Chukchi | Sea ice | 13 | 11-23 | 20.5 | 11 | 03-04 | 22.6 | 11 | 101 | 32.9 |
| Chukchi | Land | 46 | 11-15 | 36.4 | 34 | 03-13 | 23.1 | 34 | 116 | 39.5 |
| Southern Beaufort | Sea ice | 72 | 11-16 | 27.6 | 61 | 02-25 | 27.3 | 61 | 100 | 38.5 |
| Southern Beaufort | Land | 59 | 11-11 | 18.5 | 54 | 03-03 | 24.7 | 54 | 112 | 26.0 |

Table 2-2: Trends in the average, minimum sea-ice extent during September measured as (a) the minimum distance from pack ice of 50% concentration to the continental shelf, and (b) the number of reduced ice days where there was <6250 km² of sea ice at 50% concentration over the continental shelf.

| Observed with dependent young | Entrance | | | Emergence | | | Duration (days) | | |
|-------------------------------|----------|-------|------|-----------|-------|------|-----------------|-------|-------|
| | n | x | SD | n | x | SD | n | x | SD |
| No | 33 | 11-16 | 30.3 | 28 | 02-19 | 20.8 | 28 | 91.57 | 32.7 |
| Yes | 60 | 11-14 | 21.0 | 54 | 03-08 | 23.0 | 54 | 114.6 | 27.97 |