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Denning phenology of polar bears (*Ursus maritimus*) in the Barents Sea population

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Marine Ecology and Resource Biology

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Table of Contents

List of Tables

List of Figures

Abstract

Timing reproductive effort to match food availability is important due to high energetic costs of reproduction. Female polar bears need sufficient time in the den to nurse cubs until they are big enough to withstand the Arctic environment, however females' emergence from the den needs to be synchronized with ringed seal pupping peak, which is a crucial energy source for polar bears. The phenology of polar bear maternity denning may shift over time due to changing environmental conditions. Denning phenology of polar bears from Barents Sea population (BS) from 2011 to 2017 was detected using satellite telemetry GPS locations, temperature and activity data. This resulted in full length records of 29 maternity denning events, with estimated dates of entry and emergence. This study found that 64 % (0.49-0.78, n=45) of all reproductively available females went into den. Additionally, 15 % (0.04-0.35, n=26) of females initially accompanied by cubs of the year and 11 % (0.00-0.48, n=9) of females accompanied by yearlings went into den following autumn, possibly due to early loss of cubs which allowed for subsequent mating and denning. Females started denning between Oct 4th and Jan 5th, mean Nov 5th (SD=29 [Oct 7th - Dec 4th], n=35), and emerged from it from Dec 12th to May 1st, mean Mar 14th (SD=32 [Feb 10th – Apr 15th], n=29). Bears entering den later in the year denned for a shorter period. Den emergence dates were less variable than den entry dates, which supports the hypothesis that bears time den emergence to the peak seal pup availability. Additionally, young females were less likely to go into den and if denning, they emerged from den earlier, possibly due to reproductive failure. Warmer weather in spring, indicated by negative Arctic Oscillation Index values, was associated with later den entry, suggesting that spring conditions potentially influence polar bears hunting success and may play a role in collecting energy stores to undertake successful maternity denning.

Key words*: Arctic, denning ecology, den use, maternity denning, seasonality, Svalbard, *Ursus maritimus*

1 Introduction

Polar bear (*Ursus maritimus*) populations are predicted to be negatively affected by climate warming, but due to the harshness of the environment in which they life and their isolated lifestyle, some elements of polar bear denning ecology still remains unknown. Studies investigating reproductive ecology can provide necessary insight into the condition of polar bear populations and detect changes in bears' distribution and behaviour that signal shift in the environment. This is necessary for population management conservation status decisions. Such predictions are difficult to obtain from historic data directly because past and predicted environmental conditions differ substantially. In this thesis, I explore maternity denning behaviour of polar bears in the Barents Sea subpopulation in relation to the environment and compare this with existing studies to further investigate polar bear population responses under climate change.

Yearlong life at high latitudes requires adaptations that allow to accumulate energy when food is available (Schultz and Conover 1997) and to reduce energy consumption when food is scarce (Watts and Hansen 1987). Denning has been defined as an example of a behavioral adaptation that enables animals to conserve energy at times of limited access to food (Johnson 1931, Folk et al. 1974, Reynolds et al. 1974, Sandell 1990). For this reason, most bears from the Holarctic genus *Ursus* go into den in response to seasonal fluctuations of resources (Bunnell and Tait, 1981; Johnson and Pelton 1980), and the variability of food availability influences the bears' physiological processes. When food is abundant, ursids go through a period of hyperphagia to gather energy reserves (Kingsley et al. 1983) or undergo prolonged fast when food availability is significantly restricted (Nelson et al.1983). Environmental seasonality, especially pronounced periods of fasting, has been shown to additionally influence reproductive physiological processes such as implantation, gestation and lactation (Gittleman and Oftedal 1987, Ramsay and Dunbrack 1986).

Polar bears (*Ursus maritimus*), in contrast to terrestrial ursids, inhabit environments where food was available throughout winter, thus only pregnant females overwinter in dens. Polar bears are large, solitary carnivores that feed primarily on ringed seal (*Phoca hipsida*) and other ice-obligate Arctic pinnipeds like bearded seal (*Erignathus barbatus*) and harp seals (*Phoca groenlandica*) (Derocher at al. 2002, Iversen et al. 2013). Polar bears' prey is available for most of the year, but its accessibility changes seasonally. Especially in spring, susceptible seal pups are particularly easy to hunt (Hammill and Smith, 1991). Ringed seals require sea ice for

reproduction and, in Svalbard and western Barents Sea, they breed during spring on land-fast ice (Smith and Lydersen 1991) and drift ice (Wiig et al. 1999). Additionally, seals use sea ice as moulting and resting platforms as well as feed on ice-associated species (Reeves 1998, Hamilton et al. 2017). Polar bears' seasonal patterns of activity consequently follow changes in prey availability. Even though polar bears are more active between April and June and less active throughout the winter (Messier et al. 1992), the accessibility to food is rarely completely restricted. Although some individuals den temporarily in shelters to conserve energy, denning behavior in polar bears is primarily dictated by giving birth to underdeveloped newborn cubs, who require protection from the harsh environment thought first 3-4 months of their life (Blix and Lentfer 1979, Ramsay and Stirling 1988).

Maternity denning, the prolonged denning restricted to pregnant females, is a crucial stage in the polar bear life cycle (Messier et al. 1994, Amstrup 2003, Van de Velde et al. 2003). In order to go through pregnancy and raise cubs in winter, a female polar bear has to obtain enough energy reserves feeding though spring and summer (Robbins et al. 2012). The timing of sea ice formation can affect the arrival of females to the denning area (Lønø 1970, Derocher et al. 2011). Additionally, the beginning of denning relies on the accumulation of sufficient compact snow to excavate a den (Amstrup and Gardner 1994). Across the range, polar bears are using various features and topography types – from mountainous ridges (Lønø 1970, Uspenski and Kistchinski 1972, Wiig 1998, Andersen et al. 2012) to snowdrifts on riverbanks and tree-supporting ridges on flat tundra (Ramsay and Andriashek 1986, Ramsay and Stirling 1990, Messier et al. 1994).

Across most of the Arctic, pregnant polar bears excavate and enter their dens in late autumn (Harington 1968, Lentfer and Hensel 1980, Ramsay and Stirling 1990, Wiig 1998). While in the den, the females do not eat or drink, relying entirely on their stored energy reserves, while undergoing delayed implantation, gestation, parturition, and lactation (Blix and Lentfer 1979, Ramsay and Stirling 1988, Amstrup 2003). In mid-winter, females give birth to, on average, two altricial cubs, who weigh only around 0.6 kg (Derocher et. al 1992, Amstrup 2003). Thus, the thermal refuge of the den is critical to the survival of the cubs until they are big enough to survive outdoors and travel to the sea ice. After nursing cubs for about 3-4 months, who then weigh around 10-12 kg, females break the den in spring, around late March to early April (Ramsay and Stirling 1988, Wiig 1998, Andersen et al. 2012) and accompanied by their cubs return the sea ice to hunt seals and regain their lost energy reserves. The emergence from the den corresponds with the birth of ringed seal pups in lairs on the sea ice (Lydersen and Gjertz

1986, Smith and Lydersen 1991) and the increased availability of prey allows females to restore energy reserves depleted during denning, and supports their continuous lactation and survival of the cubs. Since less developed young are more susceptible to heat loss, the duration of denning may affect cub survival (Blix and Lentfer 1979).

Cub survival is frequently low, less than half may survive their first year (Amstrup 2003). Surviving cubs stay with their mother for 2.5 years until weaning (Ramsay and Stirling 1988). If successfully raising her cubs until weaning, a polar bear female may enter a den every third year. If a female loses her cubs early, in den or soon after emergence, she may enter the den following season (Ramsay and Stirling 1988, Amstrup. 2003).

While only pregnant females overwinter in den, males and non-pregnant females may use temporary den shelters to rest during unfavorable ice conditions and seasons of low food availability (Harington 1968, Jonkel et al. 1972, Schweinsburg 1979, Derocher and Stirling 1992, Messier et al. 1994, Ferguson et al. 2000). Messier et al. (1994) originally described maternity denning as periods exceeding 4 months, and defined shorter periods as sheltering (temporary denning). Amstrup. (2003) points out that sheltering periods of several months may be most typical for areas with low prey availability. In practice, a failed attempt of maternity denning after a shorter period would always be looked at as temporal denning if one has a specific limit for number of days to separate the two. It is nearly impossible to follow maternity denning of female polar bears directly and observe their reproductive success or failure.

As technology advances, finer means of scientific investigations become available, allowing for increasingly detailed spatial and temporal data. At first polar bear maternity denning was described through observation, where den entries and emergences would be spotted and their dates recorded (Lønø 1970, Jonkel et al. 1972, Larsen 1985, Hansson and Thomassen 1983, Ramsay and Stirling 1990) with a high likelihood of biases. Later capture-recapture surveys coupled with Argos and Iridium telemetry system provided a modern tool collecting data remotely (Messier et al. 1992, 1994, Wiig 1998, Fischbach et al. 2007, Andersen et al. 2012). Although telemetry collars are deployed on a relatively small sample of bears and are only on adult females, the analysis of data can complement previous knowledge and characterize maternity denning trends in light of the ongoing climate changes (Escajeda et al. 2018, Rode et al. 2018).

While polar bears are adapted to high environmental variability, they are currently experiencing extreme long-term reductions in sea ice extent and thickness, in addition to shortening of the duration of seasonal ice cover and changing snowfall patterns (Stroeve et al. 2012, Laidre et al. 2015a, Lone at al. 2018). Those changes may negatively affect polar bears' condition and body size (Rode et al. 2010, 2012, 2014), decrease the survival (Regehr et al. 2007, 2010; Bromaghin et al. 2015), shifts bears into lower ice concentration areas (Laidre et al. 2015b) or terrestrial habitats (Fischbach et al. 2007, Schliebe et al. 2008, Rode et al. 2015, Olson et al. 2017) and are likely to cause a shift in trophic coupling with seals (Derocher et al. 2004). Although the reduction in sea ice and increasing temperatures are expected to affect population of polar bears (Ferguson et al. 2000, Derocher et al. 2004, Stirling and Derocher 2012, Molnár et al. 2014, Descamps et al. 2017), its direct impact on denning timing and length still poorly understood.

The cascading impact of spatial and temporal sea-ice changes is likely to decrease the reproductive success of polar bear females, as females will have less fat to invest in winter or will not be able to reach hunting areas and feed during lactation (Derocher et al. 2004). Polar bears from Barents Sea subpopulations have spent more time on energy-costly swimming during summer months (Lone et al. 2018) while in Chukchi Sea, Beaufort Sea, and Hudson Bay, bears have spent more time on land in months prior to denning than they have in the past (Rode et al. 2015b; Atwood et al. 2016). Lower hunting success and increased energy expenditure can influence female body condition prior to denning (Stirling et al. 1999). Additionally, increasingly variable and less predictable weather (Krupnik and Jolly 2002) may cause denning failure through events such as earlier snowmelt (Stone et al. 2002; Derksen and Brown 2012), den collapse (Stirling and Derocher 1993), or rain on snow, when cold water would seep into den before mothers and cubs have departed.

Studies of polar bear denning phenology are few and rarely focus on subsequent monitoring of the subpopulations (Ramsay and Stirling 1990, Messier et al. 1994, Fischbach et al. 2007, Derocher et al 2011, Laidre et al. 2015b, Olson et al. 2017). Polar bears reportedly changed denning behavior in some areas by moving to more land-based denning sites (Derocher et al. 2011, Fishbach et al. 2017), by denning at higher latitudes (Derocher et al. 2011, Rode et al. 2015b), at higher elevations (Escajeda et al. 2018), and by changing the time of den entry (Escajeda et al. 2018). The implications of those changes in polar bear maternity denning on reproductive success and cub survival are not clear. Complementing knowledge about denning phenology of polar bears belonging to Barents Sea subpopulation can determine any

shifts in denning phenology and provide further insight into polar bear maternity denning in changing environment.

The aim of this study is to use GPS telemetry data collected in Barents Sea region from 2011 to 2017, to identify and describe maternity denning as well as to identify factors determining maternity denning. First, I want to identify all maternity denning events and describe their phenology and length. I hypothesize that the den emergence is less variable than den entry dates due to the bears' need to match seal pupping peak. Thus, females going into den late would den for a shorter period. Secondly, I want to determine how denning probability varies with reproductive life history stage and age, an indicator of experience. I predict that solitary females will be most likely to den, however shifts in the environmental conditions may lower the rates of reproductively available females going into den. Additionally, I hypothesize that young, less experienced females are less likely to go into den and if denning, due to lower hunting success and limited energy stores, they are likely to den for a shorter period. Next, I want to investigate if the spring Arctic Oscillation Index, which may be an indicator of sea ice conditions in time crucial for polar bears in building their energy reserves, influences maternity denning entry. Additionally, considering the fast pace of climatic changes underway in Barents Sea area and reported shifts in den distribution and loss of good denning areas (Derocher et al. 2011, Andersen et al. 2012), this study provides a very good system for monitoring denning phenology changes in light of changing climate. Finally, I want to compare the results of this study with literature to relate the described denning phenology to denning habits of polar bears from different subpopulations, exposed to varying conditions and prey availability.

2 Materials and Methods

2.1 Study site
Svalbard is a high Arctic archipelago, with most of its islands stretched between 10'E and 35'E and between 74'N and 81'N. It is surrounded by the Arctic Ocean to the north, Barents Sea to the east and south and by a branch of the North Atlantic current on the west. Cold currents influence island from northeast bringing drift sea ice, and the warmer Atlantic waters from the southwest influence the archipelago creating relatively mild climate (Vinje 1985). Consequently, there is an east-west temperature gradient of temperature and sea ice conditions, with the eastern part having on average a few degrees C colder climate than west Svalbard (Vinje 1985). North-East of Svalbard lies Franz Josef Land, which together with Novaya

Zemlya delineates the Barents Sea subpopulation of polar bears to the east (Figure 2., Aars et al. 2009). Sea ice in the area is predominantly seasonal, but multi-year ice is regularly advected from Arctic Ocean basin (Gerland et al. 2008, Stroeve et al. 2012). Sea ice, on which polar bears depend for hunting, resting and travelling (Amstrup 2003), varies interanually in its conditions and arrival time, but the ice thickness and distribution have dramatically declined since the late 1990s and this trend is predicted to continue (Lone at al. 2018).

2.2 Sampling

Since 1987, Norwegian Polar Institute (NPI) researchers have captured polar bears annually, each spring, while building an extensive capture-recapture database. During the capture effort bears were found and collared opportunistically, which was dictated by the environmental and logistic constraints in the high Arctic. Only females were collared and the collar battery lasted from few months to years. The sex, and for females the reproductive status, was recorded for each bear. A vestigial premolar was extracted for estimating age based on counts of cementum growth layers (Calvert and Ramsay 1998). Additionally, notes were taken providing observational data providing history of sampled bears.

Reproductive status was determined by the absence or presence of cubs and their age at the moment of capture. Females were classified as lone (if they were solitary of accompanied by a male at time of capture), accompanied by cubs of the year (COYs) or yearlings (Yrlg).

Age was estimated based on the analysis of the extracted premolar. Preparation and reading of the teeth were performed by the company Age Dynamics, Denmark (Christensen-Dalsgaard et al. 2010), following the methods described in Stirling et al. (1977a), Stewart et al. (1996), Hensel and Sørensen (1980) and Christensen-Dalsgaard et al. (2010).

In this thesis, I used data from 2011 to 2017, when the new generation collars Telonics Inc. (Mesa, AZ, USA) were introduced, providing highly accurate GPS positions in addition to recording the ambient temperature and activity. Temperature was measured by a thermistor inside a collar (Fischbach et al. 2007), and although temperature readings were influenced by animal's body temperature, the data measurements were a good indicator of the ambient temperature of the surrounding environment (Harris et al. 1990). Activity was measured by a mercury-tip switch inside the collar that recorded state changes at 1-s intervals within 2h (7200s) periods (Fischbach et al. 2007). Collected data was transmitted every 2h.

2.3 Data analysis

All numerical and statistical analysis were done using R version 1.1.463 (R Development Core Team 2008).

2.3.1 Determining denning

Between 2011 and 2017, a total of 102 collars were deployed on polar bear females. I excluded data from dead bears or collars that failed to record and transmit data at least until December 1st, as collars that stopped working before that date were considered less useful for maternity denning analyses.

Denning events were identified using a combination of sensors in order to pinpoint the entry and emergence dates as accurately as possible. Denning events are characterized by a low activity level, an elevated temperature, fixed geographical locations, and should at least last for 14 consecutive days (Messier et al. 1992, 1994; Wiig 1998, Fischbach et al. 2007, Andersen et al. 2012, Escajeda et al. 2018). As maternity denning was the focus of my study, I narrowed the period of investigation to October 1st and May 1st, which was expected to cover all maternity activity (Messier et al. 1992). Some bears transmitted data for more than one year, thus I considered each year to be a different potential denning period, later called bear/season.

Denning events were identified using a custom-written function (created by Marie-Anne Blanchet, December 2018), taking into account the speed and activity count during the tracking period. Raw GPS locations were modelled through a correlated random walk in a state space model framework using the "CRAWL" R package (Johnson and London 2008). This was done in order to account for the error around each location and missing location associated with a time stamp. Speed was calculated between two consecutive modelled locations. Speed and activity were smoothed using a weighted moving average with a window of 24 hours and weights following a Gaussian distribution. A segmentation algorithm was then applied to the smoothed speed and activity curves. The algorithm finds the optimal segmentation using a dynamic programming approach. The number of segment was then chosen using Lavielle's (2005) procedure based on locating rupture in the penalized likelihood. We used the R package "segclust2d" (Patin et al. 2018). Each segmentation event was then visually inspected to confirm that the algorithm actually identified a denning event. A denning event had to be at

least 14 days and start between October 1st and December 31st, as this was after the December cut-off. One denning event was however added manually, where a female entered a den on January 19th. I performed the analysis consistently in one session to unify the measurements. Using the function, and with manual inspection and adjustments, I estimated den entrance and emergence dates, converted them as day-of-year while accounting for leap years (DOY; Day no. 1 is January 1st) and consequently calculated the duration of denning as the number of days between those dates. Nine bears left their dens for less than a day during the denning period, either changing to new den location (n=9) or returning to the initial den, those events were manually tagged as breaks within the function. The data signatures of temperature, activity data, and movement in general gave very clear indications of denning events. Therefore, I was confident that data provided useful estimates on the maternity den chronology.

2.3.2 Determining denning phenology

I used length of denning to distinguish temporary denning from maternity denning. I classified dennings as temporary if they lasted from 14 to 60 days and maternity denning to be longer than 60 days. As it was impossible to determine whether short denning events were failed maternity dennings or temporary dennings defined as periods in which a female rested in a shelter to conserve energy, I plotted lengths of all recorded dennings and based my division in the bimodal distribution of denning lengths. I referred to notes from field sampling and confirmed that the second shortest denning classified as maternal (81 days) was indeed an attempt to produce cubs, as the female was lactating when recaptured in spring after emergence. Statistics on frequency of temporal denning is provided, but was not further analyzed, as this thesis focuses on maternity denning phenology.

2.3.3 Determining maternity den position

I estimated den positions based on stationary bear locations with the lowest GPS error (range 5-23m, n=28 dens) within each recognized maternity denning period.

2.3.4 Reproductive status

The reproductive status of polar bear females was recorded at capture at the time a female received the collar. For bears where a collar transmitted data for more than one winter season, this data was thus only known from capture data for the first season. Capture data on reproduction was missing for 14 bear/seasons. For those bear/seasons, I assumed lone females

entering a den in the first winter following capture to be with cubs the following spring (n=4), and that lone females that failed to den necessarily would also be lone the following spring (n=4). Females that were with yearlings the year of capture, and that did not go into den (n=2), I assumed to be alone the next spring (or with 2-year old cubs in early spring, but lone in later spring). I set the reproductive status of females accompanied by cubs in the capture year, that did not enter a den the following year, as NA the following spring, this because she could either be with yearling cubs or alone (n=4). One bear accompanied by cubs of the year in spring was confirmed to lose her cubs in autumn, so after she did not den in winter, her status the following spring was set to lone.

I modelled probability of denning of bears belonging to each reproductive category using binomial test.

2.3.5 Arctic Oscillation Index

The Arctic Oscillation Index (AOI) is a measure of climate variability poleward of 20°N, related to sea-level pressure variations (Thomson and Wallace 1998) and has been shown to correlate with demography of Svalbard plants and reindeer (Aanes et al. 2003) and polar bears (Derocher 2005). Higher AOI values indicate colder temperatures and negative AOI corresponds to higher than average temperatures (Thomson and Wallace 1998). I obtained monthly values for the Arctic Oscillation Index from https://www.cpc.ncep.noaa.gov/products/precip/ CWlink/daily_ao_index/ao.shtml and created a spring AOI index for April – June for the months preceding denning.

2.4 Statistical modelling

2.4.1 Den phenology analyses

Using linear regression models, I tested for a correlation between duration of denning and den entry date as well as correlation between duration of denning and den emergence date. In order to test for year-dependent differences between den entry and den emergence dates, I used an analysis of variance (one-way ANOVA) model on the maternity denning matrix.

To determine influence of the bear's age, year and AOI spring average on den entry and den emergence, I used a linear regression model. The best fitting model was selected based on

stepwise evaluation of Akaike's Information Criterion AIC. Fitness of the model was evaluated by visual inspection of the residual plots and tested with type one ANOVA.

2.4.2 Reproductive status

I calculated the probability of denning of bears belonging to each reproductive category using binomial test.

2.4.3 Age class

As lone females were suspected candidates for maternity denning, I used binomial test to calculate the probability of denning of young, prime age, and old females with lone reproductive status.

2.4.4 Maternity denning occurrence

I run a generalized linear model (GLM, binomial family) to determine possible influence of bears' reproductive status, age and AOI spring average on maternity denning occurrence. The best fitting model was selected based on stepwise evaluation of Akaike's Information Criterion (AIC). Fitness of the model was evaluated by visual inspection of the residual plots. Reproductive status was used as a categorical variable with three defined levels "lone", "COY" and "Yrlg". Similarly, age was categorical variable divided into three classes of ecological importance (Ramsay and Stirling 1988) "young", "prime age" and "old". AOI spring average was a categorical variable for each year, from 2011 to 2017. Individuals bears were not included as a random effect since only 3 bears (n=47) denned more than once.

3 Results

3.1 Dataset

A total of 47 collared females provided frequent information long enough into the winter that I could reveal if maternity denning took place (providing data at least until 1 December). In total, these females provided data for 84 bear/seasons, as 25 bears gave data for one winter, 10 bears were tracked for 2 winters, 9 bears for 3 winters, and 3 bears for 4 winters. Two females denned twice and one female denned three times. The youngest tracked female was 5, and the oldest 28 was years old (average 13 years, SD=5).

3.2 Shelter dens

Nine females went into den for longer than the two weeks, a period used as a limit to define a denning event, but shorter than the two months, a minimum period to categorize maternity denning. The average entry date for the shelter dens was 29th December (9th November – 13th February). The length of the period ranged from 17 to 42 days, with an average of 33.5 days (SD=9 days). The days of emergence ranged from 7th December to 27th March (average February 2nd). None of the nine females that entered shelter dens were later classified as maternity denning bears the same winter. Thus, for all further analyses, these nine females are grouped with "non-denning" bears. For simplicity, hereafter the term 'denning' will refer to maternity denning, not shelter events.

3.3 Maternity denning

All maternity dens were located on land dispersed throughout Svalbard, except from one den located in Franz Josef Land (**Error! Reference source not found.**). Over all winter bear-seasons (n=84), 35 maternity denning events were recorded (**Error! Reference source not found.**). This gives a denning proportion of 0.42 (Cl 0.31-0.53).
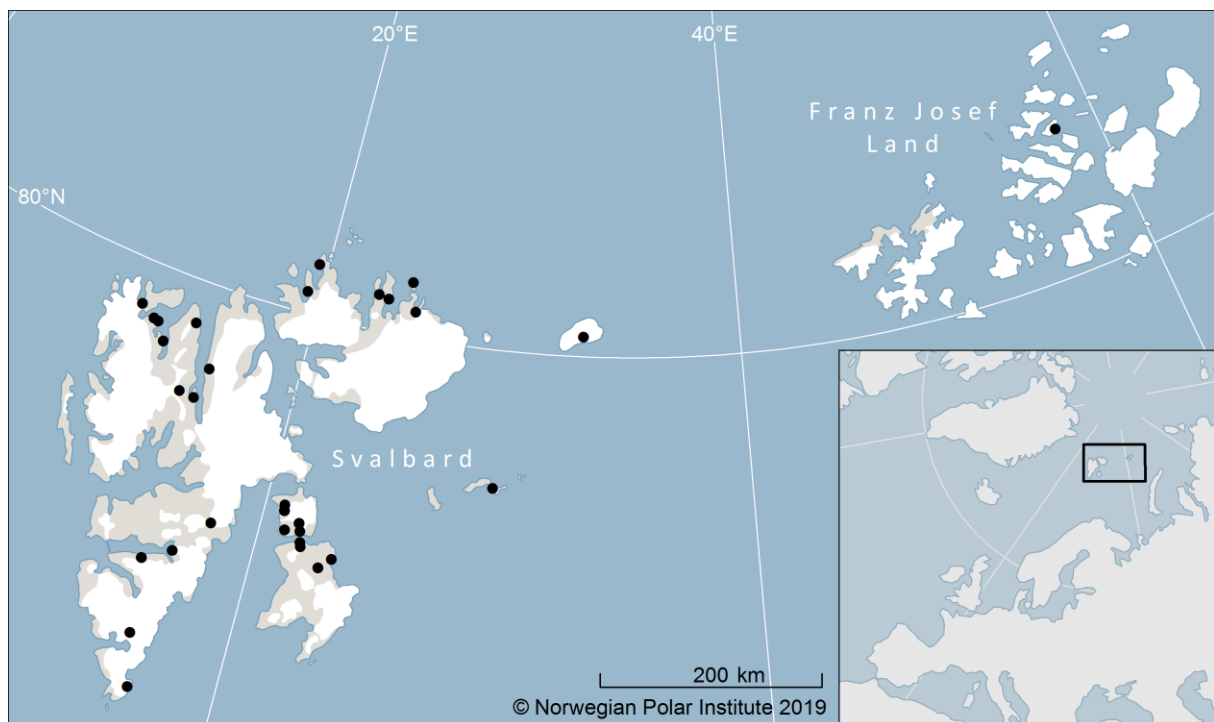

Figure 1. Map showing locations of maternity dens (n=35) used by female polar bears in Svalbard and Franz Josef Land from 2011 to 2017.
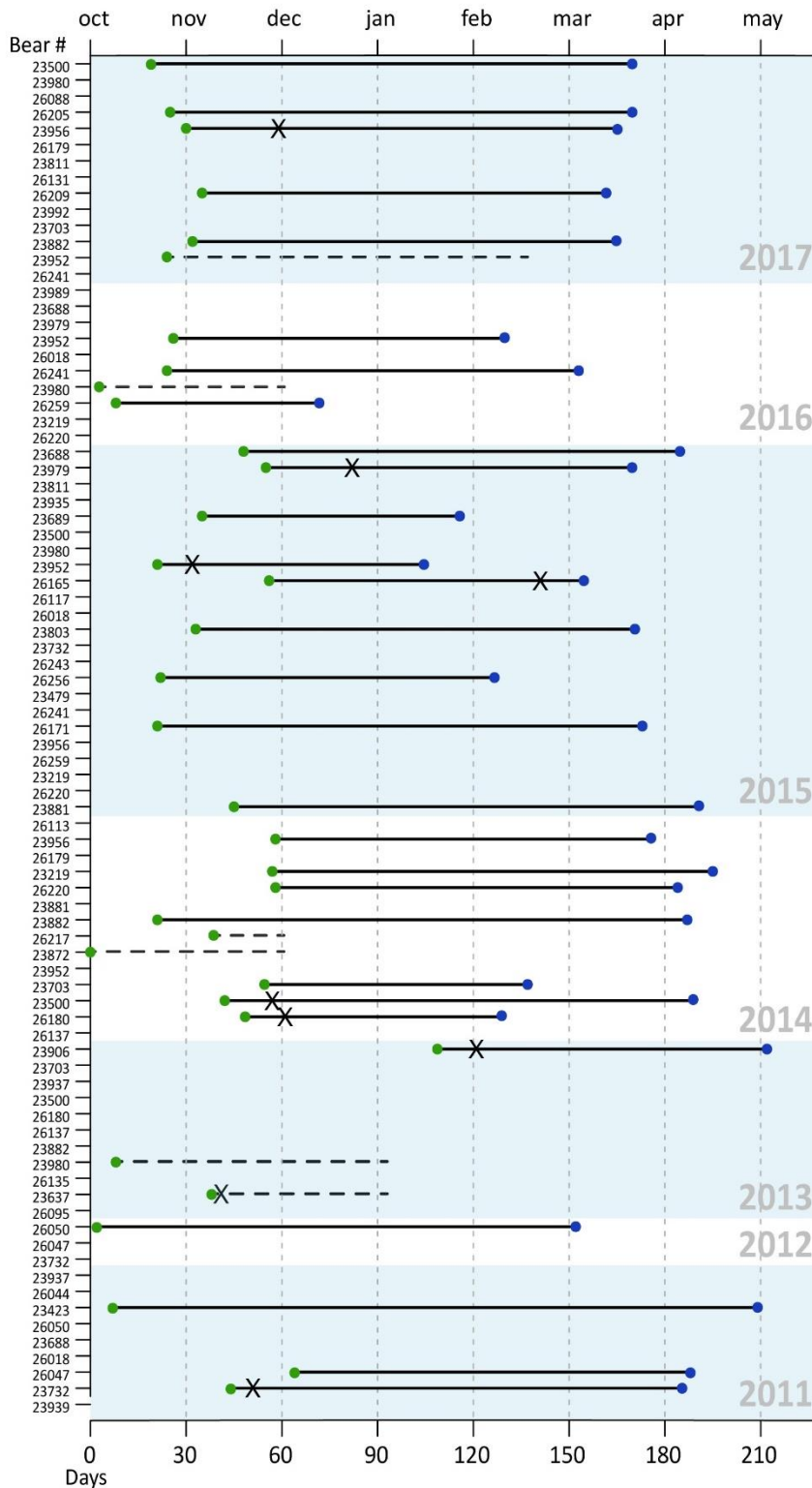
Figure 2. Den entry dates and duration of maternity denning (n=35) and over 84 bear/seasons. Green point indicates entry date, blue point indicates emergence date and black cross indicates recorded break in denning. Dotted line shows recorded data until collars

The GLM analysis of all denning females showed that over all of the bear seasons (n=84), maternity denning was strongly influenced by reproductive status (F=16.17, 2 df, p<0.001) and not influenced by AOI (F=3.48, 6 df, p=0.746) or age class (F=0.68, 2 df, p=0.713). Among

females that were lone, and thus expected to mate and den, 37% failed to go into maternity den. Five out of thirty five females that had cubs of the year or yearlings did also den, so would have lost their litter and mated again (Table 1).

Table 1. Bears going into maternity den divided by their known reproductive status (n=80).

	Lone	With cubs of the year	With yearlings
N maternity denning / total	29 / 45	4 / 26	1 / 9
Proportion of denning	0.644 (0.489-0.781)	0.154 (0.044-0.349)	0.111 (0.003-0.482)

Young solitary females were less likely to den compared to solitary mature bears, represented by prime age and old females (ANOVA: $F=5.24$, 1 df, $p=0.022$) (Table 2).

Table 2. Maternity denning probability of lone bears (n=45) of different age classes.

	Young	Prime age	Old
N denning/total	8 / 18	14 / 18	7 / 9
Proportion of denning	0.444 (0.215-0.692)	0.778 (0.524-0.936)	0.778 (0.340-0.972)

Females went into maternity den from October 4th to January 5th, mean November 5th (SD=29 [October 7th - December 4th], n=35) and emerged from it between Dec 12th and May 1st, mean March 14 (SD=32 [February 10th – April 15th], n=29) (Figure 2). One bear showed a very unusual denning phenology as she entered the den January 19th and emerged May 1st with cub footprints observed at the den in April, during the polar bear capture program. The bear was later seen by others, with a cub in early May not far from the den, with telemetry data confirming it was the actual family (Aars, pers. comm. November 2018).
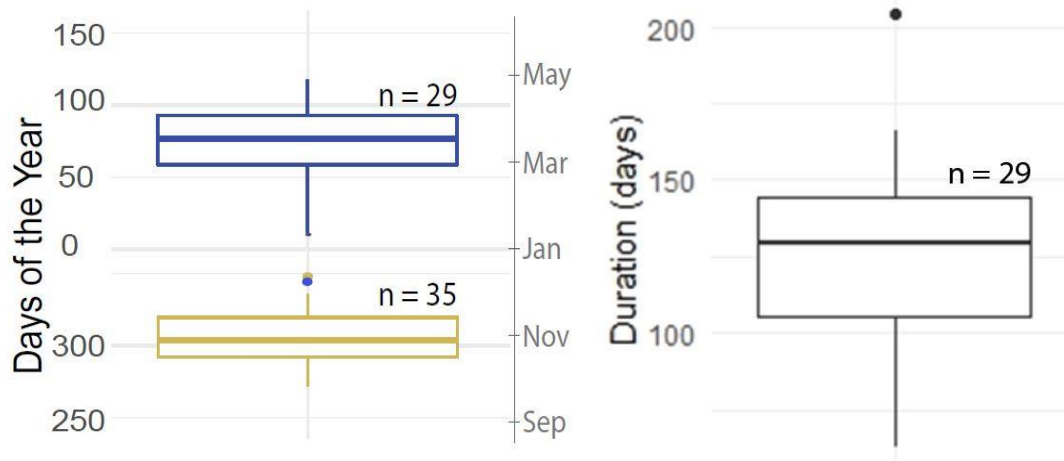
Figure 3. Maternity den entry (in yellow) and emergence (in blue) dates and denning duration of polar bear females denning between 2011 and 2017.

The LM analysis revealed that den entry date was best described as influenced by spring AOI (F=4.268, 1 df, p=0.047), but not by the age class of denning females (F=0.107, 2 df, p=0.900) or year of denning (F=1.574, 6 df, p=0.192). Den entry dates varied over the years (Figure 6), although they were not significantly different (ANOVA F=9.45, 6 df, p=0.15).
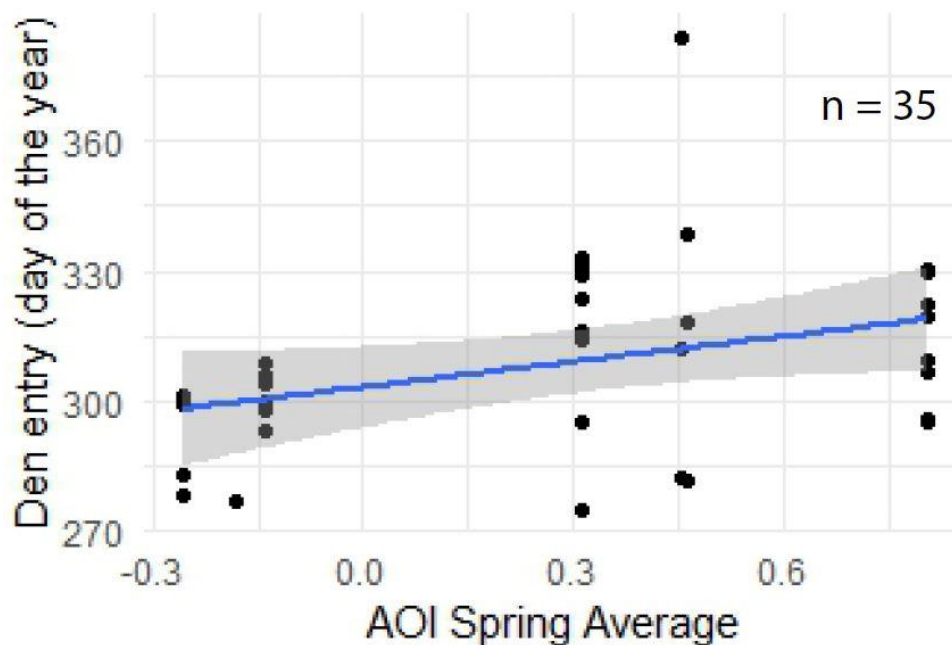

Figure 4. Function of Arctic Oscillation Index (AOI) in spring before denning and den entry date (ANOVA p=0.036) the following season (n=35).

Den emergence date varied accordingly to age class (LM: F=9.077, 2 df, p=0.007), AOI in the spring prior to denning (F=5.282, 6 df, p=0. 031) and den entry date (F=8.447, 1 df, p<0.001).

Bears showed an increase of emergence date with increasing age until reaching maturity, where young females emerged on average 3 weeks earlier than prime and old age females. In colder conditions during spring prior to denning, expressed as higher AOI, females emerged from dens later than in warmer spring conditions. Den emergence dates were different over the years (ANOVA F=17.31, 6 df, p=0.008) (Figure 7).

Additionally, emergence date was predicted by den entry date (LM: emergence = -115.98 + 0.6*entry, P<0.05) (Figure 5).
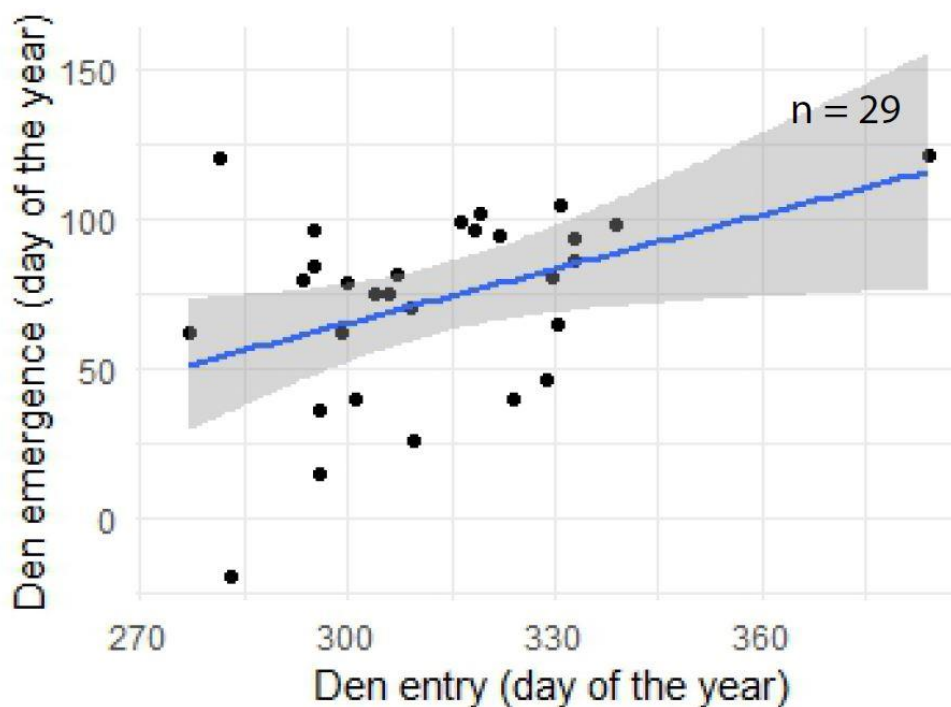

Figure 5. Denning entry in relation to den emergence from maternity dens between 2011 and 2017.

Maternity denning duration was between 63 and 204 days, with a mean of 125 days (SD=30, n=29) (Figure 2). From all dennings with recorded duration (n=29), 11 dennings lasted less than 4 months. The best fitted LM model analysis showed that denning duration was influenced by the females' age class (F=17, 2 df, p<0.001), den entry (F=72783, 1 df, p<0.001) and emergence (F=153768, 1 df, p<0.001).
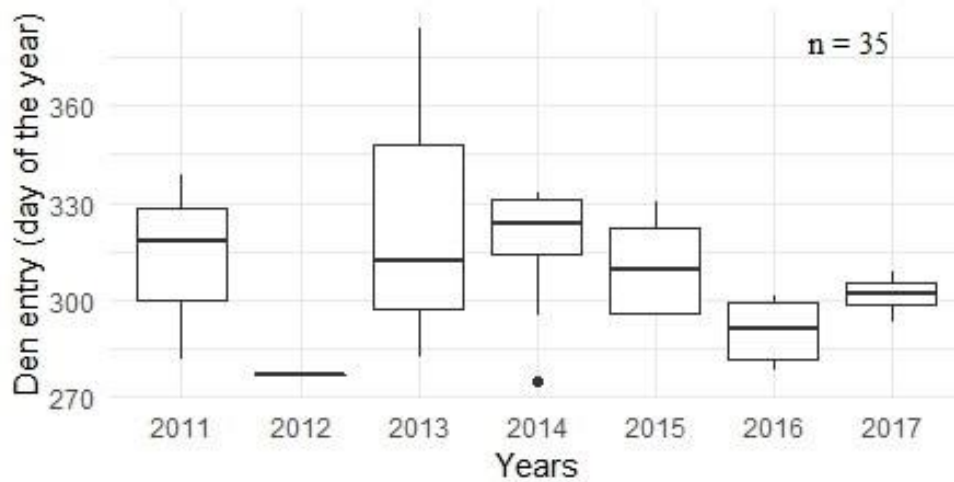
Figure 6. Boxplot of polar bear maternity den entry dates over the years 2011 to 2017.
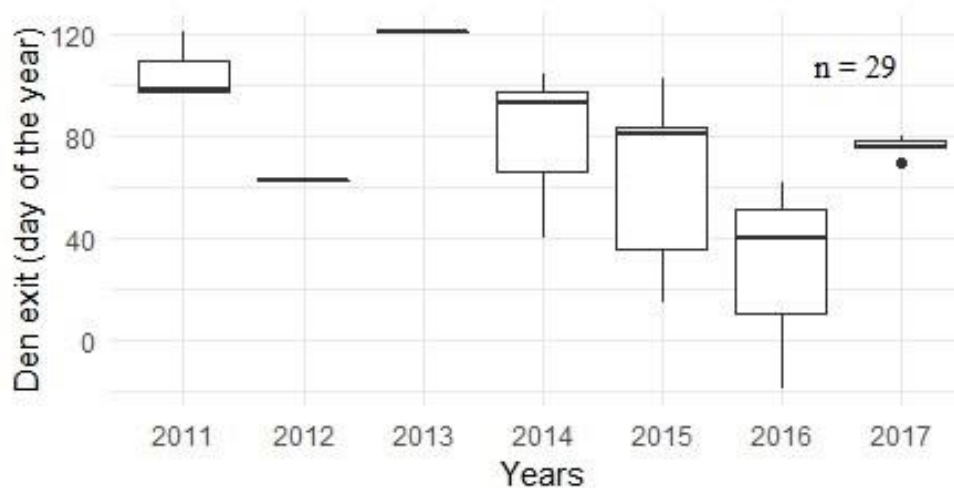
Figure 7. Boxplot comparison of polar bear maternity den emergence dates over the years 2011 to 2017.

4 Discussion

4.1 Proportion of bears going into den

Denning behavior was most strongly influenced by a females' reproductive status, however 15% of females with cubs of the year (n=26) and 11% with yearlings (n=9) went into den the following autumn. That means that females with cubs most likely lost cubs early in the spring and undertook the reproductive effort the same year, as mating usually occurs between March and May. Such reproductive plasticity of females who lost cubs was previously reported by Smith and Aars (2015), who described a female that had lost her cubs to be denning in June, go into den and successfully produce cubs.

Out of all reproductively available females, solitary in the spring prior to denning, 64% went into maternity dens between 2011 and 2017. This proportion was considerably lower than the 82% (n = 28) reported for the same subpopulation for the period 1988 to 1993 (Wiig 1998). Additionally, during 1977 to 1983, 77% of females that denned on Svalbard emerged in spring with produced cubs (Larsen 1986). Studies investigating the Alaskan (Lenfer et al. 1980) and Canadian (Taylor et al. 1987b) coastline, the Southern Beaufort and the Chukchi Sea subpopulations, reported similar (40-70%) rates of reproductively available females going into den. Productivity of polar bear populations strongly depends on the number and productivity of ringed seals (Amstrup 2003). Therefore, the difference between denning rates in different polar bear subpopulations could result from different area productivity (Amstrup 2003), as well as different sample sizes (Wiig 1998) or study method (Lenfer et al. 1980, Taylor et al. 1987b, Wiig 1998).

Among all lone reproductively available females, young bears were less likely to den compared to prime aged and old females. Derocher et al. (1992) noted that in the western Hudson Bay, of all females pregnant in autumn, 33% were not accompanied by cubs when captured the following year. Assumed reasons were neonatal mortality, failure to implant, or spontaneous abortion. In this study, it is impossible to clearly deduce the reason for denning failure among reproductively available females, yet it could be caused by female's inability to mate in spring or her poor body condition in autumn preventing successful implantation or causing abortion before denning season. The fact that young females were less likely to den compared to older ones could be explained by their inexperience and consequent failure to build up sufficient fat reserves, as polar bears depend on their cognitive skills and learning for hunting and survival (Amstrup 2003). Later age of reaching maturity and commencing reproduction was reported in areas less productive in ringed seals (Ramsay and Stirling 1988, Lentfer and Hensel 1980).

4.2 Den entry

The entry date mean and variability recorded in this study (November 5th) were similar to those recorded in Svalbard in 1988-96 (Wiig 1998), despite spanning months later in the year (September 7th – December 12th, mean = November 7th, SD = 25, n = 26).

Start of denning was best described by spring Arctic Oscillation Index average. Colder weather, indicated by higher AOI values, correlated with later den entry. Positive AOI indicates low pressure level over the Arctic, which locks cold air in the polar area (Thomson and Wallace 1998). This in turn is associated with greater sea ice extent (Rigor et al. 2002), which facilitates

successful hunting and the bears consequently gaining energy needed for successful reproduction and lactation (Derocher 2005, Descamps et al. 2017).

Food availability influences timing of entry into den in brown bears and black bears (Van Daele et al. 1990, Schooley et al. 1994, Friebe et al. 2014, Pigeon et al. 2016, Johnson et al. 2017), which enter den later if food is abundant. For polar bears, Rode et al. (2018) attempted to use sea ice extent in autumn as a proxy for hunting conditions, yet found no relationship between den entry date and food availability. The AOI average used in this study was calculated for spring months, period crucial for gathering energy reserved of polar bears to work as a proxy of food availability due to the strong dependence of ringed seals on sea ice (Freitas et al. 2008). Pregnant polar bear females are more prone to accumulate fat in preparation to denning due to hormonal changes related to pregnancy (Ramsay and Stirling 1988), which results in higher activity compared to non-pregnant females. Previous observations recorded pregnant females hunting on the sea ice as late as December (Koettliz 1898, Harington 1962). Additionally, movements of females during colder periods could be extended due to greater ice cover, and restricted and more energy costly during warmer years (Lone et al. 2018), which could result in shorter travel distance to potential den sites and earlier den entry. However, pregnant females were previously recorded resting for extended periods before moving to a den location, (Messier et al. 1994, Wiig 1998), behavior which was observed in this study as well. AOI, despite being an easily available climate proxy with a documented relationship to polar bear demography (Derocher 2005), is a general indicator insensitive to local microclimates and conditions that adabwide dispersing bears can exploit.

Den entry was not significantly influenced by year, but variation over the years and seasonal similarities, especially in bears denning in geographical proximity, could be observed. Similarly to AOI, year can be a general indicator of environmental conditions, but it may fail to indicate local environmental parameters, for example temperature or snow arrival date. Even detailed environmental variables, like monthly ice variability, monthly temperature and snowfall have not directly explained bear denning phenology in southern Beaufort Sea and Chukchi Sea polar bear populations (Rode et al. 2018), suggesting that more research is needed to understand that relationship.

Age of individual bears did not have an effect on den entry dates. Although age influences denning phenology in brown bears (Friebe et al. 2001, Manchi and Svenson 2005), brown bears are generally obligate hibernators, while only pregnant polar bear females go into den.

Moreover, if young inexperienced females attempt reproduction, it is possible that their poorer energy reserves compared to older bears were sufficient to go into den but not to support the nursing period.

4.3 Den emergence

The timing of den emergence was less variable than den entry while bears entering den later in the year denned for shorter period. This may suggest an existing females' preference for leaving the den in time of peak prey availability. Den emergence dates differed between years in this study and were twice as widely distributed as in 1988-96 (Wiig 1998) (March 2nd to April 27th, mean = April 5th, SD = 14 days, n = 32). Females left dens in this study over 3 weeks earlier than reported by Wiig (1998). Andersen et al. (2012) observed females emerging from their dens between March 29th and April 27th (mean = April 17th, n = 55), on average a month later then in this study. Synchrony between den emergence and seal pupping of ringed seals on sea ice is important to optimize cub development for withstand harsh external conditions (Derocher and Stirling 1996). In 2006 the sea-ice regime around Svalbard underwent a collapse never observed before that has since persisted (Hamilton et al. 2015). Progressing climate changes resulting in decreased sea ice extent may cause trophic decoupling (Hamilton et al. 2017), where female polar bear may leave dens earlier in order to feed, compromising the survival of their underdeveloped young.

Since in this study females entering den later stayed in den for the shorter period, it is likely that bears giving birth later are emerging from the den with smaller cubs.

4.4 Denning duration

Denning duration was influenced by the age class of females and its' 125 days average was shorter than the mean denning duration of polar bear populations in the Canadian archipelago (Messier et al. 1994: 186 days), Baffin Bay and Kane Basin (Escajeda et al. 2018: 167-194 days) and longer than Beaufort and Chukchi populations (Rode et al. 2018: 113.8 days).

Comparing to the 1988-1996 study of the same polar bear population (Wiig 1998), females denned 4 weeks shorter, mainly due to earlier average emergence date which was twice as

variable as previously reported. Wiig (1998), building primarily on temperature data, estimated denning duration to be between 90 and 197 days, with a mean of 153 days (SD = 26, n =24).

Out of all recorded dennings (n=29), 5 were fitting the 5-months length typically described for maternity denning (Messier et al. 1994), 19 were around 4-months and shorter, while 5 dennings were around 3 months and shorter.

The shortest maternity denning period observed was 81 days. That female was lactating when captured by field researchers in the beginning of April, yet was not accompanied by cubs of the year. In such cases, it is not possible to say if the female have lost the litter when in den, and thus abandoned the den, or whether they lost cubs after emergence. Rode et al. (2018) reports an instance of two female producing cubs after denning lasting 42 and 59 days, suggesting that there is a flexibility to den duration needed to produce cubs.

Longer denning duration is associated with likelihood of producing and raising cubs successfully within first 100 days after leaving the den (Rode et al. 2018). Rode et al. (2018) reports that all the females that emerged from den late in the spring were subsequently observed with cubs, while half of females that emerged early, until the end of February, have either not produced or have lost cubs. Although in my study scarce observational data was available concerning the reproductive success of denning females, reproductive success may follow the pattern observed by Rode et al. (2018). As young polar bears denned for shorter periods than prime age and older ones, females emerging from dens earlier were on average younger, consequently likely less experienced, and thus having less energy reserves to support pregnancy or continuous lactation within the den.

4.5 Den locations

All dens were located on land, distributed across the Svalbard archipelago. No dens were located in the western part of Svalbard or in Hopen, a previously important denning site for polar bears (Derocher et al. 2011, Andersen et al. 2012). Andersen et al. (2012) reports a similarly wide distribution, with particular importance of the eastern islands.

In this study, a statistical procedure modelling denning duration was developed and den positions were estimated based on GPS locations. Consequently, given locations are approximates and, in the majority of cases, were not confirmed by on-ground surveys. However, the precision and frequency of den positions in high as in working collar transmitters successfully send the data despite mountainous terrain, or snow and ice layers of the den itself.

4.6 Conclusions

Studies of phenology aimed in detecting biological impact of climate change are recommended to contain minimum 20 years of continuous data (Brown et al. 2016, Rozenzweig et al. 2008). This study, focusing on a subset of polar bear populations, is examining denning phenology of polar bears from Barents Sea population that has been a subject of maternity den studies dating back to 1980's (Wiig 1998, Andersen et al. 2012). However, more continuous studies are necessary to estimate potential changes in polar bear ecology and behavior. For maternity denning to be successful, timing is critical. Over the past decades, the Arctic has been warming twice as fast as global average (IPCC 2013), and is expected to be ice-free before 2040 (Wang and Overland 2009). Such changes are likely to transform to the northern ecosystems (Kovatc et al. 2011, Post et al. 2013). Although polar bears have been documented to behaviorally adjust their reproductive strategy to the environment, it may be challenging to keep up with the pace of developing changes as the breeding success strongly relies on accumulated energy stores (Spady et al. 2007). Further insight into the bears' reproductive success in relation to denning length could provide a reliable measure for population monitoring.

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