Polar Biology (2022) 45:481–490
https://doi.org/10.1007/s00300-022-03016-5

ORIGINAL PAPER

Shifting polar bear *Ursus maritimus* denning habitat availability in the European Arctic

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Received: 16 November 2021 / Revised: 18 January 2022 / Accepted: 19 January 2022 / Published online: 30 January 2022

Abstract

Climate warming has resulted in extensive sea ice loss across the Arctic. Polar bears (*Ursus maritimus*) rely on sea ice for hunting, resting, travelling and in some parts of the Arctic also maternity denning. In the European Arctic, polar bears rely on snow drifts on land to den and give birth. Consequently, timely arrival of sea ice around land masses during autumn is important for pregnant females to reach their denning habitat from their sea ice hunting grounds. We defined denning habitat as landforms necessary to accumulate snow to a depth sufficient for dens. We quantified availability of terrestrial denning habitat across the three European Arctic archipelagos throughout the last four (1979–2020) and the next eight decades (until 2100) using arrival of autumn sea ice around these islands. Across the study area, a clear trend was visible towards later sea ice arrival, varying up to 102 days. Female polar bears in the European Arctic now have 33% denning habitat available compared to the 1980's as many areas became inaccessible in time to start maternity denning. By the 2090's, all areas were projected to be inaccessible to pregnant bears. This decline was unequally distributed, with most reduction in Svalbard and Novaya Zemlya until 2020, whilst denning habitat availability in Franz Josef Land remained unchanged until 2020 but is predicted to become inaccessible by the end of the century. This work emphasizes the importance of the temporal dimension of sea ice dynamics for the persistence of polar bear populations.

Keywords Climate change · Maternity denning · Phenology · Prediction · Reproduction

Introduction

Climate change impacts are already evident in every ecosystem globally (Scheffers et al. 2016). But, effects are nowhere more pronounced than in northern latitudes (Scheffers et al. 2016; Overland et al. 2019) and especially in the European Arctic (Lind et al. 2018). Ice-associated species such as polar bears *Ursus maritimus* are particularly vulnerable to the effects of climate change due to the recent dramatic losses of Arctic sea ice and warming of their environment in general (Laidre et al. 2015b). This apex predator has a circumpolar distribution (Amstrup 2003) and uses sea ice as its primary habitat, as a platform to travel and hunt, the main prey being ice-associated seal species, in particular the ringed seal *Pusa hispida* and bearded seal *Erignathus barbatus* (Stirling et al. 1993; Derocher et al. 2002; Amstrup 2003). Shifts in polar bear sea ice habitat have been documented with a median loss of sea ice throughout their range corresponding to 1.26 d year^{-1} since 1979 with the most dramatic shifts occurring in the European Arctic, with 4.11 d year^{-1} (Regehr et al. 2016). These shifts already forced behavioural changes in some populations, such as longer fasting periods on land in the summer (Molnár et al. 2020) and increased movements and swimming over greater distances to reach the retreating sea ice (Pilfold et al. 2017; Lone et al. 2018).

A critical aspect of polar bear life history is the use of over-winter maternity dens, typically dug into snow drifts, to give birth and protect newborn cubs from the harsh environmental conditions (Ramsay and Stirling 1986; Messier et al. 1994; Stirling 2011). Pregnant females usually enter maternity dens sometime in October to mid-December (Amstrup and Gardner 1994; Messier et al. 1994; Wiig 1998; Amstrup 2003; Derocher et al. 2011; Laidre et al. 2015a; Olson et al. 2017; Escajeda et al. 2018), where they give birth to one to three altricial cubs in mid-November to mid-January

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(Harington 1968). In Svalbard, European Arctic, Derocher et al. (2011) demonstrated that plasticity in how late females enter the dens is limited. Females failed to den on an island if sea ice had not formed before December around it. Females spend up to 8 months in dens and emerge between February and May when the cubs weigh about 10 kg (Amstrup 2003). Dens typical occur on land, although they have also been found on land-fast ice (Laidre and Stirling 2020) or on multiyear sea ice in the Beaufort Sea (Lentfer 1975; Amstrup and Gardner 1994; Fischbach et al. 2007). Also, females in some areas in Canada are observed to enter dens made into peat banks during autumn. These later get extended into the adjacent snow drifts in winter (Stirling 2011). As polar bears in general spend much of the year on sea ice, their life cycle is tightly linked to its seasonality, as it retreats in the spring and advances in the fall. Hence, timing of arrival of pregnant females in maternity denning areas varies amongst populations ranging from months to days before den entry, depending on local sea ice dynamics around these denning areas (Ramsay and Stirling 1990; Fischbach et al. 2007). Derocher et al. (2011) showed that later arrival of sea ice around a denning area in Svalbard negatively correlated with the number of dens found there the following spring. Additionally, it negatively correlated with body mass of adult females and their cubs at den emergence. Thus, Derocher et al. (2011) highlighted that for polar bears to persist not only the amount of available sea ice habitat for hunting is essential, but crucially its seasonal availability and accessibility around denning areas must be sufficient for successful polar bear reproduction.

How maternity dens are distributed varies considerably throughout the Arctic, depending on land topography, sea ice dynamics, climate and other factors. Whilst bears in the Southern Beaufort Sea area frequently den out in the multiyear ice or if on land, close to the coast (Amstrup and Gardner 1994; Durner et al. 2010), bears in other areas, such as Western Hudson Bay frequently den far inland (Stirling 2011). Whilst polar bear maternity dens in most areas are widely separate and found at low densities, high aggregations have been found in some areas in east Svalbard and on Herald and Wrangel island in the eastern Russian Arctic (Amstrup 2003).

The goal of this study was to quantify observed and projected availability of maternity denning habitat in the European Arctic, focussing on the changing availability of sea ice corridors to reach denning areas and assuming that snow cover is no limiting factor. This part of the Arctic experienced dramatic shifts in sea ice distribution in the mid-2000's and a marked reduction since then (Lind et al. 2018). It has experienced a loss of sea ice habitat that has been more than twice the rate than in any other part of the Arctic occupied by polar bears (Regehr et al. 2016), a pattern predicted to continue in coming decades (Durner et al. 2009). Quantifying the historical impact of sea ice loss on the availability of terrestrial denning habitat for polar bears, and how availability is likely to decline throughout the twenty-first century, can improve our understanding on how climate change impacts polar bear populations and better inform conservation decisions.

Materials and methods

Our study area encompasses the Barents Sea polar bear subpopulation (Obbard et al. 2010) and consisted of the three archipelagos surrounding the Barents Sea (70–82 °N, 10–70 °E) in the European Arctic (Fig. 1). These include the Svalbard Archipelago (SVB) on its western edge (74–82 °N, 10–35 °E), Franz Josef Land (FJL) in the north-eastern Barents Sea (79–82 °N, 44 62 °E) and Novaya Zemlya (NZ) on its eastern edge (70–77 °N, 52–69 °E). We subdivided Svalbard into a western (WSVB) and eastern (ESVB) part based on the oceanography around this island group (Loeng 1991) and known space use ecology (site fidelity) of the Barents Sea polar bear population (Lone et al. 2013). Similar, we subdivided Novaya Zemlya into a southern (SNZ) and northern (NNZ) island group. Next, we estimated potential polar bear maternity denning habitat and observed and predicted arrival timing of sea ice during autumn and early winter around these archipelagos to quantify past and future availability of maternity denning habitat. In the following, we identified areas that are suitable for maternity denning, modelled using topography and assumed to be constant (assumption is based on snow not being a limited factor). Then, we identified which of those areas were and would be accessible based on past (observed) and future (predicted) sea ice distribution, respectively.

Estimating potential maternity denning habitat

Potential maternity denning habitat was estimated using a topographic habitat selection model (using elevation and slope) built for denning habitat in eastern Svalbard (details in Merkel et al. 2020). This model was chosen over a superior snow drift model as it predicts potential maternity denning habitat based on static predictors and does not rely on yearly meteorological input data. It models prime den habitat within areas of ~ 15 to 35° slope and ~ 50 to 250-m altitude. Other parameters like distance from the coast did not improve the model fit (see Merkel et al. 2020 for details). This model was applied to all island groups in our study area. The model utilizes data from an Arctic wide 10-m high-resolution (10 × 10-m pixels) digital elevation model (Porter et al. 2018) to calculate the relative probability of finding maternity den habitat on any given island across the Barents Sea. These probability surfaces were then

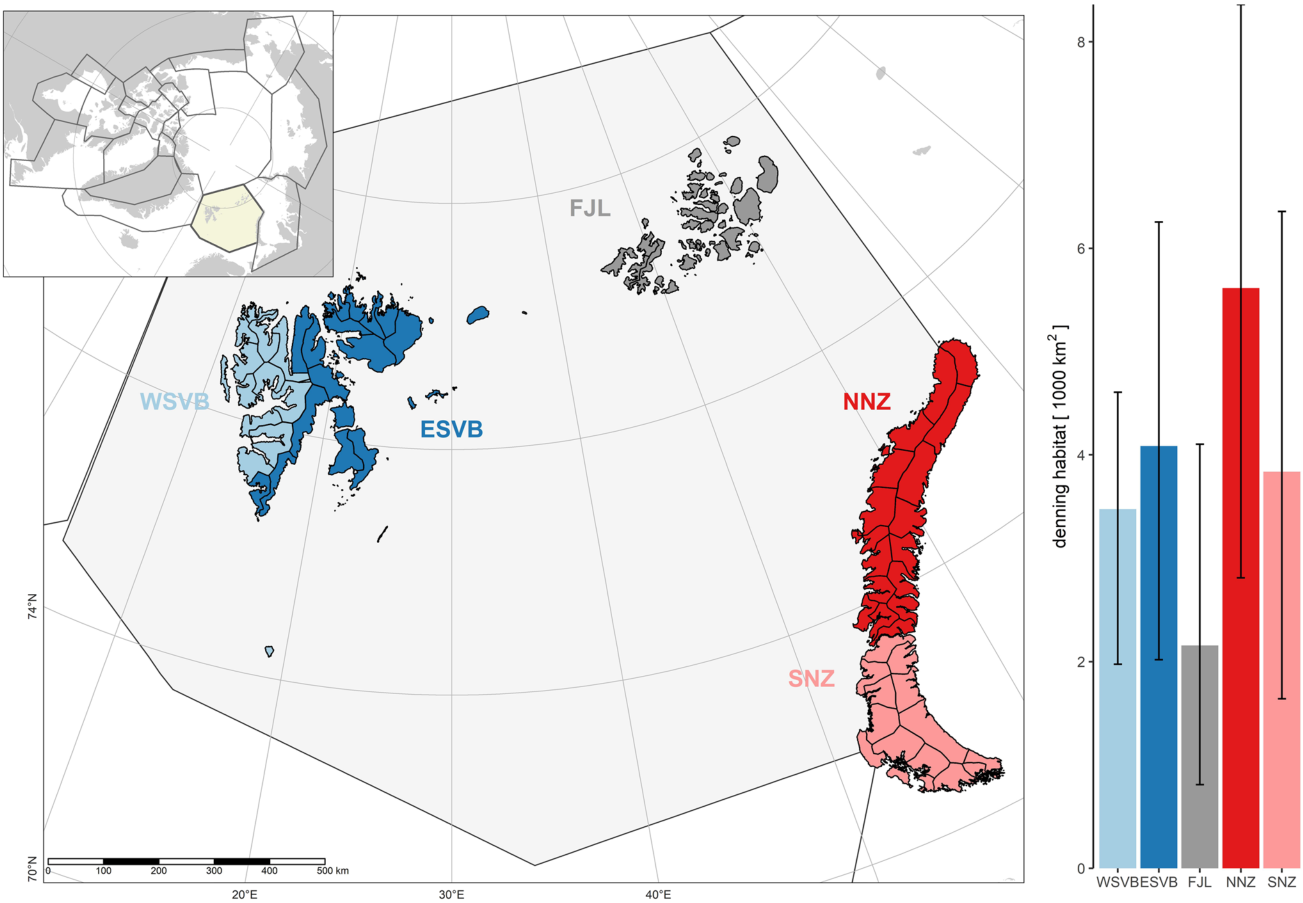


Fig. 1 *The study area*. A map including the three archipelagos in the Barents Sea. These are: Svalbard—divided into a western (WSVB) and eastern section (ESVB), Franz Josef Land (FJL) as well as Novaya Zemlya a southern (SNZ) and northern part (NNZ). All land masses have been split into coastline section of 200 km in length. Inset illustrates the 19 Polar bear subpopulations (Obbard et al. 2010) with the relative location of the Barents Sea subpopulation highlighted. Barplots on the right denote modelled potentially available denning habitat on each island group based on its topography with the likely model variability shown as error bars

transformed into areas of potential maternity denning habitat using probability thresholds derived from observed denning locations recorded in Svalbard during 1972 to 2010 (553-dens, Andersen et al. 2012). Accordingly, potential maternity denning habitat was defined as the areas of the estimated probability surface encompassed by all probabilities more or equal than 0.22 (corresponding to 33% of all known dens). Denning habitat variability in turn was assessed by estimating potential denning habitat using all probabilities included by 0.13 (25% of known dens) and 0.43 (50% of known dens). The resulting binary denning habitat surface was used to weigh the different archipelagos within the study area in terms of denning habitat.

Assessing autumn sea ice arrival date

All larger land masses in the study area (> 300-km coastline length) were divided into 200-km long coastline segments to evaluate sea ice arrival in different areas of the Barents Sea (Fig. 1). Date of sea ice arrival was calculated following Derocher et al. (2011). Sea ice arrival date for each coastline segment or smaller island, with its respective denning habitat, was defined as the first instance sea ice concentration reached or exceed 60% within a 50-km buffer around the coastline segment or island after 1 September. Historical observed sea ice arrival was estimated using daily (every second day until 1987) remote sensed sea ice concentration from 1979 to 2020 with a 25-km resolution (Stroeve and Meier 2018). Predicted future sea ice arrival was estimated using daily modelled sea ice concentration until 2100 based on seven CMIP6 models (ACCESS-CM2, NorESM2-LM, NorESM2-MM, BCC-CSM2-MR, CanESM5, CNRM-ESM2-1 and EC-Earth3; SIMIP Community 2020; Smith et al. 2020) with a resolution of 100-km and using SSP2-4.5—"moderate mitigations", the combination of shared socioeconomic pathway (SSP) 2—development along historical patterns ("middle of the road")—and climate scenario 4.5-W m^{-2}—radiative forcing applied as the change in net, downward minus upward, radiative flux taken up by the earth system due to enhanced greenhouse effect (corresponding to RCP (Representative Concentration Pathway) 4.5 in CMIP5). Here we use the first ensemble member (r1i1p1f1 or r1i1p1f2) from each model. These CMIP6 models were selected based on their ability to predict sea ice freeze-up dynamics during autumn, the target period for this study (Smith et al. 2020). Observed and predicted availability of denning habitat was then estimated as all potential islands and coastline segments reachable within 1 December or at last 1 January. We chose these conservative cut offs based on previous work on polar bear denning phenology in the Barents Sea (last observed day of den entry: 12 Dec, Wiig 1998), East Greenland (24 Nov, Laidre et al. 2015a), Baffin Bay (20 Nov, Escajeda et al. 2018), Canadian Arctic archipelago (12 Oct, Messier et al. 1994; Ferguson et al. 2000) and Southern Beaufort Sea (25 Nov, Amstrup and Gardner 1994; Olson et al. 2017). Derocher et al. (2011) showed that females in eastern Svalbard did not reach the Hopen island denning area if sea ice did not form before December, but variation in denning phenology both amongst and within areas made it relevant to include the later date (1 January) in our study. All analyses have been conducted using R 4.0.4 (R Development Core Team 2021).

Results

Potential maternity denning habitat in the Barents Sea was estimated to be 19,176-km^2 (9260–29,682-km^2), with most habitat in Svalbard and Novaya Zemlya (Fig. 1). On average 13% (6–19%) of each island group was estimated to be denning habitat (WSVB: 15% (8–20%), ESVB: 12% (6–18%), FJL: 14% (5–26%), NNZ: 13% (6–19%), SNZ: 11% (5–19%)). During the 1980's, 53% of potential denning habitat in the Barents Sea was reachable for pregnant females before 1 December (Fig. 2). The average date when sea ice had formed around the different denning areas, weighted by the area of its potential denning habitat, varied from 8 October to 31 December (WSVB: 31 Dec, ESVB: 13 Nov, FJL: 8 Oct, NNZ: 23 Nov, SNZ: 16 Dec, Fig. 3). This average moved forward in time by 29–55 and 13–102 days by the 2010's (observed) and 2090's (predicted), respectively, whilst some areas now remain or are predicted to remain ice-free year-round (Fig. 3). This resulted in a reduction of available denning habitat of 67% and 100% compared to 1980's by the 2010's and 2090's, respectively. This reduction was not homogenous across the study area, but rather followed a southwest to northeast gradient (Fig. 4), with most loss visible early in WSVB (100% loss by 2010's), whilst denning habitat availability on FJL remained unchanged (0% reduction by 2010's) but is predicted to decrease by 100% until the end of the century.

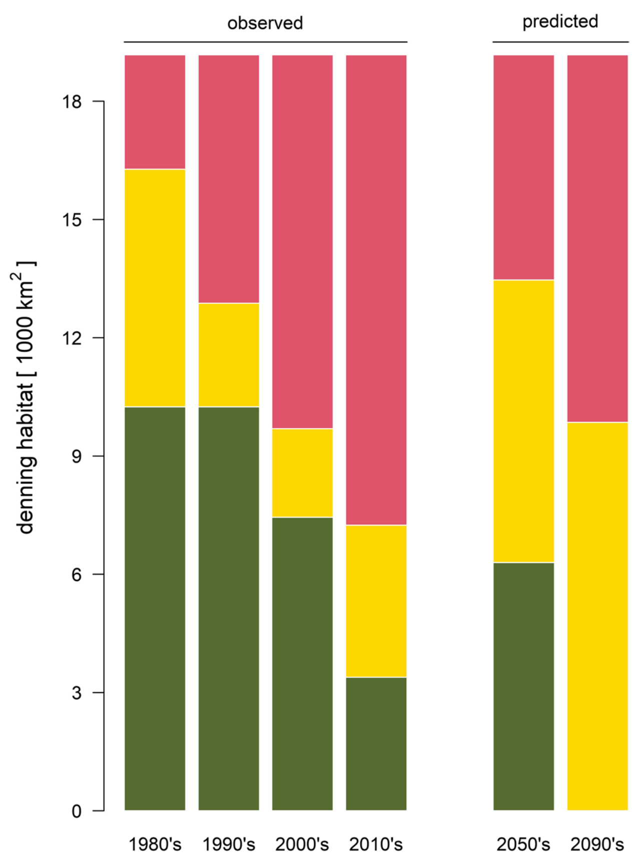


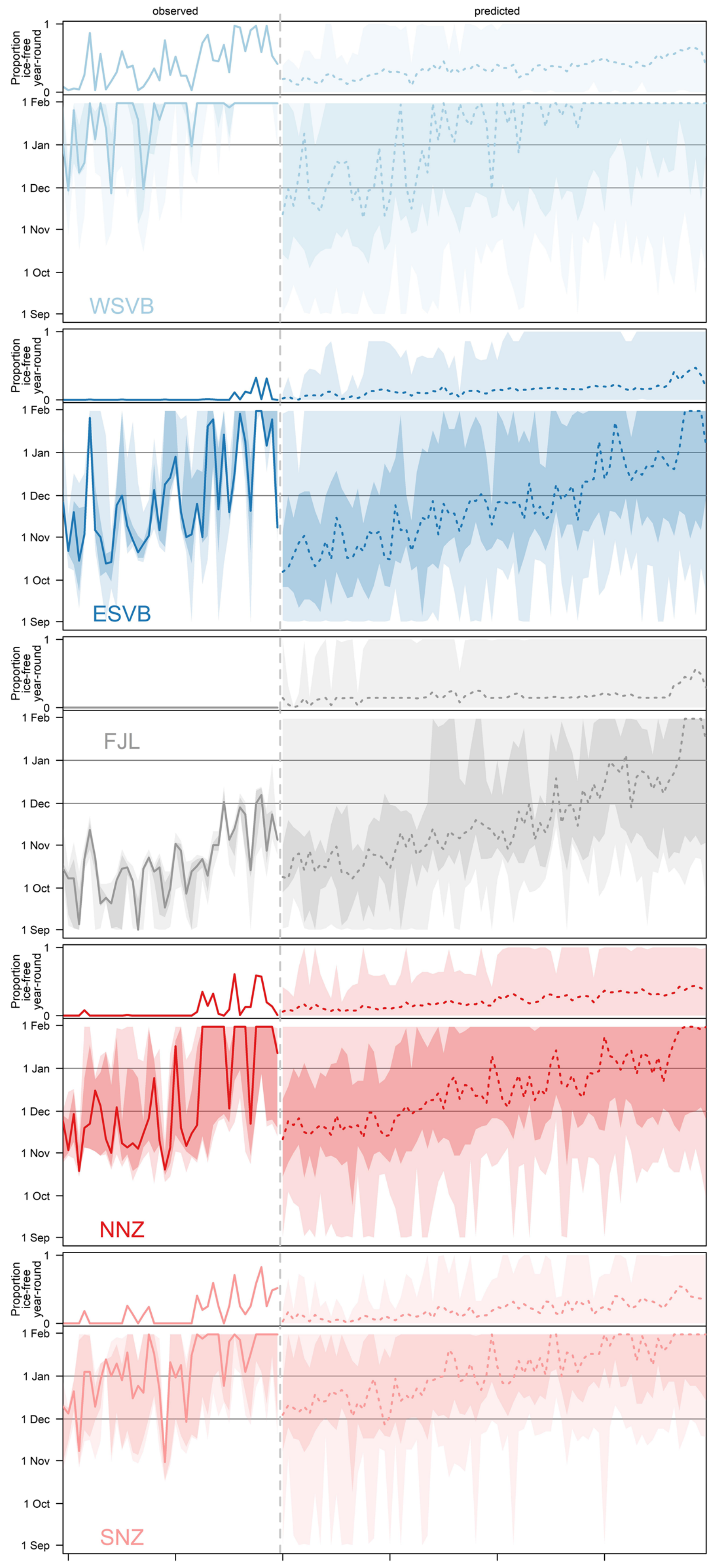
Fig. 2 *Shift in availability of potential denning habitat*. Observed and predicted shift in decadal average denning habitat availability in the Barents Sea. Green, yellow and red denote areas with sea ice arrival in time (≤ 1 December), potentially still in time (> 1 December and ≤ 1 January), and not in time (> 1 January) for pregnant females roaming the pack ice to reach maternity denning areas, respectively

Discussion

Here we quantified the observed (1979–2020) and predicted (until 2100) availability of terrestrial polar bear maternal denning habitat across the European Arctic and identified a clear decreasing trend. Potential denning habitat was considered constant throughout the decades included in our study. Therefore, the observed trend was the consequence of a decreasing ability to reach these habitats, under the assumption that presence of sea ice around denning areas is essential to allow polar bears to reach them, in accordance with earlier ecological findings from the area (Derocher et al. 2011).

During the 1980's and 90's, important denning areas in the Barents Sea were accessible in time to enter maternity dens for bears spending their summer in the open pack ice (Derocher et al. 2011; Andersen et al. 2012; Aars 2013). Since the early 2000's a clear southwest to northeast decreasing trend in maternity denning habitat availability is apparent, with the most visible reduction in sea ice in western

Fig. 3 *Regional timing of sea ice arrival*. Shift in timing of available observed and predicted potential maternity denning habitat throughout 1979 to 2020 and 2020 to 2100, respectively. Each panel illustrates the median (as line), 25–75% quantile (as dark shape) and 5–95% quantile (as light shape) in west (WSVB) and east Svalbard (ESVB), Franz Josef Land (FJL) and northern (NNZ) and southern Novaya Zemlya (SNZ), respectively. All arrival timings are weighted by potential denning habitat for each coastline section and island in each group. The proportion of each island group ice-free year-round is displayed in the top of each panel. Coloured shapes for the predicted future time frame denote the spread of model predictions



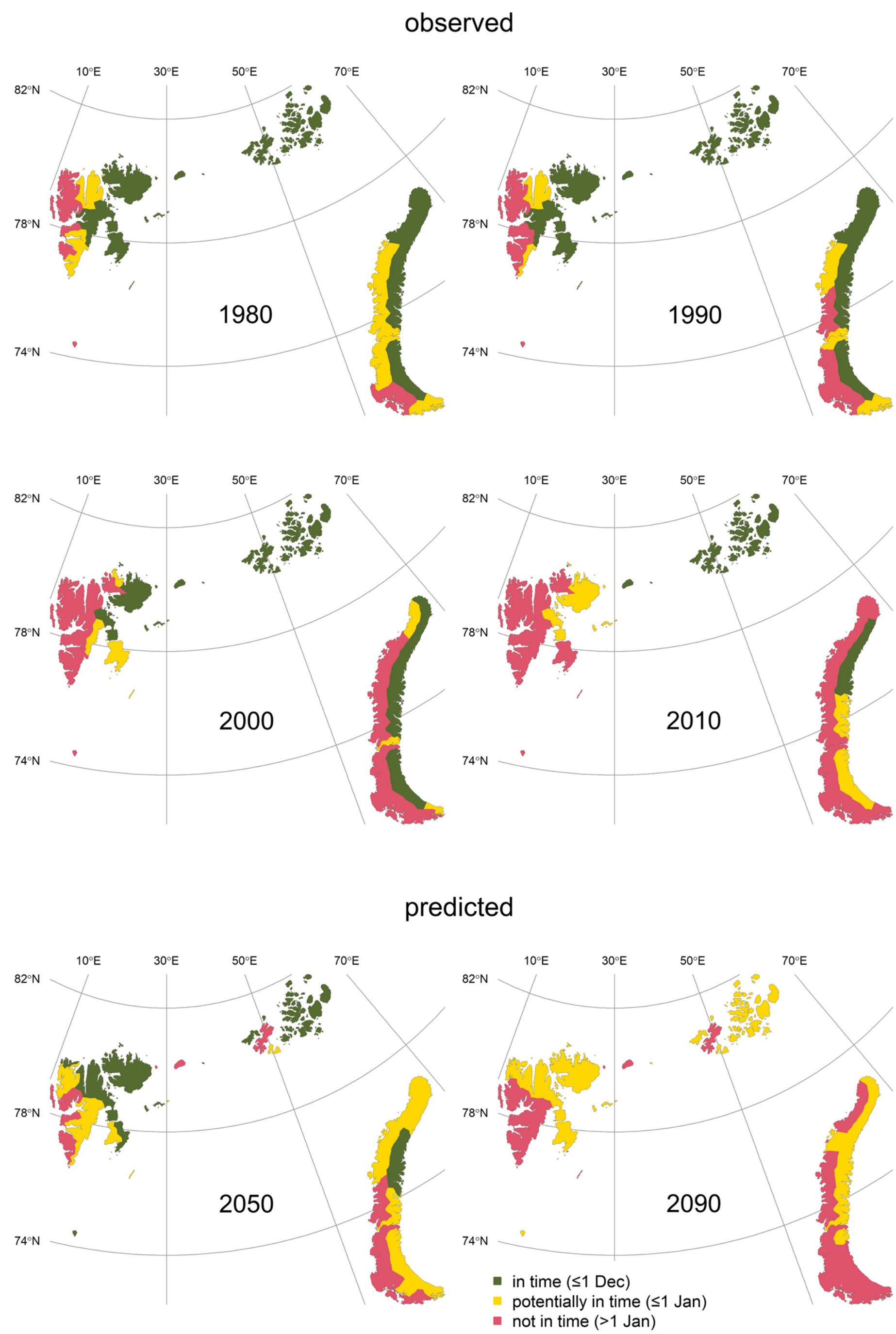


Fig. 4 *Spatial change in sea ice arrival timing*. Observed and predicted shift in decadal average arrival of sea ice around different island groups in the Barents Sea

Svalbard and southern Novaya Zemlya. This coincided with an observed reduction in the number of dens found in the eastern parts of Svalbard during a similar time period (Derocher et al. 2011; Andersen et al. 2012; Aars 2013; Norwegian Polar Institute 2021). The lack of sea ice formation in some areas leading to a reduced availability of these denning areas could have led to a shift in denning distribution, and thus not necessarily a reduction in the number of dens in the Barents Sea area (Andersen et al. 2012). Another area where changes in sea ice availability have significantly affected den distribution is the Beaufort Sea. The number of offshore dens in the preferred multiyear sea ice habitat decreased by 40% by the early 2000's (Fischbach et al. 2007), which was directly related to sea ice distance from the coast (Olson et al. 2017). In difference from the Barents Sea, where denning on land is the only option due to lack of stable multiyear ice, a warmer climate and habitat loss may thus lead to more bears denning on land, because they may not be able to reach their earlier preferred denning habitat in the multiyear ice. In both cases, less sea ice hinders bears to reach preferred denning areas due to a warmer climate and melting of sea ice. Franz Josef Land is predicted to undergo the same reduction in denning habitat availability as the rest of the Barents Sea archipelagos due to later sea ice arrival. Later arrival is already observable around these islands in recent decades, but still sea ice forms in time for pregnant females to reach them. It must be noted however that CMIP6 models, used to project future autumn sea ice arrival timings, showed most uncertainty when modelling the sea ice freeze onset dates in inflow regions into the Arctic Ocean (areas connected to Atlantic or Pacific seas) such as the Barents Sea (Shu et al. 2020; SIMIP Community 2020; Smith et al. 2020). This is apparent in the large variations visible in the model predictions (Fig. 3). Although the decreasing trend is clear, the future magnitude of change and timing in available denning habitat is uncertain. This is also visible in earlier freeze-up timings predicted by the models compared to the observed timings thus far, suggesting that our predictions might be on the conservative side.

This study builds on the assumption that polar bears inhabit the open pack ice of the Barents Sea and Arctic Ocean during most of the year and hence require sea ice around land masses to reach appropriate denning habitat in the autumn. Previous studies have identified two distinct ecotypes of polar bear females in the Barents Sea: (1) 'coastal' bears remain within the Archipelago of Svalbard year-round, whereas (2) 'offshore' bears follow the marginal ice zone in the Barents Sea and Arctic Ocean (Mauritzen et al. 2002; Blanchet et al. 2020). Consequently, the results of this study apply to the 'offshore' part of the population only, as denning habitat availability was defined based on sea ice concentration around land masses. However, this 'offshore' ecotype potentially constitutes 90% of the total population as the number of 'coastal' Svalbard bears are likely less than 300 (Aars et al. 2009, 2017). Some (an unknown proportion) more bears may have a similar local strategy in Franz Josef Land, also being independent of sea ice to reach denning areas. This number is not likely higher than the number of 'coastal' Svalbard bears, as only about 300 bears were estimated to be in FJL during August 2004, and many of those could have been 'offshore bears', given the ice edge intersected the archipelago during the survey period (Aars et al. 2009). 'Coastal' bears will be able to reach denning areas, but ever shorter periods with sea ice around islands, resulting in ever longer fasting periods during the summer may impose other challenges to this ecotype (Pagano et al. 2018; Pagano and Williams 2021).

Another aspect of the main assumption of this study is the requirement of sea ice as platform to reach denning habitat. Long distance swimming has been documented for polar bears (Pagano et al. 2012), including in the European Arctic (Lone et al. 2018). Females are also documented swimming about 100-km from denning areas to the ice edge in August (Aars et al. 2017), but Lone et al. (2018) noted that, whilst swimming is not uncommon throughout the spring and summer, females did not seem to swim from the open pack ice to reach their traditional denning areas in late autumn. This is supported by Derocher et al. (2011), Aars (2013) and Norwegian Polar Institute (2021) finding that few, if any, females went into maternity dens in eastern Svalbard in years when sea ice did not form around the islands before December. Possible explanations include an inability to detect prospective denning habitat and its relative position for females roaming the open pack ice far from land as well as the high energetic costs that swimming long distances entails (Pagano et al. 2018), which might limit pregnant females to travel by sea ice. Similarly, after emerging from the den in spring, young polar bear cubs are vulnerable to hypothermia when exposed to cold water (Blix and Lentfer 1979), restricting them to sea ice for travelling. This reinforces the importance of sea ice not only as hunting grounds, but also as travel platform to and from maternity denning habitats.

Maternity denning habitat in the European Arctic was estimated to be abundant in all archipelagos given enough snow, and the amount of snow in winter has actually been increasing at least in Svalbard in recent decades (Van Pelt et al. 2016). Reduced availability of denning habitat in some areas, due to later freeze-up, may not be critical as long as denning habitat in other areas remains accessible to pregnant polar bears. Females have been observed to shift denning areas given no alternative (Norwegian Polar Institute, unpublished), something that is also supported by the observed genetic structure on different scales amongst adult females in Svalbard (Zeyl et al. 2010), where significant within denning area structure was found whilst little structure was apparent on the larger scale between denning areas. But loss of denning areas does present a form of habitat fragmentation that might result in reduced connectivity across the population if it persists over a longer period. This is supported by the exhibited high degree of site fidelity in Barents Sea polar bears in terms of denning areas as well as year-round area use, which is even visible across generations (Zeyl et al. 2009; Lone et al. 2013; Brun et al. 2021), and a recent increased genetic structure between different areas within Svalbard that best may be explained by less gene flow from the bears living offshore (Maduna et al. 2021).

Here we showed a clear decreasing trend in polar bear denning habitat availability across the European Arctic. This is a result of successively later sea ice arrival around denning areas in autumn over the last decades, and a further predicted significant reduction that could make most denning areas unavailable to bears that hunt in open pack ice. Our analysis show how Svalbard already was less accessible to 'offshore' bears in the 2010's, supporting the empirical data (Derocher et al. 2011; Aars 2013; Norwegian Polar Institute 2021), and the prediction under the SSP2-4.5 scenario is that by the 2050's, only the northern part of FJL may allow 'offshore' bears to reach denning habitat by 1 December. By the 2090's, also FJL may be unavailable by that date, and only if plasticity in denning phenology allows successful reproduction for females arriving denning areas as late as between 1 December and 1 January, 'offshore' bears may still have some restricted areas for reproduction in the European Arctic. Our findings indicate that a future scenario with smaller and more local populations of polar bears may be more likely, given that local conditions under future climate scenarios will be able to support these populations, and if not, that further loss of sea ice may be a threat to the Barents Sea population. Thereby, we highlight the importance of the temporal dimension of sea ice dynamics for the persistence of polar bear populations. A potentially abundant food resource in the open pack ice becomes irrelevant if reproduction becomes impossible due to an inability to reach denning habitats.

Author contributions BM & JA designed the study, BM conducted the analyses, BM & JA wrote the manuscript.

Funding Open Access funding provided by Norwegian Polar Institute. The work was funded by program HAV-3, Norwegian Ministry of Climate and Environment.

Data availability This study is based on remote sensed data, model simulations and published results. The R scripts used for the analyses are available at https://github.com/benjamin-merkel/Polar-bear-den-habitat.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval This study is based on remote sensed data, model simulations and published results.

Informed consent This study is based on remote sensed data, model simulations and published results.

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