

Sea ice resource selection models for polar bears in the Barents Sea subpopulation

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Abstract

The extent, thickness and age of Arctic sea ice has dramatically declined since the late 1990's, and these trends are predicted to continue. Exploring the habitat use of sea-ice-dependent species can help us understand which resources they use and how their distribution depends on sea ice conditions in a changing environment. The goal of this study was to develop predictive models of the habitat use of an arctic apex predator. Polar bear (*Ursus maritimus*) habitat use of the Barents Sea subpopulation was modelled with seasonal resource selection functions (RSFs) using satellite-linked telemetry data from 294 collars deployed on female polar bears between 1991 and 2015. Polar bears selected habitat in the Marginal Ice Zone, with a preference for intermediate sea ice concentrations [40-80%]. They spent most time in areas with relatively short travel distances to 15% or 75% ice concentration, and during spring and autumn they exhibited a preference for sea ice areas over the continental shelf (i.e. over shallow water). Predictions of the distribution of polar bears in the Barents Sea area can be made for specific sea ice scenarios using these models. Two such predictive distribution maps based on the autumn seasonal model were made and validated against two independent polar bear survey datasets collected in August 2004 and August 2015. The distribution of optimal polar bear habitat has shifted strongly northwards in all seasons of the year during the 25 year study period.

Keywords: arctic marine ecosystem, biotelemetry, Resource Selection Function (RSF), Marginal Ice Zone, spatial distribution

Introduction

Polar bears (*Ursus maritimus*) live in a highly variable, dynamic environment. The sea ice they rely on for hunting, resting and travelling changes daily, seasonally and annually (Falk-Petersen et al. 2000). While polar bears have evolved in the Arctic and are accustomed to high levels of environmental variability, they are currently experiencing dramatic long-term reductions in sea ice extent and volume (ice is thinner and younger), as well as a shorter duration of seasonal ice cover, that clearly exceeds the normal variability that characterizes the system (Laidre et al. 2015a, Stroeve et al. 2012). Climate models predict continued declines of sea ice across all months, and possibly an ice free Arctic occurring for the first time as early as in 2037 (Wang and Overland 2009). This is expected to have large negative consequences for polar bears across their range (Amstrup et al. 2008, Regehr et al. 2010, Stirling and Derocher 2012). Negative consequences on reproduction, condition and survival rates have already been reported in southern Beaufort Sea and western Hudson Bay subpopulations (Lunn et al. 2016, Regehr et al. 2010, Rode et al. 2014). These trends have been linked to habitat availability, habitat use and/or foraging ecology. Habitat selection has been investigated across several polar bear subpopulations, and a general model developed for the Arctic as a whole indicates a large decline in high quality polar bear habitat in the 21st century (Durner et al. 2009). However, sea ice conditions, oceanographic conditions, foraging conditions, human impacts and other ecologically relevant variables vary greatly regionally, so there is a need to develop more area specific habitat selection models for different subpopulations of polar bears, where such data are used for conservation purposes.

Earlier studies have consistently shown the importance of sea ice conditions for polar bear habitat selection (Arthur et al. 1996, Durner et al. 2004, Durner et al. 2009, Ferguson et al. 2000, Mauritzen et al. 2003, Wilson et al. 2014), in addition to other environmental variables such as distance to land or bathymetry. However, the dynamic nature of sea ice means that it can be challenging to obtain datasets that adequately describe it. Size of floes, surface roughness, whether it is first year ice or multiyear ice, land-fast ice or drift ice, have all been used in different models to better elucidate how polar bears relate to the sea ice (Ferguson et al. 2000, Freitas et al. 2011, Mauritzen et al. 2003, Pilfold et al. 2014a). Polar bear habitat selection varies through the year with respect to ice conditions for all subpopulations investigated. This is thought to reflect the occurrence and availability of their seal prey species in different seasons. Yet only a few recent studies have modelled foraging habitat explicitly, and then only for a short period in spring (Pilfold et al. 2014a, Pilfold et al. 2014b, Pilfold et al. 2015). Polar bear habitat selection studies remains a useful exercise to understand how this species interacts with their prey and to explore their foraging ecology under changing sea ice conditions.

How recent changes in sea ice impact habitat selection and habitat use by polar bears has been studied in a few subpopulations. Polar bears in Eastern Greenland have shifted their use of sea ice in terms of concentration; they now spend more time in lower concentrations and are typically found much closer to the ice edge in the 2000s than in the 1990s (Laidre et al. 2015b). However, this difference in habitat use was not due to polar bears selecting habitat differently - their preferences were largely the same in both decades - but due to reduced availability of their preferred sea ice types in the 2000s (Laidre et al. 2015b). Potential changes in habitat selection have also been investigated

in the Chukchi Sea subpopulation using data collected in 1986-1994 and data collected in 2008-2013. The annual patterns in selection of sea ice concentration remained very similar between the two periods, and there were no statistical differences in selection of ocean depth or sea ice concentration (Wilson et al. 2016). Over the last 30 years, the Barents Sea has undergone the greatest reduction in extent and duration of sea ice cover of any of the areas where subpopulations of polar bears are found (Laidre et al. 2015a). Projections of continued sea ice loss in the 21st century form the basis for an expected high rate of loss of good quality habitat in the decades to come (Durner et al. 2009), making it a particularly interesting case study.

Earlier studies of polar bears in the Barents Sea subpopulation show a preference for intermediate sea ice concentrations, but also that selection patterns depend on the availability of different sea ice types (Mauritzen et al. 2003). Polar bears in this area tend to either stay close to the islands within the Svalbard Archipelago, or to wander extensively in the marginal ice zone (MIZ) (Mauritzen et al. 2001). These strategies are repeatable to the extent that the bears using them belong to either a “coastal” or “offshore” ecotype (terms “local” and “pelagic” were used in Mauritzen et al. 2001). Both types of bears use sea ice extensively. The aim of this study was to develop Resource Selection Function (RSF) models for polar bear habitat use in the Barents Sea across a twenty-five year time frame (1991-2015) that perform well under changing sea ice conditions, so they can be used for predicting polar bear habitat use for this region into the future. This knowledge will be essential for management and conservation planning for the Barents Sea polar bear subpopulation as the region gradually becomes ice free for longer periods of the year and faces increased anthropogenic impacts (e.g. ship traffic and interest in offshore oil and gas development).

Methods

Study area and capture data

The Barents Sea is a shallow shelf sea in the European Arctic, with an average depth of 230 m. This sea encompasses the Svalbard and Franz Josef Land (FJL) archipelagos (Fig. 1). It extends from the deep Norwegian Sea in the west to the west coast of Novaya Zemlya in the east and from the Norwegian mainland and Russian coast in the south to the shelf edge that marks the transition to the Arctic Ocean basin in the north. Polar bears in the Barents Sea area also use surrounding areas, for instance to the north of the shelf at the edges of the Arctic Ocean. As sea ice declines, areas farther north may become the only area where sea ice is available to the polar bears in this subpopulation, at least during summer and autumn. Therefore the study area extended northwards of the main areas used today, using 86°N as the northern limit of the area of inference for the models developed herein (Fig. 1).

Location data for 226 individual adult female polar bears, from 294 satellite-linked transmitters (producers: ATS, Insanti, MS, USA; SirTrack, Havelock North, New Zealand; SMRU, St Andrews, UK; Telonics, Mesa, AZ, USA) deployed in Svalbard and the Barents Sea area are used herein. These data cover a period starting in 1991. Captures of polar bears for collar deployments in this study followed standard protocols (Stirling et al. 1989) and occurred mainly in April, but also in some years during March, May, August and September.

Location data

Polar bear locations were obtained using Argos (Toulouse, France) or GPS (Global Positioning System). Positioning became more accurate with a gradual transition from using mainly Argos location systems to GPS; the first GPS deployments occurred in

2000. Different collars used either Argos or Iridium (McLean, Virginia, U.S.A.) satellite systems to transfer the data, with either of these systems also providing a position in the cases where obtaining one by GPS failed. Activity and temperature data were recorded in addition to positional data. Sampling regimes of deployed tags ranged from one position every 2 hours to one position every 7th day across the study period. For the analyses presented herein, we used only the most accurate positions (classes 1, 2 and 3) for Argos data. All locations were run through a speed filter with a $10 \text{ km}\cdot\text{h}^{-1}$ threshold (McConnell et al. 1992). The polar bears rarely move more than $4 \text{ km}\cdot\text{h}^{-1}$ over extended periods, unless actively helped by sea ice drift or water currents when swimming (Andersen et al. 2008). For Argos derived positions, the best position for each day was retained, while for GPS data the first position from each day was kept. Subsequently, the data were subsampled to include only one position for every 6 days, as this frequency was the most used sampling regime prior to the year 2000. Under the different sampling regimes, positions used were not always exactly 6 days apart, so we split the tracking period into a series of 6 day periods for which we only retained a single position, but we did accept data for intervals between 4 and 9 days. Positions on land, including positions where females had maternity dens, were excluded from the analyses because the focus of this study was movement patterns in relation to sea ice. Denning activity was assessed based on positions, temperatures, and frequency of signals reaching the satellites, with methods described earlier (Andersen et al. 2012, Messier et al. 1994). Bear location data was not limited to the delineated area of inference for the models, but only 1% of the used locations were outside this box (Fig. 1).

To account for changing habitat selection throughout the year and the uneven distribution of location data (i.e. most data in May due to most captures happening in spring), the data were divided into three seasons based on annual sea ice conditions and the ecology of the annual cycle of polar bears. The three seasons considered were: 1 November to 31 March (“winter”); 1 April to 31 July (“spring”) and; 1 August to 31 October (“autumn”).

Habitat data

Daily estimates of sea ice concentration (12.5 km resolution) were obtained from the ASI algorithm Special Sensor Microwave Imager / Sounder instrumentation data (SSMIS). The ASI-SSMIS sea ice concentration data were originally computed at the Institut Français de Recherche pour l'Exploitation de la MER (IFREMER, Brest, France, <http://wwz.ifremer.fr/>), but were further processed and provided as a 5-day median-filtered and gap-filled product by the Integrated Climate Data Center (ICDC, University of Hamburg, Hamburg, Germany, <http://icdc.zmaw.de/>, accessed 14 January 2016) (Kaleschke et al. 2001, Spreen et al. 2008). In this study, only sea ice concentration data from this single source were used to avoid the possible biases arising when using data sets from two or more sensors. This sea ice data product was available for every day starting from 5 December 1991 through to 2015 (when it was accessed for this study); it will be continued with regular updates. In calculations of distance to various sea ice concentration thresholds, it was assumed that there was 100% sea ice cover in the area surrounding the North Pole (north of the study area) where this dataset did not provide coverage. Ocean depth estimates were obtained from the International Bathymetric Chart of the Arctic Ocean (IBCAO, Jakobsson et al. 2012) and rescaled from the original 500 m resolution to match the 12.5 km resolution of the sea ice data. A

raster with distance to land was also calculated at the same resolution, using open source vector maps of coastlines downloaded from <http://geodata.npolar.no/> for Svalbard's islands, and <http://www.naturalearthdata.com/> for all other landmasses.

Resource selection modelling

Seasonal RSFs were developed to estimate the relative probability of use of available habitat by polar bears. Only pairs of consecutive locations separated by 4 to 9 days (“steps”) were retained for this analysis, since resource availability was defined based on the previous location of the bear along with speed and time. What resources are considered available is critical in the application and interpretation of step selection functions (Thurfjell et al. 2014). A circular buffer method was used to consider what was regionally available to the bear, without including areas the bear would be unable to reach (paralleling the approach of Durner et al. 2009). An alternative approach, which potentially describes animal movement more precisely, uses empirical distributions of step lengths and angles to define available locations (Forester et al. 2009). The application of this method was explored but not implemented for three main reasons. One, at the time scale considered in this paper, bear movement was not markedly directional. Two, restricting possible locations to on-sea ice and excluding all other locations from the analysis altered the distribution of step lengths such that it no longer reflected the empirical distribution. And finally, it was considered too restrictive at times when sea ice distribution changed rapidly. Thus, habitat availability for each step was defined as the area encompassed by a circle with a radius the size of which was defined by the distance a bear could have covered in the time since the last relocation if it travelled at the population-wide 97.5th quantile speed ($1.78 \text{ km}\cdot\text{h}^{-1}$). Month-specific speed cut offs were not used because month explained only 0.3% of the variation in

speed. Each 12.5 x 12.5 km pixel within the circle was defined as "available", and 25 of these pixels were selected as inputs to the model, to be paired with the pixel containing the polar bear's position (this was defined as "used"). Twenty five points were selected to limit processing time, while providing a sufficient measure of variability in each area (see Thurfjell et al. 2014). Only pixels including all covariates of interest were included in the modelling process, hence restricting used and available positions to sea ice areas. Covariates in the models included sea ice concentration, distance to either 15 %, 50 % or 75 % sea ice concentration, distance to land, and either bathymetry or the categorical variable on or off the continental shelf (defined by the 600 m isobath). A complete list of the candidate models is provided in Table 2. Accounting for "ecotype" of the bears in the models was explored, either as an interaction with distance to land, as this was the main covariate for which a difference was expected, or by fitting separate models for bears considered to belong to the "coastal" or "offshore" ecotypes. Both approaches were rejected as they necessitated excluding bears with insufficient data to determine ecotype (N=57), and the resulting models did not have better predictive capacities for each group compared to the common model all polar bear locations on sea ice.

The exponential RSF was estimated by modelling the used versus available pixels as a conditional logistic regression using the "survival" package (Therneau 2015) in R 3.2.2 (R Development Core Team 2015). The conditionality in the model was specified by using a unique identity assigned to each used position and the set of available pixels associated with it as 'strata'. Because the correlation between multiple observations from a bear can cause underestimation of the variance in the model, bear identity was included as a 'cluster' term to help control for unequal number of observations across individuals and compute a robust variance for the model.

Model selection and 3-way K-fold validation

One set of candidate models was developed in common for the three seasons (Table 2). The covariate ‘sea ice concentration’ and its second order effect were included in all candidate models due to its importance in defining polar bear habitat (see Durner et al. 2009). Then, for each season, the set of candidate models were screened so as to exclude any that contained strongly correlated covariates (Spearman correlation > 0.6). Final model selection was based on three-way k-fold cross-validation and AIC scores. Three-way k-fold cross-validation is a valid selection criteria when prediction is the main purpose of the modelling, because it ensures that the selected model has a good predictive capacity across random, temporal and spatial folds of the data (Wiens et al. 2008).

For each model, three separate five-fold cross-validations were conducted (see Wiens et al. 2008). First, the data were divided into 5 equal-sized parts, or folds, by random selection using the ‘sample’ function in *r* (“random” folds). Four of these parts were used to train the model – estimating model coefficients by fitting the model only to this subset of the data – while the fifth part was used as a test of this model. The model was trained 5 times in this way, so that each part was predicted by the other 4. This was repeated twice more, once with data split into year-based folds (4 to 5 years long, “temporal” folds) and once with the data split into 5 spatial folds (“spatial” folds, Fig. 1). The aim of the temporal and spatial elements was to assess the temporal and spatial predictability and consistency of the candidate models. This test of predictive ability in the retained fold evaluated whether an area ranked better in RSF value actually had a higher chance of being used by the animals (Boyce et al. 2002). We used “equal-area” bins of RSF values, for which the bin cut-offs were set so that equal numbers of

available locations fell into each RSF bin, hence each bin should represent approximately the same area in the physical landscape. The number of used positions with RSF scores within each bin should be higher for higher RSF-value bins. This is then tested using a Spearman rank correlation test. Each fold is evaluated using $\alpha = 0.05$ as the statistical criterion that the model performs better than random, and the average passing rate of this criterion is calculated across the random, spatial and temporal folds separately.

Although three-way K-fold cross-validation is more commonly used for model validation than as a model selection criterion in resource selection modelling, it is a valid selection criteria for predictive models (Wiens et al. 2008). Ideally, the selected model should have high correlation values and a predictive capacity (statistically shown to be better than random) across all folds. If, in a season, multiple models fulfilled this criterion, the best model among these was chosen based on AIC scores. If, in a season, no model made good predictions across all folds, the K-fold plots of the models that failed in the fewest folds were inspected, and final model selection was based on the best overall positive predictive abilities across all folds, with an emphasis on the main ice covered areas of the Barents Sea east of Svalbard.

Independent model validation

Two independent datasets of polar bear locations in the MIZ, obtained during aerial surveys in August 2004 (Aars et al. 2009) and August 2015 (Aars et al., submitted) were used to validate the autumn (August to October) RSFs. In 2004 the survey area included both Svalbard and FJL archipelagos, as well as the ice-edge between 10°E and 60°E. In 2015, the survey covered only Norwegian territories, west of 35°E. Transect lines were flown between 13 and 28 August in 2004 and 55 polar bears (or bear

families) were sighted. In 2015, the transect lines were flown between 5 and 29 August and 37 polar bears (or bear families) were sighted. When the survey transects were flown, they typically started at a clearly defined ice/no ice boundary.

Survey data was used to evaluate the August to October seasonal RSF by comparing them with model predictions using daily sea ice data at the time of the survey. An average RSF grid in each year was computed using all the daily maps from the start to the end of each survey period. These grids were overlaid with all line transects and polar bear observations. RSF values were compared with the number of observed individuals in each pixel. Spearman rank correlations were computed across equal-area bins of RSF values as in the K-fold procedure. Further, Wilcoxon rank sum tests were used to compare RSF values of pixels with and without polar bear observations. In this manner, RSF values from the entire surveyed area was compared with the RSF values at all polar bear locations from the systematic surveys. Daily RSF maps matched with flight day were tested on the 2015 data, but resulted in lower correlation values (Supplementary material Figure S1). This may be because the 12.5km resolution of the sea ice data is coarse relative to the scale operated on, and the accuracy of the daily sea ice maps may suffer from them being 5-day medians.

Predictive RSF maps and change in optimal habitat

Daily binary maps of optimal habitat were created, by predicting daily RSF maps and using a season specific RSF cut-off. This cut-off was set to include 70% of all used locations, and this corresponds to the top 50-55% RSF values in the different seasons. After classifying each pixel as optimal habitat or non-optimal habitat for each day, changes in distribution of available habitat over the study period could be visualized. The number of days an area was classified as optimal polar bear habitat during the five

earliest years of this study (1992-1996) was compared with the situation one (2001-2005) and two (2011-2015) decades later.

Results

Resource selection functions

The three seasonal RSFs were based on 7069 time steps by 226 polar bears in 294 tracks over 25 years (Table 1). The most influential track contributed 157 steps (2%), while the average number of steps from each track was 24 (standard deviation SD = 24). All seasons had data in at least 23 of the 25 years. The spring season had data comprised of almost all polar bears and with each track contributing on average 15 (SD = 13) steps. Data for autumn and winter were based on about half the number of individuals (162 and 121, respectively), with a similar average contribution of 10 (SD = 9) and 8 (SD = 7) steps per track, respectively (Table 1).

The three-way five-fold cross-validation for the seasons winter, spring, and autumn identified three, one and three models to be most useful, respectively (Table 3). In winter, all models failed in at least two folds and the top model was selected based on the best K-fold validation relationships overall (Table 4, Supplementary figure S2). Model 4 performed better than the rest as it passed spatial fold 3 and the temporal fold that failed (fold 3: 2001-2005) was close to statistical significance, with $p = 0.077$ (Table 4). The best winter model failed in spatial fold 1, containing 404 used positions. The spring model failed in one temporal fold, fold 1 (1991-1995) and two spatial folds, 4 and 5 (Table 4, Supplementary figure S3), containing 43% of all data and 7% of all data during this season, respectively. In autumn, the three best models were all classified as being statistically better than random in all folds, and out of these one top model was recognised ($\Delta AIC > 2$, Table 3).

The three seasonal habitat selection models included different covariates, and the pattern and effects of the covariates also varied, but they did have certain elements in common (Fig. 2, model coefficients are available in Supplementary Material Table S1). Polar bears selected an intermediate level of sea ice concentration over both lower concentrations and higher concentrations. Sea ice concentration had the greatest impact in the winter model, with a clear peak at about 60%, while it was selected the least strongly in the autumn model. Probability of selection decreased with distance to a sea ice concentration threshold in all seasons (Fig. 2). During spring and autumn, the threshold included in the model was the 15% sea ice concentration, with the strongest selection occurring in autumn. During winter, the threshold included in the top model was the 75% sea ice concentration. Distance to land did not have an effect in any of the top models. The models including distance to land typically performed poorly in the spatial folds 4 and 5 (these areas also had larger distances to land in the dataset than the other areas). Bathymetry was included in the top model for spring, with a higher probability of selecting shallower waters (compared to deeper waters; Fig. 2). A similar preference for shallow areas was apparent during autumn, but in these models the categorical variable “shelf” was included rather than bathymetry as continuous variable (Fig. 2).

Independent model validation

The survey in 2004 was spatially extensive and covered most of the areas with high predicted density of polar bears, with only one notable gap along the ice edge. The survey in 2015 was more limited spatially, and its southern extent did not align very well with the extent of the predicted distribution of polar bears across the month of August (Fig. 3). This is in part because the survey took place over a longer time

interval, 25 days (compared to 16 days), and the ice edge was moving a lot during this period.

Considering only the variability in RSF values within the surveyed areas, polar bear observations occurred in areas with significantly higher RSF values compared to surveyed areas without observations (Wilcoxon rank sum test, p-value = 0.044 for 2004, p-value < 0.001 for 2015). In 2004, the upper 10 % and 40 % of RSF values contained 29% and 57% of all individual polar bear observations (total 56), respectively. In 2015, the corresponding numbers were 32% and 78% of the 32 bear observations in the two RSF strata. When evaluating this by the metric used in the K-fold validation (correlation between equal-area bin rank and frequency of observations), the August 2015 results are good (Spearman rank correlation = 0.89, $p = 0.0005$), while August 2004 results are poor (Spearman rank correlation = 0.25, $p = 0.48$).

Polar bear optimal habitat defined on an annual basis and then considered in 5-year blocks (Fig. 4) shows a clear northward shift over the study period. The shift had already begun between the first two time periods considered, but continued even more strongly, resulting in a dramatic change by the end of this study.

Discussion

Habitat Selection Patterns

Habitat selection patterns were successfully identified for polar bears in the Barents Sea subpopulation using three seasonal RSFs. Polar bears in this area preferentially used intermediate rather than high or low ice concentrations, confirming patterns seen in studies from many other areas (Arthur et al. 1996, Durner et al. 2009, Wilson et al. 2014). Prior studies on this population indicate that this is a robust preference, which

holds across high and low availability levels for this ice type (Mauritzen et al. 2003). Some of the other environmental variables explored in this study had notable seasonal differences in selection. During spring and autumn, the polar bears had a higher probability of using sea ice over shallow water, and selected for short distances to the ice edge, defined by the 15% ice concentration. Taken together, the selection of these variables indicates a general selection for the MIZ, which is a highly productive region during the period with daylight in the Arctic. Not surprisingly, polar bears' sea ice preferences in the MIZ corresponds closely with those of their main prey, ringed seals (*Pusa hispida*). Part of the ringed seal population in Svalbard, mainly sub-adult individuals (Hamilton et al. 2015), travel from coastal areas where they overwinter, into the MIZ where they select habitat with 40-80% ice cover, during the summer feeding period that extends from post-moulting in July through until near the time when fjords typically froze in Svalbard, in November (Freitas et al. 2008a).

Most subpopulations of polar bears occur over shelf seas, and Durner et al.'s (2009) circumpolar model identified ocean depth to be a strong determinant of polar bear habitat selection on a year-round basis. Increasing probability of use with decreasing depth was also seen in models for the Beaufort Sea (Durner et al. 2004). Only in one region that is relatively shallow in its entirety, has the opposite trend been found, i.e. a selection for deeper depths (Western Hudson Bay – see McCall et al. 2016). The preference for shallow shelf areas where sea ice can be found, has been linked to higher productivity and consequently higher abundance of prey for polar bears compared to areas with deep water (Hamilton et al. 2015). Despite a wide range of ocean depths in the study area, ocean depth was only retained as being important in the spring and autumn models in this study. Shelf areas had roughly twice as a high probability of use

compared to non-shelf areas, all other things being equal. While during the spring season, the sea ice retreats away from the shelf, during autumn it advances back over the shelf. Thus, in the autumn models, this covariate may partly reflect the polar bears' tendency to follow the movement of the MIZ back over the shelf.

Ringed seals did not select their key habitats on the basis of water depth when they were tracked during offshore trips from Svalbard to the MIZ in the summer (Freitas et al. 2008b), even during recent years when the MIZ has been located over the deep Arctic Basin (Hamilton et al. 2015). They did, however, alter their behaviour by swimming greater distances, showing less area-restricted search behaviour, diving for longer periods, exhibiting shorter surface intervals and resting less on sea-ice when over deep water, indicating that foraging conditions have become more challenging for seals now that the MIZ is not located over the shelf (Hamilton et al. 2015). Another potential driver of the preference for shallow areas by polar bears could be access to bearded seals (*Erignatus barbatus*). Bearded seals occur in the diet of polar bears throughout the spring and autumn, and since bearded seals feed on benthic and demersal prey that occupies shallow water (Hjelset et al. 1999, Krafft et al. 2000), they are typically found over the continental shelf. Although ringed seals are identified as the main prey of polar bears, bearded seals can make up a large portion of the diet in the pack ice of the Barents Sea (Derocher et al. 2002). The harp seal (*Pagophilus groenlandicus*) is a third ice-associated seal species with known importance to polar bears in the Barents Sea area (Derocher et al. 2002). Although data are scarce, it is likely that their importance could be significant in some areas in the MIZ, which these seals occupy seasonally between June and October, particularly in the central Barents Sea (Haug et al. 1994).

Distance to the sea ice edge is an important factor for where polar bears occur during spring and autumn, but is a very strong determinant only in the autumn RSF models. This fits reasonably well with June-August being the period of highest biological productivity in the MIZ, and a period when a lot of different wildlife is attracted to this region (Falk-Petersen et al. 2000). During winter, polar bears selected for shorter distances to the 75% ice cover boundary, rather than the 15% ice cover boundary, indicating that the best habitat in this season is farther into the ice compared to spring and autumn. The reason is not clear but may be related to prey abundance and the polar bears' ability to catch food items of various types on a seasonal basis. Alternatively, they might select the higher concentrations of ice because these are more stable; edges break up in storms. The relative importance of prey is lower in winter; polar bears hunt most extensively in spring and summer, and accumulate fat reserves that are utilized during winter (Amstrup 2003).

The broad-scale patterns of resource selection found for Barents Sea polar bears in this study are shared with polar bears in most subpopulations studied previously. However, distance to land was not significant in this study, but is retained in models constructed for other areas. Many of those models deal with subpopulations where land is a relatively linear feature (e.g. in Western Hudson Bay; McCall et al. 2016), while the islands in the Barents Sea are heterogeneously distributed and cover a very small proportion of the polar bear range in the region. The lack of a consistent pattern with respect to distance to land may also be related to heterogeneity in the timing of selection of land, or because of the mix of space-use strategies in the Barents Sea population (Mauritzen et al. 2001); both coastal and offshore bears are represented in this study.

The autumn RSF has good predictive abilities as seen in the K-fold validations and the validation against independent survey data. The independent survey data is an optimal test of whether the models make good predictions for the population as a whole, as it also includes observations of males and subadults, while our models are based on adult female tracking data only. The extrapolation of RSFs from adult females to the population level is further supported by a lack of any observed age or sex structure during the surveys. Unfortunately, data to test the predictive abilities of the winter and spring models with similar thoroughness, are lacking, so they are evaluated herein only based on the K-fold validation. However, this suggests that the models performed well across random subsets of the data, but also that the models from these seasons were not as robust across spatial and temporal folds as the autumn models. There may be several underlying reasons for these seasons being more difficult to model. One is that there is greater variability in sea ice conditions during the rest of the year compared to the autumn when a clear sea ice edge occurs offshore. Polar bears have more choices and flexibility in the selection of sea ice, particularly in their use of sea ice close to land. An additional factor in this study is that the autumn model of sea ice use mainly relates to offshore bears, while the winter and spring models include both sea ice use by coastal and offshore ecotypes, since the sea ice is accessible to both when it is in coastal areas.

Denning and reproductive constraints during winter and spring might also have led to greater variability in the basis for sea ice selection by the bears during these seasons.

Reproductive denning only happens on land in this subpopulation (Andersen et al. 2012), and with a high degree of site fidelity in denning areas (Zeyl et al. 2010).

Females preparing to enter a den will necessarily make different choices than females not facing such a constraint. Leaving the den in early spring, females with cubs of the

year adjust their habitat selection relative to other bears, too. They may do this to avoid intraspecific competition and confrontation, to avoid long open water crossings, or because relative hunting success in different habitat types is different from that of lone females (Freitas et al. 2011, Pilfold et al. 2014b). Polar bears hunt ringed seal pups extensively during spring in the Svalbard area (Iversen et al. 2013), as ringed seals are very accessible during their pupping and moulting period. In April, females with small cubs in particular hunt ringed seal pups in front of glaciers, a prime ringed seal pupping habitat (Freitas et al. 2011). Ringed seal abundance is very high in coastal areas with fast ice (Lydersen and Gjertz 1986), but polar bears using alternative strategies in the drifting pack ice of the Barents Sea can also find ringed seals breeding and moulting there, albeit at much lower densities (Wiig et al. 1999). However, because the satellite data does not quantify sea ice cover close to landmasses well, the near-shore hunting habitat is not represented optimally in our RSF. Additionally, there are characteristics of the sea ice that was not considered in this study, for instance age, thickness or surface roughness, that could be important for polar bear habitat selection because they influence seal habitat preferences or polar bear hunting success (Ferguson et al. 2000, Pilfold et al. 2014a). No such data was included in this study because the temporal and/or spatial resolution of the data sets available were not high enough (e.g. they did not cover the entire time period or they did not include land buffers or they masked parts of the study area).

Change in optimal habitat

Climate change has, and will continue to have, profound impacts on the Arctic ecosystem. This is already apparent in the geographical shift in polar bear sea ice habitat in the Barents Sea, and how the number of days that such optimal habitat is available

around Svalbard has declined between the start and end of our 25-year study period (Fig. 4). Summarizing the changes in terms of day-pixels and assuming a linear underlying trend, the geographical shift goes hand in hand with a 27% decrease in optimal habitat between 1992 and 2015, or a rate of 11.7% decline per decade. Breaking down by season gives rates of 6.1% decline per decade in winter, and 18.8% and 18.9% for spring and autumn, respectively. The overall statistic from the current study is very similar the 10.7% reduction in optimal habitat per decade estimated by Durner et al. (2009) for the Barents Sea subpopulation over their study period (1985-2006). While the two models are very similar, they have been developed independently, and the consistency between them is worth noting.

The ice edge, which was identified to be the main offshore polar bear habitat in the Barents Sea, has moved northward and is still moving north and east, away from the continental shelf (as exemplified by the predictive maps for specific dates in 1996 and 2013 in Fig. S3; Laidre et al. 2015a). As the sea ice retreats farther and farther north, it is a question whether the bears will select habitat in the same manner or respond to this change by altering their behaviour. Two studies that set out to identify changes in habitat selection over recent decades have shown largely unaltered preferences, although geographical space use patterns changed, both in the Chukchi Sea and in Eastern Greenland (Laidre et al. 2015b, Wilson et al. 2016). That polar bears adhere to their selection criteria is not necessarily the case across all conditions into the future.

The northwards shift of the ice edge poses a challenge to the polar bears in the Barents Sea subpopulation, which have to implement their space use strategies in an altered physical and biological landscape. The two main ecotypes of bears, coastal and offshore

(also called "local" and "pelagic"; Mauritzen et al. 2001), will face different challenges. Coastal bears will have a shorter season in which the sea ice habitat will be available around the islands, while offshore bears may have a challenge in moving between denning areas on land and sea ice habitat in the MIZ. Polar bears are very capable swimmers that can also cross long distances of open water, although young-of-the-year likely set a limit for female bears, as they tolerate cold water less well, particularly in spring or early summer (Aars and Plumb 2010, Derocher et al. 2011, Durner et al. 2011, Pagano et al. 2012). Females using the offshore strategy may therefore have to decide between running an ever increasing risk of losing their offspring while trying to reach the MIZ with young cubs, or change their strategy and become coastal bears either permanently, or in years following birthing. Additionally, the cost of swimming may be considerable if bears have to cross stretches of several hundreds of kilometres to reach denning islands. One consequence may be a shift in denning distribution from eastern islands in Svalbard to FJL, which is further north, and surrounded by sea ice habitat in seasons (and years) when Svalbard is not. This again may induce a shift in preferred sea ice habitat further east along the ice edge.

Coastal bears do not have a problem reaching denning habitat, but may be stuck on land for longer periods of the year, akin to how polar bears in the Chukchi Sea have increased their use of land, particularly in High Arctic islands, in response to sea ice loss (Rode et al. 2015). Less access to sea ice habitats and spending more time on land is expected to lead to reduced energetic intake and poorer body condition, even after considering possible alternative terrestrial prey (Dey et al. 2016). Trends in demography and body condition have been linked to sea ice changes on a decadal time scale in several subpopulations already (Lunn et al. 2016, Obbard et al. 2016, Rode et al. 2014),

while the Chukchi Sea is an example of a subpopulation showing some resilience in this regard (Rode et al. 2014). While monitoring data does not show any change in body condition of polar bears in Svalbard in the period 1993 to 2016, there is a small shift towards fewer females having COYs in a given year and fewer cubs in each litter (MOSJ (Environmental Monitoring of Svalbard and Jan Mayen): www.mosj.no). The observed geographical shift and reduction of optimal habitat in the Barents Sea has the potential to impact space use strategies, body condition and reproductive rates of Barents Sea polar bears. There seems to be a certain degree of resilience also in this population, and it will be important to follow how these develop over time, and find out if the degree of resilience persists.

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Figure Legends

Figure 1. Locations of female polar bear captured and equipped with satellite transmitters in the larger Barents Sea area, from 1991 – 2015 (black dots, N=296). The black box shows the area of inference for the models run in this study (which encompasses 99% of the data). The locations of the five spatial folds for the K-fold validation are shown in white. The dark blue line is the 600 m bathymetry contour used to define the continental shelf break.

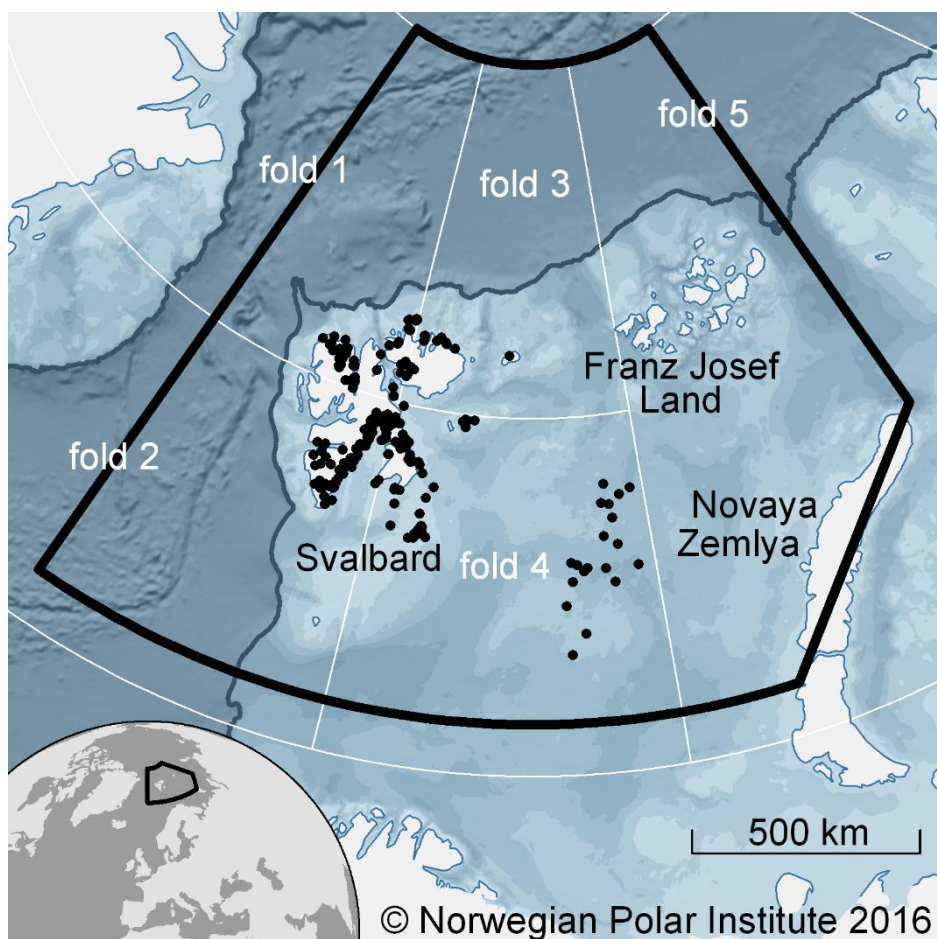


Figure 2. Model predictions showing how the RSF value (relative probability of use) depends on each covariate in the model. RSF prediction values are scaled so 1 is the maximum prediction during each season.

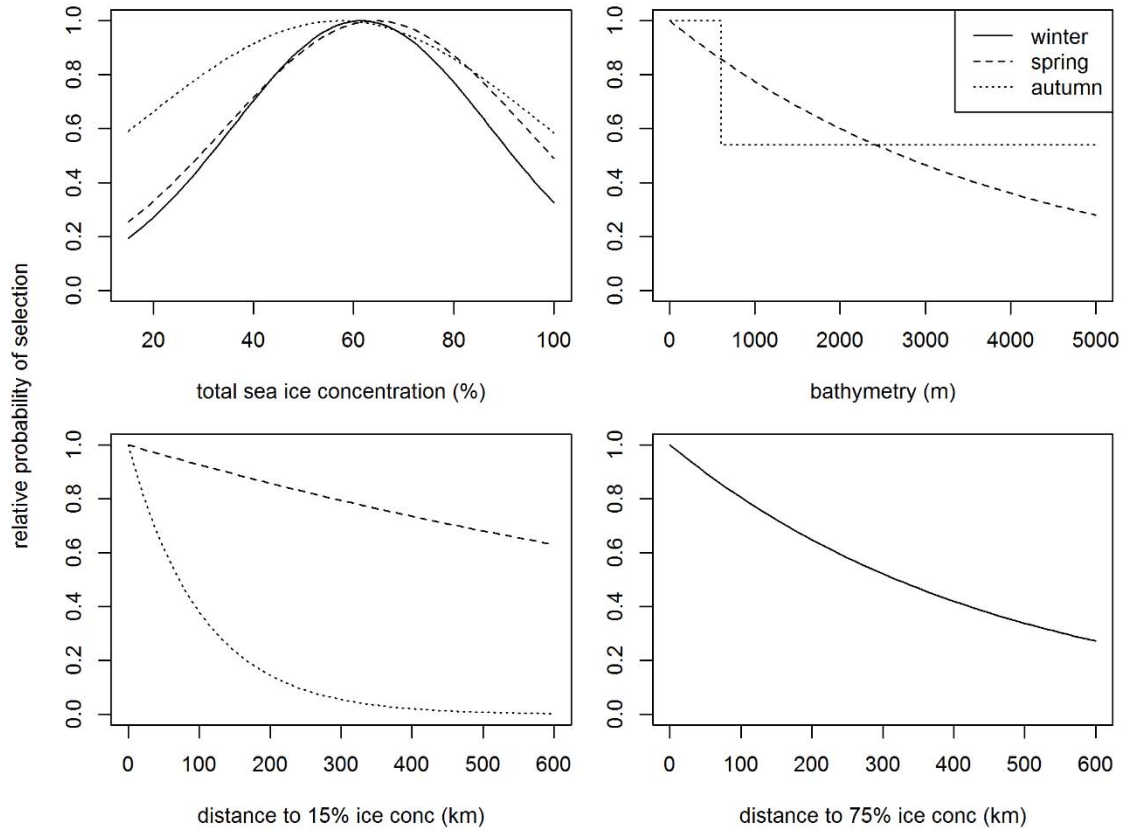


Figure 3. Comparison of the predicted unscaled RSF values (averaged for survey periods) for polar bear distribution in the marginal ice zone in combination with the empirical distribution of polar bears (black points) seen during surveys in August 2004 (upper panel) and August 2015 (lower panel). The actual areas covered by the surveys (via parallel transects lines) are outlined.

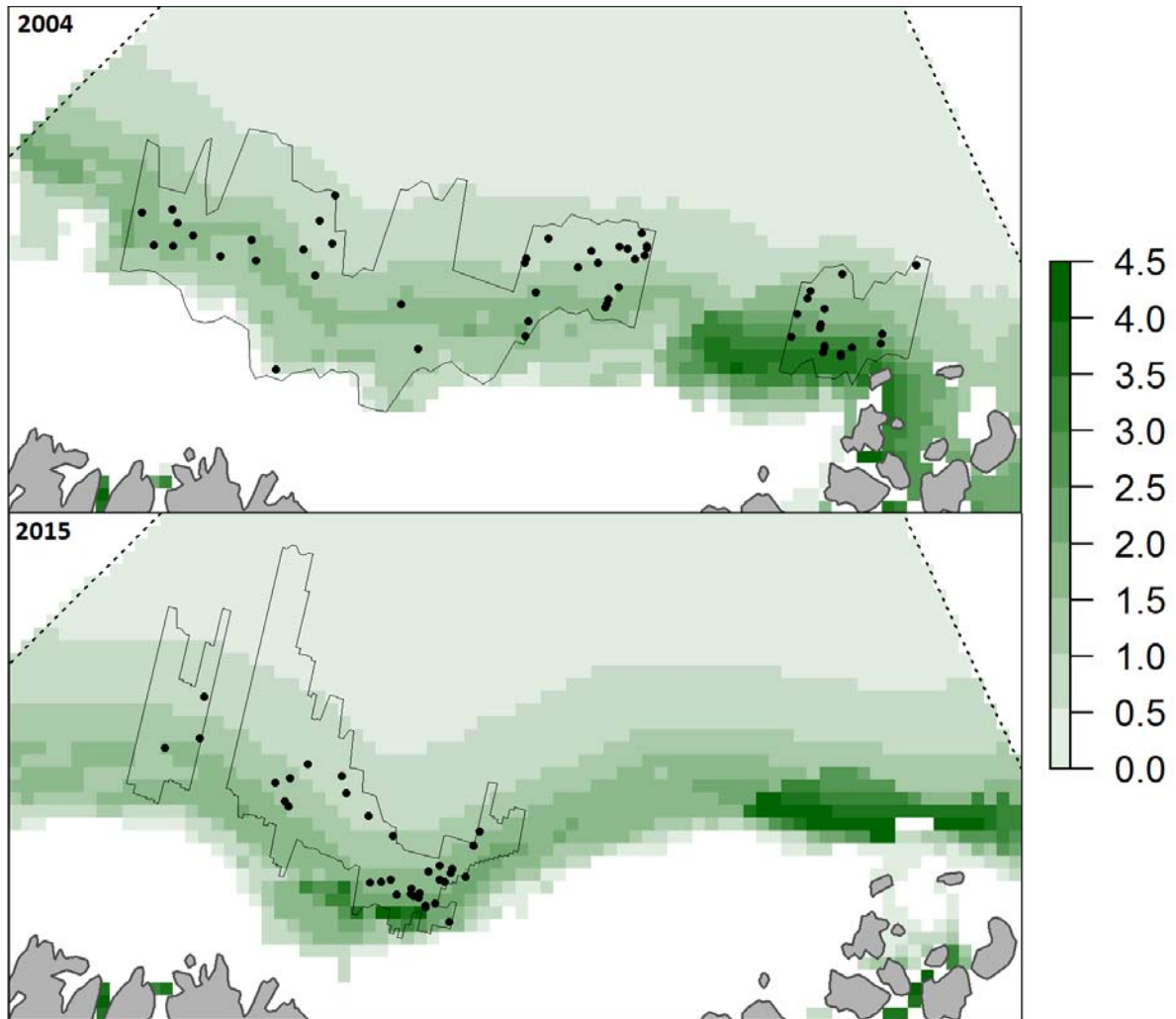


Figure 4. Change in average number of days with optimal habitat, relative to a 1992-1996 reference period.

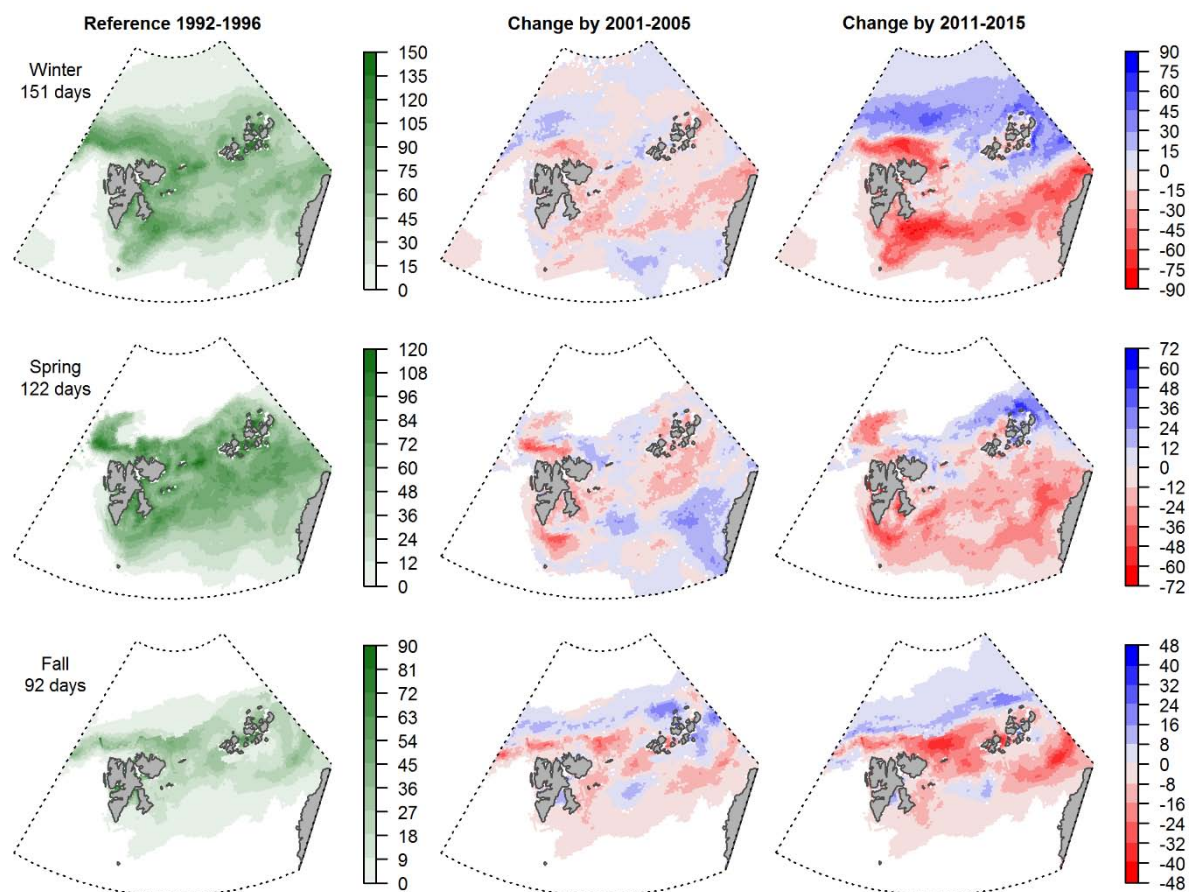


Table legends

Table 1. Summary of the data material underlying each seasonal model, including number of unique bears, number of tracks (some bears were collared multiple times), and number of steps (used locations on sea ice and their associated set of available locations) considered in the model.

Season	Years of data (range)	# of bears	# of tracks	# of steps	# of steps in a track			
					Mean	SD	Min	Max
Winter								
Nov-Mar	1991-2015	121	140	1347	9.6	8.6	1	40
Spring								
Apr-Jul	1992-2015	219	280	4268	15.2	12.6	1	69
Autumn								
Aug-Oct	1992-2015	161	186	1454	7.8	7.5	1	51
Across all	1991-2015	226	294	7069	24.0	24.5	1	157

Table 2. Candidate models.

Model	Covariates	Model structure
1	2	$\text{totcon} + \text{totcon}^2$
2	3	$\text{totcon} + \text{totcon}^2 + \text{dist_ice}.15$
3	3	$\text{totcon} + \text{totcon}^2 + \text{dist_ice}.50$
4	3	$\text{totcon} + \text{totcon}^2 + \text{dist_ice}.75$
5	3	$\text{totcon} + \text{totcon}^2 + \text{shelf}$
6	4	$\text{totcon} + \text{totcon}^2 + \text{shelf} + \text{dist_ice}.15$
7	4	$\text{totcon} + \text{totcon}^2 + \text{shelf} + \text{dist_ice}.50$
8	4	$\text{totcon} + \text{totcon}^2 + \text{shelf} + \text{dist_ice}.75$
9	3	$\text{totcon} + \text{totcon}^2 + \text{bath}$
10	4	$\text{totcon} + \text{totcon}^2 + \text{bath} + \text{dist_ice}.15$

11	4	$\text{totcon} + \text{totcon}^2 + \text{bath} + \text{dist_ice}.50$
12	4	$\text{totcon} + \text{totcon}^2 + \text{bath} + \text{dist_ice}.75$
13	3	$\text{totcon} + \text{totcon}^2 + \text{dist2land}$
14	4	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{dist_ice}.15$
15	4	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{dist_ice}.50$
16	4	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{dist_ice}.75$
17	4	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{shelf}$
18	5	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{shelf} + \text{dist_ice}.15$
19	5	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{shelf} + \text{dist_ice}.50$
20	5	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{shelf} + \text{dist_ice}.75$
21	4	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{bath}$
22	5	$\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{bath} + \text{dist_ice}.15$

23 5 $\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{bath} + \text{dist_ice}.50$

24 5 $\text{totcon} + \text{totcon}^2 + \text{dist2land} + \text{bath} + \text{dist_ice}.75$

Table 3. Best models from each season with the selected top model in bold.

Season	Model	Covariates in model	AIC	dAIC	wAIC	Proportion of folds passed			Mean rho across folds		
						random	temporal	spatial	random	temporal	spatial
winter	7	totcon + totcon ² + dist_ice.50 + shelf	8574	0	0.59	5/5	5/5	3/5	0.82	0.80	0.55
winter	11	totcon + totcon ² + dist_ice.50 + bath	8575	1	0.36	4/5	5/5	3/5	0.80	0.77	0.50
winter	4	totcon + totcon² + dist_ice.75	8579	5	0.05	5/5	4/5	4/5	0.83	0.81	0.70
spring	8	totcon + totcon² + dist_ice.15 + bath	27466	0	1	5/5	4/5	3/5	0.75	0.70	0.56
autumn	6	totcon + totcon² + dist_ice.15 + shelf	8834	0	1	5/5	5/5	5/5	0.93	0.89	0.83
autumn	8	totcon + totcon ² + dist_ice.15 + bath	8855	21	0	5/5	5/5	5/5	0.92	0.88	0.88
autumn	9	totcon + totcon ² + bath	9046	212	0	5/5	5/5	5/5	0.87	0.87	0.85

Table 4. K-fold validation results from all folds for the top models from winter and spring. Model 4 was selected as the top winter model. Folds that did not pass (i.e. not statistically better than random, $p > 0.05$) is presented with a grey background.

model	fold	random		temporal		spatial	
		p-value	rho	p-value	rho	p-value	rho
Winter							
7	1	0.0052	0.8	0.0056	0.83	0.7244	0.13
	2	0.0009	0.88	0.0014	0.89	0.0018	0.85
	3	0.0009	0.88	0.0104	0.76	0.6751	0.15
	4	0.0263	0.69	0.0153	0.74	0.0005	0.92
	5	0.0026	0.84	0.0064	0.79	0.0295	0.68
11	1	0.0041	0.81	0.0137	0.77	0.625	0.18
	2	0.0012	0.87	0.0027	0.87	0.0041	0.81
	3	0.0544	0.64	0.0409	0.65	0.8667	0.06
	4	0.0018	0.85	0.0125	0.75	0.0098	0.77
	5	0.0056	0.83	0.0052	0.8	0.036	0.66
4	1	0.0018	0.85	0.0035	0.85	0.5423	0.22
	2	0.0045	0.84	0.0014	0.89	0.0005	0.92
	3	0.0014	0.89	0.077	0.58	0.0461	0.64
	4	0.019	0.72	0.0002	0.91	0.0009	0.9

	5	0.0035	0.85	0.0043	0.81	0.0021	0.84
Spring							
8	1	0.0275	0.71	0.0972	0.55	0.0302	0.68
	2	0.0137	0.77	0.0311	0.7	0.0108	0.76
	3	0.0041	0.81	0.0137	0.77	0.0275	0.71
	4	0.0394	0.67	0.0275	0.71	0.2505	0.4
	5	0.0117	0.78	0.0098	0.79	0.4483	0.27
