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A Model for Autumn Pelagic Distribution of Adult Female Polar Bears in the Chukchi Sea, 1987-1994

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Abstract

We made predictions of polar bear (*Ursus maritimus*) autumn distribution in the Chukchi Sea with a Resource Selection Function (RSF) developed from 1198 satellite radio-collar locations on 124 adult female polar bears, 1987 – 1994. The RSF was created to assist in an aerial survey design for polar bears proposed by the U.S. Fish and Wildlife Service. The RSF was based on bathymetry and daily sea ice covariates extracted from passive microwave satellite imagery within the pelagic region > 25 km from shore. The RSF indicated that polar bears selected habitats with intermediate amounts (~50%) of ice cover in close proximity to higher ice concentrations, and over relatively shallow waters. The RSF showed good predictive abilities for the years of its construct, worked best in October, and was robust to inter-annual variability. When evaluated with recent (1997 – 2005) data, the RSF performed well for October and November but poorly in September. This loss of predictive abilities appeared to be related to recent changes in habitat due to longer melt seasons and younger sea ice, and testing the retrospective model with a small sample of recent polar bears locations from a limited region of the Chukchi Sea. Contemporary applications of this RSF must consider three factors that could limit its utility: 1)

different sea ice phenology; 2) distributions of males and sub-adults; and 3) occupancy in nearshore habitats.

Introduction

Polar bears (*Ursus maritimus*) are dependent on the seasonally and permanently ice-covered seas throughout the Arctic basin to hunt for seals. Sea ice composition and distribution vary both within and among years. Minimal sea ice extent occurs throughout the Arctic basin during September. During autumn and into winter, new ice is created in areas of open water and between unconsolidated floes and eventually covers most Arctic seas. By early winter this new ice thickens and becomes first year ice that may be > 1 m thick. First year sea ice that survives the summer melt becomes multi-year ice in autumn. Multi-year ice may persist for a decade or more and become more than 2 m thick. The actions of winds and currents reshape the ice surface into a mosaic of pressure ridges, leads, and floes of various diameters and thicknesses.

Polar bear distribution, while generally limited to the distribution of sea ice (Garner et al. 1990), is further influenced by the habitat requirements and availability of ice dependent prey. Polar bears prey primarily on ringed seals (*Phoca hispida*) and secondarily on bearded seals (*Erignathus barbatus*) (Amstrup 2003). Hence, polar bear distribution usually reflects the distribution of ice habitats that optimizes seal availability (Stirling et al. 1993, Ferguson et al. 2000). However, the requirement for suitable hunting habitat is balanced by the requirement for stable habitat necessary for resting between hunting bouts (Mauritzen et al. 2003). Polar bears appear to respond to habitat parameters including ice concentration, ice thickness or age (ice stage), floe size (ice form), the proximity of active ice edges, and ocean depth (Stirling et al. 1993, Arthur et al. 1996, Ferguson et al. 2000, Mauritzen et al. 2003, Durner et al. 2004) in their quest for food. Breeding takes place on the sea ice during the season of maximal ice extent in early spring. In Alaska, many pregnant polar bears depend on a stable sea ice platform for

successful denning (Amstrup and Gardner 1994). Therefore, the use of different sea ice types by polar bears is dependent on certain life history requirements. Throughout much of their range, polar bear habitat use changes with seasonal changes in sea ice (Arthur et al. 1996, Ferguson et al. 2000, Mauritzen et al. 2003, Durner et al. 2004).

The vulnerability of polar bears to climate change is well recognized (Stirling et al. 1999, Wiig 2005, Stirling and Parkinson 2006). An understanding of polar bear sea ice requirements will allow prediction of likely responses of polar bears to sea ice change from climate warming. This will allow adjustment of current management strategies where humans and polar bears interact, and to provide baseline data to identify future habitat refugia in a diminished sea ice environment. Also, current management strategies are dependent on knowledge of polar bear population size and trends. This information has been traditionally obtained through intensive field work involving aerial surveys and mark-recapture studies of free-ranging polar bears, both of which involve a large amount of personnel time and funding (Evans et al. 2003). Therefore, the efficiency of capture and survey field work may be increased through an understanding of polar bear habitat selection patterns.

To help address ecologic and management questions, we examined the relationship between polar bears in the Chukchi Sea and the sea ice environment during the autumn months of 1987 – 1994. We used archived data of satellite telemetry locations of free-ranging female polar bears, daily sea ice distributions from satellite remote sensing, and ocean depth to develop predictive models of polar bear distributions. The analyses were structured in a geographic information system (GIS) to facilitate use of the data for designing future USFWS aerial surveys of polar bears in the pelagic realm of the Chukchi Sea. This report does not address the distribution of polar bears on land.

Our report is organized into 3 sections. Beginning on page 4, we present the derivation of a predictive polar bear resource selection model based on habitat covariates characterizing the sea ice

environment and ocean depth. The model constructed is a resource selection function (RSF), which predicts the relative probability of use, or values proportional to the probability of use, of habitats (Manly et al. 2002, McDonald et al. 2006). Starting on page 13, we evaluate the RSF model by examining the association between predicted and observed polar bear distributions. We quantified these associations with the monthly and interannual variability of sea ice in the Chukchi Sea during autumn. We also investigated sensitivity of the predictive ability of the final model to daily concordance between measured sea ice conditions and polar bear locations. Finally, the robustness of the final RSF for predicting recent polar bear distributions is explored and discussed with respect to recent sea ice conditions, which have changed substantially since 1994. The overall results and implications of this study, with management applications, are presented in the Discussion.

Deriving the Resource Selection Function

This section describes the formulation and evaluation of an RSF for polar bears in the Chukchi Sea during autumn, 1987 – 1994. The RSF is a function that is proportional to the probability of use of resources by an animal (Manly et al. 2002). The analysis was developed to allow for changes in habitat availability over time (Arthur et al. 1996).

Study area

Our study area was the Chukchi Sea within the region bounded by 156º W to 170º E, and 66º 30' N to 80º N (Fig. 1). Boundaries were chosen to represent the extent of Chukchi Sea ice conditions and typical polar bear movements on the sea ice during 15 September – 14 November (autumn). The study area was further delineated based on two factors. First, this analysis used passive microwave imagery (SSMR, SSM/I; National Snow and Ice Data Center, Boulder, Co.) as the source of sea ice data. These data are in a raster format with a pixel size of 25 × 25 km. Because passive microwave data are not

reliable along shorelines (Cavalieri et al. 1990) we excluded passive microwave pixels, and polar bear location data that were within 25 km of land. A rasterized land mask (1:10^6-scale Digital Chart of the World; Defense Mapping Agency, 1992) with a 25 km buffer effectively removed most of the coastal pixels. Because this land mask mimicked the resolution of passive microwave data, the resulting 25 km shoreline buffer was blocky rather than smooth (Fig. 2).

The study area also was allowed to vary by day depending on sea ice extent. Because polar bears cannot forage effectively in open water, and because polar bears swimming in large expanses of open water are likely enroute to ice covered areas or land, we defined the southern boundary of the study area for each day as the southern extent of sea ice on that day. Open water regions were not considered as available habitat so polar bear locations south of the ice edge were excluded. The coarse resolution of microwave satellite imagery meant that some pixels classified as 'open water' may have contained undetected sea ice. To account for this lack of precision we buffered areas of pack ice recorded with ≥15% ice concentration with a 50 km polygon. We then retained the single, very large polygon of pack ice that always occupies the central Arctic. Consequently, any small parcels (islands) of sea ice (≥15% ice concentration) south of the main pack were not included in the study area. The periphery of the single large polygon was considered the edge of the main ice pack, and is hereafter termed the 15% ice contour.

Polar bear location data

We used location data from satellite radio collars deployed on adult female polar bears captured in the Chukchi and the Beaufort seas during 1987 – 1993. Polar bears were captured with standard animal immobilization techniques (Stirling et al. 1989) each spring from 15 March – 5 May, 1987 – 1993, and during autumn 1988 and 1989. Bears were equipped with a PTT (platform transmitter terminal; Telonics, Inc., Mesa, AZ) radio collar. PTTs transmitted to polar-orbiting satellites which

then relayed the information to various ground receiving stations worldwide, and ultimately to Service

Argos in Largo, MD. PTT locations were calculated by the Argos Data Collection and Location System

(Fancy et al. 1988). Most PTTs transmitted for 4 – 8 hours every 1 – 7 days (duty cycle). Several

locations were typically collected during each duty cycle. For analysis we used locations that were

within 1.2 km of the true location of the bear (Argos location-quality1, 2, or 3; Keating et al. 1991) and

only one location per duty cycle. From these, we retained only those locations that fell within our study

area (see *Study area*). Because pregnant polar bears may enter dens as early as 8 October (Amstrup and

Gardner 1994), we removed all locations that may have been associated with maternal denning.

We were interested in the habitat choice that a bear made as it departed point A and arrived at

point B. We also wanted to maintain relative independence of observations.   Therefore, we used only

consecutive locations that were separated by 2 – 7 days (44 – 172 hours). The second observation of

each pair would become the first observation for the next pair. Lastly, we removed near shore locations

that fell on passive microwave pixels with land contamination. Generally this excluded most polar bear

locations < 25 km from shore.   However, the blocky shape of the rasterized shoreline excluded some

polar bear locations 25 – 40 km from the coast (Fig. 2).

Habitat data

Sea ice habitat covariates (Table 1) were derived from daily sea ice concentration (National

Snow and Ice Data Center, Boulder, CO) maps produced from satellite image analyses of passive

microwave brightness temperatures using the NASA Team Algorithm (Cavalieri et al. 1990). These

data were disseminated in raster format with 25×25 km pixel size in polar stereographic projection.

Sea ice concentration (NTICE) is the areal proportion of sea ice occupying each ~625 km^2 pixel.

Within each pixel, we also calculated the distance (A15) to the nearest boundary (contour) of the

polygon that encompassed all NTICE >15% concentration. This boundary is equivalent to the 15%

contour described in Study area. We constructed a 50% contour and a 75% contour using the same

methodology, and calculated each pixel's distance to these contours. These contours partition the ice

environment into 2 classes based on the respective thresholds of ice concentration (15, 50, or 75%).

Offshore, these boundaries generally represent ice concentration contours where there is a gradient of

ice concentrations above and below the threshold to either side of the boundary. However, this is not

the case in the late-autumn nearshore environment when sea ice abuts the coastline. In this situation,

passive microwave ice concentrations often exceed 90% from the coastline outward so the boundaries

that partition ice greater than 15, 50, and 75% all converge to the same place – the coastline (or in our

case, the 25 km coastal buffer that defined the edge of our study area). These coincident contours along

the coastline are no longer descriptive of the actual ice concentrations that are present, but their

geographic position does make them a spatial proxy for the coastal zone in general.

Hence, "contour", as used in our analysis, gives two different distance measurements. First,

contours provide a distance measurement between a sample point and a coarse-resolution transition

between thresholds of ice concentration. For example, A15 is the distance from a particular pixel to the

nearest transition zone between pixels containing no ice and pixels containing ≥15% ice. Likewise A50

is the distance from any particular pixel to the transition from pixels containing < 50% ice and those

greater, and A75 is the distance from any particular pixel to the transition between pixels containing <

75% and those pixels ≥ 75% ice. However, as autumn progressed and ice formed adjacent to the

shoreline, the 3 contours became synonymous and concordant with the coastal borders of the study area.

In late autumn, the distance to the contour covariates (A15, A50, and A75) all effectively become

proxies for a coastal effect.

We used the International Bathymetric Chart of the Arctic Ocean (IBCAO,

http://www.ngdc.noaa.gov/mgg/bathymetry/arctic/arctic.html) for data on ocean depth (BATHY).

These data are provided in a polar stereographic projection grid with 2500 m pixel resolution.

Defining Habitat Available to Polar Bears

We defined the habitat available to a bear at a particular time as the area within a circle with its

center at the first of 2 consecutive observations (Arthur et al. 1996, Durner et al. 2004). The radius of

that circle was determined by the duration of time between the previous observation and the next

observation, and by the rate of bear movement. Because movement rates of female polar bears in the

southern Beaufort Sea vary by month (Amstrup et al. 2000), we calculated a unique radius for each

unique bear/date observation with the following equation:

radius of available habitat = $\{a + (b \times 2)\} \times c$;

where a equals the mean hourly movement rate for all bears within the respective month; b is the

standard deviation of the movement rate; $\{a + (b \times 2)\}$ gives an approximation of the upper limit to the

hourly movement rate; and c equals the number of hours between locations. On rare occasions, the

actual straight-line distance traveled by a bear between observations exceeded the calculated radius. In

these cases, the radius of available habitat was defined as the straight-line distance actually traveled.

Creating Discrete Choice Habitat Units

Data extracted from the daily sea ice concentration maps and the bathymetry chart (Table 1)

were combined to produce units of discrete habitat units. We defined a discrete habitat unit as a point

on a map representing a 1000 × 1000 m area (pixel size) that was associated with several layers of

habitat covariates, including total ice concentration, distances to the three ice class interfaces (contours),

and ocean depth.

Generating Available Locations and Attaching Habitat Variables

Available locations represented the discrete choice set of the possible habitat units that a bear may select as it traveled from point A to point B. For each bear location, we generated up to 100 random available locations within the respective available habitat. To each available location we attached habitat covariates, including measured distances to ice concentration boundaries (i.e., A15, A50, and A75) and associated quadratics and interactions (Table 1). Available locations had a minimum spacing of 1000 m.

Generating a Resource Selection Function

Estimating the RSF followed the methods for discrete choice modeling as described in Arthur et al. (1996), McCracken et al. (1998), Cooper and Millspaugh (1999) and Durner et al. (2004). The discrete choice model is estimated by maximizing the multinomial logit likelihood (Manly et al. 2002). This was accomplished using the stratified Cox proportional hazards likelihood maximization routine available in the SAS procedure PROC PHREG (SAS Institute 2000). Although PROC PHREG was not designed to fit discrete choice habitat selection functions, Kuhfeld (2000) describes a method by which PROC PHREG can be adapted to maximize the appropriate discrete choice likelihood function.

Prior to model building, Pearson's Correlation Coefficient (r; Conover 1980) was calculated for all pairs of main effects. If a pair of covariates had a value of $|r| \geq 0.6$, one of the variables was excluded from the analysis to avoid multicolinearity. Stepwise model building began with developing a single-term model based on each covariate. We set the critical level for covariate entry into the model as $\alpha = 0.05$ for the adjusted score χ^2 statistic (Klein and Moeschberger 1997). The single-term model with the largest significant score χ^2 was selected as the start of a forward selection model building process. We allowed each step of the forward-selection process to add one other term only when the p-value for the adjusted score χ^2 value for that term was ≤ 0.05. Each forward selection step was preceded

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by a backward removal step, where the variable with the smallest Wald χ^2 value was dropped from the model if its statistical significance was > 0.05. An interaction or quadratic term was not allowed in the model if the associated main effect was not already in the model. If a backward selection step identified a main effect for exclusion, and that covariate was also present in the model as a quadratic or as an interaction with another main effect, the main effect was not dropped from the RSF model. The RSF was considered complete when no other terms could be entered or removed under the constraint of α = 0.05.

Testing the final resource selection function

The predictive ability of the final RSF was tested with a *k*-fold cross-validation technique similar to that described by Boyce et al. (2002) and Johnson et al. (2006). We randomly subdivided the data into groups based on the number of covariates in the final model. Groups were composed of all sampled locations, used and available, for individual bears rather than random subsets from all bears, meaning that all of the observations for any particular bear fell within only one group in any iteration of the *k*-fold process. In the *k*-fold process, one group was used for testing the model and the other groups were used for model training (re-estimating model coefficients). We used Huberty's rule of thumb (Huberty 1994) to determine the number of groups for any particular model. Using this rule, we randomly selected 2 groups for testing 2 covariate models, 3 groups for 3 – 6 covariate models, and 4 groups for 7 – 12 covariate models. One of these groups was then set aside for testing and the remaining groups were used for training. For example, during each iteration of the validation process for a 2-covariate model, half of the bears were randomly placed into the training group, and half of the bears were placed in the testing group. Coefficients for the 2 variable model were then re-estimated using all data from the training group, and model predictions (relative probability of selection) were made for all locations (used and available) in the testing group. Predictions were scaled to sum to 1, and

the predictions for the available locations (testing group) were grouped into 10 bins based on percentiles. Thus, each bin represented the same amount of area as each of the other bins. The used locations for the testing data were then assigned to the appropriate bin, based on the model prediction for that point. For example, if bin 10 had minimum and maximum RSF values of 0.9 and 1.0, all polar bear locations with predictions in this range would be assigned to bin 10. Spearman's rank correlation coefficient was then calculated to estimate the strength of the relationship between the bin rank (10 in this example), and the number of polar bear locations associated with that bin. Higher ranks correspond to higher relative probabilities of selection, and thus a good predictive model would correctly identify more polar bear locations with bins of higher rank (Boyce et al. 2002). This process was repeated 100 times, and the average correlation coefficient was reported.

Results

There were a total of 1862 polar bear relocations within the spatial and temporal bounds of the study area. The coastal 25 km buffer excluded 246 of these relocations from the analysis. The majority of relocations associated with land or the coast occurred on Wrangel Island (n = 141). Fifty-six relocations occurred along the Russia coast and 49 were along the Alaska coast, primarily in the vicinity of Barrow. Final temporal filtering left a total of 1198 observations from 124 individual polar bears for building the RSF model (observations per bear: min. = 1, max. = 47, mean = 9.7 ± 7.3 STD). Bear locations (used locations) were associated with 115,092 available locations, where each bear contributed between 71 – 4293 available locations (mean = 928.2 ± 693.9 STD), and each used location was associated with 21 – 100 available locations (mean = 96.1 ± 9.2 STD).

Pearson correlations indicated high colinearity between A15 and A50, A50 and A75, and A15 and NTICE (Table 2). A15, A50, A75, and BATHY all had highly significant score χ^2 results as single covariate models (Table 3), indicating the importance of these variables in explaining polar bear

distribution. Because A50 had the highest score χ^2 it was chosen as the initial covariate for model building. Due to significant correlations between A50 and A15, and between A50 and A75, A15 and A75 were excluded from further model building. The second model building step entered the quadratic for A50 (Table 3). This was followed by the inclusion of BATHY, and concluded with the entry of the quadratic for NTICE (NTICE^2; Table 3). No covariates were identified for removal from the model during any of the backward steps. The final RSF model was:

$$RSF = \exp((-0.01116 * A50) + (0.0000107 * A50^2) + (0.0003442 * BATHY) +$$

$$(0.06377 * NTICE) + (-0.0006086 * NTICE^2)).$$

Cross validation of the final model (Boyce et al. 2002) indicated the RSF distribution had high concordance with actual polar bear locations. Three subgroups of polar bear locations, each with 100 replicates, had mean correlations of 0.88, 0.92, and 0.88. The average of these three correlations was 0.89 ± 0.03 STD.

The RSF model predicts that polar bears selected ice concentrations near 53% and habitats near the 50 % ice contour (Fig. 3). The response of polar bears to the 50 % contour was not linear; selection declined abruptly with increasing distance (Fig. 3). Selection showed a slight increase at very great distances from the 50 % contour, which was likely an artifact of the A50 quadratic term since all observed polar bear locations were within 700 km of the 50 % contour. Ice concentration by itself was not a useful predictor of polar bear distribution, but it became a useful predictor when considered collectively with A50 and BATHY (Table 3). As with distance to the 50 % contour, the predicted response to ice concentration was not linear. While polar bears were predicted to select high concentrations of sea ice by virtue of the positive contribution of NTICE in the model, predicted selection peaked at 52.7 % sea ice concentration owing to the model's negative NTICE quadratic term.

The predicted response of polar bear locations varied inversely to ocean depth at a constant rate: as depth increased, predicted selection decreased at a constant rate.

Assessing the Resource Selection Function

In this section we evaluated the RSF model by examining the association between predicted and observed polar bear distributions. We quantified these associations with the monthly and interannual variability of sea ice in the Chukchi Sea during autumn, and we also investigated sensitivity of the predictive ability of the final model to daily concordance between measured sea ice conditions and polar bear locations. The robustness of this retrospective RSF for predicting recent polar bear distributions is explored and discussed with respect to recent sea ice conditions, which have changed substantially since 1994.

Extrapolating the RSF

Every day between 1 September and 30 November (91 days), 1987 – 1994, and 1997 – 2005, we used the 1987 – 1994 model to calculate RSF values for each pixel across a 5 × 5 km pixel resolution grid. This was done by subdividing each 25 km cell into twenty-five 5 km cells and calculating a RSF using sea ice covariates derived from the respective day's passive microwave sea ice concentration estimates (Cavalieri et al. 1990), and bathymetry. Within the grid of daily RSF values, all pixels outside the full study area were excluded (Fig. 1), as well as all open water (<15% ice concentration) pixels > 50 km south of the 15 % ice concentration contour. The remaining pixels were partitioned (Arc/Grid Slice Function, ESRI, Redlands, CA) into 20 intervals with the equivalent number of pixels, based on ranked percentiles of the RSF values. Hence, the highest RSF interval (# 20) was comprised of the units with the uppermost 5% of the daily RSF values, and so forth, to the lowest RSF interval (# 1) which was comprised of the lowest 5%.

Although each of the 20 daily RSF intervals contained approximately the same number of pixels, their geographic areas were not exactly equivalent, because polar stereographic is not an equal area map projection. Therefore, the area-extent of each daily RSF interval (N = 20) was adjusted using a Lambert azimuthal equal area map projection The daily mean of the 20 intervals was used to represent the physical area for all 20 intervals of the respective day. Ramifications of partitioning the RSF intervals in the polar stereographic projection were, however, found to be minor (~1 % error); the average CV among all of the adjusted daily means (N = 1729) was only 0.010 ± 0.003 STD.

The characteristics of the daily RSF extrapolations reveal several important aspects about the behavior of the RSF in relation to the autumn sea ice dynamics (Fig. 4). For a pixel to have membership in the daily study area, the pixel must occur: 1) within the primary study area (which excluded the nearshore zone, Figure 1); and 2) where sea ice concentration estimates were >15 % or within 50 km south of the 15 % ice concentration contour. Because sea ice extent increased during the study period as the Chukchi Sea froze, size of the daily study area increased, and so the size of RSF intervals. Total size of the daily study area is depicted by the combined extents of the upper 10 (individually gray shaded) and the lower 10 (identical blue shade) RSF intervals (Fig. 4). Hence, half of the daily study area is shaded gray and the other half is shaded blue. Size of the daily study area is, by definition, approximately 20-times the size of any single respective-date RSF interval. The seasonal effect on study area size, and size of the corresponding RSF intervals, caused by changes in sea ice extent is clearly apparent in Figure 4. In this example, each RSF interval occupies approximately 29,700 km^2 on 15 September 1993, and 57,100 km^2 on 15 November 1993.

The 25 km coastal buffer did not fully exclude all nearshore pixels (Fig. 4). This occurred where the presence of land caused the ice concentration estimates to incorrectly exceed 0 %, so they were retained within the daily study area. Although inclusion of these anomalous pixels affected the total

daily study area size, their impact was considered to be minor since they represented such a small fraction of the total area.

The highest RSF values predominated along the 50 % ice contour (Fig. 4). Northward of the 50 % edge, the RSF values generally declined along a distance continuum unless modified by a discontinuity in ice concentration or bathymetry. Since depth of the Chukchi Sea is relatively uniform over the continental shelf, effect of the bathymetry covariate only occurred when the ice edge was at high latitudes (e.g., 15 September 1993 in the north central Chukchi Sea ($\sim 172°$ W $- 177°$ W, $> 75°$ N) when the 50 % ice contour was over relatively deep water). RSF values also declined southward from the 50 % contour along a distance continuum, but this gradient was more strongly modified by the greater spatial variability of ice concentrations along the ice pack's southern margin. South of the 15 % ice contour, a pronounced drop in RSF values was realized as the ice concentrations rapidly yielded to open water. Note the inclusion of ice-free water, as estimated by the 25 km resolution satellite sensor, was terminated, by definition, 50 km south of the 15 % ice contour.

Seasonal and inter-annual variations among the RSF-interval distributions are illustrated in Figure 5. A qualitative appreciation of the broad range of sea ice conditions that occurs in the Chukchi Sea during autumn can be attained by noting inter-annual differences in the general locations of the ice edge and the annual rates of ice formation (freeze up). This variability has been attributed to variations in atmospheric circulation patterns that strongly influence regional air temperatures and ice motion regimes (for examples see: Maslanik et al. 1996, Rigor et al. 2002, Drobot and Maslanik 2003, Belchansky et al. 2005a). Climate conditions during the previous winter can influence sea ice conditions the following autumn through heat exchange mechanisms affecting the onset of spring melt and duration of the summer melt season (Belchansky et al. 2004).

A fairly consistent pattern of within-year ice variability is revealed in Figure 5. In 1987 – 1994, between-year autumn sea ice conditions were most variable during early September and then again during mid November. Little variability exists in late November after the entire Chukchi Sea freezes. In early September, between-year variability was high with respect to total sea ice extent (e.g., 1988 vs. 1990), and, it was also high with respect to the amount of area between the 15 % and 50 % ice contours (hereafter referred to as the marginal ice zone) (e.g. ,1987 vs. 1992). Then, in mid-November, total sea ice extent was again highly variable between years (e.g.,1991 vs. 1994). Notably, however, October was generally a period with less inter-annual variability. During October, sea ice conditions in the Chukchi Sea more or less attained a balance between the extent of open and ice-covered water, while breadth of the marginal ice zone tended to be more consolidated as the lead systems froze and the ice edge propagated southward.

Polar Bear Location Data

We used all polar bear locations between during 1 September to 30 November, 1987 – 2005, for assessing the RSF (Fig. 1). We maintained the filtering criteria of 1 standard-quality location per transmitter duty cycle (see page 5), however we did not use the temporal filter that was imposed in model building (restriction to consecutive locations separated by 2 – 7 days). We also included locations during the first 2 weeks of September and the latter 2 weeks of November to assess the RSF outside of the seasonal window of its construct. Thus, our assessment of the RSF examined more polar bear locations than were used to develop the RSF.

We considered 2 time periods for the RSF assessment. First, 2709 locations collected between 1987 and 1994 from 155 polar bears were selected for RSF evaluation during the period of its construct (Table 4). Following 1994 satellite telemetry research in Alaska essentially ended. Telemetry research resumed in the Beaufort Sea in 1997, resulting in a smaller number of polar bear locations (n = 827)

occurring in the Chukchi Sea between 1997 and 2005 (Table 4). This second sample of 1997 – 2005 locations was used for assessing performance of the retrospective RSF to contemporary conditions in the Chukchi Sea.

Assigning Bear Locations to RSF Intervals

Each polar bear location (Table 4) was intersected with its respective (same date) daily RSF-value and RSF-interval map. In addition to the RSF attributes, values of the RSF covariates and other ancillary data were recorded for each bear location: distance to the 15 %, 50 % and 75 % ice contours, bathymetry, sea ice concentration, and distance to the coast. Bear locations outside the bounds of the daily study area including those on land, within the nearshore buffer zone, or on open water > 50 km south of the 15 % ice contour (Fig. 6) were excluded from the analysis (n = 606, or 17% of total) . Hence, the RSF assessment was restricted to polar bear locations that occurred >40 km from shore (termed "pelagic"), unless otherwise stated. This left 2193 and 737 locations from 1987 – 1994, and 1997 – 2005, respectively, for RSF assessment (Table 5). The loss of polar bear locations due to coastal proximity became more important during the latter part of autumn, as the sea ice became more proximate to, or convergent with, the shoreline (Fig. 7). Of the 606 bear locations that were < 40 km from the coast (Fig. 6), approximately 25% occurred in September, 25% in October, and 50% in November. Although only 17% of the locations occurred <40 km offshore, 131 of the 250 (52%) total within-year bear individuals (Table 4) were relocated at least once within the nearshore (<40 km) zone during the 3-month autumn period.

Polar Bear – RSF Associations

When the polar bear location data in Table 5 were pooled over 16 September – 15 November and across 1987 – 1994 (the approximate analogous period used to derive the RSF), the frequencies of

polar bear locations (n=1425) occurring along an increasing RSF-interval gradient showed an exponential relationship (Fig. 8). Over half (54%, n=766) of the polar bear locations occurred within the upper 2 combined RSF intervals, suggesting that approximately half of the bears in the Chukchi Sea were distributed across about 10% of the daily study area. The proportion of polar bear occurrences increased to 68% within the upper 3 combined intervals (~ 15% of the area), and to 77% within the upper 4 combined intervals (~ 20% of the area).

A very small fraction of bear locations (< 0.6 %, n = 8) occurred outside the daily study area during 16 September to 15 November, and were thus excluded from the assessment. These 8 locations all occurred during the latter 2 weeks of September (over 3 different years) at open water (0 % ice) pixels that were >50 km south of the 15% ice contour. These bears may have been using remnant ice floes that drifted south from the main ice pack that were too small to provide a sufficient passive microwave signature for detection by the ice concentration algorithm.

Roughly 5% of all autumn (16 September – 15 November) pelagic bear locations across all years occurred south of the 15% ice contour. Approximately 80% of these locations occurred within 50 km of the edge. This 50 km zone was systematically retained in the daily study area because polar bears routinely utilize the southernmost fringe of the ice pack, but the 25 km resolution sea ice concentration maps often fail to accurately detect the presence of very low ice concentrations. The majority of bear locations within the 50 km zone were associated with intermediate RSF intervals, because a very low (or nonexistent) ice concentration value (NTICE covariate) otherwise reduced the extrapolated RSF value (Fig. 4).

We observed a modest amount of annual variability among the proportions of bear locations that occupied the upper 4 RSF intervals (Fig. 9). When data from 1987 – 1994 were pooled, the upper 4 RSF intervals contained 77% of the bear locations (Fig. 8), but when each year was examined

individually, the proportion of bear locations in the upper 4 intervals ranged from 65% in 1988 to 86% in 1990 (Fig. 9). Between-year comparisons dramatically reduces sample sizes (Table 5), so they are less robust to issues of inter-annual transmitter deployment biases, the influences of different inter-annual climate regimes, or behavioral nuances among individual bears. Given that polar bear occupancy of the upper 4 RSF intervals ranged as little as 65 – 86% suggests that, for the years used to derive the RSF, the RSF was unaffected by the year-specific suite of sample sizes, environmental conditions, or behavioral repertoires.

When bear location frequencies within the RSF intervals were partitioned across 2-week intervals spanning the autumn season, issues of inter-annual sampling bias are relaxed because each 2-week interval more or less includes the same component of inter-annual variation. The between-interval sampling intensity during 1987 –1993 was fairly equitable (Table 5). Seasonally, the strongest associations between bear locations and the RSF intervals were observed in October, when the frequency of bear locations within the upper 4 combined intervals attained about 77 % (Fig. 10). The frequency of bear locations in the uppermost RSF interval (# 20) imposed the greatest influence on the 4-interval sum. Before and after October, the bear-RSF associations diminished in a somewhat linear fashion. The bear-RSF associations were strongest during the period of the RSF's derivation (15 September – 15 November).

The early September and late November intervals in Figure 10 are outside the temporal range of polar bear data that were used to derive the RSF. The diminished bear-RSF association during these very-early and very-late autumn periods suggests that either the bears' habitat selection criteria changed, or that environmental conditions changed, or both. Addressing the former is beyond the scope of this study, but annual differences in very early and very late season sea ice conditions compared to the mid-autumn period are apparent in Figure 5.

Freeze onset typically occurs after mid-September in the Chukchi Sea, so the marginal ice zone tended to be broader in early September compared to conditions after freeze up. Breadth of the marginal ice zone under melt conditions is further exacerbated by melt ponding on the ice surface, which tends to reduce ice concentration estimates derived from microwave data (Comiso and Kwok 1996). After freeze conditions commence, ice forms within the melt ponds and open water leads of marginal ice zone, and thus the zone tends to shrinks in size.

When the marginal ice zone is very broad, the specific "line" delineating the 50% ice contour is probably too explicit to possess robust RSF covariate qualities, compared to conditions when the marginal ice zone is narrow and a greater range of ice habitats (concentrations) are maintained within closer proximity to the 50% contour. In other words, it is unlikely that polar bears specifically select the 50% contour per se. Rather, it is more likely that the 50% ice contour is spatially proximate to the density of ice concentration that is best for polar bear foraging.

By late November, sea ice typically occupies the entire Chukchi Sea and the pelagic ice edge is often south of the Bering Strait (Fig. 5). Bears selecting the pelagic ice edge would have presumably moved south of the study area. Recall that most bears tend to move closer to the coast as the autumn season progresses (Fig. 7). The bears that moved toward the coast tended to maintain fidelity with the higher RSF intervals because the 15%, 50% and 75% ice contours become coincident with the study area's coastal boundary when the sea ice converges to within 25 km of shore (Figs. 4 and 5).

Over the Chukchi Sea as a whole, the upper RSF intervals encompassed a majority of the unconsolidated pelagic pack ice during early autumn. Additionally, a majority of the study area paralleled the coast after the ice converged with the shore during the latter part of the season (Fig. 5). This seasonal ice pattern also reflects the overall seasonal change in polar bear distributions, from the pelagic ice edge to more coastal environments. Since the 50% ice contour parallels the coastline when

the ice converges with shore, the A50 covariate essentially served as a "distance to coast" surrogate in the RSF model. Consequently, the RSF was able to maintain robust association with the bear locations throughout the entire autumn season, despite the bears' general mid-season distributional shift from the pelagic ice edge to more coastal regions.

Distance to the 50% ice contour is the dominant covariate of the RSF, after which sea ice concentration influences the RSF magnitude (bathymetry notwithstanding since its effect is only realized at the northernmost latitudes). The highest RSF interval (# 20) is associated with habitats that are in close proximity to the 50% contour and that contain intermediate ice concentrations (Fig. 11). In conditions when the 50% contour abuts the study area's coastline boundary, magnitude of the ice concentration covariate strongly influences the resulting RSF value, since distance to the 50% contour is effectively constant.

When the 50% ice contour abuts the study area boundary and sea ice concentrations are high near the coast, the RSF values are diminished by virtue of the negative coefficient to the squared ice concentration covariate in the RSF. If sea ice concentrations along the coastal boundary are intermediate, the RSF values remain relatively high. An example contrasting these two conditions is captured by the RSF interval distributions on 15 November 1993 in Figure 5. The 50% contour abuts the study area's coastal boundary along northwest Alaska, and along the Chukotka Peninsula south and west of Wrangel Island. On the Russian side, sea ice concentrations in the pixels along the coastal boundary of the study area on 15 November 1993 typically exceeded 90%, which reduced their RSF values and precluded their membership in the uppermost RSF interval (#20). However, along the Alaska coastal boundary, sea ice concentrations were less (albeit > 50%), so the coastal RSF pixel values remained high and were assigned to the uppermost RSF interval.

Differential behavior of the RSF along the study area's coastal boundary (when the 50% ice contour is coincident with the boundary) is solely dependent on local sea ice concentrations (since distance to the 50% contour and bathymetry are effectively constant). Along coastal regions with prevalent ice motion, shearing, flaw lead zones, or persistent polynyas, ice concentrations along the boundary will typically be lower and the RSF values consistently higher than for coastal regions where more stable ice conditions favor higher ice concentrations, which in turn, slightly diminish the RSF values. Whether these results indicate that bears "prefer" coastal regions with the former conditions (less ice), or whether it is an artificial expression of the bears' selection for marginal ice concentrations along the pelagic ice edge is unclear. The question requires further study. In the meantime, caution should be exercised not to over interpret subtle differences among the upper RSF intervals when they occur along the study area's coastal boundary.

Temporal Sensitivity of the Bear–RSF Associations

Above we evaluated actual observed bear-RSF associations, when the RSF extrapolations and the polar bear locations were the same date. In this section, sensitivity of this temporal synchrony is evaluated. For this analysis, the polar bear locations were offset ± 7 days, in 1-day increments, relative to the RSF date, and the bear-RSF associations were quantified for each daily offset.

The proportion of polar bear locations occupying the combined upper-4 RSF intervals decreased by about 3% for each day the RSF map predated or post-dated the bear locations (Fig. 12). Given the arguably high degree of temporal autocorrelation among daily increments of both sea ice conditions and the relocations of individual polar bears, it is not surprising that the bear-RSF associations maintained their integrity after the events were modestly desynchronized. Nevertheless, the association consistently diminished over the ± 1-week intervals indicating that, on average, there is a functional near-real-time component to the bear-RSF association.

The proportion of bear locations occupying the uppermost RSF interval (# 20) was most sensitive to daily offsets between bear location dates and RSF dates (Fig. 13). Strength of the association with the uppermost RSF interval rapidly diminished after about a ± 1 day period. The effect was postponed and less pronounced in RSF interval # 19; effectively absent in RSF interval # 18, and was partially compensated within interval # 17. Ice drift alone contributes, at least partially to disassociation between bear locations and the RSF intervals. During autumn in the Chukchi Sea, ice drift velocities frequently exceed 10 km/d, and can be much greater during periods of strong winds (Norton and Gaylord 2004). To what degree the polar bears passively drift with the ice and/or make compensatory movements to selected habitats is beyond the scope of this study, but the combination of these factors within the expanding autumn sea ice environment dictated the observed temporal sensitivity of the bear-RSF associations.

Bear-RSF Associations During Recent Years

In this section, RSF associations are examined for a recent (1997 – 2005) data set of tracking locations from satellite transmitters that were exclusively deployed on polar bears captured in the Beaufort Sea. Occasionally, some Beaufort Sea bears range west into the Chukchi Sea. All such autumn occurrences were extracted and evaluated with respect to extrapolations of the original, unmodified (1987 – 1994) RSF to assess robustness of the retrospective RSF under more contemporary sea ice conditions, albeit for a distinctly different population of polar bears.

The recent bear locations were fully independent of those used to derive the RSF, but sample sizes were relatively small (Table 5) and their spatial distribution over the Chukchi Sea possessed an eastward and northern bias (Fig. 1). Nevertheless, these were the best data available to evaluate how recent changes in sea ice conditions may have impacted the degree of association between bear distributions and the retrospectively-derived RSF.

The exponential character of the bear-RSF associations observed in the historical assessment (Fig. 8) is far less pronounced for the 1997 – 2005 polar bear locations (Fig. 14). The relationship essentially plateaus over the upper RSF intervals, resulting in only 55 % of bear locations collectively occupying the 4 highest intervals, or top 20% of the study area. The most striking difference between the two periods is the dramatic loss of association between the recent bear locations and the uppermost (# 20) RSF interval (Fig. 8 and 14).

Seasonally partitioning the recent bear-RSF associations revealed useful insights into probable causes of the diminished relationship. Throughout September, the proportion of recent bear locations occupying the upper 4 RSF intervals remained quite low (~ 30 %), but then increased to about 60% for the remainder of the autumn season (Fig. 15). RSF performance for October, 1997 – 2005 (approximately 62%; Fig. 15) is similar to RSF performance for September, 1987 – 1994 (approximately 70%; Fig. 10), which suggests a delay in autumn ice conditions during the later period. These results are likely the consequence of longer melt seasons in the Chukchi Sea during recent years (Belchansky et al. 2004). Effectively, seasonal evolution of the sea ice environment to conditions resembling those of the 1987 – 1994 has been delayed later into the season.

Freeze onset and the corresponding reduction in size of the marginal ice zone occurred, on average, about 2 weeks later during 1997 – 2005 compared to 1987 – 1994 (Fig. 16). Since the RSF was derived from 1987 – 1994 data, after the marginal ice zone had decreased in size and more or less stabilized (mid September), it is not surprising that this retrospective RSF lacked strong association with recent polar bear distributions until similar seasonal ice conditions were established (i.e., early October).

Average size of the daily study area decreased relative to the earlier period (1987 – 1994). Since the daily study area is essentially defined by regions with > 0% ice cover (plus a 50 km southward

extension along the 15% ice contour), seasonal changes in study area size between the early and recent periods are effectively illustrated by the dynamics of open water area in the Chukchi Sea (Fig. 17).

Figure 17 corroborates extension of the melt season during recent years. It also illustrates a greater persistence of open water well into late November. Note, however, these are generalized patterns that do not reflect the conditions of every year, as exemplified by 1999, 2000, and 2001 whose patterns are essentially indistinguishable from those of 1987 – 1994.

Since average size of the study area decreased during recent years while size of the marginal ice zone increased, the proportional area of marginal ice relative to the daily study area increased to an even greater degree (Table 6). Consider October, a month when sea ice conditions are somewhat standardized between the two periods because freeze onset had largely commenced but there was still a large fraction of open water in the Chukchi Sea (Figs. 5 and 18). Average size of the daily study area in October was about 17% smaller during the recent years compared to the early years, and size of the marginal sea ice zone was about 25% larger (Table 6). The net effect of these two changes in October resulted in a ~50% increase in the amount of the study area occupied by marginal ice. This may be due, in part, to the younger age composition of sea ice in the Chukchi Sea (Belchansky et al. 2005b), which would enhance its propensity to shear and disperse under conditions of wind-driven divergent forcing.

We speculate that lack of an exponential bear-RSF association during the recent years (Fig. 14) is partly due to the larger proportions of marginal ice occupying the recent study area. Recall that distance to the 50 % ice contour has the greatest influence on the RSF magnitude. As suggested earlier, if the marginal ice zone is small, a greater diversity of sea ice habitats will be positioned in closer proximity to the 50% contour compared to conditions when the marginal ice zone is large and more dispersed. Thus, when the RSF is extrapolated over marginal ice zones that are considerably larger than those encountered in its retrospective derivation (i.e., the 1987 – 1994 period), the precise location of

the 50 % ice contour may be too spatially specific to maintain robust association with the habitats that are actually selected and used by polar bears in the pelagic sea ice environment. However, this effect becomes irrelevant once the ice converges with shore and the 50% ice contour coincides with the study area's coastal boundary.

Caution should be exercised not to over-interpret any environmental explanations regarding bear-RSF associations that may differ between the early (1987 – 1994) and recent (1997 – 2005) periods. The relatively small sample size of recent bears, which ranged primarily in the north-eastern Chukchi Sea, may have introduced a spatial bias sufficient to dominate the observed results.

Seasonal RSF-Area Interactions

Size of the daily study area increased during autumn as the sea ice expanded, so size of RSF intervals increased accordingly. Consequently, a statement like "75% of the bear locations were associated with the upper 4 combined RSF intervals" is ambiguous in terms of the area (km^2) encompassed by those intervals, the area of which is solely dependent on ice extent (i.e., date). Figure 19 illustrates this phenomenon by including an area component with the results presented in Figure 10. Information can be ascertained from Figure 19 by comparing bi-monthly responses for fixed values of interest on both the axes. For example, 50% of the bear locations were associated with RSF intervals that occupied a cumulative area of about 70,000 km^2 in early October, 90,000 km^2 in late October, 95,000 km^2 in late September, 105,000 km^2 in early September, 125,000 km^2 in early November, and 180,000 km^2 in late November. Alternatively, the area encompassing the uppermost 100,000 km^2 of RSF values was associated with roughly 28% of the bear locations in late November, 42 % in early November, 48% in early September, 50% in late September, 56% in late October, and 64% in early October.

In terms of area-efficiency, bear-RSF associations were most favorable during the first half of October, when the cumulative proportion of polar bear locations over the cumulative RSF interval area consistently exceeded all other 2-week periods. The logarithmic character of the curves in Figure 19 suggests that the inflection points within each respective 2-week period may represent optimal conditions of RSF area-efficiency in terms of bear density.

When results based on the recent polar bear locations (1997 – 2005) are illustrated analogously (Fig. 19, bottom), the logarithmic character of the bi-monthly curves yields to more linear ones because the bear-RSF relationship over the upper RSF intervals was generally flat (Fig. 14) versus exponential (Fig. 8). The recent curves also encompass fewer bear locations per RSF unit area (a downward shift on the y-axis), owing to the diminished bear-RSF relationships throughout the season as described above. Similar to 1987 – 1994, the early half of October in 1997 – 2005 had the highest RSF-area efficiency, although the latter half of October was almost indistinguishable. Both September periods were very inefficient during the recent years. The compressed range of cumulative September RSF area along the x-axis during the recent years results from larger fractions of open water in the Chukchi Sea (Fig. 17), which causes a corresponding decrease in the RSF interval area. For the 16 – 30 November period, the RSF-area efficiency was slightly higher during recent years compared to early years, which is not surprising given that the progression of autumn sea ice conditions has shifted later in the season.

Discussion

The distribution of polar bears in the Chukchi Sea is closely associated with the pelagic sea ice edge during autumn. While the area of potential usable habitat is very large throughout autumn, most bears appeared to select a relatively narrow band of habitat composed of an even mixture of sea ice and open water. Polar bears appeared to select the habitat zone where this even mixture of ice and open water transformed into higher proportions of sea ice. The change in selected habitat was relatively

abrupt. As the distance from the 50% ice contour increased , habitat selection rapidly decreased. North of this contour the decrease in RSF was more gradual. Therefore, while bears selected regions of ice comprised of approximately half ice and half water, the habitats in closer proximity to higher ice concentrations were selected most often. The RSF was skewed to slightly higher concentrations of sea ice (Fig. 3 and 11).

Polar bears also selected sea ice habitats where ocean depth was minimal. The response to ocean depth is most pronounced during early autumn for years when the minimum ice extent places the bears' ice habitat over deep waters of the Arctic basin. As autumn freeze progresses the effect of ocean depth becomes less influential because most of the Chukchi Sea is relatively shallow and uniform.

Selection for an even mixture of ice and open water in close proximity to higher concentrations of ice may reflect a strategy for choosing optimal hunting habitats while maintaining access to stable refuge habitats (Mauritzen et al. 2003). A large proportion of water interspersed by an equal proportion of ice floes may provide a necessary mixture of stable platforms and abundant hunting habitats in leads between floes.

Arthur et al. (1996), also using passive microwave data, examined habitat use by five female polar bears in the Chukchi Sea during 1990 and showed that those individuals used habitats with 25 – 50 % ice cover, and secondarily habitats with 51 – 75 % ice cover. Locations of the five bears investigated by Arthur et al. are part of this study. The habitat selection we observed from a much larger sample size is similar to that reported by Arthur et al. (1996). Our result differs, however, from the reported use of high ice concentrations by polar bears in the Beaufort Sea (Durner et al. 2004) and in the Canadian Arctic (Ferguson et al. 2000) where polar bears selected habitats with 95 % ice concentrations. This suggests that habitat use may not be consistent among regions within the range of polar bear populations.

As autumn progressed and sea ice extent advanced toward and ultimately converged with the coastline, most bears tended to follow the advancing ice edge so their distribution generally shifted shoreward and southward. The RSF was able to emulate this seasonal distribution shift through its dependence on proximity to the 50% ice contour. During early autumn, the 50% contour effectively tracked the southward propagation of unconsolidated ice as it approached the coastline. Once the ice converged with shore, the 50% contour essentially coincided with the coastal periphery of the study area and acted as a proxy covariate for "distance to coast". Consequently, bears that followed the ice into coastal regions remained in high-value RSF habitats, as did any bears that remained affiliated with the pelagic ice contour. This dual versatility of the RSF is its foremost attribute. The RSF not only performed well overall (Fig. 8), it was fairly robust to inter-annual variability (Fig. 9).

Bear-RSF associations were strongest in October (Fig. 10) because the sea ice was still mostly offshore, and breadth of the marginal ice zone was generally less than during September. Under these conditions, regions in closer proximity to the 50% ice contour encompassed a majority of the unconsolidated sea ice habitats, and coastal habitats were largely unavailable. Regardless if bears were using the unconsolidated ice contour for hunting or as a vehicle to gain imminent coastal access (e.g., females seeking maternity dens), the majority of this zone received high RSF values owing to both its close proximity to the 50% contour and its intermediate ice concentrations (Fig. 4).

The RSF associations were lower in September (Fig. 10) possibly because September was a transitory month for ice formation. During early September and prior to the onset of freeze, the marginal ice zone tends to be broader (Fig. 16), so areas proximate to the 50% ice contour encompass proportionally less of the unconsolidated ice margin. Since it is unlikely that polar bears specifically select the boundary of 50% ice concentration per se, the 50% contour lost its value as a robust spatial proxy to the habitat diversity of the overall marginal ice zone.

The diminished early-autumn RSF performance was exacerbated in the evaluation of recent (1997 – 2005) polar bear distributions (Fig. 15). The poor September bear-RSF associations during recent years are consistent with extended melt seasons (Belchansky et al. 2004) and younger ice (Belchansky et al. 2005b) that would cause broader marginal ice zones to persist longer into the autumn season (Fig. 16). After September, although the RSF never attained performance equitable to the earlier years (Figs. 10 and 15), approximately 60% of the recent bear locations did consistently occupy the 4 upper RSF intervals – but a strong association with the uppermost RSF interval (# 20) was conspicuously lacking (Fig. 15). This tells us that a retrospective RSF may not be useful for current September ice conditions in the Chukchi Sea, but the model continues to work reasonably well after September.

Changes in the autumn sea ice in the Chukchi Sea over the past decade, raises the question as to whether the response by polar bears to contemporary sea ice features may be different from those of 1987 – 1994. A "functional response" (Mauritzen et al. 2003) of polar bears to changes in the proportion of likely hunting habitat and the proportion of stable refuge habitat is plausible. Hence, there are additional questions concerning the applicability of this retrospective RSF for predicting contemporary polar bear distributions; however the efficacy of application to similar conditions appears to remain strong. Insufficient data exist, however, to examine if behavior of the present-day Chukchi Sea polar bear population still adheres to a model of retrospective selection criteria, especially in light of today's substantially different sea ice conditions. Although we present some results of bear-RSF associations using recent location data, it is very important to keep in mind that this is from a relatively small number of bears tracked in the northeast Chukchi Sea during recent autumns. Most likely this is not a defensible surrogate for making inferences about the behavior of the entire Chukchi Sea population, which ranges as far west as Wrangel Island (Amstrup et al. 2004). We can't offer a solution

to this conundrum, except to suggest renewed research efforts in the Chukchi Sea. The topic may

warrant further consideration, but, because recent distribution data for the Chukchi Sea population do

not exist, a contemporary RSF cannot be developed nor can a retrospective RSF be adequately assessed.

Any ad hoc solutions require imposition of one or more assumptions that may or may not be defensible.

Also, this study is based exclusively on tracking data of adult female polar bears and makes the

assumption that they are representative of all members of the population. There is little data of autumn

movements for other ages and sexes of polar bears to test this assumption, however.

The methodology we employed necessarily omitted the nearshore coastal zone owing to the

coarse resolution of the sea ice concentration data. Consequently, the RSF model domain does not

address the occupancy of habitats adjacent to the coastline, yet a considerable proportion of the Chukchi

Sea polar bear population is known to utilize coastal areas during autumn (Fig. 6). Hence, the RSF

predictions of bear distribution become less and less comprehensive as the season progresses and more

bears select habitats along the coast (Fig. 7). Resource selection by the coastal component of the

Chukchi Sea polar bear population during autumn is not addressed by this study, nor does it lend itself

to the analysis of covariates derived from 25 km resolution sea ice concentration data. A different RSF

modeling approach is justified for polar bears occupying the coastal zone, perhaps one that considers

different habitat covariates, and certainly one with higher spatial resolution. Renewed research efforts

on polar bears in the Chukchi Sea could address this concern.

Stirling et al. (1993) suggested that the distribution of polar bears in the Arctic is dominated by a

complex of sea ice characteristics rather than simply the presence or absence of ice. Several studies in

various regions of the Arctic (Arthur et al. 1996, Ferguson et al. 2000, Mauritzen et al. 2003, Durner et

al. 2004) support this notion and bring forth some limitations of this study. Our work is limited by the

coarse resolution of passive microwave data (25 x 25 km pixels), and lacks information about ice age

and average floe size, which were important habitat features affecting polar bear distributions in the Beaufort Sea (Durner et al. 2004) and in the Canadian Arctic (Ferguson et al. 2000). Nevertheless, our results agree with Stirling et al. (1993) and are generally consistent with other studies, suggesting our RSF model of polar bear habitat use during autumn in the Chukchi Sea for 1987 – 1994 is sound. This also suggests that some patterns of habitat use may be consistent among polar bear populations in many different regions of the Arctic.

There is utility in this RSF model for polar bear management. Determining the status of wildlife populations is important for effective wildlife management. Population status is also the most difficult information to obtain. Polar bears are no exception to this. Polar bears occur at low densities in a dynamic environment where it is logistically difficult to collect data. Hence, it is useful to know where to look for polar bears if the interest is in determining population status. The model that we present here may be applied by researchers in the field, mindful of the caveats that we have explained, to near-real time passive microwave imagery so that daily maps of the expected distribution of polar bears may be derived. Such information is useful for allocating efforts in traditionally resource-limited field methods of polar bear studies, including line transect methodologies and mark-and-recapture techniques. The model provides a relative probability of occurrence, which may be applied as a correction factor to encounter rates and field effort. In the field, our model has practical significance for the day-to-day operations for researchers attempting to collect population data on polar bears. The model lends itself well to standard GIS tools and could be used in stratifying survey effort (Fig. 20).

In this report, we elucidated some complexities of polar bear habitat selection, revealing that bear distributions are affected by varying ice concentrations, distances to contours between ice concentration classes, and ocean depth. We also demonstrated that the dynamics of autumn polar bear distribution in the Chukchi Sea can be generalized using habitat features extracted from coarse

resolution satellite imagery. After applying our retrospective RSF model to a limited data set of contemporary polar bear locations, we found that the bear-RSF generalities persisted in the recent period, but strength of the associations diminished. Renewed research efforts on polar bears in the Chukchi Sea are necessary to better understand the applied limitations of this retrospective RSF in present-day conditions. Until then, we strongly caution against the use of this RSF for any contemporary applications without first giving thorough consideration to all of the topics discussed above that could severely limit its utility: 1) the implications of different sea ice conditions; 2) the distributions of males and subadults; and 3) the occupancy of nearshore habitats.

Acknowledgements

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Table 1. Main effects (covariates), quadratics of main effects, and interactions

between main effects for a resource selection function of polar bear habitat use in the

Chukchi Sea, 1987-1994.

Covariate code	Description
A15	Distance (km) to the 15 % ice concentration contour
A50	Distance (km) to the 50 % ice concentration contour
A75	Distance (km) to the 75 % ice concentration contour
$A15^2$	A15 quadratic
$A50^2$	A50 quadratic
$A75^2$	A75 quadratic
NTICE	Ice concentration (%)
$NTICE^2$	NTICE quadratic
BATHY	Ocean depth (m)
$BATHY^2$	BATHY quadratic
A15*NTICE	A15 and NTICE interaction
A50*NTICE	A50 and NTICE interaction
A75*NTICE	A75 and NTICE interaction
A15*BATH	A15 and BATHY interaction
A50*BATH	A15 and BATHY interaction
A75*BATH	A15 and BATHY interaction
NTICE*BATH	NTICE and BATHY interaction

Table 2. Correlation matrix of covariates considered for a resource selection function for polar bears in the Chukchi Sea, 15 September to 14 November, 1987 – 1994. Significant correlations ($r \geq |0.6|$) are indicated in bold text. See Table 1 for a description of covariates.

	bathy	a15	a50	a75
ntice	-0.23	**0.60**	0.37	-0.07
	<.0001	<.0001	<.0001	<.0001
bathy	-	-0.43	-0.42	-0.25
		<.0001	<.0001	<.0001
a15		-	**0.89**	0.46
			<.0001	<.0001
a50			-	**0.66**
				<.0001

Table 3. Sequence of model building of a resource selection function for polar bears in the Chukchi Sea, 15 September to 14 November, 1987 – 1994. Model building began with A50 (largest single covariate score chi-sq.)

Model	Parameter estimate (standard error)	Score χ^2 (covariate entry)	P (covariate entry)
A15	-0.00741(0.0006279)	144.6026	<0.0001
A50	-0.01479(0.0008452)	335.4296	<0.0001
A75	-0.00685(0.0006842)	102.9724	<0.0001
NTICE	-0.0003150(0.00125)	0.0636	0.9354
BATHY	0.0005074(0.0000739)	51.5663	<0.0001
A50	-0.02074(0.00110)		
$A50^2$	0.0000212(0.00000227998)	126.4511	<0.0001
A50	-0.02022(0.00111)		
$A50^2$	0.0000209(0.00000229346)		
BATHY	0.0002742(0.0000765)	13.1083	0.0003
A50	-0.02062(0.00112)		
$A50^2$	0.0000213(0.00000229969)		
BATHY	0.0003064(0.0000775)		
NTICE	0.00481(0.00143)	11.3501	0.0008
A50	-0.01116 (0.00147)		
$A50^2$	0.0000107(0.00000259101)		
BATHY	0.0003442(0.0000777)		
NTICE	0.06377(0.00672)		
$NTICE^2$	-0.0006086(0.0000662)	86.9893	<0.0001

Table 4. Total number of all satellite telemetry locations and polar bears considered for the RSF assessment, including observations < 40 km from the coast, by year and 2-week interval during autumn in the Chukchi Sea.

	Number of Locations									Number of Individual Bears						
Year	Sep 01-15	Sep 16-30	Oct 01-15	Oct 16-31	Nov 01-15	Nov 16-30	Total	% Total	Year	Sep 01-15	Sep 16-30	Oct 01-15	Oct 16-31	Nov 01-15	Nov 16-30	Total
Early									Early							
1987	31	39	35	51	58	46	260	9.6	1987	10	14	13	14	15	15	22
1988	54	35	22	27	25	37	200	7.4	1988	16	11	9	9	8	12	22
1989	74	64	70	63	71	61	403	14.9	1989	21	20	18	22	19	17	27
1990	116	109	106	103	87	99	620	22.9	1990	33	29	27	26	23	23	35
1991	50	46	49	44	42	43	274	10.1	1991	17	16	15	13	12	11	21
1992	81	53	69	91	78	83	455	16.8	1992	23	20	20	23	21	24	28
1993	79	79	68	83	60	57	426	15.7	1993	30	24	25	24	22	19	33
1994	22	13	9	7	12	8	71	2.6	1994	8	7	5	3	4	2	12
Total	507	438	428	469	433	434	2709	100.0	Total	158	141	132	134	124	123	200
Recent									Recent							
1997		1				4	5	0.6	1997		1				1	2
1998	5	14	16	20	17	20	92	11.1	1998	3	2	2	3	3	3	6
1999	2	13	28	24	15	13	95	11.5	1999	2	4	6	4	3	2	7
2000						2	2	0.2	2000						2	2
2001	2	4	11	16	14	20	67	8.1	2001	1	2	3	4	4	2	5
2002					4	3	7	0.8	2002					2	1	2
2003	3		1	2	2	1	9	1.1	2003	1		1	1	1	1	2
2004	13	11	21	19	35	55	154	18.6	2004	1	2	4	3	6	8	10
2005	27	65	86	70	80	68	396	47.9	2005	4	7	9	9	11	10	14
Total	52	108	163	151	167	186	827	100.0	Total	12	18	25	24	30	30	50

Table 5. Total number of all satellite telemetry locations and polar bears considered for the RSF assessment, after removal of observations < 40 km from the coast, by year and 2-week interval during autumn in the Chukchi Sea.

	Number of Locations									Number of Individual Bears						
Year	Sep 01-15	Sep 16-30	Oct 01-15	Oct 16-31	Nov 01-15	Nov 16-30	Total	% Total	Year	Sep 01-15	Sep 16-30	Oct 01-15	Oct 16-31	Nov 01-15	Nov 16-30	Total
Early									Early							
1987	27	33	25	47	52	40	224	10.2	1987	9	13	10	13	13	13	21
1988	41	22	14	23	17	30	147	6.7	1988	15	8	5	8	6	10	21
1989	72	63	70	61	47	51	364	16.6	1989	20	19	18	21	16	16	26
1990	111	100	96	83	59	80	529	24.1	1990	31	27	25	24	22	20	35
1991	37	40	41	39	31	27	215	9.8	1991	13	12	11	12	11	10	16
1992	65	30	56	77	63	61	352	16.1	1992	21	12	16	21	21	22	27
1993	66	68	54	55	28	37	308	14.0	1993	25	22	22	19	14	12	31
1994	15	6	6	7	12	8	54	2.5	1994	6	4	3	3	4	2	9
Total	434	362	362	392	309	334	2193	100.0	Total	140	117	110	121	107	105	186
Recent									Recent							
1997		1				4	5	0.7	1997		1				1	2
1998	5	14	16	20	17	15	87	11.8	1998	3	2	2	3	3	3	6
1999	2	13	28	20	3	8	74	10.0	1999	2	4	6	4	1	2	7
2000						2	2	0.3	2000						2	2
2001	2	4	11	14	7	17	55	7.5	2001	1	2	3	3	3	2	5
2002						2	2	0.3	2002						1	2
2003	3		1	2	2		8	1.1	2003	1		1	1	1		2
2004	13	11	21	19	31	54	149	20.2	2004	1	2	4	3	5	7	9
2005	27	65	86	64	70	43	355	48.2	2005	4	7	9	8	10	9	13
Total	52	108	163	139	130	145	737	100.0	Total	12	18	25	22	23	27	47

Table 6. Average monthly size of the daily study area, the marginal ice zone, and the proportional area of marginal ice within the study area, during (and % change between) the early (1987-1994) and recent (1997-2005) periods investigated.

PERIOD	MONTH	N	STUDY AREA (km^2 10^3)	MARGINAL ICE (km^2 10^3)	PROPORTION MARGINAL ICE
1987-1994	SEP	240	906.7	115.8	12.8
1997-2005	SEP	270	713.4	200.3	28.1
% Change	SEP		**-21.3**	**73.0**	**119.9**
1987-1994	OCT	248	1022.6	85.5	8.4
1997-2005	OCT	279	852.7	106.7	12.5
% Change	OCT		**-16.6**	**24.7**	**49.5**
1987-1994	NOV	240	1172.2	63.9	5.5
1997-2005	NOV	270	1129.2	79.9	7.1
% Change	NOV		**-3.7**	**25.0**	**29.8**
1987-1994	ALL	728	1033.7	88.4	8.6
1997-2005	ALL	819	897.9	128.7	14.3
% Change	ALL		**-13.1**	**45.6**	**67.7**

Figure 1. Boundary of the full Chukchi Sea study area (intermediate gray) as defined by a 25 km x 25 km rasterized polygon that encompassed offshore (>25 km) waters between 170°E–156°W and 66°N–80°N. Dot symbols denote all polar bear satellite relocations within 170°E–156°W and 66°N–80°N that were collected during the autumn months (September–November), mostly from an early-vintage field study (1987–1994) of the Chukchi Sea bear population (red), and exclusively from a recent-vintage field study (1997–2005) of the Beaufort Sea bear population (blue).
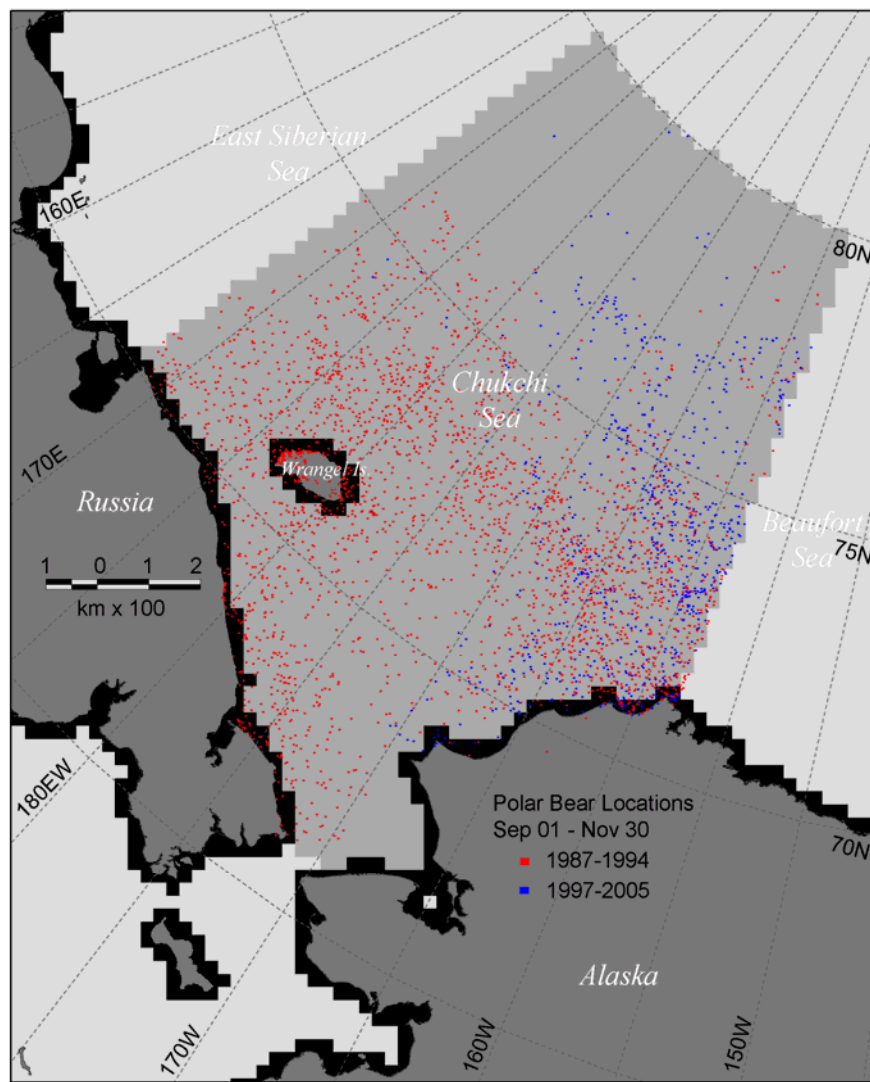
Figure 2. Example of a rasterized 25 km shoreline buffer for the Chukchi Sea, compared to a true 25 km buffer, for a polar bear resource selection function (RSF). This rasterized buffer eliminated contaminated shoreline pixels, and associated polar bear locations, from the RSF modeling.
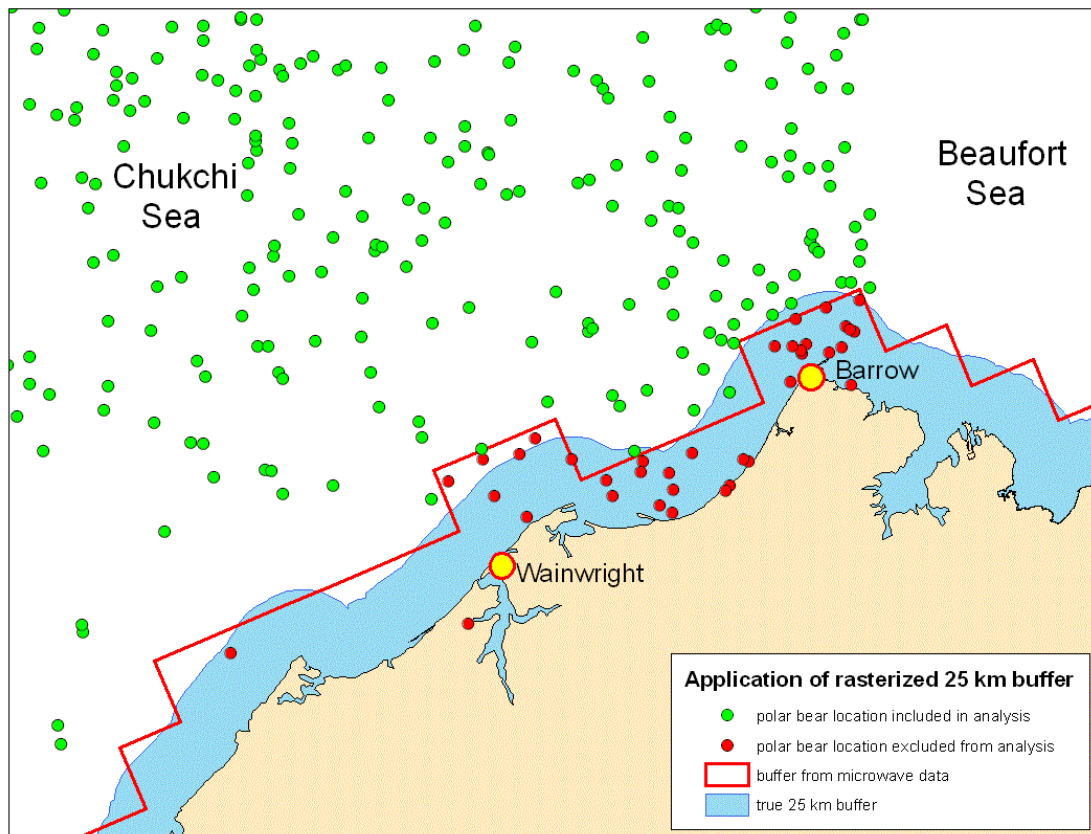
Figure 3. Response of the resource selection function for polar bears in the Chukchi Sea during autumn to changes in distance to the 50% ice edge (A), ocean depth (B), and total sea ice concentration (C). Covariates not shown in each chart were held constant at their mean values (distance to 50% edge: 78.5 km; depth: -329.3 m; ice concentration: 61.3 %).
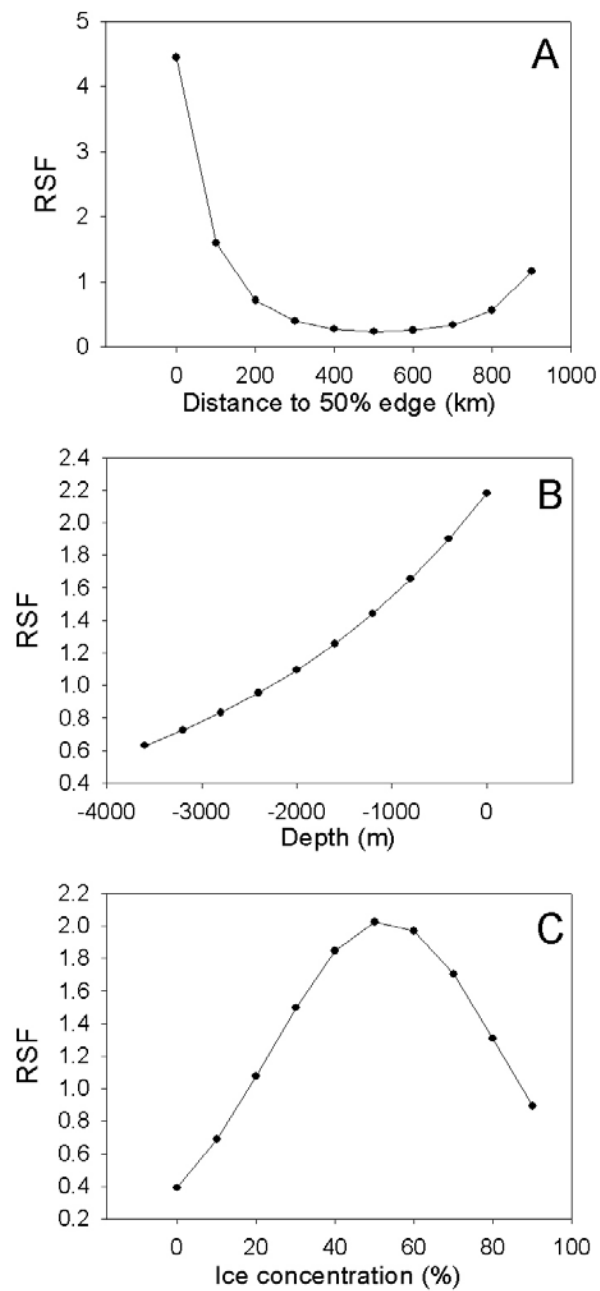
Figure 4. Distribution maps of individual RSF intervals 11-20 (gray shaded gradient, dark to light) and pooled RSF intervals 1-10 (blue) for 15 September (left) and 15 November (right), 1993. The 50% and 15% ice edges are shown as cross-hatched and broken lines. Dot symbols denote individual polar bear locations recorded on the respective day.
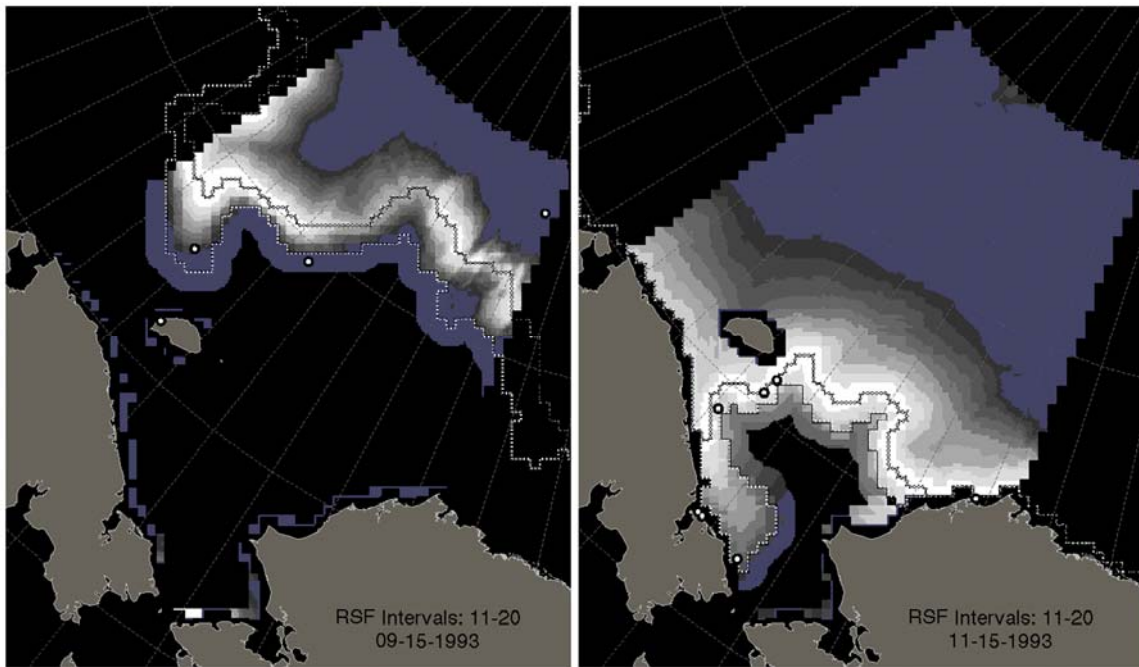
Figure 5. Daily RSF distribution maps at 15-day intervals beginning 1 September and ending 30 November, 1987-1994. Map shading and symbols are analogous to Figure 3.
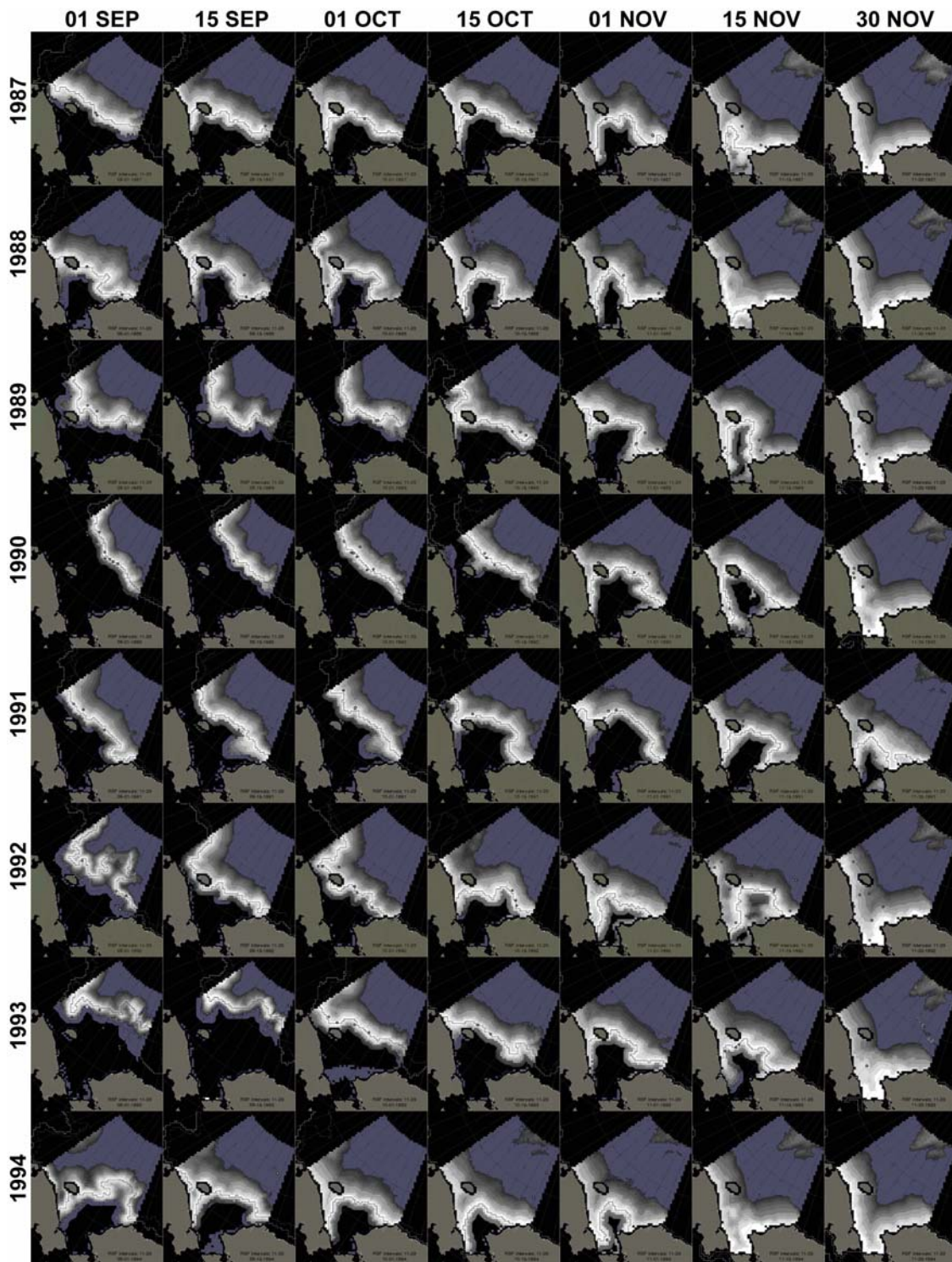
Figure 6. Frequency of autumn (Sep-Nov) polar bear locations in the Chukchi Sea (1987-2005) within distance intervals from the coastline. Negative values are onshore, positive values are offshore. Note the distance interval thresholds are not equal across the y-axis. Locations above the dashed line (< 40 km offshore) were excluded from the RSF assessment.

Distance to Coast (km)	FREQ.	PCT.	CUM. PCT.
−55	4	0.11	0.11
−45	1	0.03	0.14
−35	1	0.03	0.17
−25	4	0.11	0.28
−15	17	0.48	0.76
−5	104	2.94	3.70
5	144	4.07	7.78
15	114	3.22	11.00
25	91	2.57	13.57
35	126	3.56	17.14
45	180	5.09	22.23
75	403	11.40	33.63
125	399	11.28	44.91
175	487	13.77	58.68
250	581	16.43	75.11
350	471	13.32	88.43
450	176	4.98	93.41
550	108	3.05	96.46
650	97	2.74	99.21
750	28	0.79	100.00

Polar Bear Locations (%)
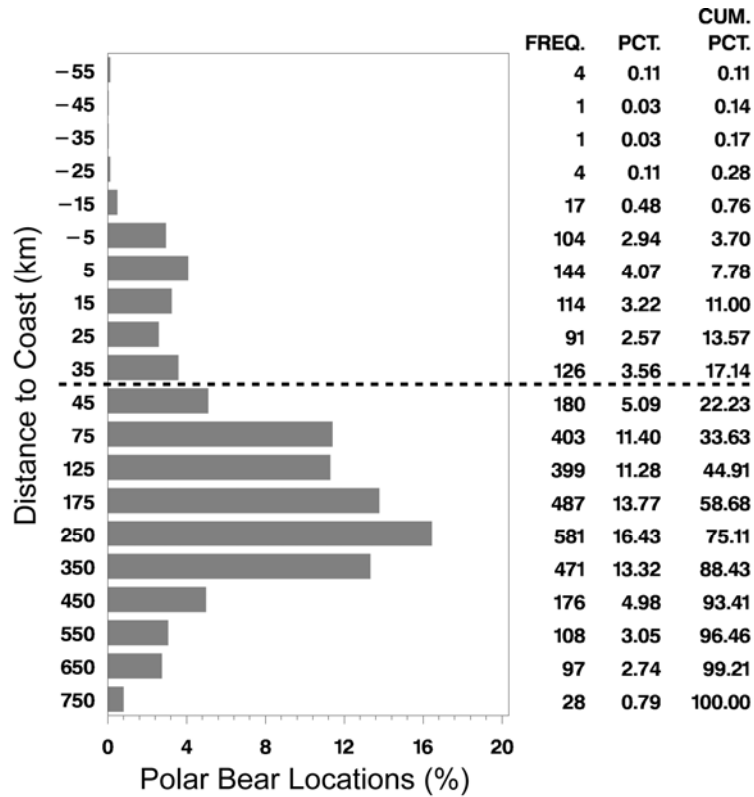
Figure 7. Proportion of all polar bear locations (Table 2) during 1-week periods, within 5 distance intervals to the coastline, 1987-1994. Note that range of the distance interval thresholds are not equivalent.
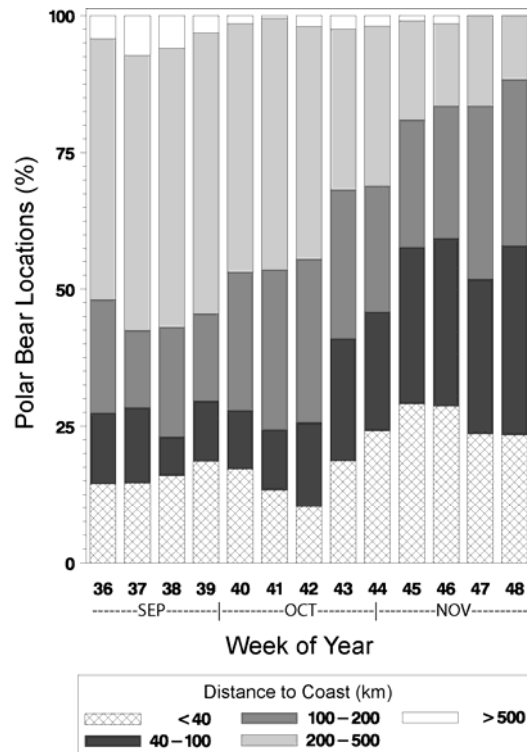
Figure 8. Frequencies of pelagic polar bear locations within 20 equal area RSF intervals along an increasing RSF-value gradient. Polar bear data from 15 September-15 November, 1987-1994.
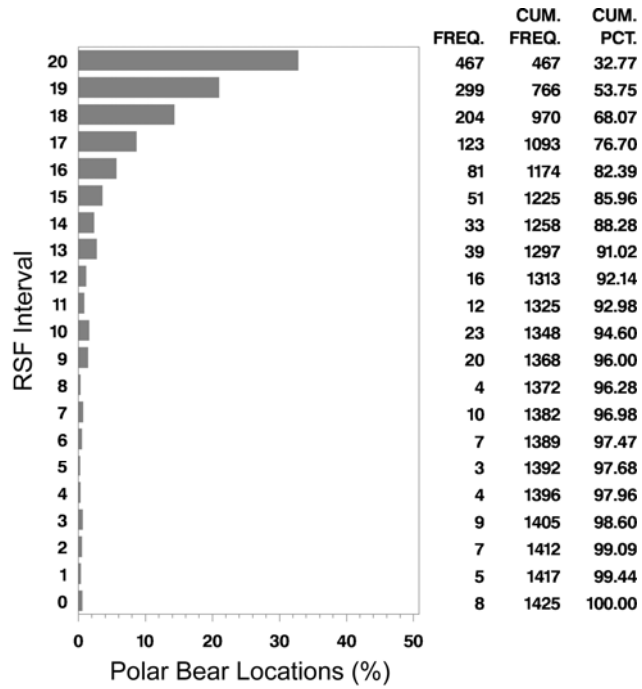

RSF Interval	FREQ.	CUM. FREQ.	CUM. PCT.
20	467	467	32.77
19	299	766	53.75
18	204	970	68.07
17	123	1093	76.70
16	81	1174	82.39
15	51	1225	85.96
14	33	1258	88.28
13	39	1297	91.02
12	16	1313	92.14
11	12	1325	92.98
10	23	1348	94.60
9	20	1368	96.00
8	4	1372	96.28
7	10	1382	96.98
6	7	1389	97.47
5	3	1392	97.68
4	4	1396	97.96
3	9	1405	98.60
2	7	1412	99.09
1	5	1417	99.44
0	8	1425	100.00

Figure 9. Annually (1987-1993) partitioned frequencies of pelagic polar bear locations within each of the respective year's 4 upper RSF intervals, and their consolidate sum. Polar bear data from 15 September-15 November. 1994 is not shown due to small sample size (Table 3).
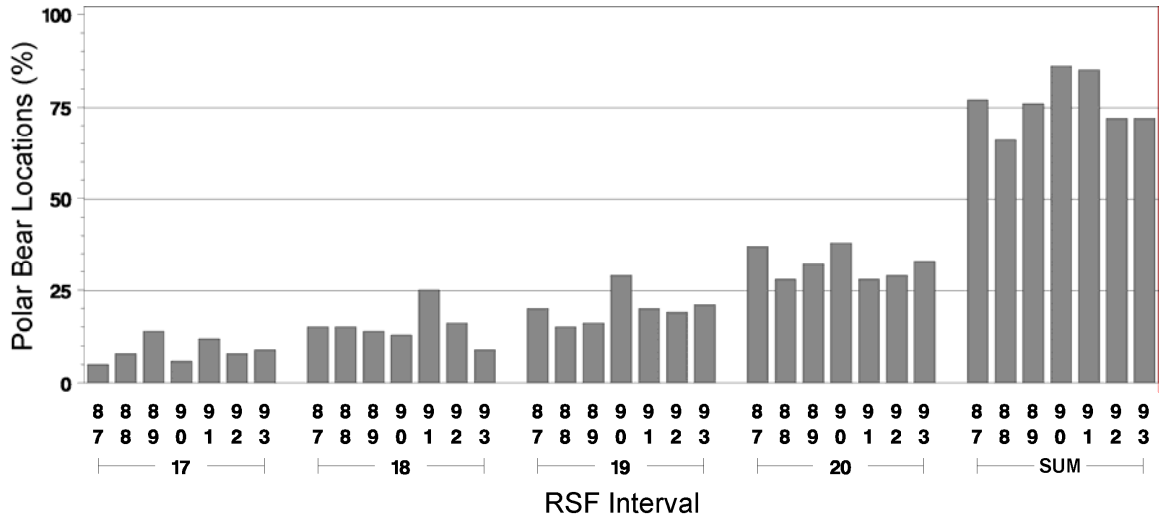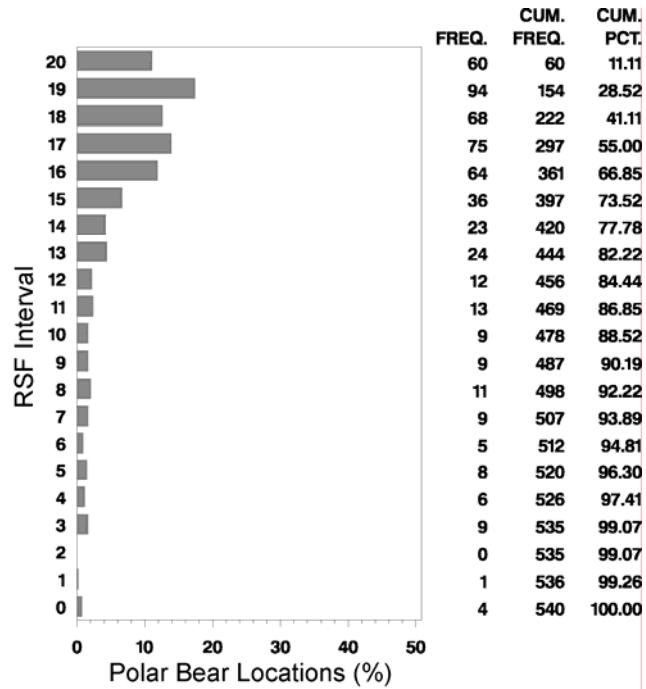

Figure 10. Seasonally partitioned frequencies of pelagic polar bear locations within 2-week periods between 01 September-30 November for the 4 upper RSF intervals, and their consolidate sum. Polar bear data from 1987-1994.
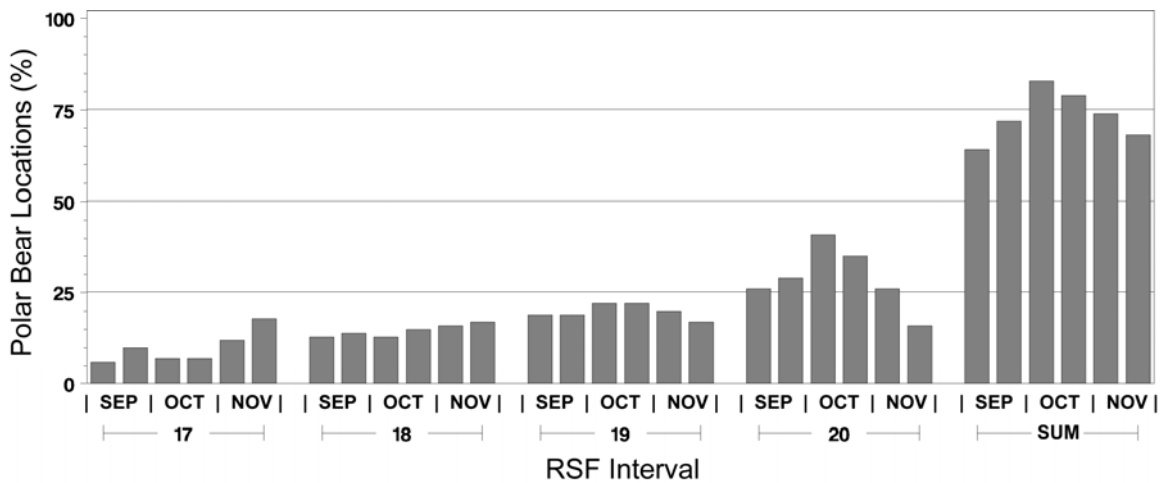
**Figure 11.** Frequency response surface of pelagic polar bear locations with respect to sea ice concentration and RSF interval. RSF intervals 17-20 are gray-shaded for visual discrimination. Polar bear data from 15 September-15 November, 1987-1994.
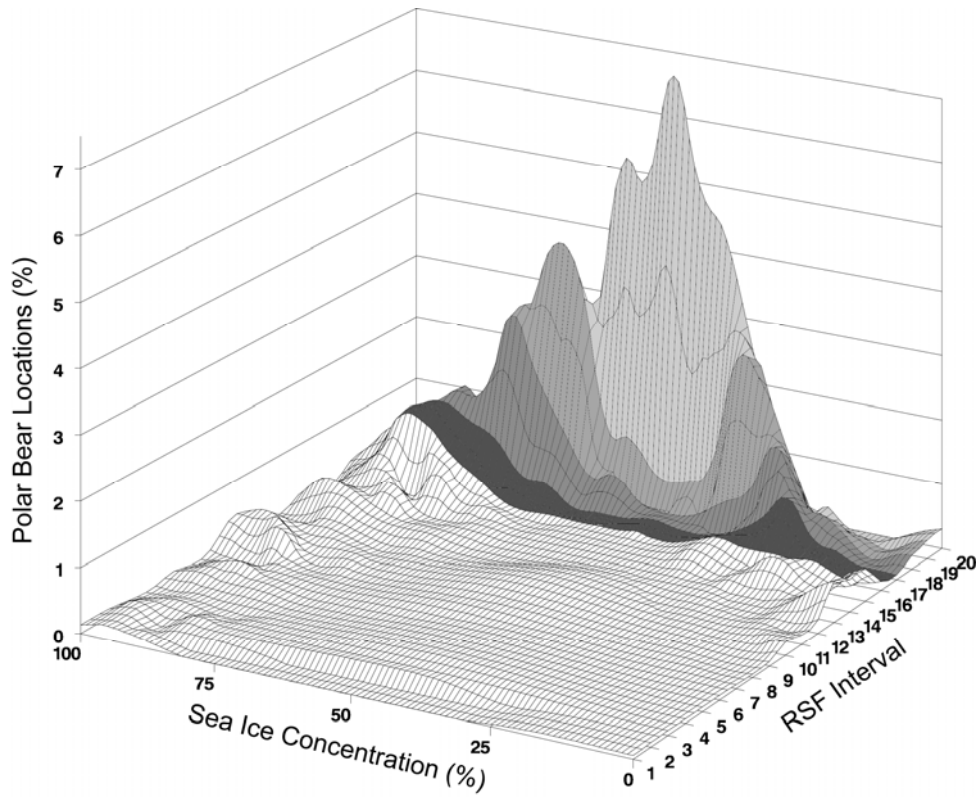
Figure 12. Frequencies of polar bear locations within the upper 4 combined RSF intervals, when the bear location dates are offset in daily increments relative to the dates of the RSF-interval maps. Polar bear data from 15 September – 15 November, 1987-1994.
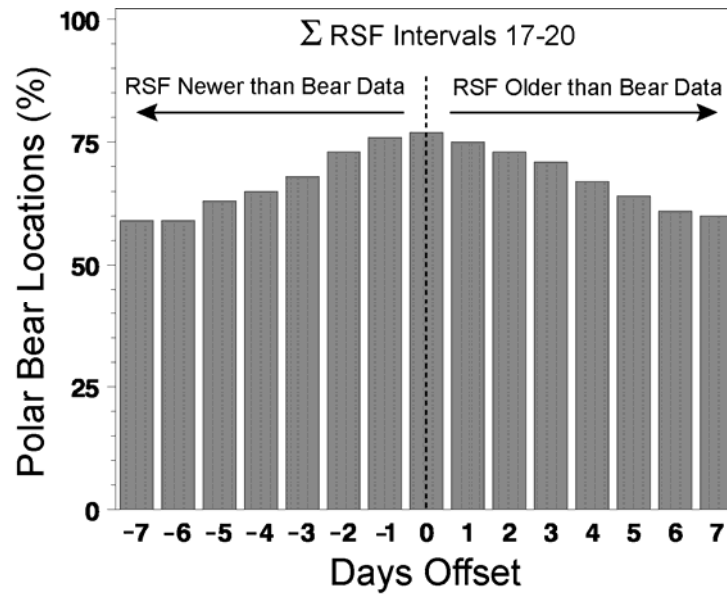
Figure 13. Frequencies of polar bear locations partitioned within each of the 4 upper RSF intervals, for bear location dates that were offset in daily increments relative to the dates of the RSF-interval maps. Relativity of the offsets is analogous to Fig. 11. Polar bear data from 15 September – 15 November, 1987-1994.
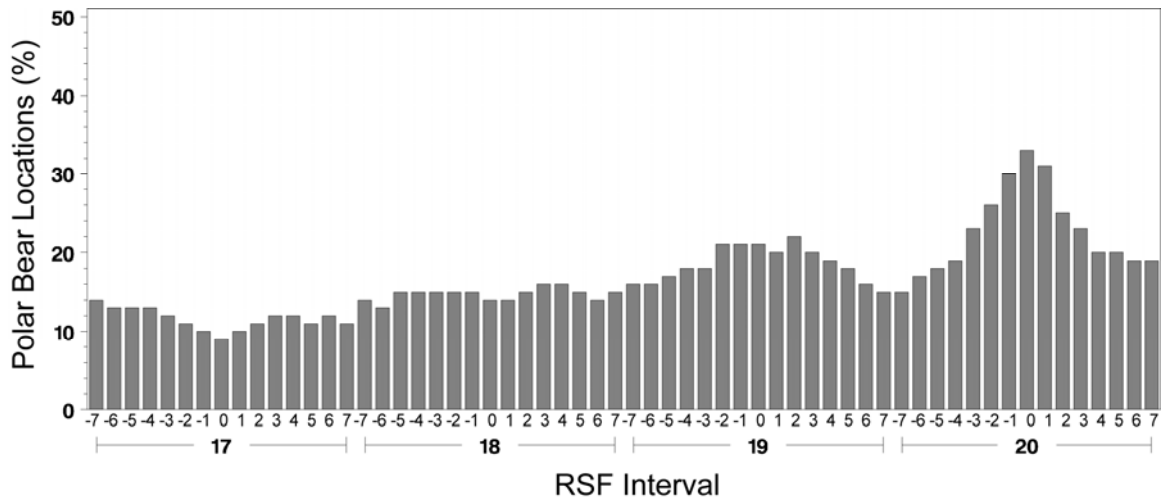
Figure 14. Frequencies of pelagic polar bear locations within 20 equal area RSF intervals along an increasing RSF-value gradient. Polar bear data from 15 September-15 November, 1997-2005.

Figure 15. Seasonally partitioned frequencies of pelagic polar bear locations within 2-week periods between 01 September-30 November for the 4 upper RSF intervals, and their consolidate sum. Polar bear data from 1997-2005.
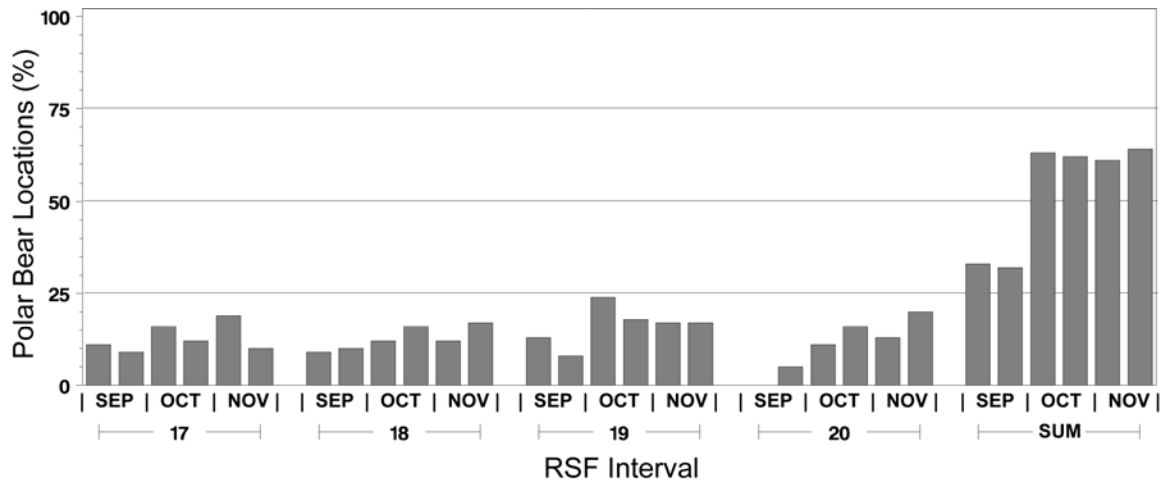
Figure 16. Daily area of the marginal ice zone (15-50% concentration) during autumn in the Chukchi Sea: 1987-1994 (top) and 1997-2005 (bottom).
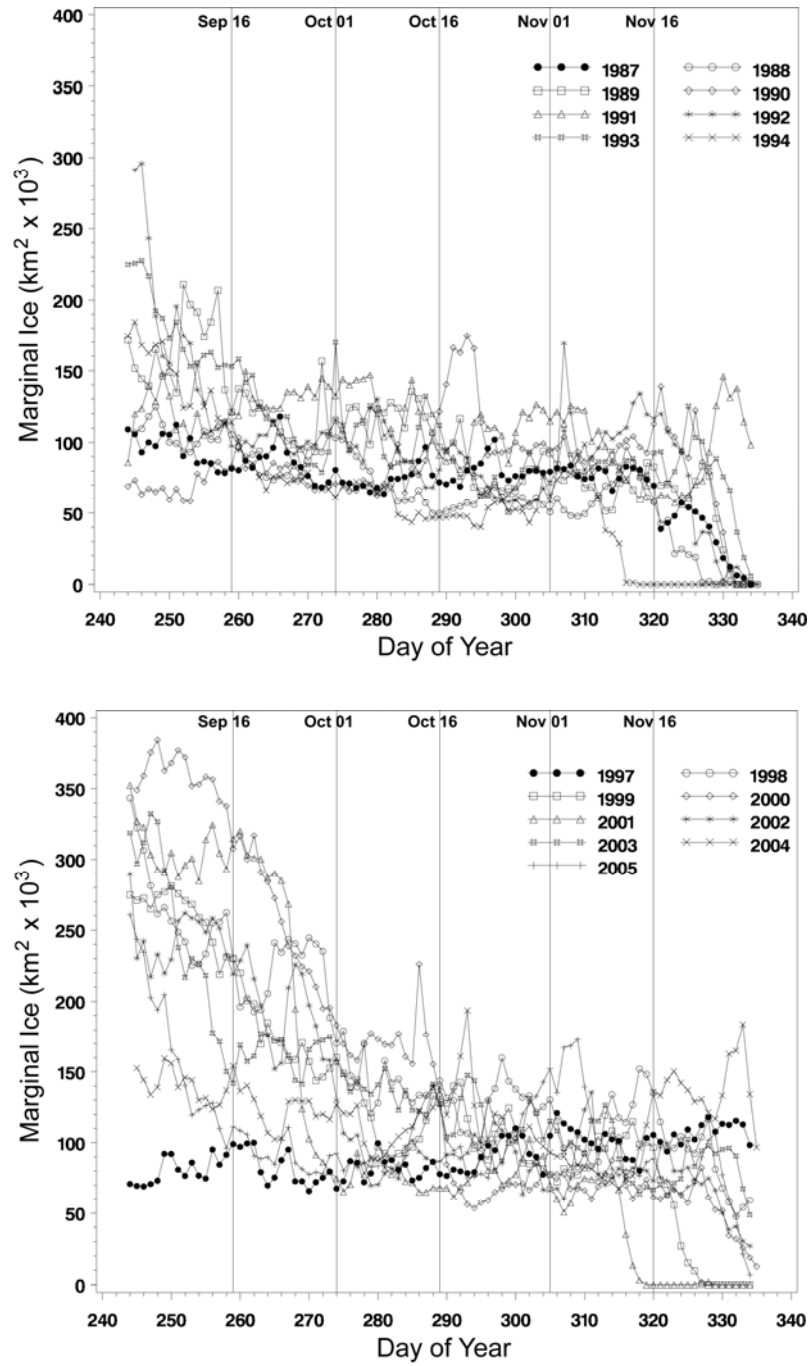
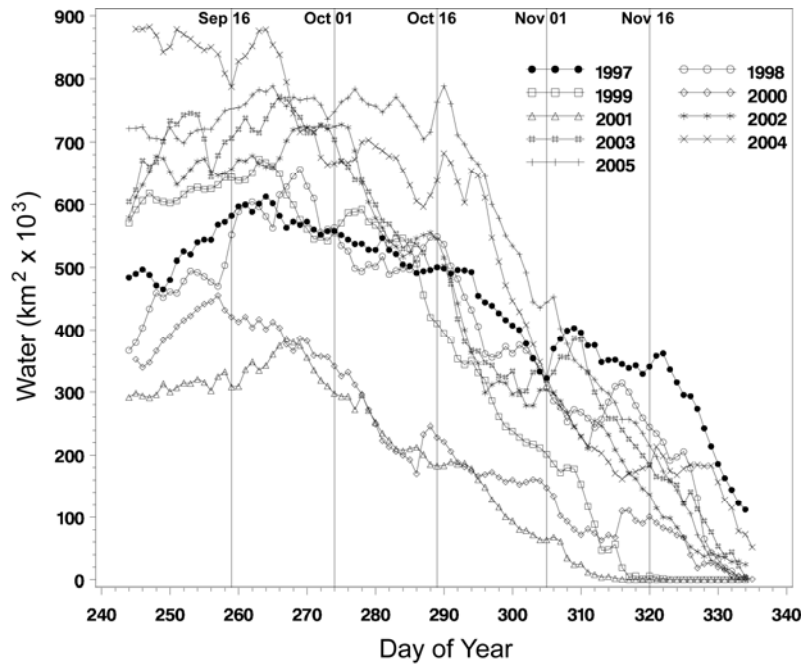**Figure 17.** Daily area of ice-free water during autumn in the Chukchi Sea: 1987-1994 (top) and 1997-2005 (bottom).
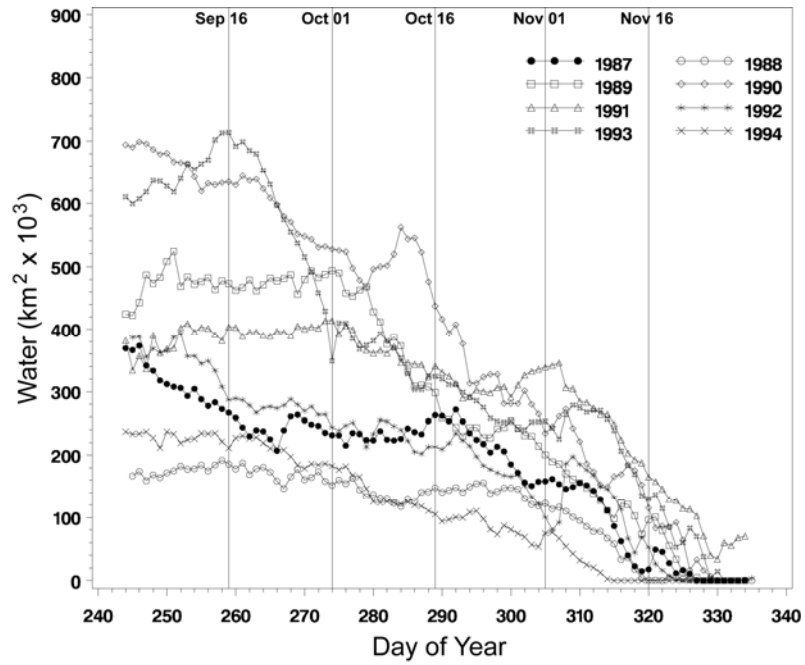
Figure 18. Daily RSF distribution maps at 15-day intervals beginning 1 September and ending 30 November, 1998-2005. Map shading and symbols are analogous to Fig. 3.
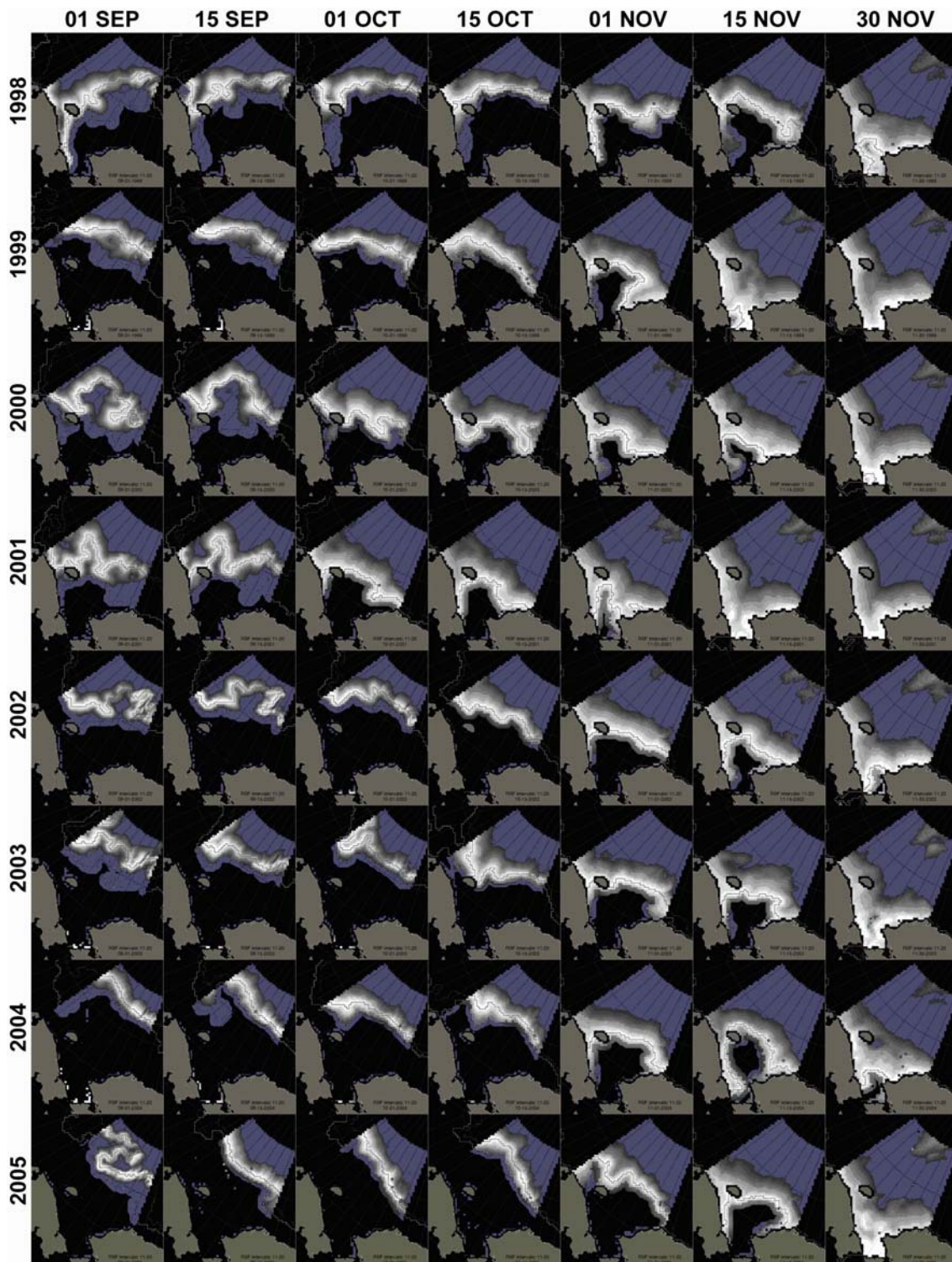
Figure 19. Cumulative frequency of polar bear locations occupying cumulative increments of the upper 6 RSF intervals as a function of the total area encompassed by the respective RSF interval, partitioned across 2-week intervals during autumn, and averaged for the periods 1987-1994 (top) and 1997-2005 (bottom).
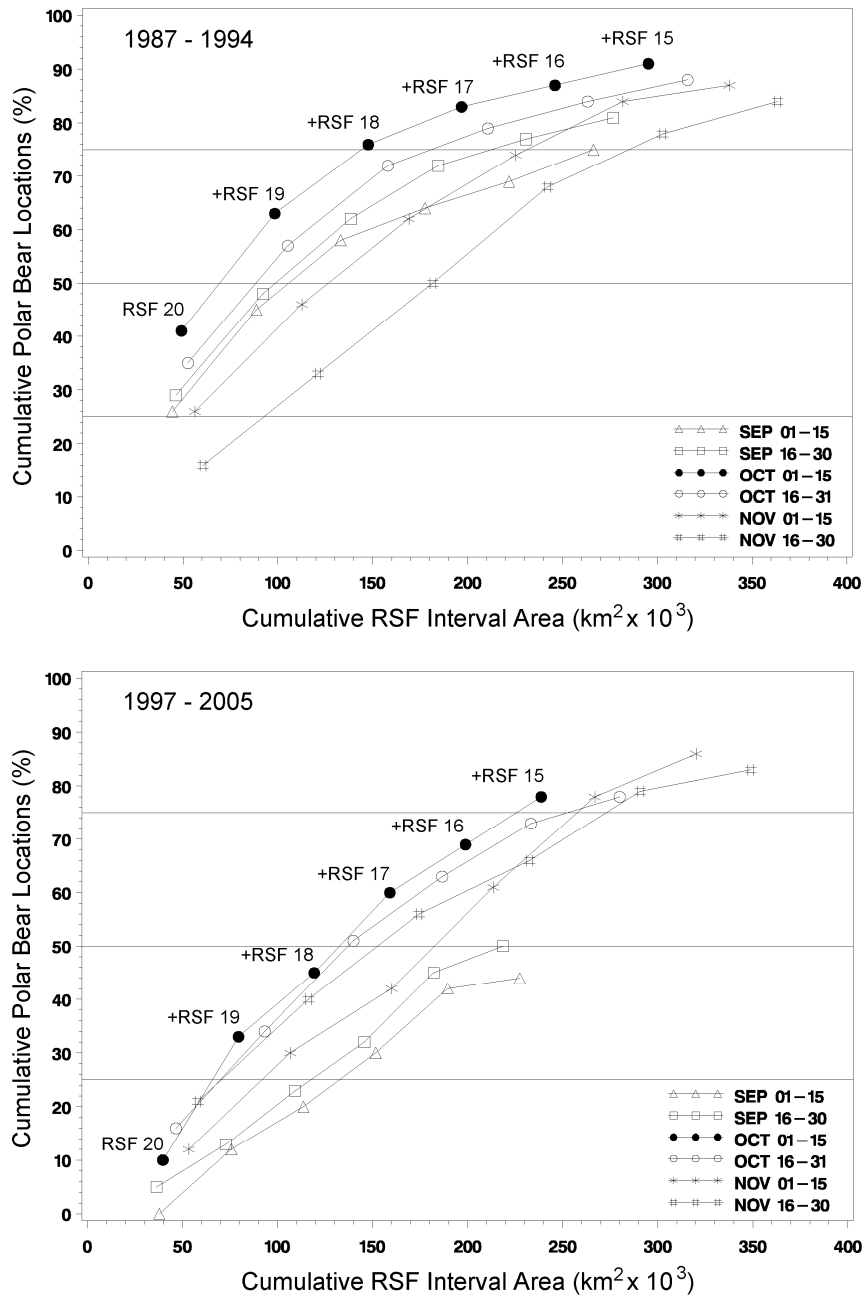
Figure 20. Example of the application of a polar bear resource selection function to help stratify aerial survey transects for polar bears in the Chukchi Sea. Transects (10 per day; length: ≥25 km – 100 km) shown were randomly selected within a 100 km radius from fictitious icebreaker ship locations and within standardized RSF values ≥ 0.5. The RSF was derived from the final model in this report (see Results) using SSM/I sea ice concentration data for each respective date shown.