Using satellite radiotelemetry data to delineate and manage wildlife populations

Steven C. Amstrup, Trent L. McDonald, and George M. Durner

Abstract The greatest promise of radiotelemetry always has been a better understanding of animal movements. Telemetry has helped us know when animals are active, how active they are, how far and how fast they move, the geographic areas they occupy, and whether individuals vary in these traits. Unfortunately, the inability to estimate the error in animals' utilization distributions (UDs), has prevented probabilistic linkage of movements data, which are always retrospective, with future management actions. We used the example of the harvested population of polar bears (*Ursus maritimus*) in the Southern Beaufort Sea to illustrate a method that provides that linkage. We employed a 2-dimensional Gaussian kernel density estimator to smooth and scale frequencies of polar bear radio locations within cells of a grid overlying our study area. True 2-dimensional smoothing allowed us to create accurate descriptions of the UDs of individuals and groups of bears. We used a new method of clustering, based upon the relative use collared bears made of each cell in our grid, to assign individual animals to populations. We applied the fast Fourier transform to make bootstrapped estimates of the error in UDs computationally feasible. Clustering and kernel smoothing identified 3 populations of polar bears in the region between Wrangel Island, Russia, and Banks Island, Canada. The relative probability of occurrence of animals from each population varied significantly among grid cells distributed across the study area. We displayed occurrence probabilities as contour maps wherein each contour line corresponded with a change in relative probability. Only at the edges of our study area and in some offshore regions were bootstrapped estimates of error in occurrence probabilities too high to allow prediction. Error estimates, which also were displayed as contours, allowed us to show that occurrence probabilities did not vary by season. Near Barrow, Alaska, 50% of bears observed are predicted to be from the Chukchi Sea population and 50% from the Southern Beaufort Sea population. At Tuktoyaktuk, Northwest Territories, Canada, 50% are from the Southern Beaufort Sea and 50% from the Northern Beaufort Sea population. The methods described here will aid managers of all wildlife that can be studied by telemetry to allocate harvests and other human perturbations to the appropriate populations, make risk assessments, and predict impacts of human activities. They will aid researchers by providing the refined descriptions of study populations that are necessary for population estimation and other investigative tasks.

Key words Arctic, Beaufort Sea, boundaries, clustering, Fourier transform, kernel, management, polar bears, population delineation, radiotelemetry, satellite, smoothing, *Ursus maritimus*

Radiotelemetry has provided previously unavailable insights into the activity, habitat use, and survival patterns of many wild animal species (Craighead 1971, Craighead et al. 1976, Amstrup et al. 1986, Whitman et al. 1986, Pollock et al. 1989, Garner et al. 1990, White and Garrott 1990, Amstrup

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and Durner 1995, Craighead 1998, Erickson et al. 2001, Kenward 2001, Winterstein et al. 2001). Analysis of movement patterns, however, has been the most common and persistent use of radiotelemetry data. With telemetry, we have learned when animals were active, how far and how fast they moved, what areas they occupied (their utilization distributions or UDs [Winkle 1975, Kernohan et al. 2001]), and whether they varied in these traits, among individuals or time frames (Amstrup et al. 2000, 2001*a*).

Radiotelemetry descriptions of animal movements are retrospective. Management decisions such as those related to harvest regulations or industrial development, on the other hand, are forward looking. Managers are interested in where animals will be in the future, how many will be in particular locations and hence might be impacted by human activities, and how numbers or distributions may change among seasons. Heretofore, methods of interpreting radiotelemetry data have failed to provide probabilistic answers to such questions.

Attempts to convert radiotelemetry data to probabilistic information necessary for management are inchoate. Even in the chapter of their recent book focusing on future needs of radiotelemetry, Millspaugh and Marzluff (2001) did not emphasize the need to make radiotelemetry data more relevant to daily needs of managers. Typically, animals have been grouped subjectively (often according to where they were captured), or according to where they are observed at particular times (e.g., breeding, calving, nesting) of the year. Polygons and other shapes have been drawn around clusters of locations to indicate individual, herd, or population UDs. Such approaches might aid population management if there never was overlap in the movements of animals from the different groups or populations. Usually, however, there is extensive geographic overlap in UDs. Individuals also commonly move among population units and occasionally move across the ranges of many others to make new homes (Durner and Amstrup 1995, Bethke et al. 1996, Amstrup et al. 2000). Geographic overlap in movements of individuals and groups they compose has not been quantified because of the inability to assign estimates of uncertainty to descriptions of animal movements.

Terms like herd, stock, or population, although necessary for communication, have not been useful in most real-life situations because there has been no way to link them to probabilities that their members will occur at various geographic locations. In this paper we provide that link by introducing a new method of clustering animal relocations that makes use of the relative intensity of use of different geographic areas within the scope of animal movements. This clustering method provides a better way to designate populations or stocks that are separate from a management perspective. We then show how radiotelemetry relocations can be used to identify the relative probabilities of occurrence of members of clustered populations with a new kernel smoother that improves UD estimates. Finally, we describe a method for assessing uncertainty in animal and population space-use patterns. That allows us to use radiotelemetry relocations to precisely identify relative probabilities of occurrence at any geographic location. We illustrate the utility of this analytical approach with the example of polar bear (*Ursus maritimus*) management in the southern Beaufort Sea of Alaska and adjacent Canada.

Methods

Field procedures

Our study area included the Chukchi Sea adjacent to northwestern Alaska and the Beaufort Sea. The portion of the Chukchi Sea included in our study area roughly extended from Wrangel Island, Russia, to Point Barrow, Alaska, while the Beaufort Sea portion of our study area extended from Point Barrow, Alaska to Banks Island, Northwest Territories, Canada (Figure 1). We captured, marked, and radiocollared polar bears in coastal portions of this area each spring between 1985 and 2003, except 1995, and each autumn of 1985, 1986, 1988, 1989, 1994, and 1997. Autumn captures occurred in October and November, and spring captures occurred between March and May. Continuous sea ice, from shore seaward, at these times allowed safe helicopter flights over the Arctic Ocean. Aerial survey, animal capture, hunter returns, and radiotelemetry data collected over the past 30 years confirm that the greatest concentrations of polar bears, during the ice seasons, occur in near-shore areas that we were able to sample by helicopter. Each capture season, we had opportunity to recapture bears that had been captured in previous seasons. Also included in our analyses were data collected by Bethke et al. (1996) from 8 polar bears that comprised their "Northern Beaufort Sea" polar bear population.
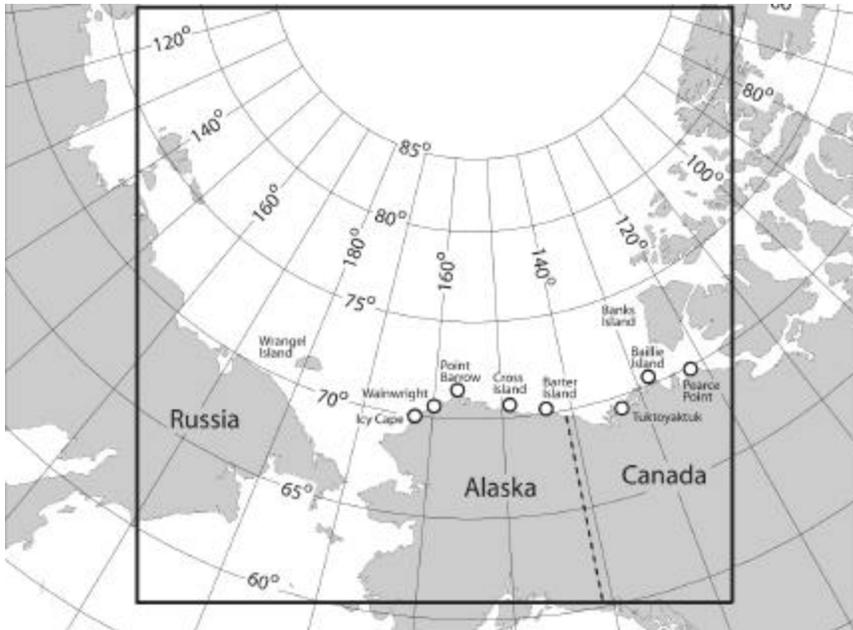
Figure 1. Approximate extent of the grid overlying our study area in the Beaufort and Chukchi seas. The grid extended 3,300 km in each direction and was comprised of 660 cells on each axis. It was used for smoothing satellite telemetry observations of polar bears collected between 1985 and 2003.

Data analysis

Overview. Whereas traditional analyses of radiotelemetry data provide a retrospective description of where instrumented animals were relocated during a study, we were interested in using radiotelemetry data to define population boundaries in ways to make them relevant to future management decisions. We also wanted to identify individuals belonging to different populations and quantify the degree of geographic overlap among members of adjacent populations. To quantify overlap, we needed to be able to predict the probability of occurrence of members of identified populations at all locations in our study area. We accomplished these goals in 7 steps.

Data standardization. Our first step was to standardize transmission schedules so that all PTTs contributed to the analysis equally. Although PTTs often reported many locations in each duty cycle, we deleted all observations that were not in ARGOS class 1, 2, or 3, for which the reported location may not have been within 1,000 m of the true location of the animal (Harris et al. 1990). From among the remaining high-quality locations we deleted all but the one with the highest-quality index in each duty cycle. If ≥2 locations shared the highest-quality rating, we chose the location for each duty cycle that was geographically closest to the best location in the previous duty cycle. We standardized duty cycles to 6 days by ignoring locations obtained <6 days apart. This prevented individual animals wearing PTTs that operated on short duty cycles from contributing more data points than individuals wearing PTTs with longer duty cycles. This filtering process reduced the number of relocations evaluated and minimized spatial autocorrelation among observations separated by short time periods. In order to prevent bears in dens from contributing numerous locations at their stationary den sites, we included only one location per

We captured adult female polar bears by injecting Telazol® (tiletamine hydrochloride plus zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, Ia.) with projectile syringes fired from helicopters (Larsen 1971, Schweinsburg et al. 1982, Stirling et al. 1989). Live-capturing was necessary to deploy radiocollars. Collars used in this study were ultra-high-frequency (UHF) platform transmitter terminals (PTTs) that were relocated by satellite. We did not radiocollar male polar bears because their necks are larger than their heads and they do not retain radiocollars.

Although some PTTs transmitted daily, most utilized an energy-saving duty cycle in which they transmitted for short periods (e.g., 4–8 hours) and were dormant for longer periods (e.g., 3–6 days). Sensors on most PTTs recorded temperature of the collar and 2 indices of activity. Collars carrying PTTs also carried VHF beacons that we located from aircraft (Amstrup and Gardner 1994). Geographic locations of PTT-collared animals were determined by sensors on the satellite that interpreted frequency shift patterns caused by changes in relative positions of the satellites and animals (Fancy et al. 1988). Data retrieved from PTTs were processed by the Argos Data Collection and Location System (ADCLS; Fancy et al. 1988).

month from denned females. This prevented denning bears from generating artificially high probability values in grid cells containing dens while assuring that areas used for denning were included in UDs.

We also strived to include bears that were located during all 12 months of the year. This ensured that all portions of a bear's UD were represented in the observations we analyzed. It also meant, however, that observations did not always come from a continuous string of locations. Radiocollars frequently were replaced as their batteries expired or as electronics components failed. For example, the year-round distribution of a particular bear might have been derived by combining spring, summer, and autumn locations obtained one year with winter locations for the same bear from a different year. Some bears had short gaps in the time span for which they were represented. However, individual re-observation histories that included data gaps ≥ 60 days were deleted from analyses.

Calculation of individual utilization distributions. In the second step of our analysis, we overlaid a prediction grid of 435,600 cells onto the study area. The grid was composed of 660 cells on each axis, and each grid cell was 5 km on each side. This grid extended from 56° north latitude to 80° north latitude and from 112° west to 170° east longitude. It covered the geographic region from west of Wrangel Island (Russia) east to Banks Island (Canada), and from near the North Pole southward into the Bering Sea (Figure 1). Each cell in the grid was defined by the coordinates of its center. We calculated the number of locations for each bear in each cell and placed the numbers into a matrix along with fields for cell number and cell location (east and north coordinates).

Our third step was to estimate the probability of occurrence for individual bears in each grid cell. We accomplished this by smoothing and scaling the number of radiolocations for each bear in each cell with a 2-dimensional (2-D) Gaussian kernel density estimator with fixed elliptical bandwidth (Kern et al. 2003). Kernel smoothing made it possible to use the location data for predictive purposes without presuming any particular statistical distribution for individual locations (Worton 1995). In effect, the kernel smoother converted frequency counts in each cell in the grid to an expected intensity of use, or density, for each cell. We used a true 2-D approach that allowed the major and minor axes of our smoother to differ in length (band-width) and orientation. Therefore, our 2-D kernel smoothers worked by defining cell weights inside an ellipse of influence and then calculating a weighted average of the number of locations in a particular cell.

Application of the 2-D kernel estimator required estimation of 3 parameters, a, b, and θ, where a was the length of the major axis of the smoothing ellipse, b was length of the minor axis of the smoothing ellipse, and θ was the angle of the major axis. We set θ equal to the angle, measured counter-clockwise from due east, of the first eigenvector of the variance–covariance matrix. The direction of the first eigenvector corresponds to the longest axis of the location point cloud and is the direction of most variance in locations. This eigenvector of the 2×2 variance–covariance matrix was calculated as the (nontrivial) solution u to the equation (V $-\lambda I)u = 0$, where V was the variance–covariance matrix, I was the 2×2 identity matrix, and λ was the largest eigenvalue of V. The largest eigenvalue was the largest root of the equation $|V - \lambda I| = 0$, or equivalently the largest root of $\lambda^2 - (v(x) + v(y))\lambda + v(x)v(y) - \text{cov}^2(x,y) = 0$, where $v(x)$ was the variance of horizontal locations, $v(y)$ was the variance of vertical locations, and $\text{cov}(x,y)$ was the covariance of horizontal and vertical locations. The direction of the first eigenvector was calculated as $\theta = \arctan(u_2/u_1)$, where $u = [u_1, u_2]'$.

To select major and minor axis lengths (a and b), we rotated the coordinate system of the original locations through the angle we calculated for θ. Rotation of the coordinate system made the long axis of the point cloud horizontal and the short axis of the point cloud vertical. Rotation of the coordinate system was accomplished by multiplying each location vector $[x,y]$ by the rotation matrix,

$$\begin{bmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{bmatrix}.$$

We estimated major and minor axis lengths in the rotated coordinate system using the 1-d "plug-in" bandwidth estimation routine of Venables and Ripley (1999). Venables and Ripley's "plug-in" bandwidth estimation routine for S-Plus, *width.SJ,* is available in the MASS library of routines associated with their book or on the web at http://www.stats.ox.ac.uk/pub/MASS3/. Length of our major axis, a, was set to the "plug-in" estimate of bandwidth applied to the horizontal dimension of our rotated data. Length of our minor axis, b, was

set to the "plug-in" estimate of bandwidth applied to the vertical dimension of our rotated data.

We then smoothed the original unrotated coordinates using the 2-D Gaussian kernel smoother presented in Kern et al. (2003). This formulation of the 2-D kernel smoother allowed specification of all 3 parameters and utilized the elliptical bandwidth matrix

$$H = \begin{bmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{bmatrix} \begin{bmatrix} 1/a^2 & 0 \\ 0 & 1/b^2 \end{bmatrix} \begin{bmatrix} \cos(\theta) & \sin(\theta) \\ -\sin(\theta) & \cos(\theta) \end{bmatrix}.$$

Clustering populations. The fourth step in our analysis was to define groups or populations of bears that occur in our study area. Polar bears are distributed throughout most sea-ice-covered portions of the Northern Hemisphere, and there are few geographic boundaries to their movements. Nonetheless, they are thought to occur in numerous groups or subpopulations rather than one continuous stock. Polar bear management worldwide has been, and is currently, based on presumption of these groups (Lunn et al. 2002). Although subpopulation differences are far below the level used to differentiate species, some differences in genetic patterns among these stocks have now been confirmed (Paetkau et al. 1999). Initial screening of telemetry data from bears captured in and adjacent to Alaska suggested there were differences in geographic areas occupied by individual polar bears and that some bears shared particular geographic areas more than others. We determined which bears shared which geographic areas by clustering (Johnson and Wichern 1988, Norusis 1994) bears into distinct populations according to the UD density values of each bear for each cell in our grid. That is, we entered estimated density values from every grid cell into a single vector, forming one multivariate vector for each bear. We then grouped vectors using regular hierarchical cluster analysis. To do this, kernel density estimates for each cell for each bear (step 3) were scaled so that they summed (integrated) to 1. Scaling in this way converted absolute intensity of use values for each bear in each grid cell into proportional use values. This assured that bears for which there were few observations were represented by the same amount of information as bears from which more observations were available. Unfortunately, vectors formed from our grid of 5-km × 5-km cells were too large

for SAS Proc Cluster (SAS Institute, 1999) to handle. Those vectors had $660 \times 660 = 435{,}600$ cell entries. Therefore, we overlaid our 5-km grid with a grid of cells 100 km on each side, and summed the probability values for all of the 400 smaller cells in each of the larger cells. The second grid was 33×33 or a total of 1,089 cells. SAS was able to cluster the resulting matrix of 194 (bears) $\times$ 1,089 (cells).

We used Ward's clustering algorithm, which calculates the means for all variables in each cluster and then determines the distances (in our case, squared Euclidean distances) among all cluster means. The distances are summed, and at each step in the agglomeration the clusters merged are those 2 that result in the smallest increase in the overall sum of the squared within-cluster distances (Norusis 1994). This makes Ward's method more robust to minor differences between cluster members than methods that measure distances between individual members and then average those differences to obtain a difference mean. This also means that Ward's method tends to emphasize major differences among clusters more effectively than other methods. Because we were trying to differentiate among populations or subpopulations of bears, we were not as interested in minor differences among individuals as we were in major differences among groups of individuals.

We measured distances between clusters, as they were amalgamated, with the semi-partial R^2 values reported by Proc Cluster of SAS. Semi-partial R^2 values for the amalgamation of 2 clusters were a direct function of the sum of the analyses of variance (ANOVA) sum-of-squares, where clusters were the "treatments" and the horizontal and vertical coordinates of cluster members were "responses." Semi-partial R^2 values were calculated in SAS by summing the ANOVA sum of squares for both horizontal and vertical coordinates, and dividing by the total sum of squares to give a proportion of variance explained by the 2 clusters. Hence, small R^2 values indicated that fairly homogeneous clusters were being merged to form the next cluster. Large R^2 values indicated that clusters containing dissimilar members were being combined to form the next cluster. When the clustering begins, the R^2 values typically are small because animals with the most similar UDs are joined first. R^2 values increase gradually as increasingly less similar UDs are joined. Steps that are distinguishable from this gradual increase in R^2 values indicate greater relative differences in the UDs of groups being merged.

We stopped agglomeration of clusters at the point where the union of 2 clusters required a much larger relative increase in R^2 value than previous steps. Large steps signaled that animals with quite different space-use patterns were being combined. We also studied the composition of groups being amalgamated to understand the relative sizes and order of each amalgamation step and to assure that each merger made biological sense. For example, if going from an agglomeration of 4 clusters to an agglomeration of 3 clusters required a large R^2 value, and if that merger did not make biological sense, we would stop agglomeration at 4 clusters rather than combine clusters known to be highly dissimilar. R^2 values and hence amalgamation distances were displayed for inspection as dendrogram branch lengths.

Population UDs and relative probabilities of occurrence. Having defined populations by clustering, our fifth step was to calculate UDs for populations as a whole. To do this, relocations of all members of each population were combined and the total number of relocations in each cell of our original 5-km grid was calculated. We calculated UDs, as we did for individual bears (step 3 above), by smoothing and scaling the raw frequencies of locations in each population with a 2-D Gaussian kernel density estimator with fixed elliptical bandwidth. This time, however, locations of all animals from each cluster or putative population were pooled before the UDs were calculated.

The sixth step in our process was to calculate the relative probability of occurrence in each grid cell for members of each population. To do this, kernel density estimates for each cell for each population (step 5) were scaled so that they summed (integrated) to 1. Scaling in this way, as with the scaling of individual bears (step 4) removed the influence of unequal numbers of relocations in different populations. This scaling was critical because the number of observed locations differed among populations.

To calculate relative probability of occurrence of bears from each population in each grid cell, we required an estimate of the size of each population. Scaled density estimates told us the estimated "fraction" of each population occurring in each cell of our grid. Multiplying those fractions by the estimated size of each population converted those fractions to expected numbers of bears from each population in each grid cell. We used population size estimates agreed to and published in the proceed-

ings of the IUCN Polar Bear Specialists Group meeting from June 2001 (Lunn et al. 2002). Based upon early telemetry and capture–recapture data, the Specialist Group identified 3 populations in this region. Because our clustering procedure also identified those 3 groups (see results), we felt comfortable incorporating the size estimates of Lunn et al. (2002) into our procedure. Population sizes listed in Table 1 of that report were 2,000 for the Chukchi Sea (CS) population, 1,200 for the Northern Beaufort Sea (NBS) population, and 1,800 for the Southern Beaufort Sea population. Because the IUCN-accepted estimates were not associated with specific time frames, and because no estimates of variance were available, we held them constant in our analysis for all years in which we had data.

It must be noted that the above population estimates were used only to convert scaled probability densities to estimates of the relative numbers of bears in each cell. We recognize that these estimates, although a necessary part of our calculation process, were crude. The important aspect of these estimates is not the absolute population levels but rather that the ratios of one population size to another were sensible; that they were based upon the best information available; and, most importantly, that they were of comparable quality for each population.

Implicit in our computations is the assumption that uncollared bears move and use space similarly to collared bears. This means that collared female polar bears were representative of other females and males in their movements and space-use patterns. Although we did not collar a strictly random sample of bears from the putative populations we identified, we did collar females over a long enough time period and over a geographically diverse enough set of locations that we feel confident in this assumption. We see no reason behavior of unmarked females in any of the populations would be fundamentally different from that of collared females. In addition, available evidence suggests little or no difference in movement patterns and space use between male and female polar bears (Stirling et al. 1980, Schweinsburg et al. 1981, Lentfer 1983, Stirling et al. 1984, Amstrup et al. 2001a). Hence, our assumption that PTT-equipped female polar bears were representative of other members of the population seems justified.

We calculated the relative probability that a bear sighted in a particular cell was a member of population *i*, as:

$$p_i = \frac{a_i \hat{n}_i}{\sum\limits_{j=1}^{k} a_j \hat{n}_j},$$

where a_i was the scaled kernel density estimate of the probability that a bear from population i was located in the cell (the fraction of population i in that cell), $\hat{n}_i$ was the estimated size of population i, and k was the number of populations. We recall that estimates of a_i were obtained by scaling the smoothed number of locations to sum to 1. Hence, if a bear is observed in any cell, this formula provides the relative probability (p_i) of that bear belonging to each population. Note also that

$$\sum_{i=1}^{k} p_i = 1.$$

This unity sum means no other populations of bears were considered. Polar bears are a circumpolar species, so we know that this is not true at either the eastern or western extremes of our grid. Although we have no data from adjacent populations with which to assess presence in our grid, the geographic region in which we want to predict encounter probabilities is well within the interior of our grid and not affected by the dearth of data on the periphery.

In our final analytical step we computed standard errors, of the relative probabilities (p_i) that a bear sighted in a particular cell is a member of population i, using bootstrap methods (Manly 1997). Bootstrapping the observed data can provide necessary estimates of uncertainty. In the 2-D kernel application, however, bootstrapping requires computation of hundreds or thousands of probability densities. If data are numerous and the area large, as in our study, calculation of bootstrap kernel estimates is computationally impractical with normal methods. To achieve the speed necessary to bootstrap an estimate of precision for our relative probability values, we used the method of Kern et al. (2003), which reduced computation time by employing the fast Fourier transform (FFT) (Cooley and Tukey 1965, Monro 1976, Yfantis and Borgman 1981) and the discrete convolution theorem (Press et al. 1988). Wand and Jones (1995: appendix D) provided a thorough account of the use of the FFT in one dimension. However, they emphasized that many "practical" issues related to 2-D FFT estimation had yet to be resolved. Kern et al. (2003) resolved those practical issues, making our approach possible.

Individual bears from each population were resampled by randomly selecting bear identification numbers and associated locations with replacement. Therefore, once a bear was selected for inclusion into a bootstrap sample, all its observations were included together. This nonstandard bootstrap sampling avoided pseudo-replication (Hurlbert 1984) by resampling the true units of replication (i.e., individual bears), and assured that any spatial autocorrelation (e.g., time dependencies) if present in the original sample also was present in the bootstrapped samples. Because numbers of locations for each bear differed, each bootstrap sample contained a different number of locations. Once a bootstrap sample was selected, the entire estimation procedure for calculation of the relative probability of memberships (p_i) was performed using the bootstrap data. We performed 1,000 bootstrap calculations of relative probabilities in order to estimate standard errors for each cell in the grid. We expressed uncertainty or error in our estimates of probability with the coefficient of variation (CV). The CV expressed the relationship between the estimated value and the standard error associated with that value (Zar 1984), and provided an intuitive gauge of the strength of our data and hence the strength of our predictions.

Polar bears in Alaska are harvested in a seasonal pattern. Along the SBS coast, they are taken frequently in the autumn and early winter and again in late winter and spring. Along the CS coast south of Barrow, they are taken almost exclusively in late winter and spring because sea ice for hunting doesn't persist along the coast until then (Schliebe et al. 1995). Therefore, we calculated p_i and associated standard errors for each cell on an annual (year-round) basis, and for the 2 seasons during which bears are most frequently hunted. We defined the fall season as September–January and spring as February–May. We explored spatial patterns in p_i from our three populations, to evaluate management ramifications of observed differences between the annual and seasonal p_i for the fall and spring seasons. Polar bears are not frequently taken in the summer months (Schliebe et al. 1995), so we did not calculate separate p_i for June–August. We tested for differences between annual and seasonal p_i by calculating t test statistics,

$$t = \frac{p_1 - p_2}{\sqrt{s_1^2 + s_2^2}}.$$

for each cell in the grid. The numerator in this sta-

tistic is simply the difference between the annual and seasonal p_i of interest, and the denominator is the square root of the sum of the squares of the standard errors associated with each p_i (Zar 1984). Grid cells in which these values exceed 1.96 revealed significant differences between the annual and seasonal values at the 0.05 level.

tered close together only if their intensity of use of our grid cells was similar. For example, among 4 SBS bears shown in Figure 2, #6153 and #1734 clustered more closely together than they did to either #1737 or #6155. The latter 2 bears, both of which

Results

Our analysis started with 412,640 satellite observations of 387 individual polar bears. After deleting observations that were not in location quality 1–3 and selecting only the best location per duty cycle, we were left with 38,809 locations. Elimination of animals with data strings shorter than 1 year and with ≥60-day data gaps left 15,308 satellite locations from 194 polar bears collared between 1985 and 2003. These were the data used to delineate populations or stocks in the Beaufort Sea region and to estimate encounter probabilities.

Population identification

We halted the clustering program when it reached the first logical step that was meaningfully larger than previous steps. In clustering, determination of the stopping point always includes some subjective input from the investigator. If the outcome is counterintuitive or not easily interpretable, the entire method may be vulnerable to criticism. With our 3-D method, 2 bears clus-
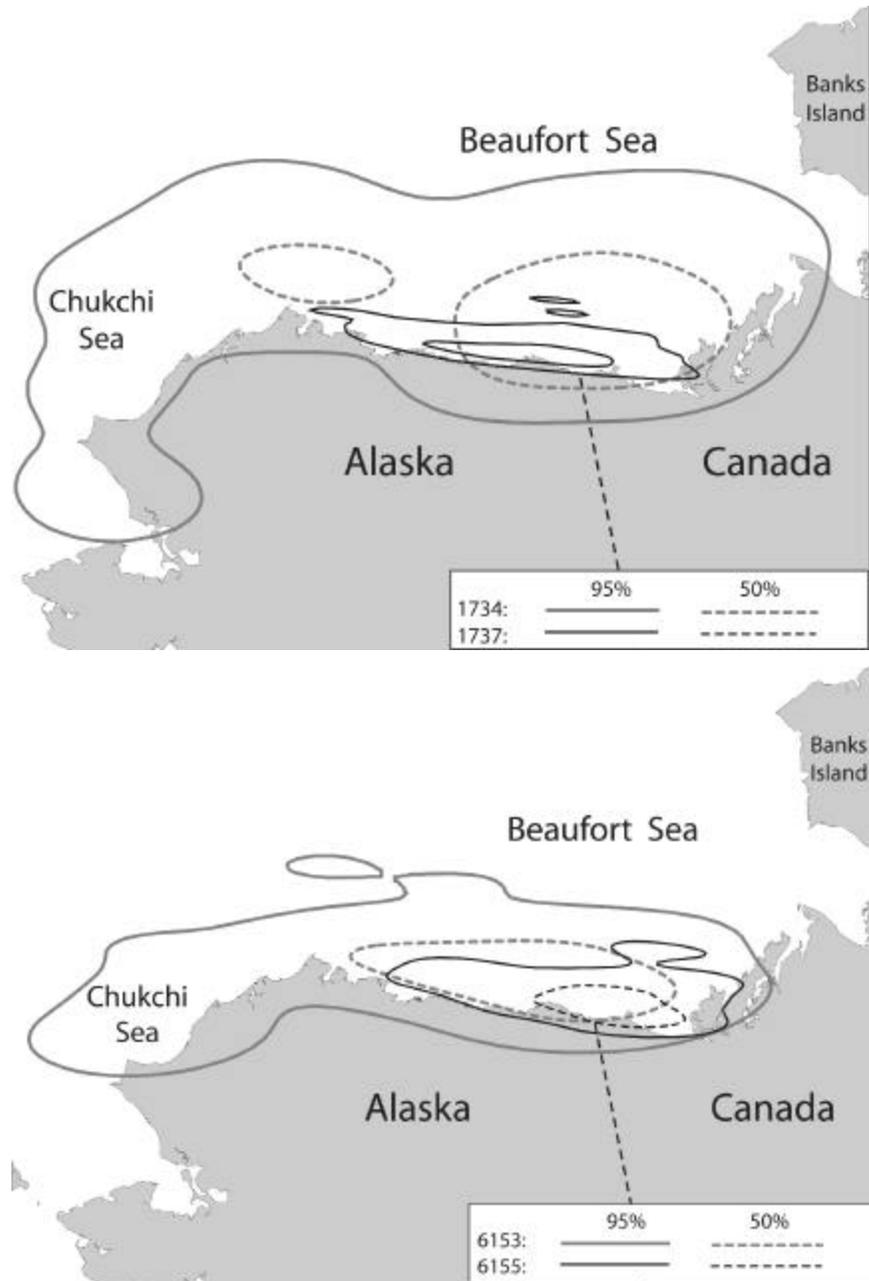

Figure 2. Two pairs of polar bears, among 194 individuals collared between 1985 and 2003 in the Beaufort and Chukchi seas, with very different utilization distributions (UDs). The "homebody" bears 1737 and 6155 clustered very close together because of the degree to which their UDs overlapped in 3-D. Similarly, 1734 and 6153 clustered close together. Although the smaller UDs were totally overlapped by the larger ones, the bears with smaller UDs did not cluster as closely with bears occupying large UDs as they did with each other (see also Figures 3, 4).
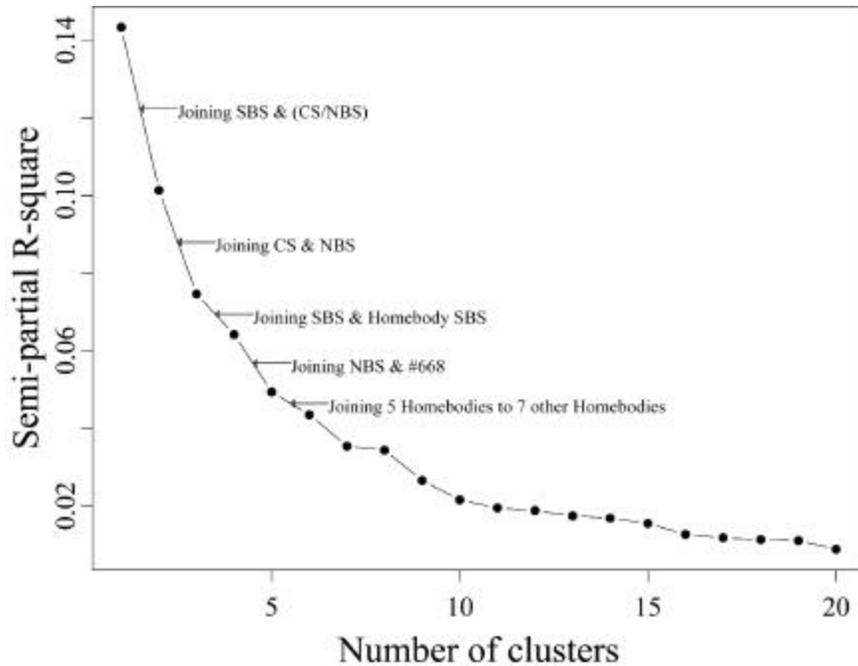
Figure 3. Steps in clustering radiolocations from 194 polar bears collared between 1985 and 2003 in the Beaufort and Chukchi seas. Clustering defined 3 primary groups or putative populations of polar bears: southern Beaufort Sea (SBS), northern Beaufort Sea (NBS), and Chukchi Sea (CS). Note the large step required to merge the CS and NBS groups and go from 3 populations into 2. The size of this step prompted us to stop our clustering at 3 populations.

The step required to go from 4 clusters to 3 also involved homebody bears and was smaller than the step required to add #668, suggesting no reason to stop there.   The step required to go from 3 clusters to 2, the largest yet encountered, was the one required to join bears spending most of their time in the NBS with bears from the CS. These 2 groups were quite separate in 2 dimensions, living at opposite ends of our study area. Clustering would have joined them, based upon the shapes of their UD surfaces in the third dimension (height), before either joined the SBS group, but their 2-D separation is clear and logical.   So, we halted the clustering algorithm there and concluded we had 3 distinct clusters or populations of bears in the study area (Figures 3, 4).

were "homebodies" with small intensively used UDs, clustered together early in the amalgamation process. Although all 4 were clearly SBS bears, homebodies clustered with other SBS bears, much later.

The combination of increasingly dissimilar clusters of polar bears came to a logical conclusion by defining 3 relatively discrete groups within our study area (Figure 3). The distance separating clusters gradually increased until the step required to combine bears from 5 clusters into 4. This was the step required to add bear #668 to the northern Beaufort Sea cluster. Bear #668 spent her whole radiotracking history in a very small area adjacent to Banks Island. The UDs of other NBS bears totally overlapped hers in 2-D. Bear #668 appeared different to the clustering algorithm because her range was so small that her UD did not overlap large areas of the UDs of any other bears. Also, the height of her 3-D probability surface in the few grid cells she occupied was greater and gradients to adjacent cells steeper than for other NBS bears. Clearly, however, this was an NBS bear, and it made no sense to stop at 5 groups, leaving bear #668 as a group of 1.

Population UDs and relative probabilities of occurrence

From west to east the 3 populations were CS, SBS, and NBS (Figure 5). Hereafter, we refer to these clusters or groups as populations, although we recognize they are not genetically distinct (Cronin et al. 1991, Paetkau et al. 1999). We used 6,151 satel-
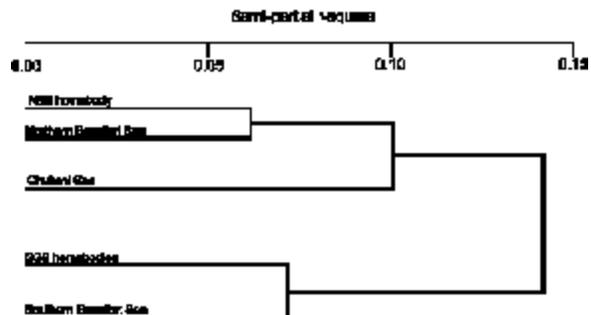

Figure 4. Clustering of 194 individual polar bears, fitted with satellite radiocollars between 1985 and 2003 in the Beaufort and Chukchi seas, suggested that 3 major groups of polar bears occur in this region: 1) southern Beaufort Sea (SBS), 2) northern Beaufort Sea (NBS), and 3) Chukchi Sea (CS).

Figure 5. Fifty and 95% annual contours of the utilization distributions (UDs) for 3 putative polar bear populations identified by clustering radiolocations from 194 individuals collared between 1985 and 2003 in the Beaufort and Chukchi seas. UDs were calculated with fixed elliptical smoothing kernels. Contour lines represent boundaries of true occurrence probabilities.

NBS bears increases to about 50%. At Baillie Island off the end of Cape Bathurst, 90% of the bears encountered are from the NBS group (Figure 6). Coefficients of variation (CVs) for our probability estimates were small across most of our study area, lending credence to our estimated probabilities (Figure 7).

Relative encounter probabilities calculated on a seasonal basis differed only slightly from those calculated from year-round data (Figure 8). In other words, although the numbers of bears available along the coast may vary greatly among seasons, their seasonal composition, with regard to the populations they represent, varies little. The *t*-tests comparing seasonal and annual probabilities of occurrence revealed significant differences only in small offshore areas where human activities are currently absent (Figure 9). Along with CV contours, *t*-test values provided insights into areas where we have too few data to attach management significance to estimated relative probabilities. Fortunately, all of those areas are far beyond the area of management interest in this study.

lite relocations of the 92 PTT-equipped bears that clustered into the CS population. We used 6,410 locations from the 71 SBS bears and 2,747 locations from the 31 NBS bears.

Kernel smoothing of bear observations provided estimates of the proportional use of each grid cell by bears from each population—in essence the fraction of each population in each cell. Multiplying those fractions by the estimated size of each population provided the estimated number of bears from each population in each cell. Ratios of the estimated numbers in each cell provide the relative probabilities (p_i) of sighting a bear from each of our 3 populations in each grid cell. Probability contours, constructed by connecting grid cells with similar (p_i's), predict that on a year-round basis polar bears seen in coastal areas of Alaska between Wainwright and Barrow are approximately 30–40% SBS bears and the remainder are CS bears (Figure 6). NBS bears have progressively lower probability of occurring in regions west of the Alaska–Canada border. At Prudhoe Bay over 90% of bear encounters are from the SBS population, with the remainder being a mix of CS and NBS bears (Figure 6). Between the village of Kaktovik on Barter Island and Tuktoyaktuk, the probability of encountering

Discussion

The methods of clustering, smoothing, and error estimation reported here have significant methodological and biological ramifications. Lunn et al. (2002) concluded there were 3 populations of polar bears in our study area. This conclusion was drawn from a variety of scientific data collected over a period exceeding 30 years as well as local knowledge. Quantifiable evidence of 3 populations discrete enough to be managed separately, however, has been lacking. Our clustering corroborates the earlier suggestion that 3 groups of bears occur in this area. That outcome justified inclusion of the Lunn et al. (2002) population estimates into our cal-
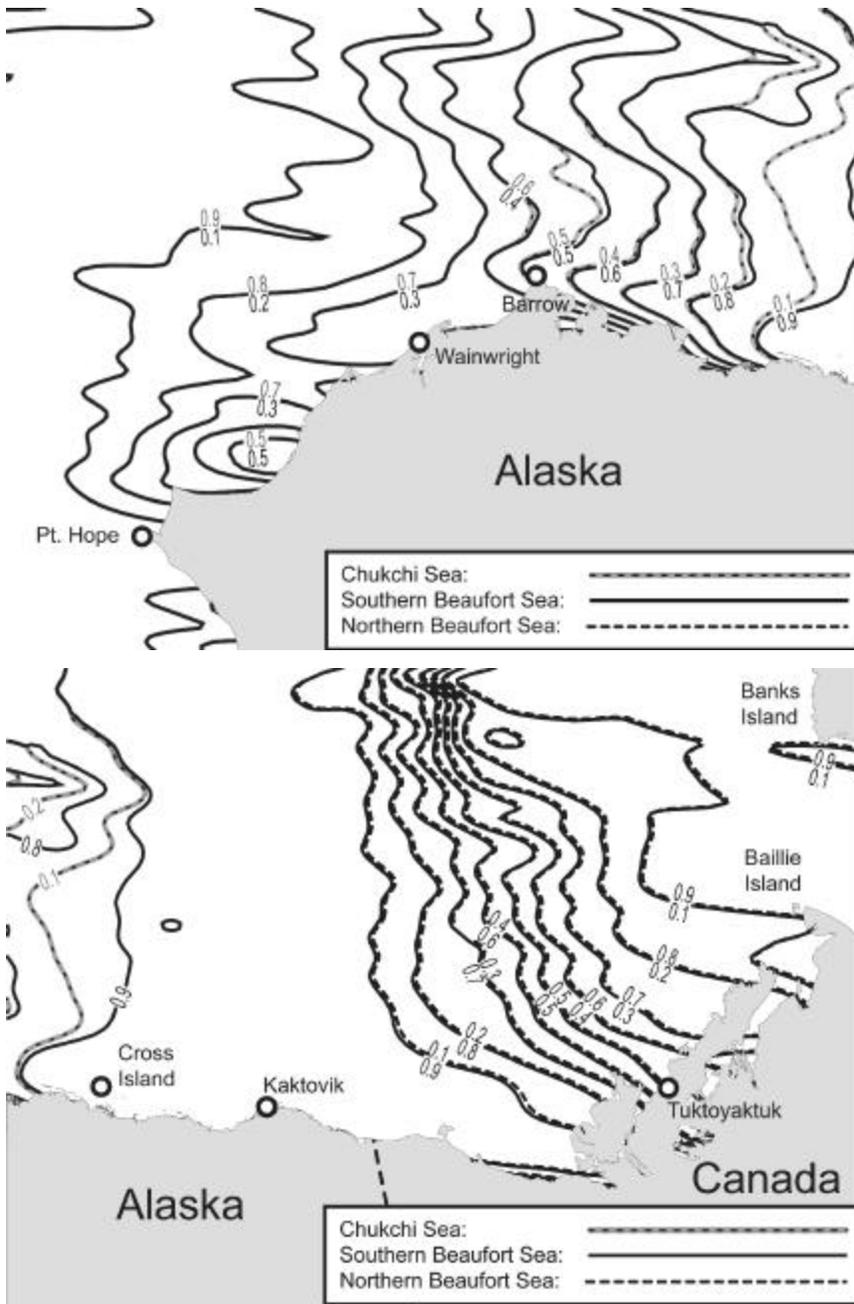
Figure 6. Annual probability of occurrence values for polar bears from 3 populations (see Figures 3 and 4) identified with radiotelemetry locations gathered between 1985 and 2003. Note that in the western part of the study area the probability of encountering NBS bears is very low (a), and in the eastern regions the probability of encountering CS bears is low (b). Low probability of NBS bears in the west and CS bears in the east results in probability contours for bears of the other 2 groups in each region that overlap almost perfectly.

culations. The results of the smoothing and error calculations reported here also, for the first time, quantify the spatial relationships between these 3 groups of polar bears. If our clustering had sug-

gested 4 clusters rather than the 3 hypothesized by Lunn et al. (2002), we would have been forced to use the proportional distribution of radiocollared bears in each cluster to derive relative size estimates for those 4 clusters. We also would have had to assume that our radiocollared bears were a random sample from the entire region. That reality emphasizes the need for radiotelemetry studies to strive for sampling distributions that are as close to random as possible.

Bethke et al. (1996) pioneered the use of clustering to assign polar bears to different groups or populations. Taylor et al. (2001) expanded the clustering procedure of Bethke et al. (1996) to a large portion of the Canadian Arctic Archipelago. In both efforts, however, the movements of individual animals were reduced to seasonal centers of activity before clustering. UD contours are 2-D representations of the hills and valleys of a 3-D surface that represents the probability distribution of the animal's locations, and they cannot be adequately represented by single points. We recognized this and clustered animals based upon the degree to which their hills and valleys matched. That is, for bears A and B to cluster together, not only must bear A share many of its "high-use" grid cells (the hills) with bear B, but bear B also must share many of its "high-use" grid cells with bear A.
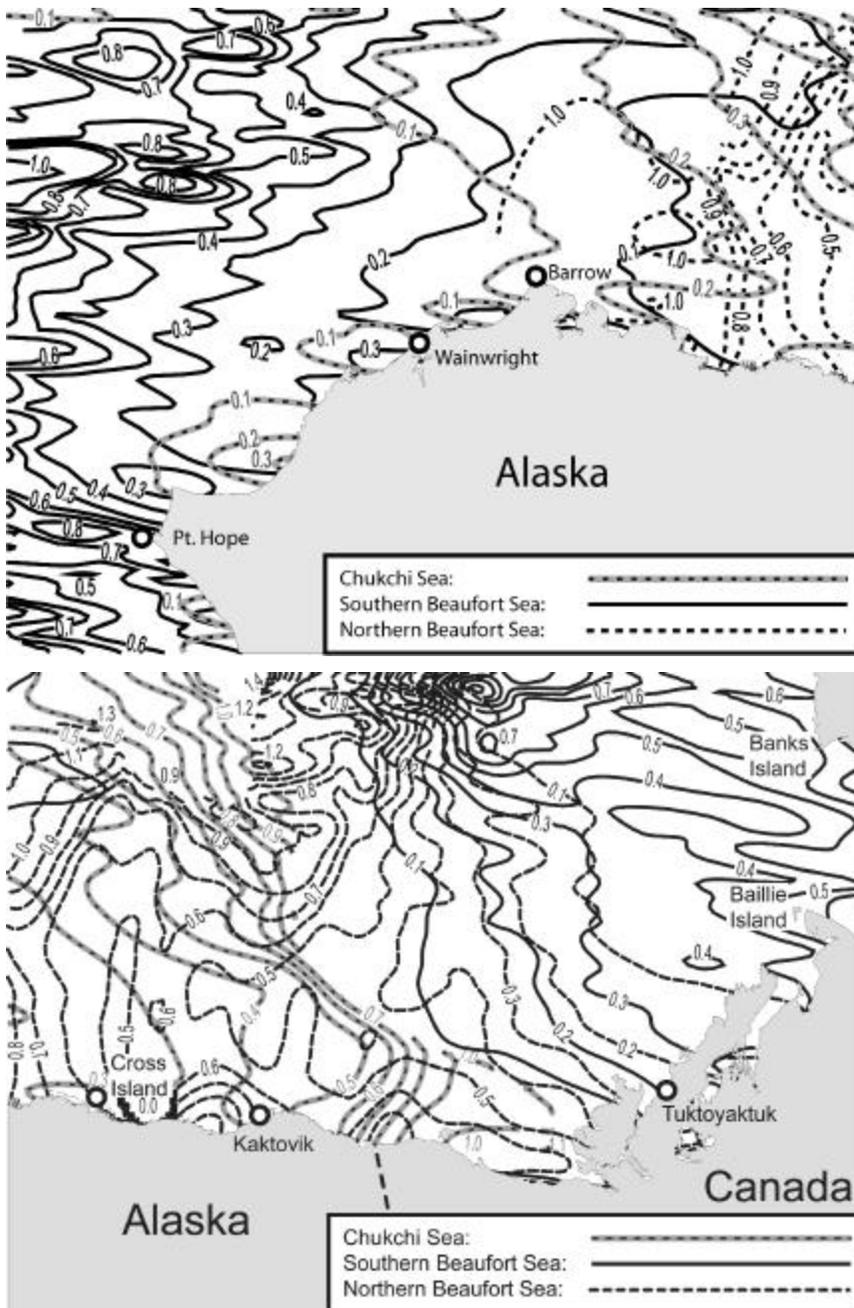
Figure 7. Coefficients of variation (CV) for probabilities of occurrence (see Figure 6) of members of 3 polar bear populations identified by clustering radiotelemetry data from 194 individuals collared between 1985 and 2003 in the Beaufort and Chukchi seas (see Figures 3 and 4). CVs were exceptionally strong in most coastal regions, suggesting good sample size and distribution of telemetry data. Note that in western coastal areas (a), where NBS bears are rare, data were too few to calculate CVs for NBS bears. Similarly, in eastern areas (b), data were too few to calculate CVs for CS bears.

steps to make sure they make biological as well as statistical sense. Our requirement for a 3-D fit makes maximum use of the UDs for each bear and assures the most reliable possible group designations. It also can result in some amalgamation steps that at first glance seem unintuitive because the heights and gradients of the 3-D surfaces, as well as their 2-D overlap, determine the steps. This point was made clear when we investigated effects of different grid-cell sizes on the results of our clustering routine.

We chose our grid of square cells 100 km on each side, as an easy multiple of the 5-km-square grid used to perform smoothing. It also divided evenly into the 3,300-km length and width of our original grid system and was within pragmatic limits for SAS to cluster. As previously described, clustering on 100-km-square cells resulted in an amalgamation process that was easily interpretable in both biological and statistical terms.

Clustering on grid cells that were 80 km, 120 km, and even 50 km square had little impact on the final clusters derived. Different grid-cell sizes, however, did alter the pattern of amalgamation and the degree of attention necessary to determine

Because determining the stopping point in clustering requires a degree of subjectivity, biologists familiar with the data must study the amalgamation stopping points. With a 50-km grid, clustering of which was tedious to perform due to the size of the data matrix involved, bear #668 did not join the
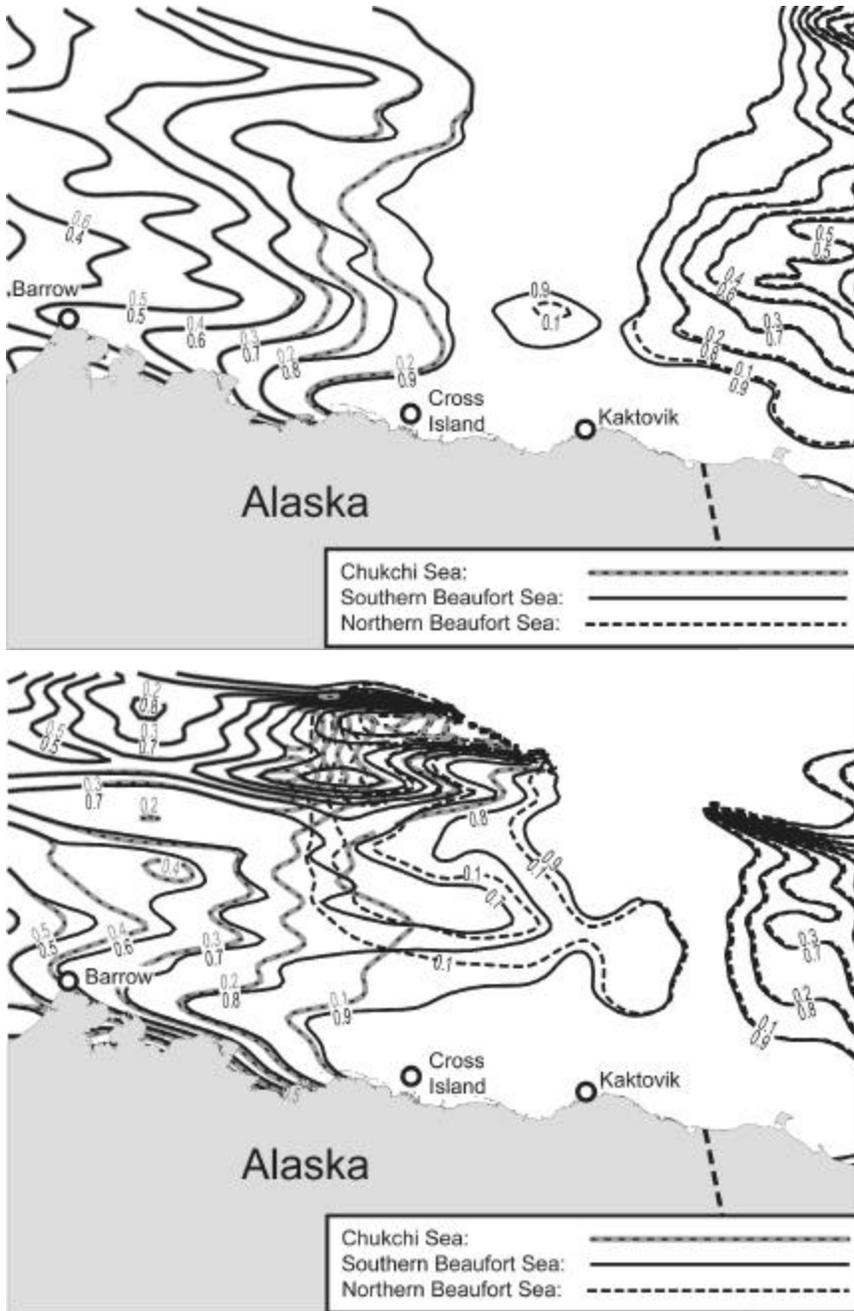
Figure 8. Seasonal probability of occurrence values for members of 3 polar bear populations identified by clustering radiotelemetry data from 194 individuals collared between 1985 and 2003 in the Beaufort and Chukchi seas (see Figures 3 and 4). Note that *P* values along coastal areas in September–January (autumn) (a) and February–May (spring) (b) are very similar to the *P* values calculated from the annual data (Figure 6). It is important to remember that *P* values represent *relative probabilities* of occurrence, not numbers of bears present. Therefore, although the numbers of bears along the coast may differ greatly among seasons, the proportional representation from each of the 3 identified populations changes little among seasons.

that #668 belonged geographically in the NBS group, stopping amalgamation prior to the step where 4 clusters amalgamated to 3, and manually adding #668 to the other NBS bears led to the same clusters as achieved with 100-km grid cells.

The first big step in amalgamation, using cells that were 80 km square, occurred when the SBS homebodies were added to the other SBS bears. Going from 4 groups to 3 occurred when #668 was added to the rest of the NBS bears. With 80-km grid cells, however, this merger occurred with a relatively small step. The step to go from 3 clusters to 2, at 80-km grid sizes, required merger of NBS and CS bears. Letting those groups merge was not biologically reasonable, even though the amalgamation distance was small when we used an 80-km-square grid. Stopping the clustering before that merger yielded the same clusters we had at 100-km grid spacing.

Clustering with a 120-km grid resulted in movement of 4 bears among final clusters. One bear moved from the 100-km SBS group into the 120-km CS group. Because there was much 2-D overlap between CS and SBS groups, the fact that only one bear made this kind of change was encouraging. The 3 other bears that changed groups, however, required more attention. Those bears
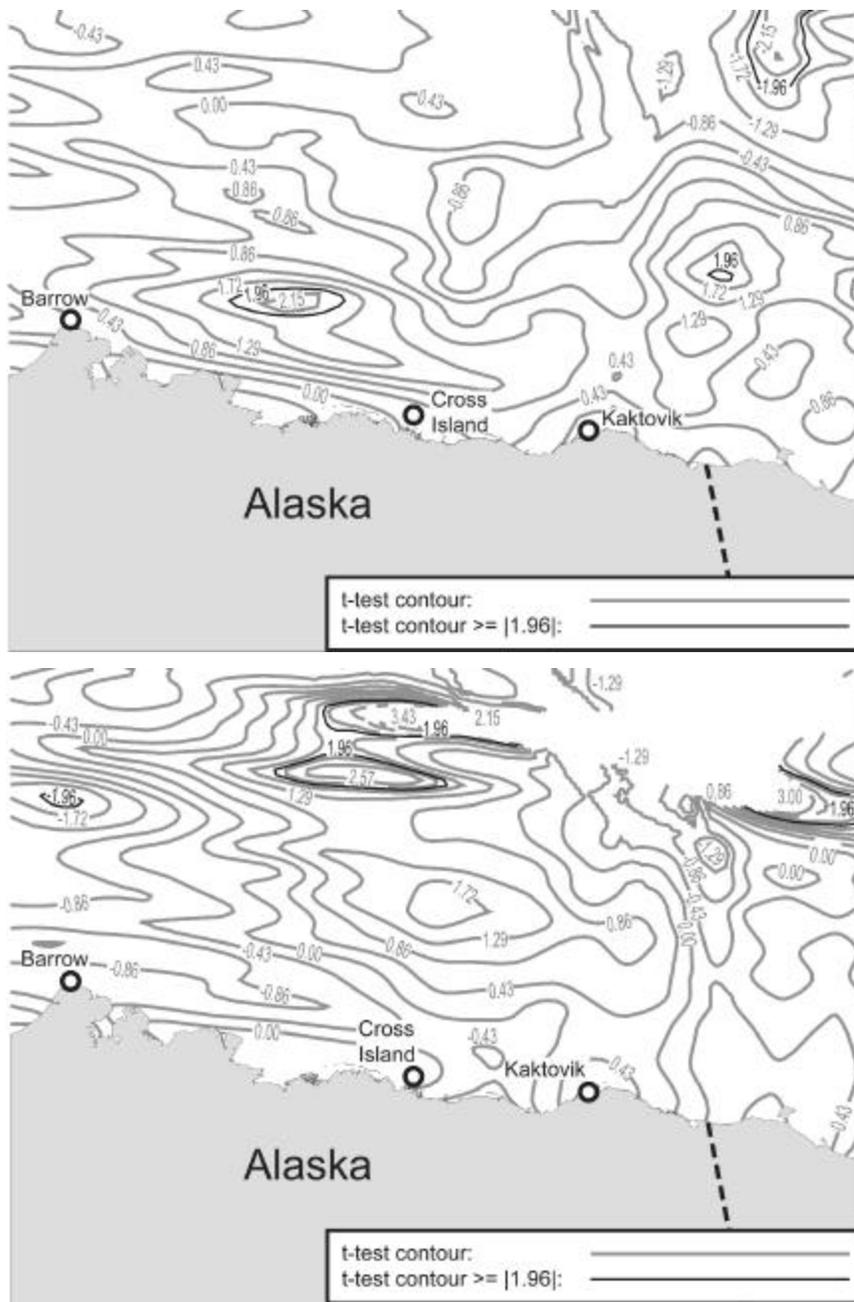
other bears until the last merger (i.e., amalgamation to 1 cluster that included all bears). Recognizing

Figure 9. Contours of *t*-test results comparing relative annual probabilities of occurrence for the southern Beaufort Sea polar bear population (see Figure 6) with probabilities of occurrence for September–January (autumn) (a) and February–May (spring) (b). Populations were identified by clustering radiotelemetry data from 194 individuals collared between 1985 and 2003 in the Beaufort and Chukchi seas (see Figures 3 and 4). Note that the only areas where significant differences occurred, at the 0.05 level of α, were relatively small and far offshore. Also note that offshore areas where contours are incomplete reflect insufficient data to perform the test.

probability surfaces for these bears were, at the 120-km grid-cell size, more similar to those of some bears in the CS group than they were to other NBS bears. Although this combination may have made statistical sense, it did not make biological sense. Those 3 bears lived at the opposite end of our study area from all CS bears with which they were grouped. Therefore, this grouping order was a failure of the procedure with regard to those animals. In that case, correcting this failure was accomplished by overriding the automatic amalgamation and forcing these 3 animals into the NBS group. That being done, final 120-km clusters differed by only one bear compared to the 100-km clusters.

Overall, our clustering was resilient to the changes in grid size for most animals. In fact, changes in grid-cell sizes from 50 km–120 km square saw only one bear move from one population to an adjacent population. Importantly, only bears with unusual movement patterns complicated the process. This near absence of shuffling of bears among clusters vouched for the rigor of our approach. Changes in amalgamation steps, however, emphasized that individual animals differ

switched from the 100-km grid NBS group to the 120-km grid CS group. This amalgamation apparently resulted because heights and gradients of in their movement patterns and that clustering them together into putative populations or other management units requires biological oversight as

well as attention to details such as grid-cell sizes.

Kernel estimates of animal UDs have been preferred to other approaches because they are free of distributional assumptions, seem to perform well in simulations, and, unlike other nonparametric methods, employ a widely used statistical smoothing technique (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999, Kernohan et al. 2001). A disadvantage of past kernel analysis, however, has been failure to recognize the asymmetry of animal movement patterns. Movements of most animals orient along coastlines, drainages, topographic features, roads, or other impediments to travel. Hence, their UDs typically have one axis (e.g., east–west) that is longer than the other (e.g., north–south). To the best of our knowledge, available "canned" programs for kernel UD estimation (Worton 1989, Kie et al. 1996, Seaman and Powell 1996, Hooge and Eichenlaub 2000) do not account for this asymmetry in UDs. Values chosen for a and b typically have been equal, and the orientation of UD axes (θ) has not been adjustable. In essence, most 2-D kernel smoothers used in the past had "round" support. Even the most up-to-date discussions of kernel approaches have not dealt with this shortcoming (Kernohan et al. 2001). Round kernel smoothers have been used in the past because elliptical smoothers are more difficult to employ. The statistics literature is replete with descriptions of one-dimensional kernel-density parameters. Previously, little has been written regarding an appropriate estimation procedure for a, b, and θ in 2 dimensions (Kern et al. 2003).

Movements of polar bears are an important example of the biological inadequacy of round smoothers. In the SBS, for example, polar bears spend most of their time relatively near shore and make extensive east–west movements paralleling the shoreline (Figure 2). Similarly, NBS bears tend to have great north–south components of movements that parallel the western shoreline of Banks

Polar bear mother with radiocollar and new cub of the year on sea ice north of Barter Island, Alaska.

Island (Amstrup et al. 2000). Forcing a round smoother onto clearly elliptical distributions (Seaman and Powell 1996, Kie et al. 1996, Hooge and Eichenlaub 2000) was not appropriate. Rotating the location point cloud through the angle of the cloud's long axis allowed the major axes of our kernels to consider the asymmetry in polar bear movements and made maximum use of the movements data derived from our study animals.

We employed fixed-kernel estimators because they have been shown to perform better than adaptive-kernel estimators in many circumstances (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999). This advantage of fixed kernels, however, depends upon use of an appropriate and objective choice of bandwidth. Bandwidth selection by least-squares cross validation (LSCV) has been most commonly used (Kernohan et al. 2001). However, despite use of thousands of polar bear relocations, bandwidths selected by LCSV created numerous small peaks of probability separated by areas in which probability of polar bear occurrence was estimated to be 0. Kernohan et al. (2001:145) cautioned users of LSCV bandwidth selection to watch for such scattered small peaks as indicators of "failure" of the LSCV method.

Least-squares cross validation failure prompted us to employ the 1-d plug-in (PI) bandwidth estimation routine of Venables and Ripley (1999). Kernohan et al. (2001) suggested that PI may tend

to over-smooth data. However, in comparative studies (Park and Turlach 1992), PI bandwidth selection was preferred to other methods (Wand and Jones 1995, Jones et al. 1996). The PI method performed well with our widespread polar bear data, yielding sensible probability estimates and UD boundaries (Figures 2, 5), and providing the ecological evaluation of this technique that thus far has been lacking (Kernohan et al. 2001).

Another disadvantage of the unknown sampling distributions of kernel UD estimators is that they suffer from lack of an obvious way to estimate standard errors. Therefore, the uncertainty of point estimates and the adequacy of sample sizes cannot be assessed (White and Garrott 1990, Kernohan et al. 2001). Kernohan et al. (2001) suggested that bootstrap variance estimates on kernel probabilities are possible and recommended they be used for future home-range analyses. Such estimates have not yet been employed in practice, however, because they are computationally impractical with standard methodologies. With the FFT and the convolution theorem, we were able to perform those computations 278 times faster than with standard methods (Kern et al. 2003), making computation of error estimates practical.

The ability to estimate error allowed us to use standard statistical tests to objectively evaluate seasonal and annual differences in distribution rather than being forced into a number of subjective decision rules. Because they lacked the ability to assess uncertainty in their estimates, Taylor et al. (2001) "validated" their results by review of ancillary information collected during their study or studies conducted by others. That sort of subjective validation can now be replaced by an entirely objective approach. Similarly, questions regarding space sharing among groups or individuals have been handled in a variety of ad hoc ways, and have failed to account for the third dimension-intensity of use of shared areas (Kernohan et al. 2001). Because, our p_i's represent the hills and valleys in the 3-D intensity-of-use surface, they provide point and interval estimates of shared space directly and objectively.

Most human activities of concern for polar bear security, notably hunting and oil and gas exploration and development, occur in the very-near-shore zone (Stirling 1990), the area in which our predictive abilities are strongest (Figure 7). Although seasonal allocation of hunting impacts does not appear to be necessary at this time, managers using our method could do so. Also, it is a simple matter to convert our relative probabilities of encountering a bear from each population to absolute probabilities of encountering any polar bear. Hence, managers could advise recreationists of the likelihood of bumping into a polar bear when they are out on the land, and they can address questions such as which areas proposed for industrial developments will minimize the risks of incidental bear encounters. They also can now calculate numbers of bears that might be exposed to oil in the event of a spill (Durner et al. 2000). This is the sort of information that makes risk assessments for environmental impact statements meaningful (Minerals Management Service, Alaska Outer Continental Shelf Region 2001).

In wildlife studies, where it is often difficult to collect large sample sizes and where samples often are not as uniform or as controlled as in laboratory experiments, strength of predictions is always an issue even when the necessary statistics are available. As shown in Figure 7, our calculated CVs were small across the majority of the study area, confirming that our samples were adequate for a robust assignment of occurrence probabilities across the cells in our grid. Had our estimated errors been much larger, however, these methods would have allowed us to determine the sample size necessary to generate narrower and more useful interval estimates.

Our findings have major ramifications for biological research as well as management. For most large mammals, estimation of population size is an enormous and complicated task. Perhaps the biggest complication in mark and recapture estimation is heterogeneity in capture probability (Pollock 1982, Pollock et al. 1990, Amstrup et al. 2001*b*, McDonald and Amstrup 2001). Attempts to estimate the size of the SBS polar bear population have been based upon the assumption that this population extended from west of Barrow to Amundsen Gulf in Canada. Radiotelemetry data confirm that members of the SBS population do travel over this range. However, the analyses presented here confirm that they do not move over the whole area equally. Fewer than 50% of polar bear encounters in northwestern Alaska are with SBS bears. The remainder of the encounter probability there is comprised of CS bears that are shared extensively with Russia. Just as the probability of harvesting a bear from the SBS is reduced in northwestern Alaska (compared with our prior assumption of one population throughout the region), the probability of capturing one

there, for population estimation, also is lower. Amstrup et al. (2001*b*) illustrated how recognition of different populations with different capture probabilities could impact population size estimates. Knowing not only that capture probabilities differ but also what the different probabilities are will be invaluable in future population estimation efforts for polar bears and other species for which telemetry data are available.

Conclusion

The methods described here can be applied to most situations in which large numbers of radio relocations are available. They will be invaluable in aiding managers making risk assessments, allocating harvests to the appropriate populations, or assessing impacts of other human activities. They will aid researchers by providing the refined descriptions of study populations that are necessary for many investigative tasks. The additional information wildlife biologists now can derive from radiotelemetry data will be applicable across a broad spectrum of management and research topics.

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