Factors contributing to the distribution and abundance of ringed seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996-1999

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ABSTRACT. Aerial surveys were conducted during late May to early June 1996-1999 in the central Beaufort Sea of Alaska using strip transect methods. Total survey effort included 40-88 transect lines per year covering 1198-2701 km^2. Observed densities ranged from 0.81 seals/km^2 in 1996 to 1.17 seals/km^2 in 1999. We examined the effects of habitat, weather, and time of day on observed seal densities using chi-square goodness-of-fit tests. We also used a generalized linear model to estimate the relationship between seal counts and covariates. The habitat-related variables water depth, location relative to the fast ice edge, and ice deformation had substantial and consistent effects. The highest densities occurred in >5-35 m depths. Densities were also highest in relatively flat ice and near the fast ice edge, with densities declining both shoreward and seaward of the edge. Univariate analysis suggested that observed densities were generally highest at about 1200 hrs local time, while time was not a significant variable in the generalized linear models. Analyses of the effects of weather factors on seal counts were inconclusive. This was likely at least partially because temperature and wind speed were measured at survey altitude rather than on the ice surface, and surveys were only conducted in weather considered suitable for hauling out.

Key Words: ringed seal, *Phoca hispida*, habitat relationships, aerial surveys, Beaufort Sea, generalized linear model

INTRODUCTION

Ringed seals (*Phoca hispida*) are a widespread, circumpolar species. They occur in the Beaufort, Chukchi and Bering seas, usually in association with sea ice (Burns, 1970). During winter ringed seals make and maintain breathing holes in sea ice (Smith and Stirling, 1975; Smith and Hammill, 1981). Some holes are enlarged to provide access to the ice surface where seals excavate lairs in the accumulated snow. As day length and temperature increase in the spring, increasing numbers of ringed seals haul out on the surface of the ice near breathing holes and lairs or along cracks. This hauling-out or basking is associated with the annual molt, which occurs in May-July (McLaren, 1958) when increased skin temperatures are needed to promote epidermal growth (Feltz and Fay, 1966). It is during this time that seals are most readily observed and counted.

Ringed seals are harvested by coastal Alaska Natives and are a primary prey of polar bears (*Ursus maritimus*) and arctic foxes (*Alopex lagopus*) at some times of year. The sea ice habitat where ringed seals occur also provides a reasonably safe and convenient surface on which various phases of petroleum exploration and development occur. Over the last several decades, there has been a warming trend in much of the Arctic, resulting in a thinning of the sea ice and changes in the annual extent of sea ice coverage (Vinnikov et al., 1999). Such changes may affect both ringed seals and humans who rely on sea ice for various activities (Huntington, 2000). It is important to document factors affecting ringed seal habitat use before warming substantially changes the available sea ice habitat and possibly impacts their distribution and abundance.

Since the earliest aerial surveys for ringed seals were conducted, observers have been aware that habitat characteristics, weather, and temporal factors affect the distribution and abundance of seals and the proportion available to be counted during surveys, and therefore introduce variability into counts and estimates of density (Burns and Harbo, 1972; Smith, 1973; Finley, 1979; Smith and Hammill, 1981). Surveys have generally been standardized to exclude very windy or stormy weather and to minimize the effects of diurnal hauling out patterns by flying in the middle of the day (Stirling et al., 1977; Kingsley et al., 1985; Frost et al., 1988; Lunn et al., 1997). Nonetheless, investigators have documented substantial within and between year variability in both survey conditions and the characteristics of sea ice and have recognized that it may be difficult to identify abundance trends or changes in distribution in light of such variability.

Variability in habitat use and hauling out behavior occurs in many pinnipeds (Smith 1965; Olesiuk et al., 1990; Thompson and Harwood, 1990; Frost et al., 1999). However, for most of these species the physical attributes of habitat that influence distribution and abundance remain similar over time. For example, physical characteristics of the rocks and sandbars on which hauled out harbor seals (*Phoca vitulina*) are counted change little from year to year. Counts may change due to factors such as weather, time, or tide, but not because of changes in the substrate itself. This makes it possible to model the effects of factors responsible for variation in counts and thus make more realistic estimates of both abundance and trend (see Frost et al., 1999; Boveng et al., 2003; Ver Hoef and Frost, 2003).

In contrast, the dynamic sea ice habitat used by ringed seals is temporally variable on short (days and weeks) as well as long (annual and decadal) time scales. A particular geographic location may have suitable ice conditions one year but not the next. Weather at the time of freeze-up and throughout the winter affects ice roughness and snow cover, which in turn determine the suitability of ice as seal habitat. Even within the same season, snow and ice conditions may change dramatically within just a few days, particularly around the time of breakup (Frost et al., 1988). There is also substantial annual variation in when break-up occurs. This type of variability makes the timing of surveys and between-year comparisons very difficult.

Many aspects of the behavior and seasonal movements of ringed seals may affect interpretation of aerial survey results. The proportion of ringed seals hauled out during late spring when surveys are conducted changes rapidly and can be highly variable (Finley, 1979; Smith and Hammill, 1981; Kelly and Quakenbush, 1990; Lydersen, 1991; Kelly et al., 2000; Born et al., 2002). In the central Beaufort Sea, the transition period from when seals rested in lairs to when ≥75% were basking on the surface ranged from 7-24 days in two consecutive years (Kelly et al., 2000). It is unknown how much geographical variation there may be in the onset of basking within a region such as the Beaufort Sea.

It was our intent in this study to evaluate the effects of environmental covariates on ringed seal distribution and abundance. We examined the effects of two types of covariates: those that we expected would affect the actual distribution and abundance of seals (habitat-related variables) and those that could affect our ability to count the seals that were present (temporal and weather-related factors).

METHODS

Collection of Survey Data

Aerial surveys were flown during late May and early June 1996-1999 in the Beaufort Sea between Oliktok Point (longitude 149°50'W) and Kaktovik (longitude 143°42'W), an east-west extent of approximately 250 km (Fig. 1). A high-wing twin-engine Aero Commander equipped with large bubble windows was used for all surveys. Surveys were conducted at groundspeeds of approximately 222 km/hr and a survey altitude of 91 m. Most surveys occurred between 1100 and 1700 hrs local time (solar noon is at approximately 1300 hrs at Prudhoe Bay) to coincide with the time of day when maximal numbers of seals haul out and bask on the ice (Burns and Harbo, 1972; Smith, 1975; Finley, 1979; Smith and Hammill, 1981). A few transects were surveyed slightly before 1100 hrs or after 1700 hrs.

Surveys were flown along lines of longitude and were therefore generally oriented perpendicular to the coast. Possible transect lines were spaced at 3.6 km between centerlines (6 minutes of longitude). A subset of the lines was surveyed each year. In some parts of the study area in 1996, 1997 and 1999, lines were spaced at 1.8 km intervals (3 minutes of longitude). Transect lines extended from approximately the 3-m depth contour to 40+ km offshore. Only data collected within 40 km of the shoreward end of the transect were used in the final analyses.

On all flights two experienced primary observers counted seals using strip transect methods. An additional observer seated behind the right primary observer counted using either strip or line transect methods. Survey strip width was 0.41 km on each side of the aircraft, with a 134 m offset from the transect centerline. Observers maintained the appropriate strip width by using inclinometers to mark survey angles (9.5° and 34° below the horizon) on the window with a grease pencil and periodically checking the angles throughout the day.

The number of ringed seals hauled out on the ice within the survey strip was counted and each was noted as being at a hole or by a crack. Seals at different holes were counted as separate groups, while those around a single hole were considered as part of the same group. When seals were spaced along cracks, the total number along a single crack (and within the survey strip) was recorded as a single group.

Each observer was paired with a data recorder who entered all sightings directly into a laptop computer. Data recorders also entered information on ice and weather conditions, evidence of on-ice industrial activity and sightings of other animals. A Global Positioning System (GPS) unit interfaced with all three computers such that positions were recorded at start and end points of survey lines, each minute along a survey line, at each seal sighting, and at all changes in ice or weather conditions

Ice characteristics were recorded independently on each side of the aircraft and included ice type (fast or pack), ice deformation (percent of the ice surface within the survey strip that was deformed by pressure ridges, ice jumbles, and snow drifts in 10% increments) and melt water (percent of the ice surface covered by standing water due to melting snow or river runoff in 10% increments). The delineation between fast and pack ice was indicated by a variety of features, including: a shear zone or large pressure ridge; the presence of open leads, broken ice and open water spots in the ice; or a large refrozen lead. In some areas the delineation between fast and pack ice was not clear from the aircraft and the location of the edge was assigned later by examining NOAA ice maps made from satellite images taken during the same time period.

Weather conditions (cloud cover, air temperature, and wind speed) were recorded at the beginning of each transect and whenever conditions changed. Because there were no on-ice weather stations and available weather reports were based on conditions over land, we based our weather information on conditions measured at survey altitude. The absence of open water in fast ice and the melted condition of the snow precluded the inference of surface winds from indicators such as white caps or blowing snow. Surveys were not conducted, or were discontinued, if wind speed at survey altitude exceeded 36 km/hr for more than a short time, or if the ceiling was below the survey altitude of 91 m.

Strip Transect Densities

The simple or "raw" density of observed ringed seals was calculated by dividing the number of seals counted on a line by the area surveyed on that line. The area surveyed was computed from the latitude and longitude of the first and last survey points on each line. Areas were computed separately for each side of the plane, although these were very close in all cases. Mean density (R) and standard error ($S(R)^2$) were then computed for each sector using the Jackknife procedure (Manly, 1991). Approximate 95% confidence intervals were computed as the mean density plus or minus the standard error multiplied by the appropriate t-statistic with n-1 degrees of freedom, where n is the number of survey lines in a sector.

Ringed seal density estimates were computed for all combinations of ice types (fast ice, pack ice and all ice) and seals (seals at holes, seals at cracks and all seals). Density was computed separately for fast and pack ice for each line.

Univariate Analyses

We compared observed ringed seal counts among habitat, weather, and time of day categories using Pearson chi-square (χ^2) goodness-of-fit tests. Analyses included all seals (seals at holes and at cracks) on any ice (fast and pack) within 40 km beyond the 3-m depth contour. Chi-square tests were conducted for each variable for every year and for all years combined. Rejection of the null hypothesis (large χ_P^2 compared to percentage points of the chi-square distribution) indicates that there is a non-random association between the variable and seal distribution. Bonferroni-adjusted 95% confidence intervals were calculated by stratum for each variable for proportion of occurrence (the observed proportion of seals within a strata relative to total seals in all strata) and for observed seals (Manly et al., 1993).

Covariate Analysis (Poisson Regression)

We used a generalized linear model (GLM) with a Poisson error distribution and log link (McCullagh and Nelder, 1989) to model the relationship between seal counts and environmental covariates. We modeled habitat variables that might affect the distribution and local abundance of seals (e.g., ice deformation, water depth, distance from the fast ice edge, and longitude) simultaneously with factors that likely to affect only the availability of seals for counting (e.g., weather or time of day).

Changes in habitat variables were noted as they occurred and locations of all such changes were assigned through a direct computer link with the aircraft GPS. Thus, each survey transect could be divided into segments based on ice type (pack or fast), ice deformation, air temperature, wind speed, and cloud cover. When any of these variables changed, a new segment was defined such that each segment was uniform with respect to the explanatory variables. Data from the left and right side observers were treated as separate transects since ice conditions sometimes differed between left and right sides. Water depth (starting with depths <5 m then in 10 m intervals) and distance from the fast ice edge (in 2 km intervals) were added to the datasets prior to creating segments. The number of seals observed and the area surveyed (segment length in km multiplied by strip width of 0.41 km) were determined for each segment.

The response variable in the regression analysis was the number of seals in a segment. The explanatory variables were year, ice type (pack or fast), percent ice deformation, distance from the fast ice edge, water depth, longitude, time of day, temperature, wind speed, and percent cloud cover. Water depth, longitude, and distance from the fast ice edge were included to account for large-scale patterns of seal abundance that were independent of local ice or weather conditions. Time was included to examine temporal changes in visibility or the proportion of seals hauled out. Year*longitude and year*distance-from-ice-edge interactions were included to account for annual large-scale changes in seal sightings that were unrelated to the other habitat variables in the model. Such changes in sighting distributions could be due to changes among years in the distribution of the population or changes in the distribution of sighting conditions.

The ln (area) of each segment was included in the regressions as an offset variable (Agresti, 1990) to account for the fact that, all other variables being equal, larger segments have more seals than smaller segments (adjusts analyses to a density basis). Quadratic terms and interactions were included for some variables or combinations of variables when we believed that relationships were not linear (on the log scale).

Based on preliminary analyses, the assumption of a Poisson distribution did not ‘fit’ the data well. We made two adjustments to the analyses to adjust for this lack of fit. First we omitted segments <0.01 km^2. These tiny segments were artifacts of combining the survey data with depth and distance-from-fast-ice-edge bands that were not part of the original data. When any seals were in these segments, very high densities resulted that had undue influence on the regression results. To account for remaining lack of fit, probably due to the presence of large groups of seals that would be unexpected with the small mean densities we observed, we adjusted tests and standard errors using the Pearson chi-square statistic as an overdispersion parameter (i.e., quasi-likelihood approach; Agresti, 1990). This resulted in somewhat larger standard errors and *P*-values than those computed without the adjustment.

To account for possible spatial correlation in the data (i.e., residuals from the regression for segments close together were more similar than for residuals from segments far apart), we included a spatial component in the variance structure. We used a spatial exponential function with a nugget effect to model the dependency in the residuals based on the distance between segments within a survey line (Littell et al., 1996). We assumed independence for data from separate survey lines and years.

All variables (including selected quadratic terms and interactions) were included in an initial model. Final regression models were then determined using a backward selection process. Terms were dropped from consideration one at-a-time based on the *P*-values from the Wald *F* statistics; those with the largest *P*-values were dropped first. This continued until all variables had *P*-values <~0.05. Continuous variables with *P*-values >0.05 were retained in the model if they were contained in a continuous by categorical interaction (e.g., longitude*year) that had a small *P*-value.

During the 1990s surveys, observations of ice deformation were recorded separately for left and right observers as they occurred instead of at 1-minute intervals. Changes in other variables were also noted as they occurred and locations of all such changes were assigned through a direct computer link with the aircraft GPS. Thus, each survey transect was divided in segments based on ice type (pack or fast), ice deformation, air temperature, wind speed, and cloud cover. When any of these variables changed, a new segment was defined such that each segment was uniform with respect to the explanatory variables. Data from the left and right side observers were treated as separate transects since ice conditions differed between left and right sides. This resulted in segments of differing sizes on the left and right sides. For both the 1980s and 1990s, water depth (starting with depths <5 m then in 10 m intervals) and distance from the fast ice edge (in 2 km intervals) were added to the datasets prior to creating segments. Because the original data in the 1980s was summarized at 1-minute intervals (although changes in depth and distance from the fast ice edge did not always match these intervals), there were generally fewer segments per transect in the 1980s than the 1990s. The number of seals observed and the area surveyed (segment length in km multiplied by strip width of 0.41 km) were determined for each segment.

RESULTS

Observed Densities

Annually, we surveyed 40-88 transects covering 1198-2701 km^2 and counted 1111-3105 seals per year (Table 1). Fast ice made up 34%-77% of the total survey area. Observed densities for fast and pack ice combined ranged from 0.81 seals/km^2 in 1996 to 1.17 seals/km^2 in 1999. In two years, pack ice densities were much greater than fast ice densities and in the other two years the densities on pack and fast ice were similar. On fast ice more seals were seen at holes than at cracks. On pack ice the relative proportions of seals at holes and cracks were more variable.

Factors Affecting Seal Distribution and Abundance

Univariate analyses using chi-square goodness-of-fit tests were performed for each year and for all years combined to individually examine the relationship between observed ringed seal counts and water depth, distance from the fast ice edge, ice deformation, and longitude (Table 2). A GLM was constructed separately from the same survey datasets (Table 3).

Depth - Univariate analysis indicated that water depth had a significant effect on observed ringed seal densities in each survey year and for all years combined (P<0.001). Densities were lowest in water $\leq$ 5 m deep (0.35-0.73 seals/km^2) and deeper than 35 m (0-0.77 seals/km^2) and highest in water depths of >5-35 m (1.00-1.33 seals/km^2; Fig. 2a). There was little annual variation in the relationship between observed density and water depth. For all years combined, the highest densities (1.17 seals/km^2) occurred in water 15-25m deep. The GLM also indicated that seal densities were lowest in water <5 m and >35 m deep and highest in water 25 m deep (Fig. 2b). Model results were significant for depth and $depth^2$ at $P<0.001$.

<u>*Fast ice edge*</u> - For all years, chi-square values for observed density relative to the position of the fast ice edge were significant ($P<0.001$). The relationship was generally consistent for each year and for all years combined, with peak densities (1.29-1.90 seals/km^2) occurring within 5 km of the edge, either on fast or pack ice (Fig. 3a). The GLM also indicated a significant, non-linear effect of distance from the fast ice edge on seal densities ($distance^2$, $P\leq 0.001$). Relative densities were highest near the fast ice edge and decreased both shoreward and seaward of the edge (Fig. 3b).

<u>*Ice deformation*</u> - Ice deformation had a significant effect on observed seal densities for each year and for all years combined in the univariate analyses (P=0.01 to <0.001). Seal densities in all individual years and in all years combined were highest in ice in the 0%-10% and 10%-20% deformation categories with gradually declining densities in rougher ice categories (Fig. 4a). Similarly, the GLM analysis for ice deformation indicated that modeled densities were highest in the flattest ice and lowest in the most highly deformed ice ($P<0.001$; Fig. 4b).

<u>*Longitude*</u> **–** Although there was some annual variability, univariate analysis indicated that observed densities were generally lowest between 146°W and 149°W and highest at about 144°W and 145°W ($P<0.001$; Fig. 5a). For all years combined, the highest density occurred at 144°, from approximately Kaktovik to Brownlow Point. The GLM indicated a more linear relationship, with the highest modeled densities occurring at the eastern end of the study area (Fig. 5b).

Factors Affecting the Proportion of Seals Hauled out

Variables that might affect either the proportion of seals hauled out and available for counting or our ability to see and count them included time of day, cloud cover, temperature, and wind speed. Results of univariate and GLM analyses of these variables are presented in Tables 2 and 3. Although we collected data on melt water, we did not use those data in this analysis since melt water was not present during the survey period in 2 of 4 years.

<u>*Time of day*</u> - Seal density was significantly related to time of day for each survey year and for all years combined based on univariate analysis ($P<0.001$). In three years, densities increased somewhat until 1200 or 1300 hrs and then gradually decreased through the afternoon. However, in 1999 the observed densities increased throughout the day and were highest after 1700 hrs (Fig. 6). The GLM indicated no significant relationship between modeled densities and time of day (P=0.226).

<u>*Weather*</u> - Univariate analysis indicated significant effects of cloud cover, temperature and wind in most years and for all years combined. However, the effects were inconsistent for all three variables. Clear skies resulted in the highest observed densities in 1999 and the lowest densities in 1996-1998 (Fig. 7). Overall, despite a significant chi-square value, there seemed to be little pattern in the relationship between seal density and cloud cover. Wind speed and temperature showed similarly variable effects (Figs. 8, 9a). The GLM indicated slightly higher densities around 0° C than when it was warmer or colder ($P<0.001$, Fig. 9b). There was no significant relationship between cloud cover or wind speed and modeled densities.

Spatial correlation

We included a spatial component in the GLM to account for possible spatial correlation in the data. The variance structure of the model showed little evidence of spatial correlation among residuals within the survey lines (Table 4). The very small estimated range (the distance between transect segments where autocorrelation is detected) indicates that there was only a relationship between residuals for neighboring segments; the pattern did not extend for sizable distances along the lines. If the model had not accounted for this short-range correlation, the variance of 10.2% (Table 4; partial sill) would have been incorrectly reduced. Two factors likely are related to the observed lack of autocorrelation. Many of our predictive variables had a direct spatial component (e.g., distance from ice edge, water depth) such that segments close together along a line had similar values for the variables; these likely removed much of the spatial pattern in the data leaving less in the residuals. Secondly, the data did not fit a Poisson distribution well, necessitating the need to adjust for overdispersion. The principal cause of the overdispersion is that, even though the mean count per segment is low, there are some large groups of seals, especially along cracks, that are much larger than would be expected under a Poisson model. The presence of these large groups also reduces the estimated positive autocorrelation, since nearby segments having similar values of predictor variables may have few or no seals.

DISCUSSION

Habitat Factors Affecting Aerial Survey Counts

Estimated densities of seals in our central Beaufort Sea study area were lowest in water shallower than 5 m or deeper than 35 m. Moulton et al. (2002) conducted surveys in a subset of our study area (from approximately 147º to 149º W) during 1997-1999 and reported the highest seal densities were generally in 5-15 m depths. They found seals to be more common in somewhat deeper water in 1999 compared to other years. Other investigators have also reported differences in densities of ringed seals relative to water depth. In the East Siberian Sea, Ognetov (1993) found higher densities in 10-30 m (0.12-0.39 seals/km^2) than in water shallower than 10 m (0.10 seals/km^2) or 30-40 m (0.01 seals/km^2). In contrast, in the eastern Canadian Beaufort Sea and the Canadian High Arctic, ringed seal densities were generally higher in deeper water (50-100 m or 50-150 m) (Stirling et al., 1982; Kingsley, 1990). The differences in distribution relative to depth between the Alaskan and East Siberian coasts on one hand and the eastern Beaufort Sea and Canadian High Arctic on the other may be related to coastal topography and the effects it has on both bathymetry and sea ice. Both the central Beaufort and East Siberian Sea coastlines are relatively linear features, with water depths generally getting deeper as one moves north and off shore. In those areas, fast ice occurs as a linear band along the coast. In the eastern Beaufort Sea and the Canadian Arctic, fast ice is more extensive and this stable habitat extends over deeper water because it is protected on all sides by land.

Univariate and GLM analyses indicated that observed as well as modeled densities of ringed seals in the central Beaufort Sea were highest near the fast ice edge and decreased both shoreward and seaward of the edge. Univariate analyses, which did not take into account the interactive effects of other factors, indicated somewhat more annual variability. However, when data were modeled in combination with other covariates, it was clear that densities were highest near the ice edge. Covariate analysis by Moulton et al. (2002) also indicated that modeled ringed seal densities in their study area decreased with increasing distance from the fast ice edge.

Some variability may have been introduced into the analysis of density relative to distance from the fast ice edge due to difficulty in visually determining the position of the edge. This boundary was not always obvious when a delineating pressure ridge was not visible, when there was a series of such ridges and/or when no open water was present in the pack ice. Furthermore, early in the season there may be a substantial amount of “attached fast ice” beyond the actual edge (Stringer et al., 1980). Until pack ice movement at the onset of breakup begins to fracture the attached fast ice, it is rarely possible to distinguish it from true fast ice.

It is unclear what makes the fast ice edge so attractive to ringed seals and results in higher densities in that region. Seals feed at a reduced rate, as indicated by stomach contents and body condition, during late spring when they are entering the molt (Lowry et al., 1980; Frost and Lowry, 1984). However, seal distribution and density in late May and early June, prior to breakup, are thought to reflect distribution patterns established earlier in the year. Higher abundance of seals in an area could indicate greater availability of prey during fall and winter when seals are actively feeding and when breathing holes are established. Alternatively, higher densities near the edge at the time of our surveys could be due to an influx of seals from other regions. During late winter and spring, ringed seals are thought to partition their habitat based on age, sex and reproductive status, with adults predominating in and near the fast ice, subadults in the flaw (or edge) zone and both occurring in drifting pack ice (McLaren, 1958; Smith, 1973). Until territoriality breaks down at the end of the breeding season, most seals seen on fast ice are single seals at holes. As the season progresses, average group size increases and it is much more common to see multiple seals at the same hole, or many seals along a crack in the ice (Smith and Hammill, 1981; Finley et al., 1983; Frost et al., 1988). Subadults wintering outside the fast ice habitat may move into the fast ice to molt, resulting in high local densities just shoreward of the edge (Finley, 1979). Seals may also move into a region as breakup progresses in other areas (Kingsley et al., 1985; Smith and Harwood, 2001). A seal tagged at Little Diomede Island, Alaska, in May 2001 moved >700 km north and east into the Chukchi Sea before its tag ceased to transmit in June (Sheffield and Menadelook, 2001). Seven ringed seals tagged in at Cape Parry in Amundsen Gulf (east of our study area) in September 2001-2002 moved west along the Alaska coast to Barrow and then into the Chukchi Sea by October or November (Lois Harwood, pers. comm. 2002. See web site www.permafrost.com/seals). It is possible that seals might return in the spring to Amundsen Gulf along a similar route.

We found a strong and consistent relationship between seal densities and the degree of ice deformation, with more seals found in flatter, less deformed ice. Similarly, Frost et al. (1988) reported that observed ringed seal densities during early June were higher in flat ice than in rough ice throughout both the Chukchi and Beaufort seas. However, once the ice began to crack and break up, they found that the correlation between ice deformation and observed density disappeared. Investigators in the eastern Beaufort Sea and the Canadian Arctic have also reported that during the molting season ringed seals bask in flat, open areas (Smith and Stirling, 1975; Stirling et al., 1977; Smith, 1980). Moulton et al. (2002) speculated that densities might be lower in rough ice because seals were harder to see. While that possibility cannot be entirely dismissed, the absence of a correlation between density and ice deformation after the beginning of breakup reported by Frost et al. (1988) suggests that the difference is related at least in part to seal distribution.

Ringed seals are a primary prey of polar bears in most parts of their range and the constant threat of predation has shaped their behavior on the ice (Smith, 1980; Kingsley and Stirling, 1991; Stirling and Øritsland, 1995). Bears generally hunt along pressure ridges, in hummocky ice and at the edges of rough ice areas. Seals in turn haul out to bask in areas where they can see and smell approaching predators and where they can escape down holes or cracks too small for a polar bear to follow (Kingsley and Stirling, 1991). It is not surprising that densities of basking ringed seals are higher in flat ice than in rough, ridged ice where polar bears hunt more commonly.

We tested the effect of longitude on the distribution and abundance of seals because we thought it possible that there might be some east-west habitat gradient that was not reflected in the other variables incorporated in our analyses. Both univariate analysis and the GLM indicated a significant longitudinal gradient, with densities generally higher at the eastern end of the study area, between Brownlow Point and Kaktovik. While the reasons for this gradient are unknown, it may be related to prey availability. Griffiths and Thomson (2001) reported that zooplankton biomass in this region during summer and autumn was much higher than the average biomass in other areas of the eastern Beaufort Sea (1000 mg/m^3 compared to the average biomass of ~260 mg/m^3).

Factors Affecting Proportion Hauled Out

Although univariate analysis suggested that observed densities were generally highest around 1200 hrs local time (solar noon is about 1300 hrs), the relationship was inconsistent. Moulton et al. (2002) found a similarly inconsistent relationship between the number of ringed seals counted and time of day, and Kingsley et al. (1985) reported that time of day was not a significant factor in multiple regression analysis of ringed seal densities in the Canadian High Arctic. In contrast to inconclusive results from analyses of aerial survey data, the results of most tagging studies indicate a strong diurnal component to ringed seal behavior, with most seals hauled out between mid morning and late afternoon (Finley, 1979; Smith and Hammill, 1981; Lydersen, 1991; Kelly and Quakenbush, 1990; Kelly et al., 2000). However, seals tagged in northwest Greenland showed no diel pattern in hauling out between June and August (Born et al., 2002). The lack of a significant correlation between seal density and time of day in aerial surveys may well be due to the fact that surveys have been conducted during the middle of the day when seals were most likely to be hauled out.

Although more ringed seals generally are seen basking on warm, sunny days with relatively light winds, it is difficult to statistically quantify this relationship. Any analysis of the effects of weather on seal counts is complicated by the lack of local, on-site information about weather conditions. Temperature and wind speed recorded from the survey aircraft at survey altitude or from weather stations on land may not accurately reflect conditions on the ice. Furthermore surveys are generally not conducted in weather considered unsuitable for hauling out (Lunn et al., 1997; Kingsley et al., 1985). Cloud cover may affect seal counts in contradictory ways, thus obfuscating any relationship that may exist. For example, seals may prefer to haul out on warm clear days, but such conditions can also result in sun glare that impairs observers' ability to count. Conversely, cloudy days might be less optimal for hauling out but better for detecting seals. Also, weather variables in the GLM were not year-specific so it was less likely to detect a pattern that was inconsistent among years. It is not surprising, then, that our analyses of these factors relative to seal counts were not very informative. Attempts by other investigators to quantify the effects of weather on aerial survey results have been similarly problematic, with multivariate regression analysis often producing results that either contradict other studies, vary across years or survey replicates, or conflict with what is known about seal behavior (Finley, 1979; Kingsley et al., 1985). In fact, Kingsley et al. (1985) concluded that multivariate regression using wide-area survey data was ineffective for determining the effects of weather, and they did not use weather variables in their multivariate analysis.

Notwithstanding the above, some investigators have been able to demonstrate effects of weather variables such as wind speed and temperature on the hauling out behavior of ringed seals as well as other as seal species. Densities were negatively correlated with wind speed for ringed seals in the Canadian Arctic (Smith and Hammill, 1981; Stirling et al., 1982) and Weddell seals (*Leptonychotes weddelli*) in the Antarctic (Wartzok, 1991). For ringed seals, as well as other ice associated seals, temperature seems to have the greatest influence when it is too warm and may exceed the animals' thermal tolerance. Densities decrease when conditions are too warm and calm (Burns and Harbo, 1972; Finley, 1979; Harrison and Kooyman, 1968). Watts (1996) suggested that temperature appears to be less significant in models that take time of day and date into account, since to some degree they measure the same thing.

Effects of Survey Date on Seal Counts

Our surveys did not include temporal replicates that would be required to investigate the effects of date on aerial survey results. Nonetheless, it is clear that date may have a substantial effect on the number of seals available for counting. Kelly et al. (2000) monitored the hauling out behavior of 18 ringed seals tagged in the central Beaufort Sea in 1999 and 2000. They found that early in spring seals hauled out exclusively in snow covered lairs where they could not be seen by observers. As the season progressed, seals gradually began to haul out on the surface of the ice where they could be counted during surveys. In 1999-2000, seals typically did not use lairs once they began to bask. In a subsequent year, however, about 40% of the tagged seals responded to a spell of cold weather by returning to lairs after the onset of basking (Brendan P. Kelly, pers. comm.). Field measurements indicated that most seals were basking when the snow temperature near the snow-ice interface had warmed to 0º C and that snow temperature might be a good predictor of peak haulout and therefore of the best time to conduct surveys. However, even though a snow temperature of 0º C predicted basking and May 31st was the day on which 50% of tagged seals were basking in both 1999 and 2000, there was a three-fold difference in the length of the transition period from resting in lairs to hauling out on the surface in the two years. Kelly et al. (2000) estimated that only 12% of the seals present in their study area were hauled out on 29 May 1999 compared to 40% just six days later. Thus our 1999 surveys, which were flown during 29 May-4 June, very likely counted a rapidly changing proportion of the population. Born et al. (2002) also found that the proportion of time ringed seals spent hauled out changed rapidly in spring.

While it is useful to know when most seals are on the surface basking, that unfortunately does not resolve other survey-related problems. Even if snow temperatures do reliably predict basking and if, as suggested by Kelly et al. (2000), a proxy can be found for actual on-ice snow temperatures, it is still not certain that counts from surveys will reflect only seals resident in the survey area. Concurrent with the increased visibility of resident seals later in the spring may be an influx of seals from the pack ice as well as from other geographic regions (Finley, 1979; Smith and Harwood, 2001). Whether or not this occurs and to what degree, has not been documented in the Alaskan Beaufort Sea. The chronology of breakup, both within the survey area as well as in areas far removed, may affect what seals are present during the survey period. Also, resident seals may not always bask in the same location as where their winter lairs were located (Kelly and Quakenbush, 1990; Kelly et al., 2000). While satellite tagging would be useful to answer some of these questions, the current method of attaching transmitters (gluing to the pelage) limits our ability to collect data during the survey period since ringed seals molt their fur at this time.

In addition to the biological factors described above, annual variability in weather conditions may also affect timing of surveys. From the perspective of observers, the optimal timing for ringed seal surveys is before sea ice break up begins and when water on the ice surface from melt and overflow of rivers is not yet extensive (Burns and Harbo, 1972; Frost and Lowry unpubl.

obs.). In the central Beaufort Sea, such conditions generally occur in late May to early June, but that is not always the case. In our surveys, melt water covered <1% of the ice we surveyed in two years and 38%-74% in the other two years. In 1998, 80%-90% of the ice near shore was covered by melt water when surveys were flown in 27-28 May, resulting in poor conditions for counting seals. Thus, conditions in 1998 had deteriorated before the usual scheduled date for surveys to begin and may have been unsuitable for surveys before the date that most seals were basking.

While the GLM enabled us to quantify and model the effects of some covariates on observed seal counts, the final model did not account for a substantial proportion of the variation in seal counts. We think that this may be largely due to the effects of temporal variation in the proportion of seals hauling out. Although we tried to minimize the effect of date as much as possible by narrowing the survey window and conducting surveys before breakup and melting occurred, our surveys were not designed to quantify effects of date on seal behavior. In the future, any efforts to improve our estimates of trend must include quantification of the effects of within and between-year temporal variation on survey counts.

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TABLE 1. Densities of ringed seals at holes and at cracks on fast ice, pack ice, and all ice combined within 40 km of shore in the central Alaskan Beaufort Sea (149º50’ W to 143º40’ W), based on aerial surveys conducted in 1996-1999.

			Fast Ice			Pack Ice			All Ice Combined		
	Dates		At Holes	At Cracks	All Seals	At Holes	At Cracks	All Seals	At Holes	At Cracks	All Seals
1996	5/29-31	Seals/ km^2	0.51	0.06	0.57	0.60	0.38	0.98	0.56	0.24	0.81
(n=61)		LCL	0.44	0.01	0.48	0.42	0.27	0.76	0.46	0.17	0.67
		UCL	0.58	0.10	0.65	0.79	0.48	1.21	0.67	0.32	0.95
		# counted			446			1064			1510
		Km^2 surveyed			787			1082			1082
1997	5/27-6/1	Seals/ km^2	0.89	0.02	0.91	0.47	0.86	1.33	0.79	0.21	1.01
(n=88)		LCL	0.79	0.00	0.80	0.33	0.57	0.96	0.70	0.14	0.88
		UCL	0.99	0.03	1.01	0.61	1.15	1.70	0.89	0.28	1.14
		# counted			1884			835			2719
		Km^2 surveyed			2074			627			2701
1998	5/27-28	Seals/ km^2	0.65	0.30	0.95	0.53	0.38	0.92	0.58	0.35	0.93
(n=40)		LCL	0.52	-0.03	0.60	0.43	0.28	0.78	0.49	0.24	0.78
		UCL	0.78	0.62	1.30	0.64	0.48	1.05	0.66	0.47	1.07
		# counted			388			723			1111
		Km^2 surveyed			408			790			1198
1999	5/29-6/4	Seals/ km^2	0.92	0.23	1.14	0.69	0.51	1.20	0.80	0.38	1.17
(n=88)		LCL	0.52	-0.03	0.60	0.43	0.28	0.78	0.49	0.24	0.78
		UCL	0.78	0.62	1.30	0.64	0.48	1.05	0.66	0.47	1.07
		# counted			1407			1698			3105
		Km^2 surveyed			1232			1415			2647

TABLE 2. Summary of chi-square analyses of density relative to variables affecting the observed distribution and abundance of ringed seals in the central Alaskan Beaufort Sea, 1996-1999.

Variable	Chi-square	*df*	*P*-value
Water Depth			
1996	154.10	4	<0.001
1997	917.10	5	<0.001
1998	72.01	5	<0.001
1999	110.77	4	<0.001
All Years	356.04	4	<0.001
Distance from Fast Ice Edge			
1996	416.17	13	<0.001
1997	294.83	13	<0.001
1998	81.02	11	<0.001
1999	409.32	13	<0.001
All Years	597.21	10	<0.001
Ice Deformation			
1996	69.27	5	<0.001
1997	195.34	5	<0.001
1998	15.03	5	0.01
1999	108.58	5	<0.001
All Years	343.81	5	<0.001
Longitude			
1996	183.21	6	<0.001
1997	464.61	6	<0.001
1998	73.27	6	<0.001
1999	266.80	6	<0.001
All Years	754.63	6	<0.001
Time of Day			
1996	256.52	6	<0.001
1997	159.31	6	<0.001
1998	51.81	6	<0.001
1999	116.70	7	<0.001
All Years	403.98	7	<0.001
Cloud Cover			
1996	44.72	3	<0.001
1997	282.36	6	<0.001
1998	57.71	5	<0.001
1999	41.59	6	<0.001
All Years	396.13	10	<0.001

TABLE 2. continued.

Variable	Chi-square	*df*	*P*-value
Temperature			
1996	93.85	2	<0.001
1997	110.91	4	<0.001
1998	14.54	3	0.002
1999	244.48	1	<0.001
All Years	370.03	6	<0.001
Wind Speed			
1996	44.15	3	<0.001
1997	131.24	4	<0.001
1998	38.19	3	<0.001
1999	61.52	5	<0.001
All Years	333.51	5	<0.001

TABLE 3. Generalized linear model coefficients from final ringed seal regression models for aerial surveys conducted in the central Beaufort Sea, 1996-1999.

Variable	Est.	SE	t	*P*
intercept (pack)	-0.0760	0.2180		
intercept (fast)	-0.3119	0.1903		
year (pack)	-0.1413	0.0536	-2.64	0.009
year (fast)	0.0643	0.0581	1.11	0.269
$dist^2$ 96	-0.0023	0.0006	-4.02	<0.001
$dist^2$ 97	-0.0004	0.0002	-1.56	0.120
$dist^2$ 98	-0.0012	0.0004	-2.71	0.007
$dist^2$ 99	-0.0009	0.0004	-2.50	0.012
longitude	0.0958	0.0227	4.23	<0.001
ice deformation	-0.0277	0.0038	-7.26	<0.001
depth	-0.0776	0.0170	-4.55	<0.001
$depth^2$	-0.0015	0.0004	-4.04	<0.001
$temp^2$	-0.0031	0.0015	-2.05	0.040

TABLE 4. Spatial covariance parameter estimates from the generalized linear model of seal counts on year and covariates based on aerial surveys in the central Beaufort Sea, 1996-1999.

Covariance parameter	Parameter estimate	Proportion of total error variance
Range (extent of autocorrelation; km)	0.012	
Partial Sill (sill-nugget)	0.811	0.102
Residual variance (nugget)	7.123	0.896
Total error variance	7.934	

FIG. 1.

FIG. 2. Densities of ringed seals relative to water depth based on aerial surveys in the central Beaufort Sea, 1996-1999: a) observed densities b) generalized linear model estimate.

FIG. 3. Densities of ringed seals relative to distance from the fast ice edge based on aerial surveys in the central Beaufort Sea, 1996-1999: a) observed densities, b) generalized linear model estimates.

FIG. 4. Densities of ringed seals relative to percent ice deformation based on aerial surveys in the central Beaufort Sea, 1996-1999: a) observed densities, b) generalized linear model estimates.

FIG. 5. Estimates of ringed seal density relative to longitude based on aerial surveys in the central Beaufort Sea, 1996-1999: a) observed densities, b) generalized linear model estimates.

FIG. 6. Observed densities of ringed seals relative time of day based on aerial surveys in the central Beaufort Sea, 1996-1999.

FIG. 7. Observed densities of ringed seals relative to percent cloud coverage based on aerial surveys in the central Beaufort Sea, 1996-1999.

FIG. 8. Observed densities of ringed seals relative to wind speed based on aerial surveys in the central Beaufort Sea, 1996-1999. Wind speed was measured at survey altitude of 91m.

FIG. 9. Densities of ringed seals relative to air temperature based on aerial surveys in the central Beaufort Sea, 1996-1999: a) observed densities b) generalized linear model estimates. Air temperatures were measured at survey altitude of 91 m.