ARCTIC
VOL. 57, NO. 2 (JUNE 2004) P. 115–128

# Factors Affecting the Observed Densities of Ringed Seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996–99

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(*Received 30 January 2003; accepted in revised form 14 October 2003*)

ABSTRACT. Aerial surveys were conducted during late May and early June 1996–99 in the central Beaufort Sea of Alaska, using strip-transect methods. The purpose of these surveys was to quantify and model the effects of environmental covariates on ringed seal counts and to provide density estimates that would be useful for evaluating trends in seal abundance. 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 univariate chi-square goodness-of-fit tests. We also used a multivariate generalized linear model to estimate the relationship between seal counts and covariates. Three habitat-related variables—water depth, location relative to the fast ice edge, and ice deformation—had substantial and consistent effects. The highest densities occurred at depths between 5 and 35 m. Densities were also highest in relatively flat ice and near the fast ice edge, declining both shoreward and seaward of that edge. Univariate analysis suggested that observed densities were generally highest at about 1200 h Alaska daylight time, but 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 conducted only in weather considered suitable for hauling out. The final multivariate model did not account for a substantial proportion of the variation in seal counts. We think this result was largely due to date-related variation in the proportion of seals hauling out, an issue our surveys were not suited to address.

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

RÉSUMÉ. De 1996 à 1999, à la fin de mai et au début de juin, on a effectué des relevés aériens dans la partie centrale de la mer de Beaufort alaskienne, en utilisant des méthodes d’échantillonnage en bande. Ces relevés avaient pour but de quantifier et de modéliser les effets de covariables environnementales sur le comptage des phoques annelés, et de fournir des estimations de densité qui pourraient servir à évaluer les tendances dans l’abondance des phoques. Le travail de relevé a porté chaque année sur un total allant de 40 à 88 lignes-transects, couvrant une superficie de 1198 à 2701 km$^2$. Les densités observées allaient de 0,81 phoque par km$^2$ en 1996 à 1,17 phoque par km$^2$ en 1999. On a étudié les effets de l’habitat, du climat et du moment de la journée sur les densités de phoques observées, à l’aide de tests d’adéquation chi carré à une variable. On a également eu recours à un modèle linéaire généralisé à plusieurs variables pour évaluer le rapport entre les comptages de phoques et les covariables. Trois variables reliées à l’habitat – profondeur de l’eau, position par rapport à la lisière de la banquise côtière et déformation de la glace – avaient des effets importants et constants. Les plus fortes densités se produisaient à des profondeurs de 5 à 35 m. Elles se retrouvaient également sur la glace relativement plane et près de la lisière de la banquise côtière, diminuant à la fois en direction du rivage et en direction de la mer depuis la lisière. L’analyse à une variable suggère que les densités observées étaient généralement plus fortes à environ 12 h (heure avancée de l’Alaska), mais le moment de la journée ne constituait pas une variable d’importance dans les modèles linéaires généralisés. Les analyses de l’impact des facteurs météorologiques sur les comptages de phoques n’ont pas donné de résultats concluants. Ceci était probablement dû au moins en partie au fait que la température et la vitesse du vent étaient mesurées à l’altitude où se faisaient les relevés plutôt qu’à la surface de la glace, et les relevés n’étaient effectués que par temps jugé approprié pour que les phoques montent sur la glace. Le modèle final à plusieurs variables ne représentait pas une proportion substantielle de la variation dans les comptages de phoques. Ce résultat, selon nous, était dû en grande partie à une fluctuation reliée à la date dans la proportion de phoques qui montaient sur la glace, question que nos relevés n’étaient pas conçus pour aborder.

Mots clés: phoque annelé, *Phoca hispida*, relations au sein de l’habitat, relevés aériens, mer de Beaufort, modèle linéaire généralisé

Traduit pour la revue *Arctic* par Nésida Loyer.

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## 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 the 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 days grow longer and temperatures 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, when increased skin temperatures are needed to promote epidermal growth (Feltz and Fay, 1966). It is during this time, from May to July (McLaren, 1958), 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 to support various phases of petroleum exploration and development, activities that could affect localized ringed seal distribution and abundance. Over the last several decades, a warming trend in much of the Arctic has resulted 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 affects their distribution and abundance.

Observers have long 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, thus introducing 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, in light of such variability, it may be difficult to identify abundance trends or changes in distribution.

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 harbor seals (*Phoca vitulina*) haul out usually change little from year to year. This makes it possible to model and incorporate the effects of factors responsible for variation in 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 (daily and weekly) 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 interannual variation in when break-up occurs. This is particularly true for ringed seal habitat along coastlines like that of Alaska, where fast ice occurs as an unprotected, linear band that abuts the pack ice and may be heavily impacted by storms and ocean currents. This unpredictable variability makes the timing of surveys and between-year comparisons along the Alaska coast very difficult. In other regions where ringed seals occur, e.g., the Canadian Arctic or Svalbard, fiords and large offshore islands stabilize the much more extensive fast ice habitat and make it less subject to dramatic short-term changes.

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 where they could not be seen to when over 75% were hauled out on the surface to bask varied in length from 7 days in one year to 24 days in the next (Kelly et al., 2000). Thus, a rapidly changing and inconsistent proportion of the population may be hauled out and available for counting during survey periods in different years. It is unknown how much geographical variation in the onset of basking there may be 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 likelihood of seals' being present in an area (habitat-related variables) and those that could affect the probability that seals, if present, were on the ice where they could be counted (temporal and weather-related factors).

## METHODS

### Collection of Survey Data

Aerial surveys were flown during late May and early June of 1996–99 in the Beaufort Sea between Oliktok

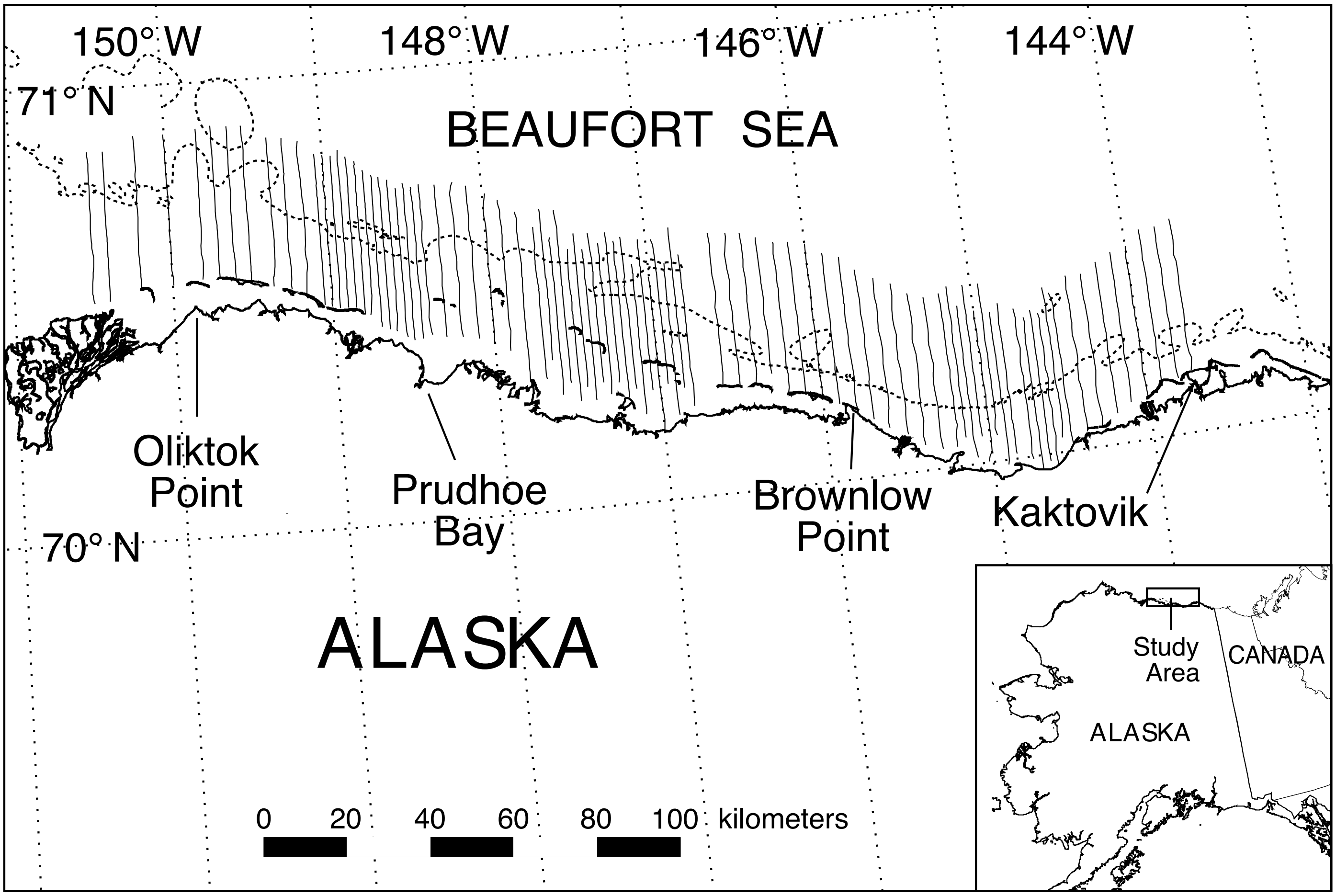

FIG. 1. Map of the central Alaskan Beaufort Sea, showing transects for aerial surveys of ringed seals conducted during May and June in 1996–99. The dotted line corresponds to the 20 m depth contour.

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/h and a survey altitude of 91 m. Most surveys occurred between 1100 and 1700 h Alaska daylight time (AKDT = GMT - 8) 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 h or after 1700 h.

Surveys were flown along lines of longitude and were therefore generally oriented perpendicular to the coast. Centerlines of possible transects were 3.6 km apart (6 minutes of longitude). A subset of the lines was randomly selected for survey 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). This additional coverage, given to areas where industrial activity was either in progress or likely to occur, was designed to facilitate future investigations of the possible impacts of such activity. 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 so that positions were recorded at the start and end points of survey lines, each minute of time 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. These included ice type (fast or pack), ice deformation (percentage of the ice surface within the survey strip that was deformed by pressure ridges, ice jumbles, and snow drifts, in 10% increments) and meltwater (percentage of the ice surface covered by standing water resulting from snowmelt or river runoff, in 10% increments). Although we collected data on meltwater, we did not use those data in this analysis since meltwater was not present during the survey period in two of the four years. The delineation between fast ice 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, observers were not able to distinguish fast and pack ice near the edge because ice coverage for both types of ice was 100% and there was no evidence of cracks or broken floes. In these instances, the location of the edge was assigned later after we examined 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 whitecaps or blowing snow. Surveys were not conducted, or were discontinued, if wind speed at survey altitude exceeded 36 km/h 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 aircraft, although these were very close in all cases. Mean density (R) and standard error ($S(R)^2$) were then computed 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 lines surveyed in a year.

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

### *Univariate Analyses*

We compared counts of ringed seals in different habitat, weather, and time-of-day categories using Pearson chi-square ($\chi^2$) goodness-of-fit tests. Analyses included all seals on any ice (fast and pack) within 40 km and beyond the 3 m depth contour. Chi-square tests were conducted for each variable for every year and for all years combined. Because we could not assume that seals were independent, comparison of our $\chi^2$ statistics with the standard $\chi^2$ distribution would be inappropriate. Therefore, we compared calculated $\chi^2$ statistics with a randomization distribution (Manly, 1991). We generated the randomization distribution by randomly associating seal counts with the categories to be tested; under the null hypothesis, there is no association between counts and categories, so random ordering will make no difference. We then calculated a $\chi^2$ statistic for this randomized version of the data. This procedure was repeated 5000 times to give the distribution of the test statistic when the null hypothesis (i.e., no association) was true. The *p*-values were calculated as the proportion of the randomization distribution that was greater than the observed $\chi^2$ statistic. Bonferroni-adjusted 95% confidence intervals were calculated by stratum for each variable for proportion of occurrence (the observed proportion of seals within a stratum 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. This model assumes that the natural log (ln) of seal counts is a linear function of the explanatory variables:

$$\ln(\text{counts}) = \beta_0 + \beta_1 {*} v_1 + \ldots + \beta_n {*} v_n + e$$

where $\beta$ is an estimated regression coefficient, v is a predictor variable, and e is the residual error. 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 were likely to affect only the availability of seals for counting (e.g., weather and 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, so 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 less than 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 × 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 large-scale interannual changes in seal sightings that were unrelated to the other habitat variables in the model. Such changes in sighting distributions could be due to year-to-year changes 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 (McCullagh and Nelder, 1989; Agresti, 1990) to account for the fact that, all other variables being equal, larger segments have more seals than smaller segments. An offset variable is a predictor with a fixed coefficient of 1 that is used to adjust the response variable for a known quantity, such as effort or availability (Agresti, 1990). In our analyses, using the ln(area) as an offset adjusts the response variable for the size of the transect segment. This is equivalent to using density as the response variable, but it allows the use of the Poisson error structure. Quadratic terms (ice deformation, distance from the fast ice edge, water depth, longitude, time of day, temperature, and wind speed) were included for some variables because we believed that relationships were not linear (on the log scale), and interactions (year*longitude, year*longitude$^2$, year*distance from ice edge, year*distance from ice edge$^2$) were included when we believed the response to a variable changed from year to year.

Preliminary analyses indicated that 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 smaller than 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. After deleting these segments, overdispersion (i.e., residual variance larger than expected under the Poisson assumption) was still present; it was probably due to the presence of large groups of seals that would be unexpected with the small mean densities we observed. When fitted Poisson GLMs have overdispersion, estimated variances are too small, resulting in confidence intervals that are too narrow and hypothesis tests that are too liberal, i.e., they reject the null hypothesis too often (McCullagh and Nelder, 1989; Littell et al., 1996). To account for this remaining overdispersion, we adjusted tests and standard errors using the Pearson chi-square statistic as an overdispersion parameter, i.e., we multiplied the variance-covariance matrix of the GLM by ($\chi^2$/df), where $\chi^2$ is the Pearson $\chi^2$ goodness-of-fit statistic and df is the residual degrees of freedom (McCullagh and Nelder, 1989; Agresti, 1990). This correctly resulted in standard errors and *p*-values somewhat larger 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 residuals for segments far apart), we included a spatial component in the variance structure. We used a spatial exponential function, based on the distance between segments within a survey line, to model the dependency in the residuals (Littell et al., 1996); a nugget effect also was included in these functions. 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 on the basis of *p*-values from the Wald F statistics: those terms with the largest *p*-values were dropped first. This process continued until all variables had *p*-values lower than ~0.05. Continuous variables with *p*-values higher than 0.05 were retained in the model if they were contained in a continuous variable by categorical variable interaction (e.g., longitude*year) that had a small *p*-value.

## RESULTS

### *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% to 77% of the total survey area, depending on year. Observed densities on fast ice over the four-year period ranged from 0.57 to 1.14 seals/km$^2$. Modeled densities from the GLM were similar (0.78 for 1996; 0.83 for 1997; 0.89 for 1998; 0.95 for 1999). On pack ice, observed densities ranged from 0.92 to 1.33 seals/km$^2$ (modeled densities: 1.42 for 1996; 1.23 for 1997; 1.07 for 1998; 0.93 for 1999). In two years, observed densities on pack ice were much greater than those on fast ice; in the other two years, the densities on pack ice and

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 (149˚50′ W to 143˚40′ W), based on aerial surveys conducted in 1996–99 (n = number of transect lines).

| | | | 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** | 29–31 May | 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 | | | 1869 |
| **1997** | 27 May–1 June | 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** | 27–28 May | 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 | 0.00 | 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** | 29 May–4 June | Seals/ km$^2$ | 0.92 | 0.23 | 1.14 | 0.69 | 0.51 | 1.20 | 0.80 | 0.38 | 1.17 |
| (n = 88) | | LCL | 0.80 | 0.09 | 0.96 | 0.60 | 0.40 | 1.05 | 0.72 | 0.29 | 1.05 |
| | | UCL | 1.03 | 0.36 | 1.32 | 0.79 | 0.61 | 1.35 | 0.87 | 0.46 | 1.30 |
| | | # counted | | | 1407 | | | 1698 | | | 3105 |
| | | km$^2$ surveyed | | | 1232 | | | 1415 | | | 2647 |

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 Densities*

Univariate analyses using chi-square goodness-of-fit tests were performed for each year and for all years combined to examine individually the relationships between observed ringed seal counts and water depth, distance from the fast ice edge, ice deformation, longitude, time of day, cloud cover, temperature, and wind speed (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 less than 5 m deep (0.35–0.73 seals/km$^2$) and more than 35 m deep (0–0.77 seals/km$^2$) and highest in water between 5 and 35 m deep (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 15–25 m deep. The GLM also indicated that seal densities were lowest in water less than 5 m or more than 35 m deep and highest in water 25 m deep (Fig. 2b). Model results were significant for depth and depth$^2$ at $p < 0.001$.

**Fast Ice Edge**: 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, on either fast ice or pack ice (Fig. 3a). The GLM also indicated a significant, nonlinear effect of distance from the fast ice edge on seal densities (distance$^2$, $p < 0.001$). Relative densities were highest near the fast ice edge and decreased both shoreward and seaward of the edge (Fig. 3b).

**Ice Deformation**: 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).

**Longitude**: 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 ($p < 0.005$ except for 1996 $p = 0.2$; Fig. 5a). For all years combined, the highest density occurred at 144˚ W, 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).

**Time of Day**: Seal density was significantly related to time of day for each survey year and for all years combined in the univariate analyses ($p$ = 0.021 to < 0.001). In three years, densities increased somewhat until 1200 or 1300 h AKDT and then gradually decreased through the afternoon. However, in 1999 the observed densities increased

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, 1996–99.

| Variable | Year | Chi-square | df | *p*-value |
|---|---|---|---|---|
| Water Depth | 1996 | 812.43 | 4 | < 0.001 |
| | 1997 | 1529.71 | 5 | < 0.001 |
| | 1998 | 452.61 | 5 | < 0.001 |
| | 1999 | 1448.76 | 4 | < 0.001 |
| | All Years | 5313.64 | 5 | < 0.001 |
| Distance from Fast Ice Edge | 1996 | 4885.07 | 19 | < 0.001 |
| | 1997 | 6966.09 | 19 | < 0.001 |
| | 1998 | 3485.80 | 19 | < 0.001 |
| | 1999 | 8447.29 | 19 | < 0.001 |
| | All Years | 26232.32 | 19 | < 0.001 |
| Ice Deformation | 1996 | 985.25 | 9 | < 0.001 |
| | 1997 | 779.79 | 6 | < 0.001 |
| | 1998 | 547.75 | 8 | 0.01 |
| | 1999 | 897.82 | 5 | < 0.001 |
| | All Years | 3941.78 | 9 | < 0.001 |
| Longitude | 1996 | 5.92 | 6 | 0.200 |
| | 1997 | 19.71 | 6 | 0.005 |
| | 1998 | 34.98 | 6 | < 0.001 |
| | 1999 | 48.94 | 6 | < 0.001 |
| | All Years | 638.89 | 6 | < 0.001 |
| Time of Day | 1996 | 160.36 | 5 | < 0.001 |
| | 1997 | 73.73 | 6 | < 0.001 |
| | 1998 | 11.82 | 5 | 0.021 |
| | 1999 | 108.04 | 7 | < 0.001 |
| | All Years | 620.80 | 7 | < 0.001 |
| Cloud Cover | 1996 | 0.03 | 4 | 0.224 |
| | 1997 | 72.78 | 6 | < 0.001 |
| | 1998 | 82.87 | 5 | < 0.001 |
| | 1999 | 77.29 | 6 | < 0.001 |
| | All Years | 776.12 | 9 | < 0.001 |
| Temperature | 1996 | 0.53 | 3 | 0.533 |
| | 1997 | 4.64 | 5 | 0.200 |
| | 1998 | 1.59 | 4 | 0.254 |
| | 1999 | 2.04 | 2 | 0.169 |
| | All Years | 531.97 | 9 | < 0.001 |
| Wind Speed | 1996 | 0.03 | 5 | 0.943 |
| | 1997 | 65.15 | 5 | < 0.001 |
| | 1998 | 22.12 | 5 | < 0.001 |
| | 1999 | 2.04 | 5 | 0.156 |
| | All Years | 627.08 | 7 | < 0.001 |

TABLE 3. Generalized linear model coefficients from final ringed seal regression models for aerial surveys conducted in the central Beaufort Sea, 1996–99.

| Variable | Est. | SE | t | *p* |
|---|---|---|---|---|
| intercept (pack ice) | -0.0760 | 0.2180 | | |
| intercept (fast ice) | -0.3119 | 0.1903 | | |
| year (pack ice) | -0.1413 | 0.0536 | -2.64 | 0.009 |
| year (fast ice) | 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 |

throughout the day and were highest after 1700 h (Fig. 6). The GLM indicated no significant relationship between modeled densities and time of day ($p = 0.226$).

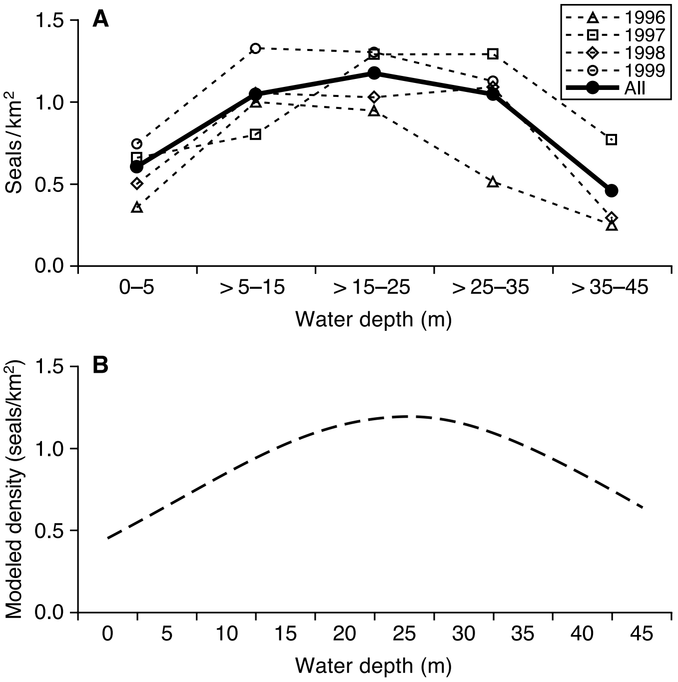

FIG. 2. Densities of ringed seals relative to water depth, based on aerial surveys in the central Beaufort Sea, 1996–99: a) Observed densities b) Generalized linear model estimate.

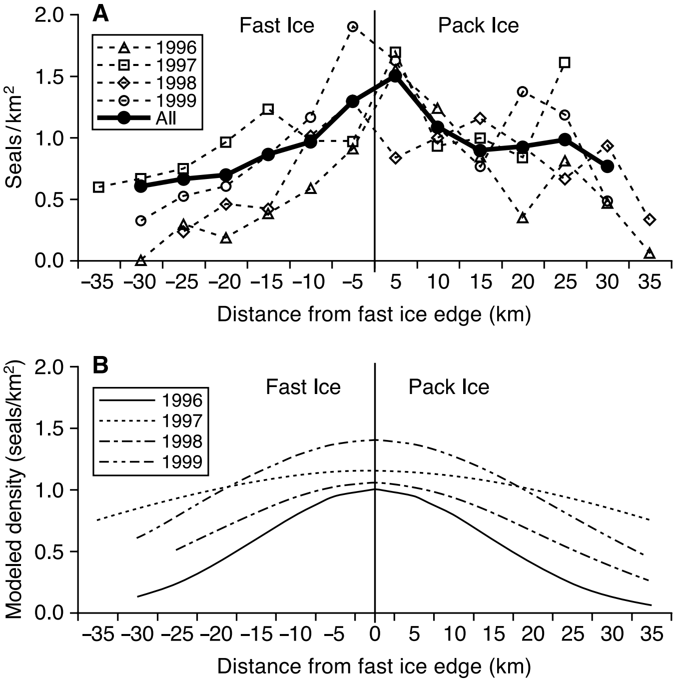

FIG. 3. Densities of ringed seals relative to distance from the fast ice edge, based on aerial surveys in the central Beaufort Sea, 1996–99: a) Observed densities, b) Generalized linear model estimates.

**Weather**: 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 1996–98. Overall, despite a significant chi-

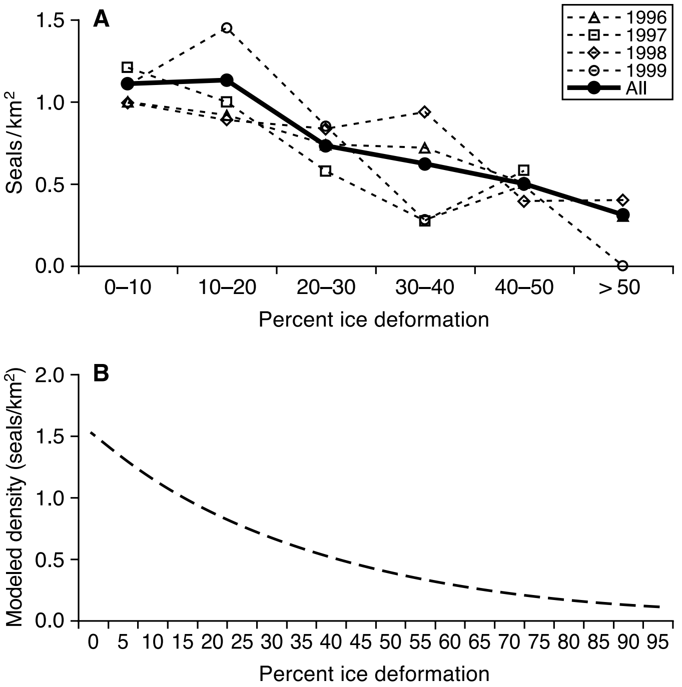

FIG. 4. Densities of ringed seals relative to percent ice deformation, based on aerial surveys in the central Beaufort Sea, 1996–99: a) Observed densities, b) Generalized linear model estimate.

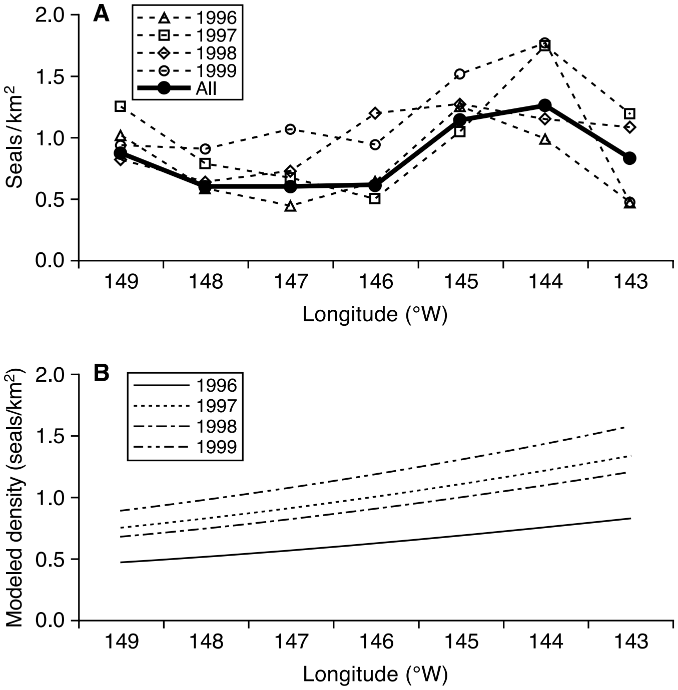

FIG. 5. Estimates of ringed seal density relative to longitude, based on aerial surveys in the central Beaufort Sea, 1996–99: a) Observed densities, b) Generalized linear model estimates.

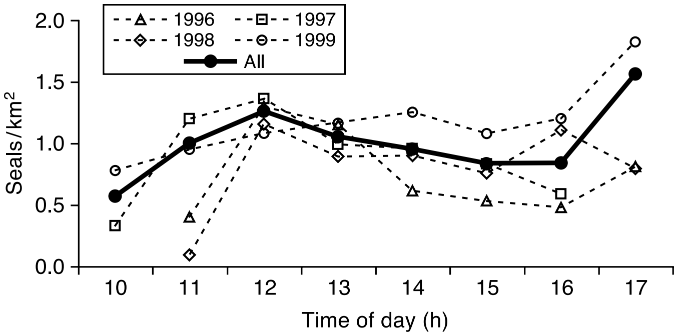

FIG. 6. Observed densities of ringed seals relative to time of day (Alaska Daylight Time), based on aerial surveys in the central Beaufort Sea, 1996–99.

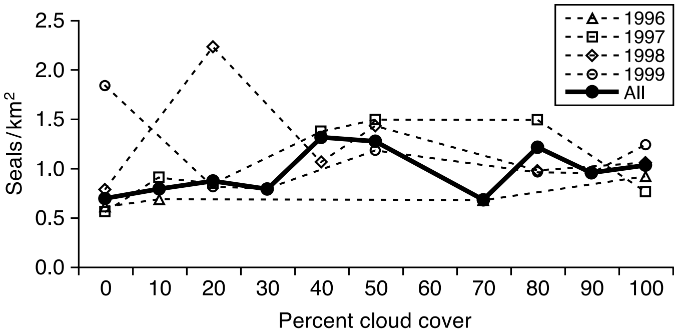

FIG. 7. Observed densities of ringed seals relative to percent cloud coverage, based on aerial surveys in the central Beaufort Sea, 1996–99.

square value, there seemed to be little pattern in the relationship between seal density and cloud cover (Fig. 7). Wind speed and temperature showed similarly variable effects (Figs. 8, 9a). The GLM indicated slightly higher densities at 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 a relationship between residuals only 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), so 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 adjustment for overdispersion. The principal cause of the overdispersion is that, even though the mean count per segment is low, there are some 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

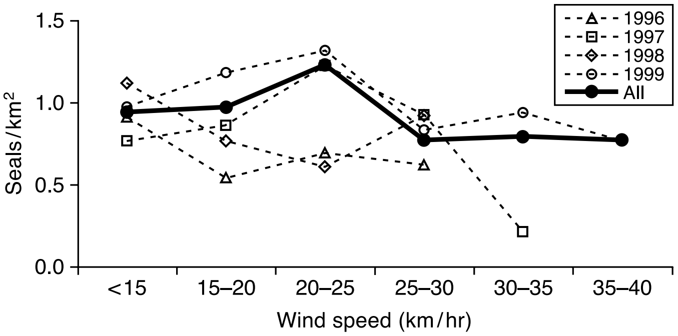

FIG. 8. Observed densities of ringed seals relative to wind speed, based on aerial surveys in the central Beaufort Sea, 1996–99. Wind speed was measured at survey altitude of 91 m.

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 147˚ to 149˚ W) during 1997–99 and reported the highest seal densities were generally found at depths of 5–15 m. They found seals to be more common in somewhat deeper water in 1999 compared to other years. For our larger study area, this was not the case. 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 at depths of 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 deep (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 the 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 offshore. 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 densities decreased with increasing distance from the fast ice edge in the subset of our study area that they surveyed.

Some variability may have been introduced into the analysis of density relative to distance from the fast ice edge by the difficulty of 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, 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.

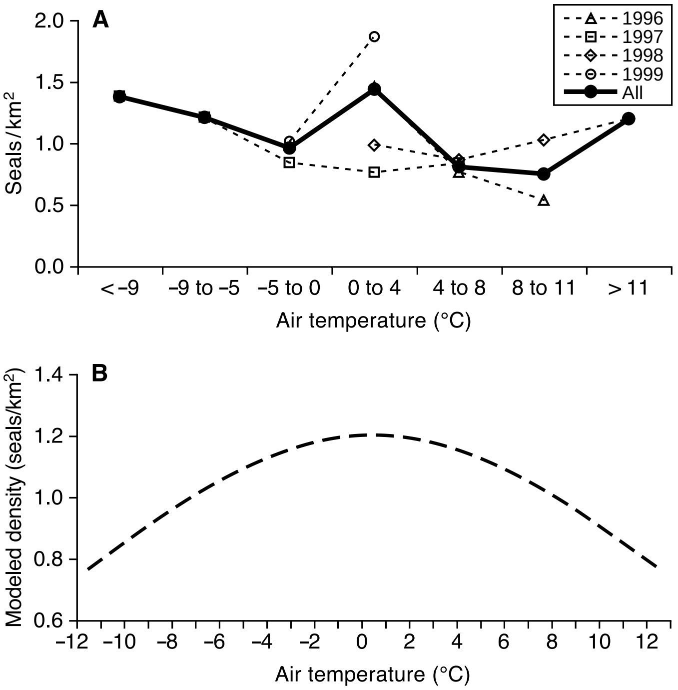

FIG. 9. Densities of ringed seals relative to air temperature, based on aerial surveys in the central Beaufort Sea, 1996–99: a) Observed densities b) Generalized linear model estimate. Air temperatures were measured at survey altitude of 91 m.

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, 1996–99.

| 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 | |

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 could indicate greater prey availability during fall and winter, when seals are actively feeding and when breathing holes are established. Alternatively, higher densities near the edge could be due to an influx of seals from other regions. During late winter and spring, ringed seals are thought to partition their habitat according to age, sex, and reproductive status, with adults predominating in and near the fast ice as single seals at holes (McLaren, 1958; Smith, 1973). After territoriality breaks down at the end of the breeding season, 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 in the pack ice 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).

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 the 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 h AKDT (solar noon is about 1330–1400 h), 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 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; Kelly and Quakenbush, 1990; Lydersen, 1991; Kelly et al., 2000). In northwest Greenland, however, Born et al. (2002) found no diel pattern in hauling out between June and August. The lack of a significant correlation between seal density and time of day in aerial surveys is probably because surveys are standardized to occur 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 quantify this relationship statistically. 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 than optimal for hauling out, but better for detecting seals. 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.

It is clear from the above discussion that investigations into how weather factors affect seal behavior are best conducted through ground-based field studies rather than through aerial surveys, since it is difficult to assess on-ice conditions at survey altitude. Aerial surveys should be standardized, on the basis of the best available information, to occur within temporal and weather windows most likely to result in comparable survey counts. Survey data are better suited to modeling fixed factors, such as the relationship of counts to habitat variables. It is important to remember that models used to interpret survey data model the behavior of seal counts, and not necessarily the behavior of the seals. For some variables, the results may be the same; for others, they may not.

### *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) found that in early spring, seals hauled out exclusively in lairs, where observers could not see them. As the season progressed, seals gradually began to haul out on the ice surface where they could be counted during surveys. In 1999–2000, seals typically did not use lairs once they began to bask outside of their lairs. 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. 2002). Field measurements indicated that most seals were basking when the snow temperature near the snow-ice interface had warmed to 0˚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 0˚C predicted basking and 31 May was the day on which 50% of tagged seals were basking in both 1999 and 2000, the transition period from resting in lairs to hauling out on the surface was more than three times as long in 2000 as in 1999. 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 that 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 if so, to what degree) has not been documented in the Alaskan Beaufort Sea. The chronology of breakup, both within the survey area and in areas far removed, may affect what seals are present during the survey period. Also, resident seals may not always bask 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 gluing transmitters to the pelage limits our ability to collect data during the survey period, since ringed seals molt their fur at this time.

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 breakup 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, meltwater covered less than 1% of the ice we surveyed in two years and 38% to 74% in the other two years. In 1998, 80% to 90% of the ice near shore was covered by meltwater when surveys were flown on 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 result 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.

### *Seal Abundance*

Densities reported for our surveys (0.57–1.14 seals/km$^2$) are generally within the ranges reported for other areas where ringed seals have been surveyed. In the eastern Beaufort Sea in the 1970s, ringed seal densities ranged from about 0.1 to 0.5 seals/km$^2$ (Stirling et al., 1977). In the Canadian High Arctic, densities were between 0.06 and 1.16 seals/km$^2$ in the early 1980s, depending on the area and year. Densities ranged from 1.3 to 1.7 seals/km$^2$ in northwestern Baffin Bay in the early 1980s (Finley et al., 1983) and from 0.38 to 1.93 seals/km$^2$ in Hudson Bay during the early 1990s (Lunn et al., 1997). In some areas, densities as high as 7–14 seals/km$^2$ have been reported (Smith and Hammill, 1981).

Both observed and modeled densities of ringed seals in our study area indicated considerable annual variability. Observed densities for all ice within 40 km of shore increased or decreased by 8% to 26% between years. Density estimates for fast ice in 1997 and 1998 were within 4% of each other, suggesting that surveys sampled a similar proportion of the population and that survey timing was similar in relation to breakup or changing social structure or both. In contrast, density estimates for fast ice in 1997 and 1999 were 20% to 60% higher than estimates for the previous years. Marked between-year variation in density estimates is common for ringed seal surveys. Such differences are variously attributed to actual changes in seal abundance or to differences in the proportion hauled out due to the timing of surveys relative to ice conditions and the annual molt (Stirling et al., 1982; Frost et al., 1988; Lunn et al., 1997). Because of problems such as this, Stirling et al. (1977) pointed out the value of having other evidence (reproductive rates, lair surveys, evidence of polar bear predation) to corroborate survey results and to help in the interpretation of population trends. Unfortunately, no such corroborative information is available for ringed seals in the central Beaufort Sea.

During three of the four years in which we conducted surveys in the central Beaufort Sea, similar surveys were also conducted by Moulton et al. (2002) to examine the effects of industrial activities, as well as natural covariates, on seal distribution and abundance. Since the study area of Moulton et al. was smaller than ours, we recalculated observed densities for only that area to facilitate comparison. Densities reported by Moulton et al. (2002) were substantially lower than those estimated from our surveys (0.43 vs. 0.73 seals/km$^2$ for 1997; 0.39 vs. 0.64 seals/km$^2$ for 1998; 0.63 vs. 0.87 seals/km$^2$ for 1999). It is unclear why observed densities for the same area should vary so much. There was considerable temporal overlap in the two survey efforts, although Moulton et al. pooled data over a broader date range (their surveys began earlier than ours in 1998 and later in 1999). Their multivariate analysis of date effects indicated that modeled seal densities would be lower earlier in the survey period, peak about 1–2 June, and then begin to decrease. The fact that two studies with such great overlap in timing and methods produced such different results (density estimates differed by 38% to 69% for the same year) suggests that comparisons of results from ringed seal aerial surveys conducted by different investigators must be done with great care.

## ACKNOWLEDGEMENTS

The Outer Continental Shelf Region of the Minerals Management Service, U.S. Department of the Interior, Anchorage, Alaska, funded this study under MMS Cooperative Agreement Number 14-35-0001-30810. The Alaska Department of Fish and Game, the National Marine Fisheries Service, the University of Alaska Fairbanks, and the North Slope Borough contributed additional support and in-kind services. We thank Tom Blaesing, Commander Northwest, for providing the aircraft used for the 1996–99 surveys and for his expert piloting. These surveys would not have been so safe or efficient without Tom's extensive experience on the North Slope and his commitment to providing the best survey aircraft possible. John Bengtson, Debbie Blaesing, Doug DeMaster, Casey Hessinger, Sue Hills, and Janice Waite served as observers and data recorders on the surveys. We thank Brendan Kelly for sharing unpublished results from his ongoing studies. Rob DeLong developed computer programs for manipulating aerial survey data. Jeff Laake provided advice on study design and data analysis.

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