Factors Influencing Local Abundance and Haul-Out Behaviour of Ringed Seals on Landfast Ice of the Alaskan Beaufort Sea

by

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Abstract

This study investigates how the local abundance of ringed seals on landfast ice of the central Alaskan Beaufort Sea is related to habitat factors, and how the haul-out behaviour of seals is influenced by temporal and weather factors. An understanding of these relationships is required before the potential impacts of industrial activity on ringed seals can be assessed. Intensive and replicated aerial surveys employing strip transect methodology were conducted during the springs of 1997-99. Data were examined with chi-square tests and Poisson regression. The overall observed densities of ringed seals over water depths >3 m was 0.43, 0.39, and 0.63 seals/km^2, in 1997 to 1999, respectively. Significantly more seals occurred over intermediate water depths, most notably 10-20 m. In all years, seals were widely distributed on the landfast ice, but during break-up, higher numbers of seals occurred near the ice edge. There was a significant trend toward lower observed densities in areas with high ice deformation and extensive melt water. There was no consistent relationship between seal sightings and time of day within the 10:00 – 18:00 period with surveys. The peak period of haulout occurred around June 1st and 2nd. Significantly more ringed seals were observed on warm, cloudy days. There was no indication that limited winter industrial activity, including ice roads and Vibroseis, occurring within the study area in 1997-99 significantly affected ringed seal density in spring.

Introduction

Several natural environmental factors are believed to affect the local abundance and haul-out behaviour of ringed seals, *Phoca hispida*, on landfast ice. However, the specific nature of these relationships is not well known. Recent and planned offshore oil developments in the central Alaskan Beaufort Sea also have potential to affect the local abundance and distribution of ringed seals in the area. A quantitative and biological understanding of the influences of natural factors on numbers of seals seen on the ice is needed as a basis for studying industry effects on observed ringed seal densities. The primary objective of this paper is to investigate how the local abundance of ringed seals is related to various habitat factors, and how the haul-out behaviour of seals is influenced by temporal and weather factors. This three-year study was conducted before the onset of intensive offshore oil development within the study area.

Ringed seals occur in both landfast and pack ice of the Beaufort Sea. Breathing holes are established in landfast ice as the ice forms in autumn and are maintained by the seals throughout the winter. As snow accumulates, ringed seals excavate lairs in snow above some breathing holes, and use these lairs for resting and giving birth (Smith and Stirling 1975). Ringed seals give birth from mid March through April, and nurse their pups in the lairs for five to eight weeks (Smith 1973b; Hammill et al. 1991; Lydersen and Hammill 1993). Mating occurs in late April and May. From mid-May through early June, ringed seals frequently begin to haul out in the open air on top of the ice. Most quantitative surveys of ringed seal abundance and distribution, including this study, are conducted during the late May – early June period when large numbers of moulting seals haul out on the landfast ice.

Habitat factors such as water depth, degree of ice deformation, snow conditions, and amount of melt water are known or suspected to influence the local abundance of ringed seals within areas of landfast ice. For instance, variations in ice deformation and snow conditions influence the locations of breathing holes and subnivean lairs (Smith and Stirling 1975, 1978). Interpretation of aerial survey results is complicated because the landfast ice that ringed seals inhabit is a dynamic environment that makes between-year, and even within-year, comparisons of abundance and distribution problematic.

Temporal and weather factors influence the proportion of ringed seals hauled out and hence available to be counted by aerial observers. As for other phocids that associate with ice, these factors are known or suspected to include date within the spring season, time of day, solar radiation, cloud cover, temperature, wind speed, and wind chill (Finley 1979; Smith and Hammill 1981; Thomas and DeMaster 1983; Kovacs 1987; Lydersen and Kovacs 1993; Moulton et al. 2000). The effects of these variables are not fully understood, and interpretation is complicated by strong correlations among some of these variables. However, the proportion of ringed seals hauled out and the observed seal densities are usually found to be negatively correlated with wind speed (Finley 1979; Smith and Hammill 1981). More ringed seals haul out around mid-day than at other times (Finley 1979; Smith and Hammill 1981; Kelly and Quakenbush 1990). The mid-day period is approximately 11:00-17:00 h in our Alaskan study area, where solar noon occurs around 14:00 local time.

Although the primary focus of this study was to investigate "natural" influences on observed densities of ringed seals in years before offshore oil production began, limited on-ice industrial activity occurred during this 1997-99 study. The relatively stable landfast ice that occurs in the central Alaskan Beaufort Sea in winter and spring provides a platform on which some oil industry activities can occur. During the ice-covered seasons in 1997-99, industrial activities within small parts of our study area consisted of on-ice seismic exploration via the Vibroseis technique, exploration drilling from an artificial island, and construction of ice roads. Some or all of these activities might have had local effects on ringed seal abundance and haul-out behaviour, so industry activities were treated as a potential confounding factor. They were expected to have less impact than the offshore oil development planned for years after 1999, whose effects will be analysed later taking account of additional years of seal survey data.

Methods

Survey Design

Each spring from 1997 to 1999, two "survey replicates" of aerial survey transects were flown between longitudes 147°06'W and 149°04.5'W, an east-west extent of about 75 km. Each survey replicate consisted of 80 north-south transects spaced 0.9 km apart. Each transect extended from the Beaufort Sea shoreline to roughly 37 km offshore or to the edge of the landfast ice if it was encountered and recognisable <37 km offshore (Fig. 1). We effectively flew two replicates (160 transects) each year, although the 1997 survey design was unbalanced (see Table 1).

Each day's flight was designed to sample 20 of the 80 distinct transects spaced evenly across the study area, rather than sampling the eastern portions one day and the western portions the next. Thus, the entire study area was to be sampled four times during each survey replicate, and eight times during each year.

Survey Procedures

We used strip transect methodology, which has been standard for previous aerial surveys of ringed seals in Alaska (Frost and Lowry 1988; Frost et al. 1997; Frost and Lowry 1998, 1999). Two primary observers occupied seats on opposite sides of the aircraft in each survey year; in 1999, a third observer operated a computerised data logger. Surveys were usually conducted at an altitude of 91 m above sea level (ASL) and a ground speed of 222 km/h. We surveyed transect strips 411 m in width on each side of the aircraft. These strips extended from 135 m to 546 m from the centreline. Table 1 summarizes the survey procedures for each year.

Data Recording Procedures

Aircraft position and time, as determined by GPS, was logged automatically every 1 s or 2 s (depending on year) via GeoLink software.

Environmental parameters were recorded at the start of each transect. These variables included cloud cover (in tenths), height of cloud ceiling (ft), visibility (n.mi.), wind speed (knots), wind direction (° T), and air temperature (°C). Wind data were acquired from the aircraft's GPS and air temperature was acquired from a thermometer mounted externally on the aircraft.

At the end of each 1-min (~3.7 km) time period along a transect, the two primary observers each dictated onto audio tape the time, visibility (n.mi.), ice cover (intervals of 10%), ice deformation (intervals of 10%), melt water (intervals of 10%), sun glare (none, moderate, or severe), and overall sightability conditions (subjectively classified as "excellent", "good", "moderately impaired", "severely impaired", or "impossible"). A timer, initialised at the start of each transect, provided an audible signal at 1-min intervals.

For each seal sighting by a primary observer, the observer dictated onto audio tape the species, number, and habitat (hole or crack) of the seal(s), and noted whether the sighting was on or off the transect strip. The observers also recorded the time of any sightings of industrial sites or previous activity, including ice roads, Vibroseis areas, or artificial islands. During our survey period in 1998 and 1999, other researchers were conducting a study of ringed seal haul-out behaviour near Reindeer Island (Kelly et al. 2000). Although aerial observers noted when they saw researchers on the ice, we do not have sufficient data on research activities to include "presence of researchers on the ice" as a factor in the analyses.

Analysis Procedures

Each seal sighting was linked to the environmental variables recorded for the corresponding 1-min time period. The location of each seal sighting was determined by matching the time of the sighting with the position recorded for that time in the GeoLink GPS logs. Time periods with severely impaired sightability conditions were excluded from all analyses. The fast-ice edge was subjectively located by mapping open leads; areas with leads were classified as pack ice and were excluded from analyses.

Hourly (or more frequent) air temperature and wind speed data for the Deadhorse airport at Prudhoe Bay (Fig. 1) were obtained from the National Climatic Data Center (Asheville, NC) for the entire study period. The airport data, with the exception of cloud cover, were used in analyses because they provided hourly coverage. Cloud cover data collected from the survey aircraft were used in analyses because cloud cover offshore often differed from that at the airport. From the airport data, an index of wind chill called heat loss (Watts/m^2) was calculated (Siple and Passel 1945). Weather conditions experienced by seals on the ice undoubtedly varied from weather data collected at the Deadhorse airport. However, we believe that the airport data provide an adequate approximation to "on-ice" weather during days when the weather was satisfactory for aerial surveys.

The percent ice deformation data collected at 1-min intervals during all surveys were contoured at 10% intervals using Vertical Mapper for MapInfo (Version 5.0.1). Water depth contours were developed based on all available depth soundings (NOAA Hydrographic Survey Data, Vol. 1, vers. 3.1; and Marine Geophysical Data/Bathymetry, Magnetics, Gravity, vers. 3.2). Five-kilometre "bins" of distance as measured from the ice edge shoreward were also plotted and used as a GIS layer. Seal sightings were overlaid on these GIS layers, and the numbers of on-transect seal sightings/km^2 and individuals/km^2 were determined for each category of ice deformation, water depth, and distance from the ice edge using MapInfo supplemented by specially written MapBASIC computer code.

Date, time-of-day, and weather effects were analysed using the 1-min periods as the common unit of observation. For example, to compare ringed seal densities with respect to time-of-day, all 1-min periods surveyed at a particular hour were combined in one bin. The number of on-transect seals was divided by the on-transect area surveyed to calculate the density for that hour.

To allow for possible industry effects, data were organised in ten 1-km bins measured from the edge of the nearest industrial area; observations >10 km from any industrial site were coded as "11". The "Distance from Industry" variable took account of "Northstar Ice Roads" in 1999; "Tern Island" (geotechnical surveys), "Eastern Vibroseis Area", and "Prudhoe Bay Vibroseis Area" in 1998; and "Tern Island" (drilling, etc.) in 1997. Figure 1 shows these locations.

Statistical Tests

Data were analysed with univariate tests and with a multivariate Poisson regression analysis. Presentation of univariate results provides a basis for observing trends in the actual direct observations and for interpreting multivariate analyses. However, they do not account for the confounding influences of other factors on observed seal density, which the multivariate analysis can do. Data collected over pack ice, during conditions of poor sightability, and in water depths <3 m were excluded from most analyses. The only exception was the inclusion of the 0-3 m water depth stratum in the univariate test of sighting density vs. water depth. The <3 m criterion for exclusion of data was used in all other tests because very few seals occurred in such shallow areas, where much or all of the water column is frozen during spring (see "Results"). Results were considered statistically significant based on the α=0.05 criterion, and marginally significant for $0.10 > \alpha > 0.05$.

Univariate Analyses

We used the chi-square (χ^2) goodness-of-fit test to assess the significance of observed differences in ringed seal densities with respect to habitat, weather, and temporal variables in each survey year. Simultaneous Bonferonni-corrected 95% confidence intervals (CIs) were calculated for the observed proportions by strata (see "Results" for stratum boundaries). An expected proportion (based on available survey area) falling outside the CI for an observed proportion was considered significantly different (Manly et al. 1993). Strata with relatively small surveyed areas (<30 km^2) are excluded from analyses, and strata with areas 30-50 km^2 are bracketed in all univariate plots (see Figs. 2, 4 and 5). All tests were based on numbers of seal sightings (singletons or groups), not numbers of individual seals, as seals within a closely spaced group are not statistically independent. Although statistical tests were always based on seal sightings (total number of singletons or groups seen), we discuss the results in terms of observed seal densities (individuals/km^2). This permitted comparison of our results to the findings of other studies.

For habitat factors that did not change during the course of a single season, such as water depth, we considered the within-year survey replicates to be non-independent. To avoid pseudoreplication problems, we examined each survey replicate (group of 80 unique transects) separately whenever possible.

In analyses of observed seal densities vs. weather and temporal variables, we pooled the data across replicates. For these variables, we assumed that the number of seal sightings in a given survey segment would vary between replicate surveys as a result of variation in temporal and weather factors.

Multivariate Analysis

A Poisson regression model (McCullagh and Nelder 1989; Cameron and Trivedi 1998) was used to assess the relationship between seal counts in small segments of the survey transects and several variables known or expected to influence seal abundance and haul-out behaviour. Prior exploratory analysis had revealed that the ringed seal count data within 1-min survey segments (approximately a 3 km^2 area) exhibited a Poisson distribution.

The unit of observation in the Poisson regression analysis was nominally the segment of transect surveyed in one minute. However, the "unit" was often reduced to allow for stratification based on covariates that changed within the 1-min segment (e.g., distance from industry). Also, the "unit" was enlarged on the infrequent occasions when all environmental conditions remained constant from one 1-min period to another. The latter approach was used to reduce concern about possible lack of independence and autocorrelation. To account for the fact that larger survey areas would probably contain more ringed seals than smaller areas, the logarithm of the survey area was fitted as an offset variable in the model (Venables and Ripley 1999). The response variable was the number of observed ringed seal sightings (singletons or groups) per square kilometre of landfast ice, with log (segment area) as an offset variable.

To obtain a single value for percent ice deformation, percent melt water, and visibility within each 1-min survey segment, we averaged the values recorded by right and left observers. Other covariates available for each survey segment included water depth, distance from edge of the landfast ice, time of day, date, air temperature, wind speed, heat loss, cloud cover, and distance from closest industry activity. All covariates were required in order for a transect segment to be included in the Poisson regression analyses. All variables in the Poisson regression, except survey replicate number and year, were considered continuous. Variables that were organized in ordered bins (e.g., distance from ice edge or industry) were considered continuous and not discrete, resulting in a model that was easier to interpret. The survey replicate and year were considered discrete and treated as factors in the models. Quadratic terms were included for the covariates water depth, ice deformation, distance from edge of the landfast ice, heat loss, wind speed, air temperature, cloud cover, time of day, and date to investigate possible non-linear trends. Table 2 provides a summary of the variables considered in the Poisson regression.

All continuous variables, including the quadratic terms, plus the interaction of year with each of these variables, were considered for inclusion in the model. Survey replicate was nested within year and within all interactions between year and each of the continuous covariates. Main effects were not considered for elimination from the model if they were involved in a statistically-significant interaction.

Forward model selection (Rawlings et al. 1998) was employed to derive the final model. At each step of the forward model selection procedure, the covariate added to the model was the one that would, if included, be most effective in "explaining" the remaining variability in seal numbers (i.e., highest *F*-value). The process was repeated until twenty covariates were added to the base model (Table 2). In considering quadratic terms for inclusion in the model, the selection procedure determined how much the model would be improved by adding the quadratic plus associated linear term in combination. We employed the Bayesian information criterion (BIC) to assess how many of these twenty covariates should be included in the final "best-fit" model (Venables and Ripley 1999). Values of BIC were calculated and plotted at each of the twenty model steps. When values of BIC increased rather than decreased from one step to the next, indicating that the model fit was not improving, the model was limited to this number of covariates. This resulted in the inclusion of seven covariates in the model (Table 2). To verify that "industry" did not significantly affect seal density, the covariate "Distance from Industry" was added to the model even though it would be excluded based on the BIC criterion.

Significance of terms in the model was assessed by approximate F-tests, which account for over-dispersion of the raw seal-sighting data using a quasi-likelihood approach (McCullagh and Nelder 1989; Venables and Ripley 1999). Calculations were done with S-Plus Version 2000 (Venables and Ripley 1999).

Due to the potential for temporal (and spatial) correlation among seal counts collected within successive transect segments, the deviance residuals of all final models were checked for correlation that might inflate reported significance levels. Correlation among residuals from adjacent transect segments would be a form of pseudoreplication and might cause model terms to appear more significant than justified by the data. To check for this autocorrelation, Moran's I statistic (Moran 1950) and associated standard error were computed using pairs of residuals from the final model that were separated by less than 5 min of survey time (about 18.5 km). Five-min intervals were chosen for testing because intervals less than 5 min did not contain a sufficient number of pairs for testing using Moran's I. Moran's I was computed separately for each transect and averaged for all transects. When this average Moran's I was not significantly different from zero or was negative, temporal correlation was deemed to have an insignificant influence on model estimation.

Final model fit was examined by computing the minimum, lower quartile, median, upper quartile, and maximum deviance residuals for the model. The absolute values of the lower and upper quartile were compared to 2.0 and, if greater, model fit was further examined for systematic factors producing the large number of high residuals. Deviance residuals greater than 2.0 were considered large because deviance residuals typically are approximately normally distributed (McCullagh and Nelder 1989; Cameron and Trivedi 1998), so 95% should be less than 2.0 if the model fits adequately.

In addition, deviance residuals were plotted against key environmental variables and examined for trends. These tests revealed that there were no residual quartiles greater than 2.0 in absolute value. No trends were observed when deviance residuals were plotted against key variables.

Results

Overall Observed Densities, Distribution, and Group Size

The overall observed ringed seal density was 0.39, 0.35, and 0.56 seals/km^2, in 1997 to 1999, respectively. The 3-year average density was only 0.06 seals/km^2 in areas where the summer water depth is <3 m. If those areas are excluded, observed densities were 0.43, 0.39, and 0.63 seals/km^2 in 1997-99, respectively.

Ringed seals were observed in all parts of the study area >3 m deep, including the deeper parts of the nearshore lagoons inshore of barrier islands. However, ringed seals were more common in deeper parts of the nearshore lagoons in 1997 and 1998 than in 1999. In 1999 there was a tendency for lower densities inside the lagoons than at corresponding depths outside the lagoons.

In 1998 and 1999, higher densities of ringed seals were observed in the western portion of the study area, but this was not evident in 1997. In 1999, the area of highest observed density occurred near a concentration of cracks in the west that appeared to extend from the pack ice into the landfast ice

The majority of ringed seals were observed near holes in all three survey years. However, in 1999, relatively more ringed seals occurred at cracks (overall 22.8%) than in either 1997 (6.5%) or 1998 (10.5%). Observed average group sizes were lower in 1997 and 1998 than in 1999 (1.4, 1.4 and 2.0, respectively). Overall, average group sizes at cracks (3.1 seals) generally were higher than group sizes at holes (1.4 seals), and more variable from day to day. In 1999, group size tended to increase as the season progressed; this increase was significant for seals at holes (Page's L Test; $L_{date} = 262$, n = 1, 9, $0.05 > P > 0.01$; Page 1963) but not for those at cracks ($L_{date} = 249$, n = 1, 9, $P > 0.10$). In 1998, average group size observed at cracks increased marginally with date ($L_{date} = 130$, n = 1, 7, $0.10 > P > 0.05$).

Habitat Factors Affecting Local Abundance

Water Depth

Univariate analyses indicated that sighting densities were significantly related to water depth during all three survey years (Table 3A and Fig. 2A). Maximum densities tended to occur in slightly shallower water in 1997 and possibly 1998 than in 1999 (5-10 m vs. 10-15 m; Fig. 2A). During all three survey years, lowest seal densities were observed in the 0-3 m stratum.

The Poisson regression model confirmed that, even after allowance for effects of other environmental variables, number of seal sightings per square kilometre was significantly related to water depth. Number of sightings tended to peak around water depths of 10 to 20 m, with fewer sightings in both shallower and deeper water (Fig. 3A). There was no significant year-to-year difference in this relationship after allowance for other factors.

Distance from Landfast Ice Edge

Univariate analyses indicated that the relationship of sighting densities to distance inshore from the landfast ice edge varied among years (Fig. 2B). During most surveys, sighting densities differed significantly with distance from ice edge, although not during replicate 1 in 1998 or 1999 (Table 3A). During 1999, sighting rates were highest near the ice edge, especially during replicate 2 (Fig. 2B).

The Poisson regression model indicated that the average sighting rate over the three spring seasons decreased as distance inshore from the ice edge increased (Fig. 3B; Table 4). There was weak evidence of interannual variation in the relationship between seal density and distance from the ice edge – the interaction among year, replicate number, and distance from the ice edge was almost strong enough to be included in the Poisson regression model. This interaction term was excluded from the model based on the BIC.

Ice Deformation

There was little variation in observed patterns of ice deformation from year to year, although in 1999 there was slightly less ice deformation (Table 5). Rougher (more deformed) ice was very evident offshore of the barrier islands each year. In this area, the ice is more subject to storm events and interactions with drifting pack ice during freeze up, and the resulting rough ice persists through the winter and spring.

Univariate analyses indicated that observed seal density on landfast ice varied significantly among categories of ice deformation during most surveys and in each year (Table 3A). In 1998 and 1999, observed seal densities were highest at intermediate levels of ice deformation (Fig. 2C). In 1997, significantly lower numbers of sightings occurred in areas of rough ice (>40% deformed) and significantly more sightings occurred in areas of smooth ice (0-10% deformed; Fig. 2C). The multivariate model showed that, after allowance for other factors, sightings decreased as ice deformation increased—the trend was negative with no significant difference among survey years (Fig. 3C; Table 4).

Melt Water

In 1999, there was very little melt water during replicate 1 (Table 5). During replicate 2, by which time melt water had increased, there was a general trend toward lower densities in areas with high melt water ($P < 0.001$; Fig. 2D). In 1997, coverage by melt water rarely exceeded 10% during the entire survey (Table 5), so a χ^2 test was not conducted. In 1998, there was more melt water than in either 1997 or 1999. Univariate analysis of 1998 data suggested that sighting rates did not differ significantly among melt water categories during either replicate 1 or 2 (Fig. 2D; Table 3A). The Poisson regression model indicated that, after allowance for other variables, sighting density was negatively related to percent melt water, and that this effect did not differ strongly from year to year (Fig. 3D; Table 4).

Factors Affecting Proportion of Seals Hauled Out

Time of Day

Univariate analyses suggested that observed ringed seal densities varied significantly with time of day (Table 3B). Sighting rates tended to decline through the day in 1997 and 1998, and to peak near mid-day in 1999 (Fig. 4A). However, the Poisson regression model indicated that, after allowance for other factors, there was no significant relationship between seal sighting rate and time of day within the 09:00 to 18:00 period when surveys were conducted.

Survey Date

Univariate analysis of the 1997 data indicated that significantly lower seal densities were observed at the beginning (26 May) and end (3 June) of the survey, with highest observed densities occurring in the middle of the survey period. Similar results were observed in 1999, when there was a general tendency toward higher densities in the middle portion of the survey. However, the 1999 survey was conducted about nine days later in the season than was the 1997 survey, in part because spring warming was delayed in 1999. In 1998, observed seal densities generally increased during the survey period (Fig. 4B; Table 3B). This may be related to the earlier start date (23 May) in 1998 than in 1997 (26 May) or especially 1999 (4 June).

The Poisson model indicated that survey date significantly influenced numbers of seal sightings, and the trend was consistent from year to year (Fig. 3E; Table 4). Number of sightings tended to peak around 2 June (day of year 152) and were lowest at the beginning and end of the study period. This non-linear effect is somewhat consistent with the univariate results, especially for 1997, but may be confounded by pooling data from years when the timing of spring break-up was different.

Air Temperature

Univariate analysis indicated that relationships between sighting rates and temperature differed among years. In 1997, there was a relatively small range of air temperatures and mean temperatures were lower than in 1998-99 (Table 5). Sighting rate was not significantly related to air temperature (Table 3B). In 1998, observed seal densities tended to be higher with higher air temperatures ($P = 0.005$; Table 3B), even though there was no one temperature category for which the number of sightings was significantly ($\alpha=0.05$) low or high (Fig. 5A). In 1999, relatively low densities of seals were observed when the air temperature was high (>7°C), and the sighting rate was higher when the temperature was moderate. The Poisson regression model indicated that the sighting rate increased significantly as air temperature increased above 5°C (Table 4; Fig. 3F). There was no evidence of any year-to-year difference in this relationship.

Wind Speed

Univariate results indicated that observed seal densities were significantly related to wind speed in each year (Table 3B). In 1997 and 1998, higher seal densities were observed at intermediate wind speeds. In particular, during 1997, significantly more seals were sighted when wind speeds were 21-30 km/h as compared with other wind speed categories (Fig. 5B). In 1999, an opposite pattern was observed; significantly fewer seals were observed when wind speeds were 11-30 km/h (Fig. 5B; Table 3B). The Poisson regression found no significant relationship between seal sightings and wind speed after allowance for other variables.

Heat Loss

Although univariate results indicated that numbers of sightings were significantly related to heat loss in each survey year (Table 3B), there were no consistent trends across years (Fig. 5C). The Poisson regression found no significant relationship between seal sightings and heat loss after allowance for other variables.

Cloud Cover

The univariate analyses indicated that, in all three survey years, higher densities of ringed seals tended to occur with high amounts of cloud (Fig. 5D). The Poisson model also showed a significant positive relationship between numbers of seal sightings and cloud cover, with no evidence of any year-to-year difference (Table 4; Fig. 3G).

Industry

The Poisson regression model suggested that distance from the industrial activities that occurred on landfast ice in 1997-99 did not significantly affect seal density in any survey year (Table 4; Fig. 3H). Industrial activities included drilling and limited Vibroseis near Tern Island (Liberty) in 1997, Vibroseis in two areas during 1998, and construction of ice roads to Seal Island (Northstar) in 1999. Numbers of seal sightings were not strongly related to distance from the closest of these sites (*P* = 0.133) after allowance for other variables.

Discussion

Observed Seal Densities

Based on our surveys, the overall observed ringed seal density on landfast ice in the central Alaskan Beaufort Sea ranged from 0.35 to 0.56 seals/km^2 in 1997-99, or 0.39 to 0.63 seals/km^2 if areas with water <3 m deep are excluded. These recent density estimates, as well as those from other researchers (Frost and Lowry 1999), are low compared to seal densities recorded via similar survey methods in the same general area in the 1980s. Then, observed densities on the landfast ice were 1.01 to 2.94 seals/km^2 (Frost and Lowry 1999). None of these density estimates are corrected for seals above the ice and snow but missed (often called perception or detection bias) or below the surface and invisible (availability bias). Thus, actual seal densities during both decades were undoubtedly higher than observed densities.

The variable observed densities are not surprising given what is known about inter-annual variations of ringed seal body condition and reproduction in the Beaufort Sea in earlier years (Stirling et al. 1977; Smith and Stirling 1978; Smith 1987; Kingsley and Byers 1998; Harwood et al. 2000). However, recent survey results suggest that the population of ringed seals in the south-central part of the Alaskan Beaufort Sea is smaller than in the early 1980s.

Habitat Factors Affecting Local Abundance

Water Depth

Prior to this study little was known about the relationship between water depth and abundance of ringed seals inhabiting landfast ice in the central Alaskan Beaufort Sea during spring. Seals inhabiting the landfast ice in our study area were limited to maximal water depths of approximately 30 m, as that was the water depth where the ice edge was typically located. Both univariate and multivariate results indicated that significantly more seals occurred in intermediate water depths, most notably 10-20 m. Univariate results suggested that seals were proportionally more common in slightly shallower waters (5-15 m, including deeper parts of lagoons) in 1997 and 1998 than in 1999. However, the multivariate model indicates that the relationship between sighting density and water depth was not strongly different from year to year. It is possible that ringed seals in the survey area are more abundant at intermediate water depths, which are generally found seaward of the barrier islands, because these waters offer more favourable habitat in terms of ice conditions and prey abundance. Ice conditions, such as deformation and stability (i.e., distance from the ice edge), are related to water depth and likely influence where ringed seals maintain holes and lairs (Smith and Stirling 1975; Smith and Lydersen 1991; Furgal et al. 1996).

Distance from Landfast Ice Edge

There are changes in the distribution and abundance of ringed seals relative to the ice edge at the onset of break-up of landfast ice in both the central Alaskan Beaufort Sea (Frost et al. 1988) and the Canadian Arctic (Smith 1973a; Finley 1979). It has generally been accepted that, prior to break-up, ringed seals are widely distributed at holes in the landfast ice away from the unstable ice edge; during break-up, large numbers of seals occur near the ice edge, particularly along cracks (Frost et al. 1988). Our results confirm that seal densities near the ice edge are indeed related to the stage of ice break-up. Prior to break-up, seals were widely distributed on the landfast ice, possibly with a slight tendency for lower densities near the ice edge. As break-up began, higher numbers of seals occurred near the ice edge than farther inshore.

Our 1999 survey (at least replicate 2) was conducted later in spring than our 1997-98 surveys (Table 1). The outer portions of the landfast ice were breaking up during the 1999 survey. This was evident from the extensive cracks that extended from the ice edge into the landfast ice and the larger proportion of seals along cracks in 1999. The overall density for 1999 was higher than in 1997-98, particularly within 5 km of the landfast ice edge. The 1999 results (especially replicate 2) may be biased upward by the presence of seals that spent the winter elsewhere. In contrast, the univariate results for 1997 and 1998 showed that higher than average densities were observed farther from the ice edge: 10-20 km from ice edge in 1997 and 10-15 km and 20-25 km from ice edge in 1998. The multivariate analysis did not find a significant among-year difference, but the year effect did approach significance.

Based on a similar multivariate analytical approach, Frost and Lowry (1999) also found that ringed seal density decreased with increasing distance from the ice edge in the central and eastern Alaskan Beaufort Sea during 1996-98. Their study area included ours, but extended much farther east and west.

The higher observed densities of ringed seals near the ice edge during the (later) 1999 surveys vs. the (earlier) 1997-98 surveys may have been related to a change in the social structure and local distribution of adult ringed seals, and an influx of seals from pack ice. Areas of prime breeding habitat in the landfast ice are thought to be used mainly by older adults (Smith 1973a, 1987). Adult male ringed seals are territorial (Smith and Hammill 1981; Smith 1987), but likely abandon their territories shortly after the mating period (Smith 1987). Therefore, it is possible that high densities of seals near the landfast ice edge may represent a collapse in the territory-based social structure that prevailed earlier in the season, providing the opportunity for animals to haul out at newly available sites (Kingsley et al. 1985). In addition to adult ringed seals, sub-adults probably move into the fringes of the landfast ice as spring progresses, as this area affords a more stable platform upon which to haul out (Smith 1973a). Sub-adult seals are known to occur near the landfast ice edge (McLaren 1958; Smith 1973b; Teilmann et al. 1999). An additional factor contributing to high apparent densities near the ice edge during break-up may be the higher sightability of ringed seals along cracks than at holes in moderately deformed ice.

Ice Deformation

There was a significant overall trend toward higher observed densities in areas with low ice deformation and lower observed densities in areas with high ice deformation. Similar results were obtained by other researchers in Alaska (Burns and Kelly 1982; Frost et al. 1988). In several areas of the Canadian Arctic, ringed seals showed a preference for fast ice with <40% deformation (Hammill and Smith 1989). It is thought that ringed seals prefer smooth ice for basking because they are better able to detect approaching predators in open areas of smooth ice (Stirling and Archibald 1977; Smith 1980; Frost et al. 1988). The apparent decline in seal numbers with increasing ice roughness may also be related, in part, to the increased difficulty in seeing seals in rough ice conditions.

A certain degree of ice deformation facilitates snow accumulation and hence provides more suitable habitat for lairs. The minimal snow depth required for lairs is 20 cm (Smith and Stirling 1975). Sufficient amounts of snow occur most frequently on the leeward (and windward) sides of ice hummocks or along pressure ridges (Smith and Stirling 1975). In western Svalbard, prime breeding habitat is near glacial fronts where debris frozen into the annual ice provides for sites of deep snow accumulation (Smith and Lydersen 1991). Similarly, Furgal et al. (1996) found ringed seal structures in the eastern Canadian Arctic primarily in deep snow, associated with large, thick ice ridges or deformations. Given these findings, we expected that higher densities of seals would be found at intermediate levels of ice deformation—sufficiently rough for lairs to form, but not sufficiently rough to obstruct vision.

One reason this relationship was not evident in either the univariate or multivariate analyses may have been that observers assessed ice deformation at 1-min intervals and not specifically when seals were sighted. Although the ice deformation estimate represented average on-transect conditions over the 1-min (~3.7 km) survey segment, it no doubt did not always accurately reflect ice deformation at specific haul-out sites. For instance, ringed seals were sometimes observed in relatively small areas of flat ice surrounded by larger areas of rough ice. Also, subtle increases in ice deformation sufficient to accumulate enough snow for lairs are not always detectable from the survey aircraft. A further possibility is that some seals redistribute themselves, at least locally, after the time of peak lair use and before or during the time of peak haul-out (when our surveys were done).

Melt Water

The amount of melt water on the ice depends on weather conditions. Air temperatures must be warm enough to melt the upper layer of snow, and wind may also be a factor (T.G. Smith, pers. comm.). Average air temperatures during the survey period were much higher in 1998 and 1999 than in 1997. This contributed to very low amounts of melt water during the 1997 surveys when most water on the ice surface was from river run-off (not melt water), and was located near shore. There was much more melt water during 1998 and 1999. All analyses indicate that increased melt water on the ice was associated with reduced numbers of seals hauled out.

Seals probably avoid hauling out in melt water because it is important for moulting animals to have dry skin. Exposure to melt water would conduct heat away from the skin, thereby inhibiting the moult process (Feltz and Fay 1966; Fay 1982). This effect may also (at least in part) explain why there was an increase in group size of ringed seals later during the survey period in 1998 and 1999. As the amount of melt water increased during the survey period, some seals may have abandoned areas with more melt water and moved into adjacent areas with little or no melt water, joining other seals at these "drier" holes or cracks.

Factors Affecting the Proportion of Seals Hauled Out

Time of Day

It appears that limiting our survey period to 10:00 to 18:00 h (ADST) eliminated significant variation in ringed seal density in relation to time of day. Many studies of ringed seal haul-out behaviour have documented diel patterns, although few have accounted for simultaneous influences of other factors on haulout. The peak hours of haulout by ringed seals vary seasonally (Smith 1973a; Smith and Hammill 1981; Kelly and Quakenbush 1990). For instance, Kelly and Quakenbush (1990) found that ringed seals near Reindeer Island (within our study area) hauled out in the evening and early morning in March and April, but this peak period shifted to midday in May and early June. In the eastern Canadian Arctic, at the beginning of the haul-out period (early June), peak numbers of ringed seals were observed between 14:00 and 19:00 local time (UTC - 4 h). Later in the moult period, the largest numbers of seals were observed from 12:00 to 14:00, and seals spent more time hauled out (Smith 1973b). Smith (1973b) suggested that these changes in the diurnal pattern of haulout may be related to the marked change in the angle of solar radiation, increases in air temperature, and (perhaps most importantly) the more advanced moult stage of ringed seals and their reluctance to enter the water in this condition.

Date

It appears that the peak period of haulout for ringed seals on the landfast ice of the central Beaufort Sea occurs around June 1st and 2nd (days 152-153 in Fig. 3E). This finding is somewhat supported by the results of a preliminary multivariate analysis by Frost et al. (1999) of their 1996-98 survey data from a larger part of the Alaskan Beaufort Sea. They found that observed ringed seal density steadily increased in late May, with the maximal density occurring on their last survey date of May 31st. We expect that, if they had continued surveying into June, they would have found a similar peak in observed density in the first few days of June and diminishing densities thereafter. It appears that the peak period of haulout in the central Beaufort Sea is shorter than in the Canadian high arctic, where the duration of peak haulout exceeded two weeks in certain areas (Finley 1979).

In general, ringed seals haul out more frequently and for longer periods later in the moult season (Smith 1973b; Finley 1979; Smith and Hammill 1981; Kelly and Quakenbush 1990; Frost and Lowry 1999; Born et al. 2002) in order to facilitate the moult process. Also, not all ringed seals begin hauling out at the same time during the spring moulting period. It is believed that, like harp seals *Pagophilus groenlandicus* (Sergeant 1991) and harbour seals *Phoca vitulina* (Kelly 1981), younger ringed seals moult first, followed by adult seals (Kelly et al. 1986; Kelly and Quakenbush 1990). Also, there is likely a great deal of individual variation in timing of haulout within different age groups. Individual variation in phocid haul-out behaviour has been noted in many studies (Cameron 1970; Ashwell-Erickson et al. 1986; Yochem et al. 1987; Thompson et al. 1989; Moulton 1997; Born et al. 2002). The dates when different ringed seals start to bask can span several weeks (Kelly et al. 2000).

Based on this study, we suggest that ringed seal surveys in the south-central Alaskan Beaufort Sea be conducted around 28 May to 4 June when maximal numbers of seals are available to be counted by aerial surveyors and break-up is usually not advanced. Researchers should consider adhering to this survey period regardless of whether spring break-up is reported as early or late in a particular year. Using a consistent survey period from year to year eliminates a source of variation that must otherwise be accounted for by statistical models, and makes it easier to characterize and compensate for relationships between seal density and other covariates.

Air Temperature

It appears that numbers of ringed seals on the ice tended to be higher on warmer days (Fig. 3F). However, there was some contrary evidence from the univariate results for 1999, which suggested that lower densities of seals were observed when the air temperature exceeded 7°C.

Previous studies have reported that responses of ringed seals to air temperature vary (Burns and Harbo 1972; Finley 1979; Smith and Hammill 1981; Frost et al. 1988). The positive relationship between air temperature and sightings agrees with findings of Frost et al. (1988) and is also consistent with the fact that increased skin temperatures facilitate moult (Feltz and Fay 1966). However, Finley (1979) suggested that, on warm, bright and relatively calm days, ringed seals retreated to the water, perhaps to avoid hyperthermia. Burns and Harbo (1972) also noted a decrease in ringed seal density in the central Alaskan Beaufort Sea during a survey day when "exceptionally warm and clear" conditions prevailed. This response has been noted in other phocids that associate with ice (Weddell seals, *Leptonychotes weddelli* – Harrison and Kooyman 1968; harp seals – Øritsland and Ronald 1978; Moulton et al. 2000). Seals may avoid hauling out on extremely warm days to avoid hyperthermia but it appears that, after allowance for other factors in the model, air temperatures experienced during our surveys were rarely, if ever high enough, to elicit this potential response.

Wind Speed

Wind speed did not appear to be strongly related to seal density. Most studies of ringed seals (and other phocids as well) have concluded that haulout is reduced when wind speed is high (Smith 1973a; Finley 1979; Smith and Hammill 1981; Frost et al. 1988). Wind speeds at the Deadhorse airport (Fig. 1) during our surveys rarely exceeded 45 km/h; that is the value above which Frost et al. (1988) found lower ringed seal densities. However, Finley (1979) showed that the wind speed effect extended to considerably lower wind speeds and he also found that seals orient away from the wind, especially when it was strong. In any event, numbers of seals on the ice may be reduced at times when winds are stronger than those encountered during our surveys. Also, we re-emphasise that weather data from Deadhorse do not fully represent conditions on the ice.

Heat Loss

This study did not find a clear relationship between heat loss (index of wind chill) and observed ringed seal density. Smith and Hammill (1981) also found no significant relationship between wind chill and ringed seal haulout. However, a study investigating the effects of aircraft overflights on ringed seal behaviour found that the probability of seals escaping into their breathing holes increased during colder wind chill conditions (Born et al. 1999).

Cloud Cover

More ringed seal sightings occurred when cloud cover was high as indicated by both the Poisson regression model and univariate results for 1997-99. Others who have investigated the relationship between cloud cover and ringed seal haul-out behaviour have reported conflicting findings. Finley (1979) found that haul-out bouts of ringed seals tended to be longer on bright clear days but a re-analysis of data from Smith (1973a) by Finley (1979) indicated that there was no significant relationship with cloud cover. Frost and Lowry (1999) found that observed numbers of ringed seals peaked with 20 to 60% cloud cover. In any event, it is likely that some combination of weather conditions including cloud cover, solar radiation, air temperature, and wind speed interact to affect ringed seal haulout. It is also possible that aerial observers may detect more ringed seals under cloudy conditions as glare is reduced.

Other Factors

Prey Availability

Although ringed seals are known to reduce feeding during the spring moult, when time spent basking on the ice increases (McLaren 1958; Smith 1973a), their broad-scale distribution is mostly predetermined during the fall freeze-up (Smith et al. 1979; Kelly et al. 1986). In fall, prey availability may be a key factor in influencing where seals form their breathing holes. In fact, feeding is particularly important at this time as ringed seals begin to deposit fat to survive the winter, and pregnant females require energy to support growing fetuses (McLaren 1958; Lowry et al. 1980; Smith 1987; Ryg et al. 1990; Ryg and Øritsland 1991). In late summer and early fall, hyperiid amphipods are an important food source for ringed seals in the central Beaufort Sea (Lowry et al. 1980). During late fall and winter, Arctic cod (*Boreogadus saida*) predominate in the ringed seal diet (Lowry et al. 1980). During the November to February period, Arctic cod occur in near shore areas and spawn (Craig et al. 1982). Food availability during freeze-up is a factor that we cannot measure, and this factor presumably accounts for some of the residual variance not "explained" by the Poisson regression model.

Industry

The industrial activities that occurred within small parts of the study area during the ice-covered seasons of 1997-99 apparently did not sufficiently affect numbers of seal sightings to be detectable by our intensive aerial surveys. Inclusion of the covariate "Distance from Industry" did not significantly improve the fit of the Poisson regression model. When this covariate was "forced" into the model, there was no indication of a significant relationship after allowance for other factors. More detailed analysis of the local distribution of seals near industrial activities has been deferred until survey data from additional years are available. Surveys of the same type are continuing during construction and initial operation of the Northstar oil development (in 2000-2002; Fig. 1).

Statistical Approach

The use and interpretation of covariates in the analysis of ringed seal densities is complicated. When dealing with a large number of covariates, including some interrelated ones like temperature, wind speed, and heat loss, even a multivariate analysis cannot entirely separate the influences of the different variables. In particular, if seals respond to one or more of a group of intercorrelated variables, multivariate analysis of uncontrolled field data (however systematically they are collected) probably will not be able to isolate the specific variable(s) to which the animals respond.

Another complication in analysing ringed seal data is that the dynamic nature of their habitat makes the definition of some covariates unclear. For instance, the covariate distance from ice edge is often difficult to determine because of shifting ice and leads. When 100% pack ice is alongside the landfast ice, the boundary between the two is sometimes difficult to identify.

Also, it is often difficult to choose which covariates to include in the model. Previous studies on ringed seal distribution have often analysed observed densities in relation to distance from the shore. Inclusion of this variable in models presents a problem in our study area because barrier islands complicate its definition.

Despite these complications, our analyses provide insight into factors, or groups of related factors, most likely to have direct effects on observed seal density. Even if the specific influences of various natural factors cannot be entirely separated, this type of analysis can help determine whether nearby industrial activities affect observed seal density after allowance for the effects of all natural factors combined. The strong influences of some natural factors on sighting density, as shown here, demonstrate that it will be important to consider those natural factors as covariates in future evaluations of industry effects on seals.

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Tables

Table 1. Summary of survey coverage and field procedures during aerial surveys in the central Alaskan Beaufort Sea, spring 1997-99.

	Year		
	1997	1998	1999
Survey Coverage			
Dates Flown Rep 1	26-29, 31 May; 1-2 June	23, 25-27 May	4-8 June
Dates Flown Rep 2	27-29, 30 May[a]	27-30 May	8-10, 12-13 June
Dates Flown Rep 3	3-4 June[a]		
Total Area (km^2)	4510	4079	3980
Linear Dist. (km)	6089	6350	5486
Survey Procedure[b]			
Aircraft	Cessna 185	Shrike Commander	Twin Otter DHC-6
Bubble Windows	No	Yes	Yes
GPS	Trimble	Trimble	Garmin

[a] In 1997, only one complete survey replicate (Replicate 1: 80 unique transects) was surveyed. Forty of the 80 transects were surveyed two additional times; referenced here as "Replicate 2" and "Replicate 3. Thus, for 1997, Replicate 1 was complete but Replicates 2 and 3 were only 50% complete.

[b] In each survey year, the data logger program used was GeoLink; it automatically recorded time and aircraft position at 1-s (in 1997-98) or 2-s (in 1999) intervals throughout the flights. All surveys were flown at a ground speed of 222 km/h between the hours of 1000 and 1800 h ADST. The transect strip width was 411 m on each side of the aircraft; the strips extended from 135 m to 546 m from the centreline of the aircraft. All transects were surveyed at an altitude of 91 m ASL, with the exception of six transects near Reindeer Island (Fig. 1) that were surveyed at an altitude of 152 m ASL on 6-9 June 1999.

Table 2. List of variables analysed in the Poisson regression model of seal sightings in relation to environmental parameters. The response variable was the number of seal sightings.

Factors	All Covariates Tested [a]	Covariates Selected in the First 20 Steps of the Model [b, c]
Year	Water Depth (m)	***Ice Deformation***
	Dist. from Ice Edge (km)	***Cloud Cover***
Survey replicate nested within year	Ice Deformation (%)	***Date*** ^{2}
	Melt Water (%)	***Dist. from Ice Edge***
	Time of Day (hr-ADST)	***Water Depth*** ^{2}
	Time from Solar Noon (+/- hr)	***Melt Water***
	Date (day of year)	***Air Temperature*** ^{2}
	Air Temperature (°C)	Year x Replicate x Dist. from Ice Edge
	Wind Speed (m/s)	Year x Air Temperature
	Heat Loss (W/m^2)	Year x Water Depth ^{2}
	Cloud Cover (%)	Year x Time of Day ^{2}
	Dist. from Industry (1-km bins)	Year x Dist. from Industry
	Visibility (n.mi.)	Year x Cloud Cover
		Year x Replicate x Time of Day ^{2}
		Year x Date ^{2}
		Year x Melt Water
		Cloud Cover ^{2}
		Year x Replicate x Cloud Cover ^{2}
		Visibility
		Year x Replicate x Dist. from Industry

[a] For all these variables, with the exception of "Time from Solar Noon", "Distance from Industry", and "Visibility", a quadratic as well as a linear term was considered for inclusion in the model. Also, the interaction of the factors with each of these covariates was analysed.

[b] These variables are presented in the order in which they entered the model. For instance, "Ice Deformation" entered the model first as it was most effective in "explaining" the variability in seal numbers and "Year x Replicate x Distance from Industry" entered last as it was least effective. A "2" indicates that the variable contained a quadratic term.

[c] Covariates highlighted with bold, italic font were included in the final model based on the BIC. "Distance from Industry" was added to the final model to verify that industry did not significantly affect seal density.

Table 3. Summary of chi-square analyses of ringed seal density in relation to variables affecting *(A)* local abundance, and *(B)* the proportion of seals hauled out.

A. Habitat Factors Affecting Local Abundance				
Variable	Chi-square	*df*	*P*-value	Pooled *P*[a]
Water Depth				
1997 Rep 1	28.44	6	0.0001	
1997 Rep 2	22.53	6	0.001	
1997 Rep 3	35.66	6	0.0001	
1998 Rep 1	15.22	5	0.010	<0.0001
1998 Rep 2	15.43	5	0.010	
1999 Rep 1	67.66	6	<0.0001	
1999 Rep 2	114.14	6	<0.0001	
Distance from Ice Edge				
1997 Rep 1	15.06	5	0.01	
1997 Rep 2	12.27	5	0.031	
1997 Rep 3	26.51	5	0.0001	
1998 Rep 1	5.32	5	0.380	<0.0001
1998 Rep 2	13.27	5	0.020	
1999 Rep 1	5.74	5	0.330	
1999 Rep 2	93.64	5	<0.0001	
Ice Deformation				
1997 Rep 1	34.39	5	<0.0001	
1997 Rep 2	18.9	5	0.002	
1997 Rep 3	33.71	5	<0.0001	
1998 Rep 1	14.84	5	0.011	<0.0001
1998 Rep 2	11.83	5	0.037	
1999 Rep 1	8.74	5	0.120	
1999 Rep 2	52.6	5	<0.0001	
Melt Water[b]				
1998 Rep 1	5.61	4	0.23	
1998 Rep 2	8.18	4	0.085	
1999 Rep 1	4.36	1	0.038	0.0001
1999 Rep 2	113.31	5	<0.0001	

B. Factors Affecting Proportion of Seals Hauled Out				
Variable	Chi-square	*df*	*P*-value	Pooled *P*[a]
Time of Day				
1997	21.01	8	0.007	
1998	36	7	<0.0001	<0.0001
1999	17.11	7	0.017	
Date				
1997	52.77	8	<0.0001	
1998	25.49	6	0.0003	<0.0001
1999	160.95	8	<0.0001	
Air Temperature				
1997	3.57	2	0.168	
1998	12.69	3	0.005	<0.0001
1999	125.99	4	<0.0001	
Wind Speed				
1997	19.29	3	0.0002	
1998	16.66	4	0.002	<0.0001
1999	100.67	3	<0.0001	
Heat Loss				
1997	10.09	3	0.0178	
1998	33.66	3	<0.0001	<0.0001
1999	93.14	4	<0.0001	
Cloud Cover				
1997	19.98	7	0.006	
1998	30.42	9	0.0004	<0.0001
1999	128.33	7	<0.0001	

[a] A pooled *P*-value was calculated for each variable by adding the standard normal deviates (Zs) associated with the *P*-values obtained from the χ^2 tests and dividing this sum by the square root of the number of replicates and/or years being combined (Rosenthal 1978). In Table 3A, this procedure may slightly overstate statistical significance because of partial lack of independence between "replicates" within a given year.

[b] There was too little melt water during 1997 to allow meaningful χ^2 tests.

Table 4. Number of ringed seal sightings in 1997-99 in relation to environmental variables, as estimated by a Poisson regression model. The reference level for the year factor was 1997.

Model Term	Coefficient	Standard Error	*F*-value (approx.)	*P*-value	% Change in sighting nos. for one unit increase of covariate	95% CI for percent change		Covariate Unit
						Lower	Upper	
Intercept	-119.3398	15.5016						
Main Effects [a]								
Ice Deformation	-0.0144	0.0013	121.01	<0.0001	-1.42	-1.68	-1.16	10%
Cloud Cover	0.0029	0.0004	42.44	<0.0001	0.29	0.20	0.38	10%
Date	1.5587	0.2025	61.52	<0.0001				
Date^2	-0.0051	0.0007	62.80	<0.0001	[b]			
Distance from Ice Edge	-0.0261	0.0041	39.88	<0.0001	-2.57	-3.38	-1.76	
Water Depth	0.0752	0.0138	31.00	<0.0001				
Water Depth^2	-0.0022	0.0003	43.89	<0.0001	[b]			
Melt Water	-0.0092	0.0015	38.91	<0.0001	-0.92	-1.21	-0.62	10%
Air Temperature	-0.0003	0.0103	0.00	0.9788				
Air Temperature^2	0.0045	0.0010	18.50	<0.0001	[b]			
Distance from Industry	0.0122	0.0082	2.26	0.1330	1.23	-0.39	2.85	1 km

Note: *df* = 1447; Overdispersion = 1.04; residual correlation (Pearson's *r*) = -0.0227.

[a] The relationships of seal sightings to these covariates did not differ significantly among years; i.e., there was no significant interaction between year and each of these covariates.

[b] This value and the corresponding CI were not calculated because it is difficult to define a covariate unit for quadratic terms.

Table 5. Summary of habitat and weather variables for each survey replicate from 1997-99.

Covariate	1997				1998			1999		
	Rep 1	Rep 2	Rep 3	Overall	Rep 1	Rep 2	Overall	Rep 1	Rep 2	Overall
Ice Deformation (%)										
Mean	20.9	20.5	22.4	21.2	24.6	21.9	23.3	14.6	16.2	15.5
s.d.	25.58	25.74	26.08	25.75	25.05	20.41	22.88	14.29	15.72	15.14
Minimum	0	0	0	0	0	0	0	0	0	0
Maximum	87.5	85	85	87.5	92.5	80	92.5	65	80	80
Melt Water (%)										
Mean	3.2	5.2	1.1	3.2	17.9	49.6	33.8	2.9	38.8	23.4
s.d.	12.53	16.52	5.53	12.56	20	18.73	25.05	8.61	20.12	24.02
Minimum	0	0	0	0	0	0	0	0	0	0
Maximum	97.5	100	70	100	100	100	100	87.5	95	95
Air Temperature (°C)										
Mean	-0.5	1.1	2.5	0.6	3.4	8.4	5.9	0.1	8.1	4.7
s.d.	2.89	1.57	2.21	2.73	1.59	1.9	3.08	0.89	4.15	5.09
Minimum	-4.3	-1.0	-1.7	-4.3	1.0	5.0	1.0	-2.8	0.0	-2.8
Maximum	5.0	4.3	5.0	5.0	8.0	12.0	12.0	1.0	13.8	13.8
Wind Speed (km/h)										
Mean	24.0	21.6	38.8	27.0	33.2	25.6	29.3	24.9	23.6	24.2
s.d.	8.35	4.32	1.40	9.29	8.35	12.67	11.38	8.28	6.52	7.34
Minimum	11.7	10.8	35.0	10.8	16.7	7.4	7.4	9.7	13.9	9.7
Maximum	38.8	29.1	44.0	44.0	44.5	46.3	46.3	34.6	35.0	35.0
Heat Loss (W/m^2)										
Mean	1141	1072	1154	1127	1079	836	957	1125	853	970
s.d.	175.8	98.78	85.97	144.3	90.66	146.3	172	107.1	190.4	208.9
Minimum	880	848	1058	848	813	608	608	899	590	590
Maximum	1398	1163	1337	1398	1199	1038	1199	1314	1224	1314
Cloud Cover (%)										
Mean	41.5	83.1	40.7	51.9	53.3	39.1	46.2	73.1	38.0	53.1
s.d.	43.65	24.13	43.08	43.46	44.04	42.87	44.03	39.44	37.78	42.24
Minimum	0	40	0	0	0	0	0	0	0	0
Maximum	100	100	100	100	100	100	100	100	100	100

Figure Captions

Fig. 1. Central Alaskan Beaufort Sea showing aerial survey transects flown in 1997-99. A similar grid of 40 transects was offset 0.9 km to the east. Industrial sites active in one or more of the three study years are also shown.

Fig. 2. Observed densities of ringed seals during 1997, 1998, and 1999 at differing *(A)* water depths, *(B)* distances from the ice edge, *(C)* percent ice deformation, and *(D)* percent melt water. For all four habitat factors, differences among strata were significant for most individual replicates and years, and highly significant when replicates and years were combined (Table 3A). Solid symbols represent strata where the number of sightings was significantly lower or higher than expected based on the overall average sighting rate (α=0.05; chi-square test with Bonferroni adjustment). Bracketed symbols indicate strata where only a relatively small area of fast ice (30-50 km^2) was surveyed. Note the difference in y-axis scales for (A) vs. (B, C, D).

Fig. 3. Number of ringed seal sightings in relation to environmental variables in 1997-99 as estimated by a Poisson regression model.

Fig. 4. Observed densities of ringed seals during 1997, 1998, and 1999 at differing *(A)* times of day, and *(B)* dates. For both factors, differences among strata were significant for each individual year, and highly significant when years were combined (Table 3B). Note the difference in y-axis scales for (A) vs. (B). Otherwise as in Fig. 2.

Fig. 5. Observed density of ringed seals during 1997, 1998, and 1999 at differing values of *(A)* air temperature, *(B)* wind speed, *(C)* heat loss, and *(D)* cloud cover. For all factors, differences among strata were significant for each individual year, except air temperature in 1997, and highly significant when years were combined (Table 3B). Note the difference in y-axis scales for (A and C) vs. (B) and (D). Otherwise as in Fig. 2.

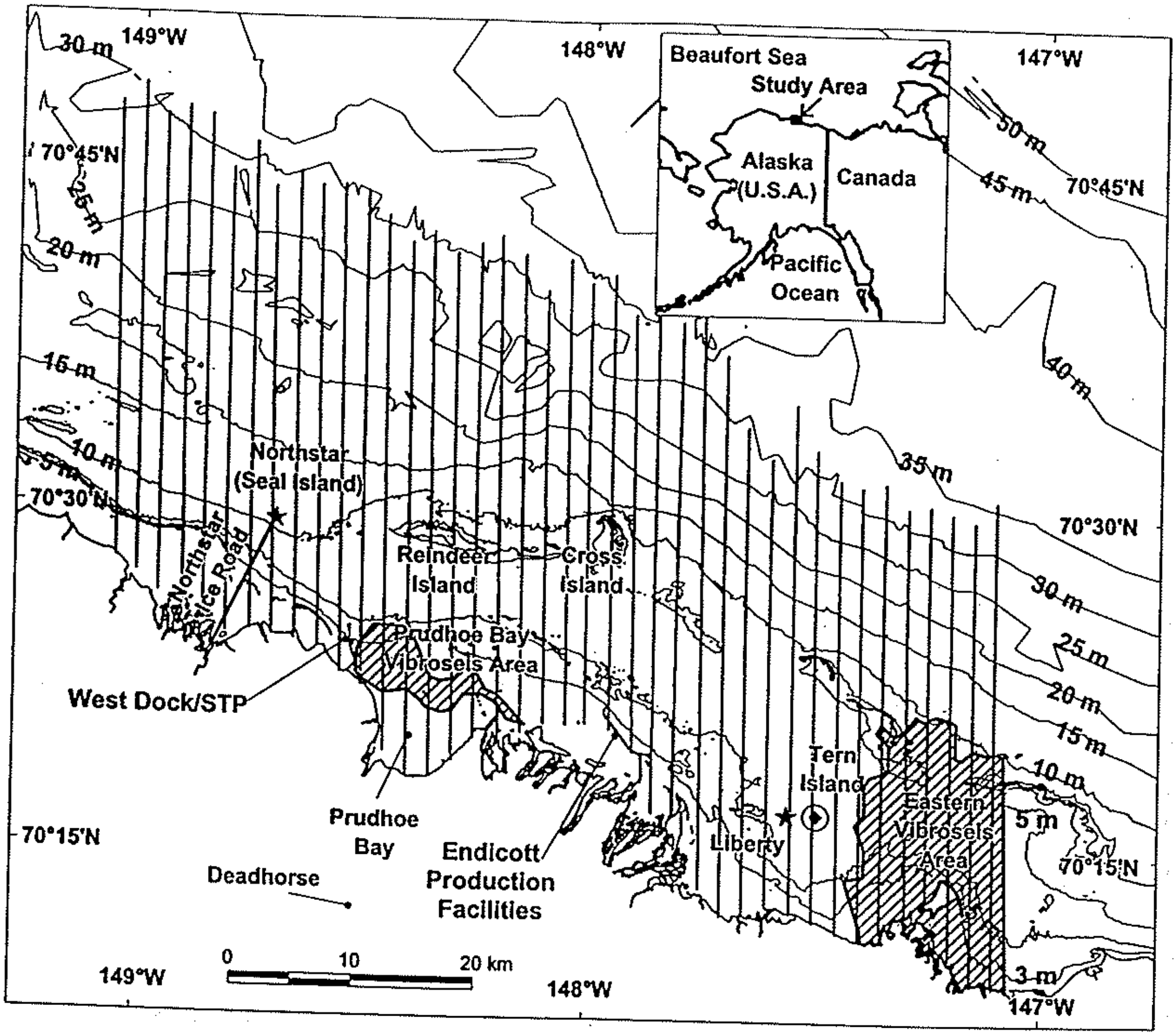
Beaufort Sea
Study Area
Alaska (U.S.A.)
Canada
Pacific Ocean
149°W
148°W
147°W
70°45'N
70°30'N
70°15'N
30 m
25 m
20 m
15 m
10 m
5 m
50 m
45 m
40 m
35 m
30 m
25 m
20 m
15 m
10 m
5 m
3 m
Northstar (Seal Island)
Northstar Ice Road
Reindeer Island
Cross Island
Prudhoe Bay Vibrosels Area
West Dock/STP
Prudhoe Bay
Deadhorse
Endicott Production Facilities
Liberty
Tern Island
Eastern Vibrosels Area
0
10
20 km

Fig. 1

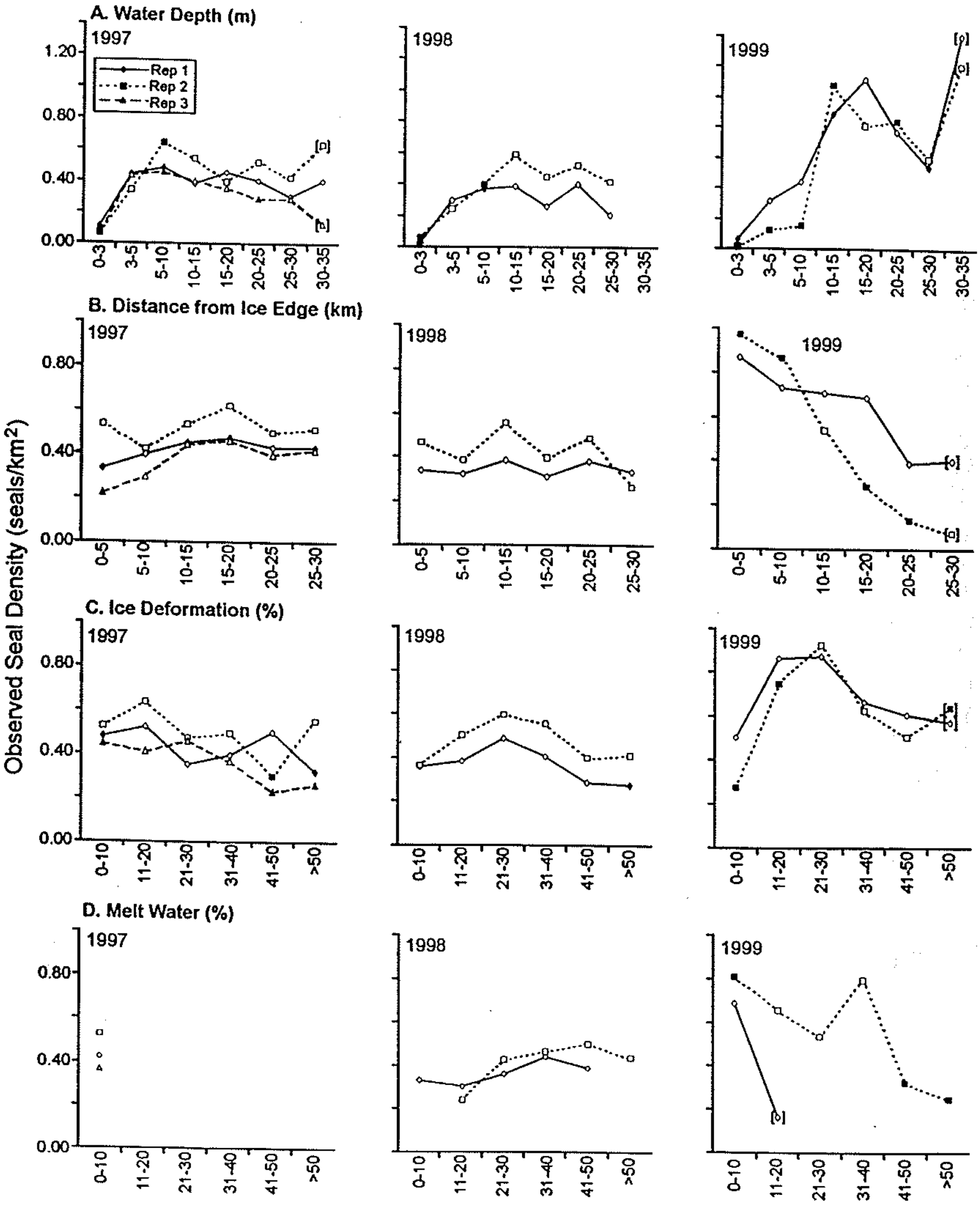
A. Water Depth (m)
1997
1998
1999
Rep 1
Rep 2
Rep 3
1.20
0.80
0.40
0.00
0-3
3-5
5-10
10-15
15-20
20-25
25-30
30-35
B. Distance from Ice Edge (km)
0-5
5-10
10-15
15-20
20-25
25-30
C. Ice Deformation (%)
0-10
11-20
21-30
31-40
41-50
>50
D. Melt Water (%)
Observed Seal Density (seals/km^2)

Fig. 2

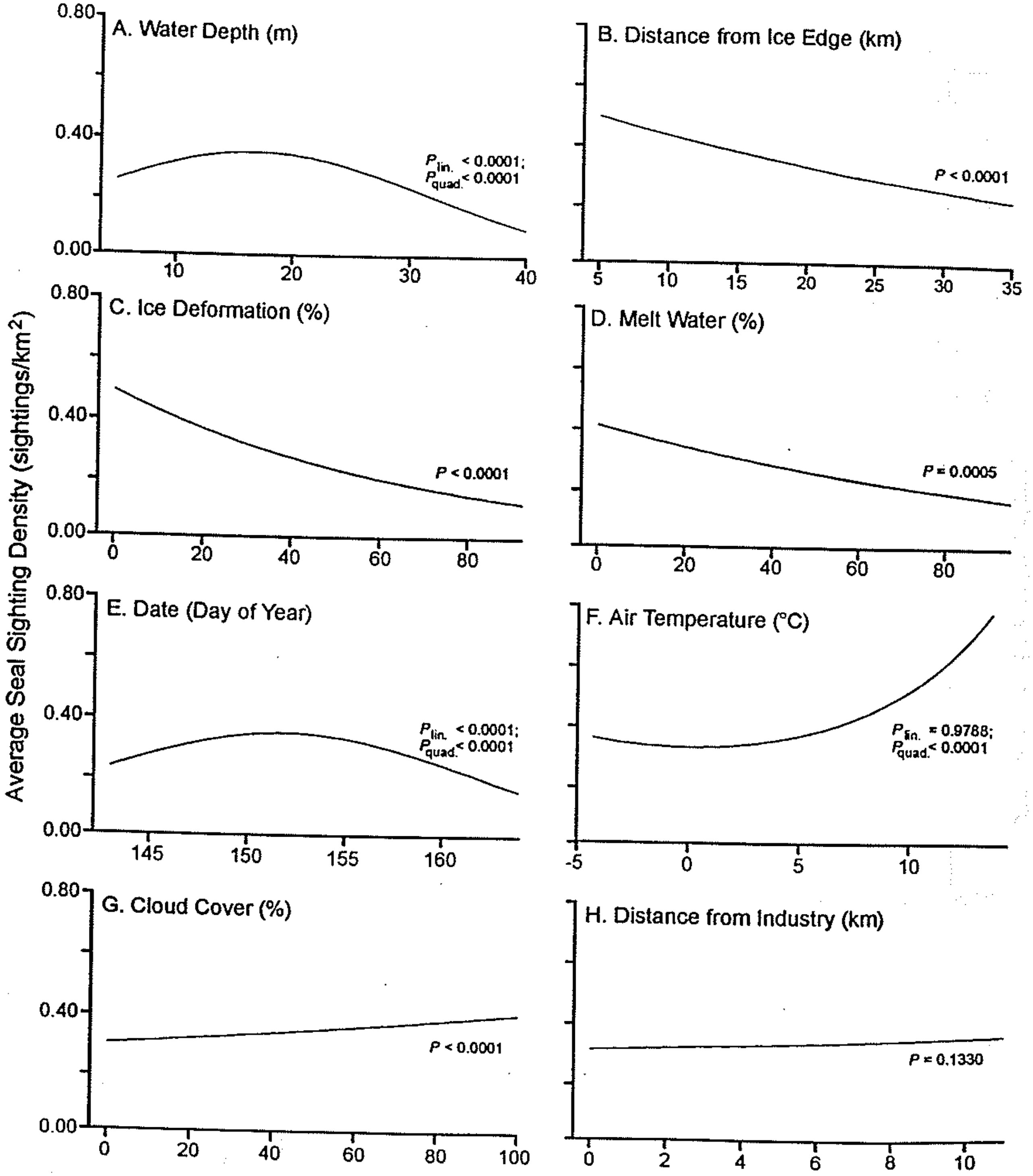
Average Seal Sighting Density (sightings/km²)
A. Water Depth (m)
0.80
0.40
0.00
10
20
30
40
P lin. < 0.0001;
P quad. < 0.0001
B. Distance from Ice Edge (km)
5
10
15
20
25
30
35
P < 0.0001
C. Ice Deformation (%)
0
20
40
60
80
P < 0.0001
D. Melt Water (%)
P = 0.0005
E. Date (Day of Year)
145
150
155
160
P lin. < 0.0001;
P quad. < 0.0001
F. Air Temperature (°C)
-5
0
5
10
P lin. = 0.9788;
P quad. < 0.0001
G. Cloud Cover (%)
100
P < 0.0001
H. Distance from Industry (km)
2
4
6
8
P = 0.1330

Fig. 3

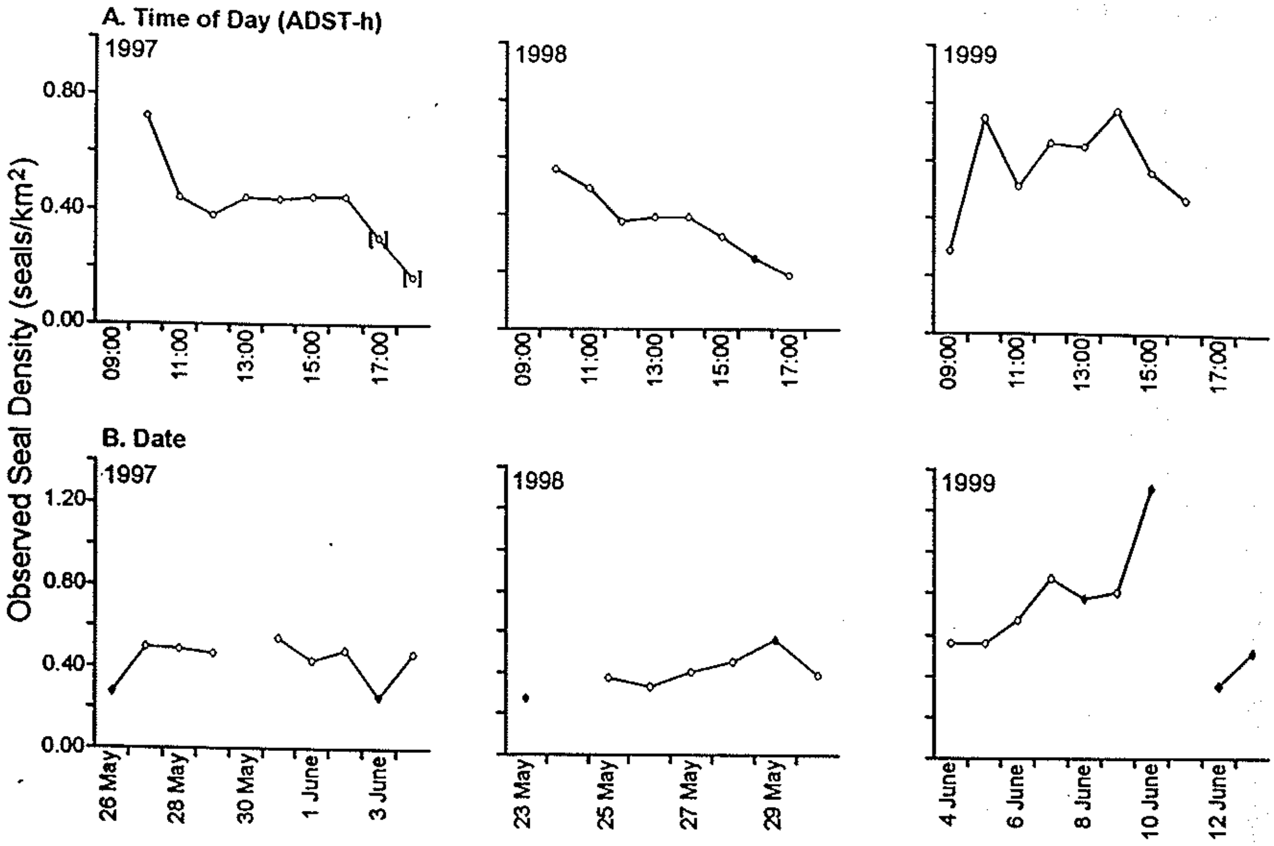
A. Time of Day (ADST-h)
1997
1998
1999
0.80
0.40
0.00
09:00
11:00
13:00
15:00
17:00
B. Date
1.20
0.80
0.40
0.00
26 May
28 May
30 May
1 June
3 June
23 May
25 May
27 May
29 May
4 June
6 June
8 June
10 June
12 June
Observed Seal Density (seals/km^2)

Fig. 4

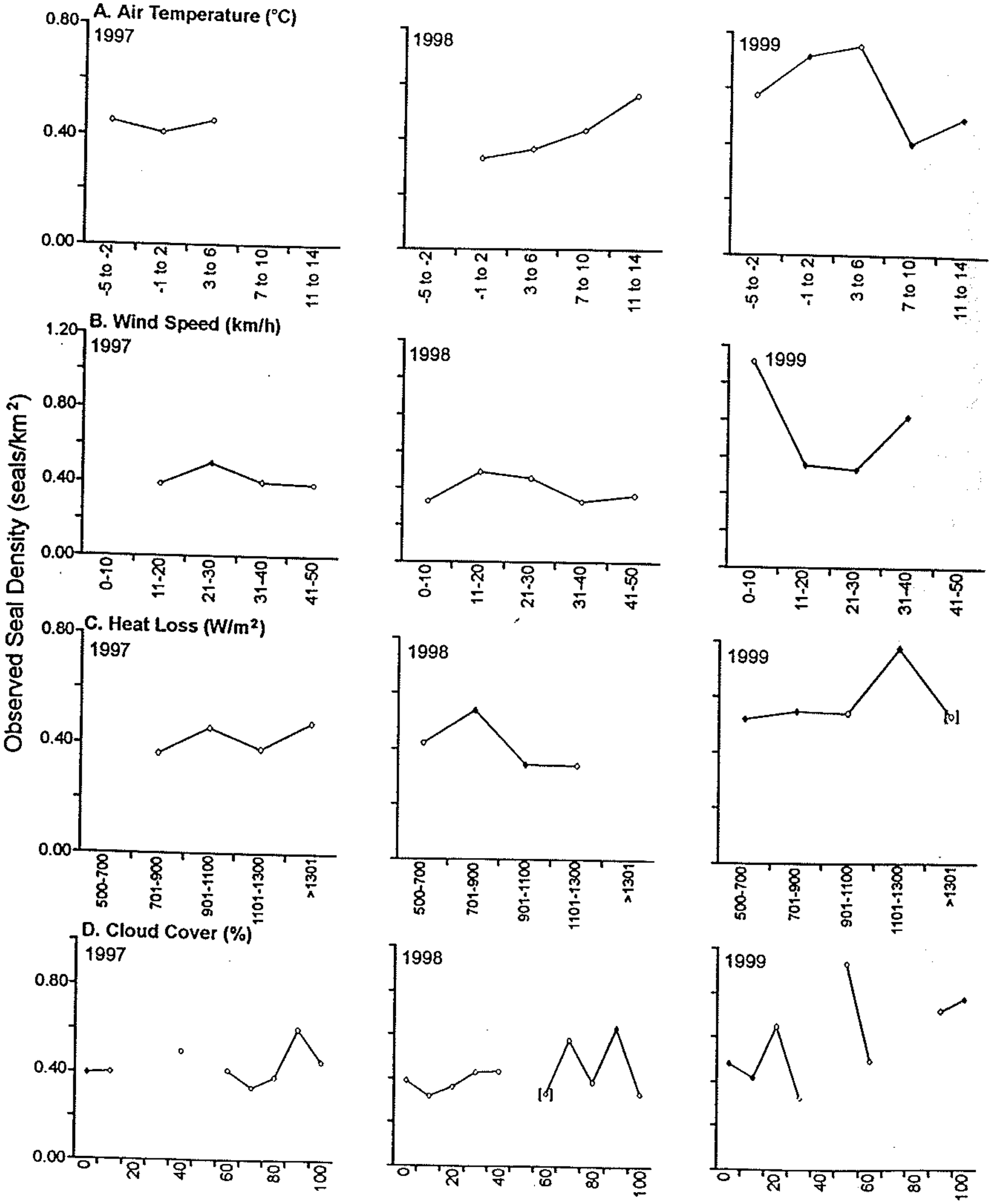
Observed Seal Density (seals/km²)
A. Air Temperature (°C)
1997
1998
1999
0.80
0.40
0.00
-5 to -2
-1 to 2
3 to 6
7 to 10
11 to 14
B. Wind Speed (km/h)
1997
1998
1999
1.20
0.80
0.40
0.00
0-10
11-20
21-30
31-40
41-50
C. Heat Loss (W/m²)
1997
1998
1999
0.80
0.40
0.00
500-700
701-900
901-1100
1101-1300
>1301
D. Cloud Cover (%)
1997
1998
1999
0.80
0.40
0.00
0
20
40
60
80
100

Fig. 5