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Abstract

Acknowledgements

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Between 1974 and 1975, there was a drop of about 50% in the numbers of ringed and bearded seals in the eastern Beaufort Sea, followed by a further 2 years of low numbers after which, in 1978, the population more than doubled. The decline in numbers appeared to be associated with particularly heavy ice conditions in the winter of 1973–74, which may have reduced the food available to seals. The resulting heavy winter mortality, combined with reduced productivity and large-scale emigration, could be responsible for the drop in numbers. Immigration appears to be responsible for the large increase in 1978.

Ringed seals prefer water with high ice cover and moderate depth. Bearded seals prefer broken-ice areas over shallow water. The greatest densities of ringed seals were recorded in the fast ice along the Yukon coast, around Cape Parry, and along the southwest coast of Banks Island. The greatest densities of bearded seals were found in the shallow water areas off the Tuktoyaktuk Peninsula.

Ecological conditions in the eastern Beaufort Sea are highly variable and cause changes in the distribution and abundance of ringed and bearded seals. Thus, management of these species as well as assessment of the possible consequences of man-made detrimental effects must be flexible, depending on the status of the populations at the time.

Ringed seal. Photo: Ian Stirling

Introduction

Aerial surveys of the ringed seal (*Phoca hispida*) and the bearded seal (*Erignathus barbatus*) in the eastern Beaufort Sea were first conducted in 1974 as part of the Beaufort Sea Project (Stirling *et al.* 1977). There were two principal objectives: to provide baseline information on the distribution and abundance of ringed and bearded seals in the eastern Beaufort Sea; and to identify critical geographical areas that might warrant protection from, or modification of, hydrocarbon exploration and production activities.

Between 1974 and 1975 there was a decline of about 50% in the numbers of ringed and bearded seals (Stirling *et al.* 1977), and a simultaneous 90% decrease in the number of ringed seal pups born in prime breeding habitat (Smith and Stirling 1975, 1978). There was also a marked decline in both numbers and natality of the polar bear (*Ursus maritimus*) (Stirling *et al.* 1975, 1976). This was the first time in the Arctic that we could quantitatively document such large-scale changes due to natural causes, even if all the mechanisms were not clear. For environmental assessment purposes, we felt it was important to document the recovery from this major decline. Also, the time required for a seal population to recover from a natural decline might indicate the time required to recover from one caused or aggravated by man. For these reasons, the survey of seals was repeated annually from 1974 to 1979.

This report analyses all 6 years of aerial survey data and describes the changes in estimated populations. We also discuss factors that influence the distributions of ringed and bearded seals.

Methods

1. Study area

The study area was a coastal strip 160 km wide along the southern and eastern shores of the Beaufort Sea and western Amundsen Gulf as far east as 123°45′W (Fig. 1).

The eastern Beaufort Sea is part of the Arctic Ocean. The distributions of sea ice, shore leads, and polynyas are influenced mainly by marine currents and winds. There is a continuous clockwise current (the Beaufort Gyre) that flows south along the west coast of Banks Island and west along the mainland coast into Alaska, after which it flows north again toward the North Pole. A more localized eddy, influenced by the outflow of the Mackenzie River, creates east-bound currents close to shore along the Tuktoyaktuk Peninsula.

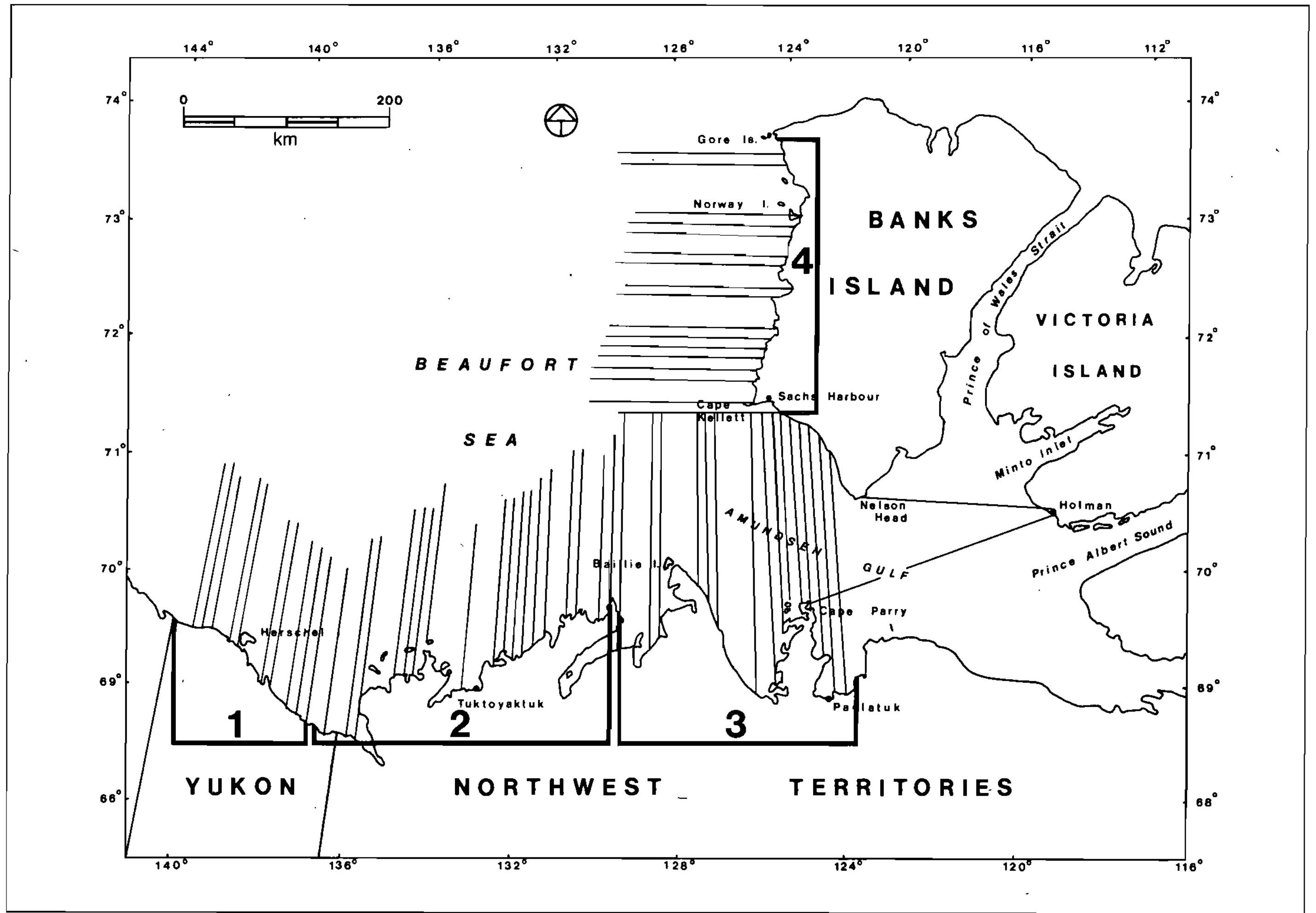
There is a continental shelf of variable width along the mainland coast and the west coast of Banks Island. Near the coast, the water is up to 50 m deep, while offshore the continental shelf may be 500 to 700 m deep. The maximum depth farther out is about 1500 m. The continental shelf is widest along the Tuktoyaktuk Peninsula, narrowest west of the mouth of the Mackenzie River, and of intermediate width along the west coast of Banks Island.

The area has a cold climate. June temperatures may reach 25°C and the January minimum is usually below −40°C (Thompson 1962); daily variations are reduced by the maritime influence. The sea begins to freeze between late September and early October and is mostly ice-covered by late November, although the pattern varies from year to year (Lindsay 1975, 1977; Smith and Rigby 1981).

The seaward boundary of the land-fast ice along the Tuktoyaktuk Peninsula roughly coincides with the 20 m depth contour (Cooper 1974) and may extend up to 50 km offshore. Beyond this, a system of recurring shoreleads and polynyas, parallel to the mainland coast, extends into the western entrance of Amundsen Gulf and north along the west coast of Banks Island. The size and distribution of these leads are largely influenced by currents and winds (Smith and Rigby 1981). In most years, there is little multi-year ice within the survey area, although the outer limit borders the edge of the permanent polar pack. Puddling on the annual ice and break-up in the Cape Bathurst polynya and along the recurring shore-lead systems begin by mid-June in most years; break-up is usually complete by mid to late July. The extent of open water along the mainland coast and the west coast of Banks Island depends mainly on the strength and direction of the wind.

The biological productivity of the Beaufort Sea is generally thought to be low, although this is poorly quantified (Davis *et al.* 1980). Although some short-term site-

Figure 1
Study area with strata and transect lines



specific studies have been done (e.g. Grainger 1975), no year-round large-scale studies have been conducted.

2. Survey design

Ringed and bearded seals are most easily seen and counted when they are resting on the sea ice. The greatest numbers of seals haul out on the ice to moult in late June, immediately before break-up (McLaren 1958*a*, Smith 1973*a,b*). After break-up, seal distributions and densities are more variable. There is also a daily cycle in the number of seals hauled out on the ice, usually reaching a maximum in early to mid afternoon (Burns and Harbo 1972, Smith 1973*a*, Finley 1979). To count the greatest number of seals hauled out on the ice, we flew as much as possible during the daily peak and during the moulting period. However, there is no accurate way to deduce the total number of seals present from the number hauled out. Consequently, these surveys are indices of abundance rather than counts of the total population.

Aerial surveys for seals have recently used a number of designs (Burns and Harbo 1972, Smith 1973*b*, Smith *et al.* 1979, Helle 1980, Stirling *et al.* 1981). This survey was a strip-transect survey flown at medium altitude, and was based on a systematic sample.

A series of transects, 15′ of longtitude apart and 160 km long was drawn north from the mainland, and a second series, also 160 km long but about 5′ of latitude apart, was drawn westward from the coast of Banks Island. In total there were 100 transects. From our previous observations of seals in the study area, we suspected that their distribution and abundance were not uniform and so we divided the study area into four strata. Stratum 1, at the western end of the study area, is most affected by the outflow of the Mackenzie River and, generally, has fairly deep water; Stratum 2 has considerable shallow water over the continental shelf, a wide band of annual landfast ice and a recurring series of east–west leads running parallel to the coast; Stratum 3, which includes the Cape Bathurst polynya, is characterized by extensive areas of relatively unstable ice over deep water; and Stratum 4, farther north than the other three strata, has north–south leads parallel to the west coast of Banks Island, a narrower continental shelf than Stratum 2, deeper water farther offshore, and relatively stable ice that often remains throughout the summer.

Because of the cost, not all transects could be surveyed, so a 60% stratified random subsample was drawn from the 8.5% systematic strip-transect sample, giving an overall sampling fraction of 5.1% (Fig. 1). In Stratum 1, 10 transects were selected out of 16; in 2, 18 out of 30; in 3, 15 out of 26; and in 4, 17 out of 28, of which, however, only 16 were flown in 1974.

Transects had been surveyed in 1972 between Holman and Cape Parry and between Holman and Nelson Head (Smith 1973*b*). In order that we could compare our results with those obtained before our surveys were started in 1974, we repeated these transects in 1977, 1978, and 1979.

3. Data collection

The survey was flown in a Cessna 337 at air speeds of 120–140 knots (220–260 km/h) and at a height of 150 m, or 90 m when fog seriously reduced visibility. The transects were 800 m wide. The 400 m wide survey strip on each side of the aircraft was divided into inner and outer 200-m-wide strips. We aligned marks on the wing struts with marks on the windows to delimit the strips. In 1977, we improved the method of placing the marks to take into account the blind area directly below the aircraft.

From 1974 to 1977, navigation was by dead reckoning with a directional gyro. Ground speed was corrected for estimated wind speed and direction. The shoreline ends of transects were confirmed from 1:250 000 topographic maps. In 1978 and 1979, we used an OMEGA-GNS 500 Global Navigation System.

Seals hauled out on the sea ice were identified to species and counted separately for the inner and outer survey strips on each side of the aircraft. Records were also kept of sightings of bowhead and white whales (*Balaena mysticetus* and *Delphinapterus leucas*) and polar bears, even when outside the transect.

We used an interval timer to facilitate recording the data in units of 2-min duration. A stopwatch was used to time intervals flown over land (small islands, spits, etc.),

Figure 2
Field sheet used to record data on the survey

RINGED SEAL AERIAL CENSUS

SURVEY DATA FORM

Date: 79/6/25

Observer(s): WC (R SIDE) wind NNE

Sight Angle:

Altitude: 500′

Air Speed: Estimated ground speed: ~177 mph

Map Number:

Transect Number: 67 Initial coordinates: 7147.0 - 12430.0 → 7007.8 - 12430.0 Headings: S

REMARKS:

Time	1/8 mi Observations	1/4 mi	Total	O	I	S	W
MDT: 1234	5LA			5	5	2	4
6	7LA	GNS: 155 kts		7			
8	" 1r hole		1r	7			
40	8LA			8			
2	7LA (lg leads opening)			7			
4	1rh	1r lead	2r	7			
6	7LM 2rh		2r	7	3		
8	8LA			8	5		
50	6LA			6	5		
2	3LA	(3 ad bel → w, narrow lead)	3 bel	3	5		
4	8LM			8	3		
6	3LA	1rh	1r	3	5		
8	7LA 1rh	1rh 1b floe	2r 1b	7	5		
1300	8LA 1rh 1rh 1rh	3rh	6r	8	5		
2	8LM 1rh		1r		3		
4	8LA	1rh	1r		5		
6	" 4rh		4r		5		
8	8LM				3		
10	8LA 1rh 1rh	1rh 1rh	4r		5		
12	" 1pb & yrlg near shore		2 bears	8	5	2	4
38′39″							
	15 ringed, 2 bears	9 ringed, 1 bearded, 3 beluga					

which were subtracted from the related 2-min intervals. We then estimated average values for ice, cloud, and wind conditions during each 2-min interval.

In 1974, seal counts and ice cover were the only variables that we recorded consistently; in later years ice type, cloud cover, and wind speed were added (Table 1). We also recorded the size of each group of seals, and whether they were at a hole, crack, lead, or floe edge on the field sheets (Fig. 2), but did not transfer this information to the data forms (Fig. 3). A data file of water depths was compiled from hydrographic charts.

In each year, the same observer sat on the same side throughout the whole survey. Over the 6 years, seven different observers took part and, generally, the quality of the surveys improved with experience.

Table 1
Frequency of collection of data (in days) on habitat and survey conditions

Year	Survey data Start	End	Ice cover (0)*	Ice type (I)*	Cloud cover (S)*	Wind speed (W)*
1974	June 15	June 29	1	0	2/3	0
1975	June 12	June 20	1	0	1/3	1/6
1976	June 16	June 25	1	1/2	1/2	1/2
1977	June 12	June 21	1	1	1	1
1978	June 13	June 25	1	1	1	1
1979	June 15	June 25	1	1	1	1

* Abbreviation used on data forms (Fig. 3).

4. Data analysis

The survey area encompasses a wide range of longitudes from 123°45′W to 140°30′W. Because the entire area was officially under Mountain Daylight Time (MDT), the time of day at which the sun was highest in the sky varied by as much as four hours from noon (12:00). Because the seals' diurnal rhythm is related to the position of the sun and not MDT, we converted all time measurements from MDT to what we call "sun time", where 12:00 is defined to be the time at which the sun reaches its highest altitude. MDT can be converted to sun time using the equation

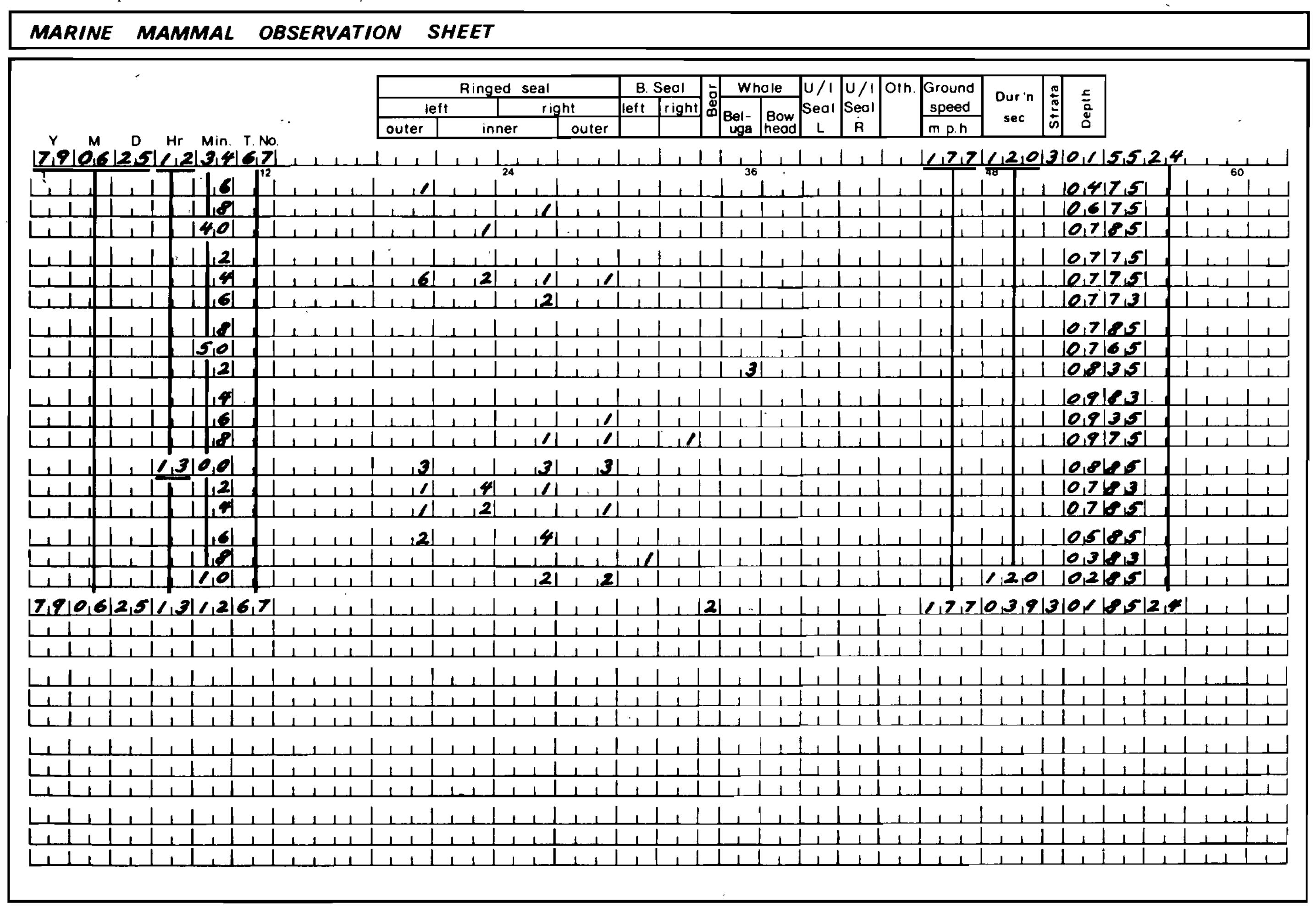
sun time = MDT + 6 − longitude/15
MDT = mountain daylight time
6 is the conversion to Greenwich mean time
15 is the earth's rate of rotation in degrees/hour.

A more accurate time correction is possible, but it changes the above calculation by at most 5 minutes.

We calculated the length and area of each 2-min interval from the recorded ground speed, and then interpolated the offshore co-ordinates (latitude and longitude) of the centres of the intervals along the transect. The water depth at those co-ordinates was taken from a separate data file.

The seal population for the entire area was estimated by extrapolating (or weighting) the counts from the flown transects.

Figure 3
Data transcription sheet used for the surveys



The weight for the east–west transects is

$$w_{ij} = 5.17 \times 1.852/0.8045$$

where w_{ij} = weight for the j^{th} interval on i^{th} transect
5.17 = transect spacing (minutes of latitude or nautical miles)
1.852 = conversion factor (nautical miles to kilometres)
0.8045 = transect width (kilometres)

The spacing of the north–south transects varied with latitude — the southerly ends, being farther apart, required the assignment of a greater weight. Thus a weight was calculated for each segment as follows:

$$w_{ij} = 15 \times \cos L_{ij} \times 1.852/0.8045$$

where 15 = transect spacing (minutes of longitude)
L_{ij} = latitude at centre of j^{th} interval

These calculations assume the earth is spherical and one minute of latitude is equal to one nautical mile.

We calculated densities of ringed and bearded seals for each interval, and used multiple linear regression to investigate habitat selection by seals, employing sets of binary variables to represent habitat factors (ice cover, ice type, stratum, and water depth) and survey conditions (sun time, cloud cover, and wind speed) (Table 2).

Regressions used each 2-min interval as a data point and were unweighted. To mitigate the effect of non-independence in successive intervals, which may produce spurious significances, a rather stringent significance level (0.005) was used. We ran regressions for all years (1974–79) using ice cover, depth, and sun time variables, and for 1977–79 using ice type, cloud cover, and wind speed as well.

We computed density estimates for each year for the whole survey area and for each stratum using transects as sampling units. The weighted total seals on each transect was obtained by:

$$Y_i = \sum_{j=1}^{m_i} w_{ij} t_{ij} \qquad [1]$$

and the weighted total area by:

$$X_i = \sum_{j=1}^{m_i} w_{ij} a_{ij} \qquad [2]$$

where Y_i = weighted total seals on i^{th} transect;
m_i = number of 2-min intervals on i^{th} transect;
w_{ij} = weight (spacing) of j^{th} interval on i^{th} transect;
t_{ij} = number of seals of j^{th} interval on i^{th} transect;
X_i = weighted total area of i^{th} transect (km²);
a_{ij} = area of j^{th} interval of i^{th} transect (km²).

A weighted ice surface area was obtained by:

$$Z_i = \sum_{j=1}^{m_i} w_{ij} a_{ij} o_{ij} \qquad [3]$$

where Z_i = weighted ice surface area of i^{th} transect (km²);
o_{ij} = ice cover fraction on j^{th} interval on i^{th} transect;

Z_i then replaced X_i in all the following expressions whenever statistics relating to ice area were required.

Then the estimate of mean density (seals/km² ice) is given by:

$$\hat{R} = \sum_{1}^{n} Y_i \Big/ \sum_{1}^{n} Z_i \qquad [4]$$

where n = number of transects flown.

Error variances of $\hat{R}$ were calculated in two ways:

$$S_1^2(\hat{R}) = n\sum_{1}^{n} d_i^2 \Big/ (n-1) \cdot (\sum_{1}^{n} Z_i)^2 \qquad [5]$$

(Cochran 1963), and

$$S_2^2(\hat{R}) = n\sum_{1}^{n-1} (d_i - d_{i+1})^2 \Big/ 2(n-1) \cdot (\sum_{1}^{n} Z_i)^2 \qquad [6]$$

(Kingsley and Smith 1981), where $d_i = Y_i - \hat{R}Z_i$.

Table 2
Variables used for habitat regressions

Variable	Type	Description
cover	continous	ice cover, minimum value zero; but 0.125 is the lowest value occurring in regressions of density/km² of ice surface.
any twoplus ↓ sevenplus eight	binary cumulative	ice cover classes: set to 1 if ice cover equals or exceeds 1/8, 2/8 . . . 7/8, 8/8; cumulative variables, e.g. if ice cover is 3/8, then 'any', 'twoplus', and 'threeplus' are set and all the others are clear.
dg1 ↓ dg10	binary cumulative	depth class variables: set to 1 if depth exceeds class 1 . . . class 10; depth equivalents are 25, 50, 75, 100, 150, 200, 300, 400, 500, 1000 m; cumulative variables.
fast lmy smy lan sman	binary exclusive	ice types: set to 1 if the ice type recorded was respectively fast, large or small multi-year floes, large or small first-year floes; large floes were more than about 400 m across; exclusive variables (i.e. only one of them can be set).
scatplus brokplus overcast	binary cumulative	cloud cover: set to 1 if the cloud cover on and adjacent to the transect was respectively non-zero, greater than 50%, or equal to 100%; cumulative.
wind1p ↓ wind4p	binary cumulative	wind speeds: set to 1 if the wind was blowing, but at respectively any speed, or more than 5, 10, or 15 knots; cumulative.
strat1 ↓ strat4	binary exclusive	stratum: set to 1 if the transect fell in the appropriate stratum.
st13	continuous	a time variable equal to sun time in hours minus 13.0, so we could look for declines in density on each side of 13:00.
st13sq	continuous	the preceding variable squared.
stgt10 ↓ stgt17	binary cumulative	set to 1 if the sun time was respectively greater than 10:00–17:00 cumulative.

We used the error variance S_2^2 for calculating standard errors to be tabulated, because it is more appropriate for systematic samples from serially correlated populations. We compared S_1^2 with S_2^2 as a measure of the efficiency of a systematic sample relative to a random one.

An estimated surveyed population (P_I) for each stratum was obtained by multiplying the weighted mean density by the weighted flown ice area:

$$P_I = \hat{R} \sum_{1}^{n} Z_i = \sum_{1}^{n} Y_i \quad [7]$$

and was then grossed up by the stratum sampling fraction to give an estimate of the total visible population (P_{II}):

$$P_{II} = P_I \, N/n \quad [8]$$

where N = total number of available transects.

The standard error of P_{II} was obtained by:

$$S_P = P_{II} \, S_2/\hat{R} \quad [9]$$

Total population estimates were obtained by summing the estimates for individual strata. Their standard errors were obtained from the root sum of squares of the stratum standard errors.

Error coefficients of variation were calculated by $e_k = S_k/\hat{R}$, where $k = 1,2$.
If seals were randomly and independently distributed with uniform average density, e_k would be approximately $1/\sqrt{\Sigma_i \Sigma_j t_{ij}}$.

Measures of the clumpiness of seal distribution (c_k) were calculated by $c_k = e_k^2 \cdot \Sigma\Sigma t_{ij}$, where $k = 1,2$.
Clump factor c_2 is a measure of the short- to medium-range clumping of seals: their tendency to haul out in groups and their response to small-scale variations in habitat over distances of the scale of that between transects; c_1 is greater than c_2 by the variation in density over the range of transects.

A components-of-variance model was created for testing differences between observers and between inner and outer strips. The error variance of a density estimate is assumed to have two components, one (σ_b^2) due to variation between observers or strips within transects, and one (σ_a^2) due to variation between transects. Under this assumption, the error variance of a density estimate obtained from a subsample (left or right observer, or inner or outer strips) is

$$V_s = \sigma_a^2 + \sigma_b^2,$$

and that of one obtained when entire transects are used is

$$V_w = \sigma_a^2 + \sigma_b^2/2.$$

V_s and V_w are estimated by the corresponding values of S_2^2. The appropriate error term for comparing observers or strips is σ_b^2, which is estimated by $\sigma_b^2 = 2(V_s - V_w)$.

5. Collection of specimens in the field

Lower jaws and reproductive organs of ringed seals were collected so we could monitor changes in population structure and possibly aid interpretation of the aerial surveys. In 1974 and 1975 we collected ringed seals from the offshore ice during April, May, and June throughout the study area, then during the summers we stationed a technician at Sachs Harbour to collect specimens from ringed seals killed by Inuk hunters. Measurements, lower jaws, and reproductive organs were collected from as many ringed seals as possible. Reproductive material was examined fresh whenever possible and then preserved in AFA (alcohol–formalin–acetic acid). From 1976 to 1979, an Inuk assistant at Sachs Harbour collected lower jaws and reproductive organs (1976–78) from seals killed by Inuk hunters during the summer and preserved them for later examination in Edmonton.

6. Analysis of field specimens

Ovaries were hand sectioned with a scalpel and the presence of a corpus luteum or corpus albicans of recent pregnancy, and follicular activity, were recorded.

Canine teeth from the lower jaws were decalcified, then sectioned and aged (Stirling *et al.* 1977).

Results and discussion

1. Comparison of left and right observers and of inner and outer strips

We counted in four survey strips so that the quality of the survey could be checked by comparing the inner and outer strips and the left and right observers. Differences between observers may be due to differences in visual acuity, experience, or concentration but may alternatively (or additionally) be due to errors in marking the struts or to a tendency for the aircraft to fly with one wing lower. The difference between left and right observers had its lowest value at 2.2% and highest at 24.9% (Table 3). However, the precision of the survey was such that none of these differences were statistically significant.

The results of comparing the inner and outer strips were more variable, although each year more seals were counted on the outer strip (Table 3). This may have several possible causes: decreased visibility of seals near the aircraft because they dive more readily, are more difficult to see, or are in sight for a briefer period; a differential increase in the width of outer strips over inner whenever the aircraft banks to correct or maintain its course; or errors in marking the struts.

The greatest difference was in 1974 when the densities in the outer strips exceeded the inner by 104%. If this difference was due to banking or attitude variation in the aircraft, then the population could have been over-estimated by at least 50%, but if it was caused by missing seals in the inner strip, then the population was under-estimated by 25%. The differences in 1975 and 1976, although still large, were not as great. The differences were statistically significant in these 3 years.

In 1977, the wing struts were marked so that the inner survey strips did not begin directly below the side of the aircraft, thus making seals near the inner border easier to see. From 1977 to 1979, there were no significant differences in the densities of seals in the inner and outer strips. In fact, in 1978 the difference was only 1.4%.

It would appear that the differences between the inner and outer strips from 1974 to 1976 were aggravated by undersampling of the inner strip. Thus, the population estimates for those years, and for 1974 in particular, are liable to be low.

2. Ice distribution

In most years, transects were flown only over areas where there was ice. The extent of the ice cover varied between years (Fig. 4*a–c*) and, in general, could be inferred from the extent of the flying.

The extent of the total ice cover and the distribution of different proportions of cover may also vary within the study area over a period of days as wind and weather change, so the following comments can be of a summary nature only. It appears that when ice begins to break up and melt, it does so quite quickly in localized areas. Thus, in the most common pattern of distribution, there is a large fraction of 7/8 to 8/8 ice cover, much less 4/8 to 6/8 cover, and usually negligible areas at 2/8 to 3/8 (Table 4). The area with only 1/8 cover is usually larger than the 2/8 or 3/8, and mainly represents strings of brash ice and fragments in the last stages of melting.

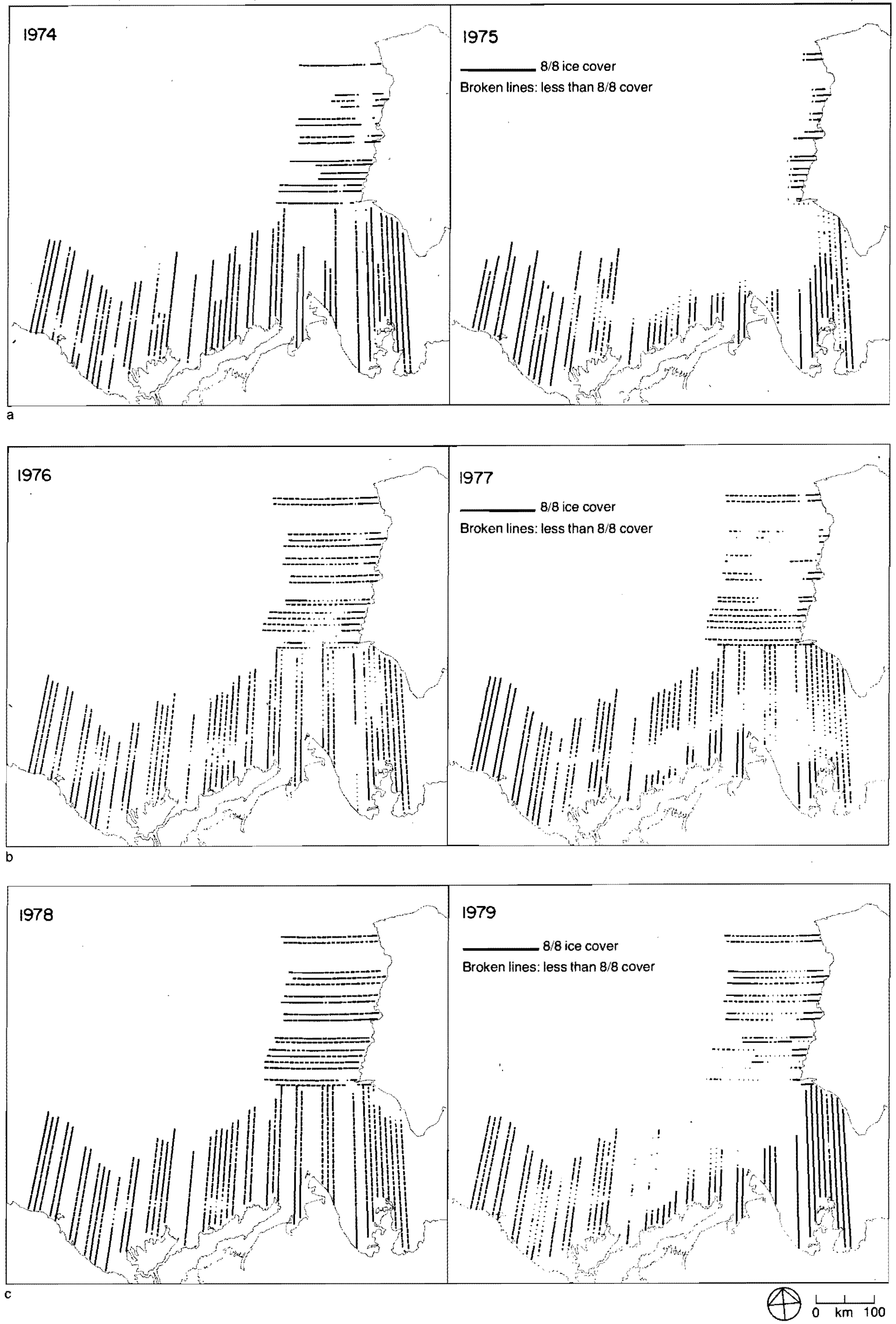
The 2 years of highest ice cover, 1976 and 1978, had relatively small fractions of 8/8 ice cover with a shift into the 7/8 and 6/8 fractions. 1977 also had a low fraction of 8/8 cover, with a shift into 6/8, which constituted 27% of the ice-covered area. 1975 was notable for its particularly low ice cover. Open water prevailed over much of the eastern Beaufort Sea and western Amundsen Gulf except for narrow shelves of fast ice along the mainland coast and the west coast of Banks Island.

Table 3
Comparison of ringed seal densities obtained by left or right observers and on inner or outer strips

	Density (seals/km² ice)				Error variances (10^{-4})			Student's t		Difference (%)*	
Year	left	right	outer	inner	V_w	V_s	σ_b^2	left-right	outer-inner	left-right	outer-inner
1974	0.447	0.358	0.541	0.265	8.26	13.22	9.91	2.00	6.20†	24.86	104.21
1975	0.369	0.361	0.410	0.320	10.38	13.72	6.69	0.22	2.45‡	2.22	27.92
1976	0.257	0.231	0.287	0.200	2.58	3.67	2.17	1.26	4.18†	11.37	43.46
1977	0.220	0.242	0.245	0.217	2.65	3.91	2.51	–0.97	1.23	–9.84	12.64
1978	0.424	0.444	0.437	0.431	9.99	13.69	7.39	–0.50	0.16	–4.55	1.44
1979	0.356	0.431	0.427	0.359	9.75	15.74	11.80	–1.53	1.38	–21.04	18.84

* As a percentage of the smaller value.
† Significant at 0.001.
‡ Significant at 0.01.

Figure 4
Distribution each year of ice in the survey area



When the proportions of ice cover in the different strata are compared between years, it is apparent that Stratum 1 has the greatest amount of cover and is the most consistent between years (Table 4*a*). It had only a 10% difference between 1978, the year of greatest total ice cover, and 1975, which had the least. Stratum 4 was the most variable with a ratio of 4.5:1 between the greatest and the least (Table 4*d*), while strata 2 and 3 were intermediate (Table 4*b*,*c*).

3. Influence of habitat and survey conditions on ringed seal density

Ringed seal densities were regressed on cover and the binary variables for ice cover classes, depth classes, and sun time to give the coefficients in Table 5*a*. The appearance of cover in all the results (except those for 1978, when cover was uniformly high) showed that density of seals would be better expressed in seals per square kilometre of ice than per square kilometre of the study area. This density was accordingly calculated and regressed on the same independent variables; the constant term, which had been optional in the previous regressions, was made compulsory.

The results obtained (Table 5*b*) varied between years. Although the coefficients of determination were usually low, certain general conclusions seem apparent. In 3 years (1974, 1977, 1979), 8/8 ice cover entered with a positive coefficient, indicating a preference for a high proportion of ice cover. However, 8/8 ice is usually first-year and landfast, and ice age and condition were not offered in these regressions. A second set of regressions run for 1977–79 (when ice type was recorded), showed a positive preference for fast ice in one of 3 years (Table 5*c*).

Depth preferences were less clear. Density increased beyond 50 m (1977) or 75 m (1979) (Table 5*c*) and decreased again in deeper water beyond 100 m (1976 and 1979) (Table 5*b*). Table 5*c* also shows a further decline in density in the very deepest water, over 300 m in 1977 and over 400 m

Table 4
Percentage distribution by stratum of ice cover, area surveyed, and area of ice cover

	Ice cover (/8)									Area (km²)*	
Year	0	1	2	3	4	5	6	7	8	surveyed	ice cover >0/8(est.)
(*a*) in Stratum 1											
1974	2.82	1.76	0.57	0.0	2.30	1.07	10.79	13.00	67.68	15 199	14 770
1975	0.45	0.0	0.0	0.0	0.94	0.0	2.26	22.86	73.48	14 186	14 121
1976	1.55	5.67	0.51	0.48	4.26	2.62	5.85	43.26	35.79	15 430	15 191
1977	0.0	0.0	0.0	0.0	0.54	3.19	12.53	22.09	61.65	15 250	15 250
1978	0.0	0.0	0.0	0.0	0.0	0.0	3.69	52.43	43.88	15 457	15 457
1979	1.77	12.27	2.62	2.06	3.07	4.03	16.61	52.71	4.86	15 305	15 034
(*b*) in Stratum 2											
1974	2.34	1.03	1.49	0.0	1.11	1.39	4.29	22.67	65.68	23 783	23 226
1975	14.97	16.25	2.95	0.42	2.86	3.13	3.81	23.90	31.72	18 722	15 919
1976	4.90	3.16	3.75	2.17	7.85	7.04	21.06	30.84	19.23	27 269	25 933
1977	19.08	3.29	1.15	2.40	4.29	3.33	24.83	27.10	14.52	26 876	21 748
1978	0.63	2.18	1.19	0.91	1.81	2.74	6.71	48.90	34.94	27 032	26 862
1979	18.18	12.21	5.02	3.82	5.64	5.65	12.89	16.44	20.15	19 932	16 308
(*c*) in Stratum 3											
1974	1.11	0.58	0.28	0.26	0.88	0.0	2.47	36.54	57.88	25 937	25 649
1975	10.94	13.63	3.28	2.52	4.05	3.49	5.25	6.37	50.47	20 144	17 940
1976	9.89	11.51	2.94	2.15	6.29	5.35	10.48	37.11	14.29	29 399	26 491
1977	18.78	9.00	6.46	4.71	7.33	7.10	19.64	12.33	14.65	29 607	24 047
1978	5.13	0.53	0.77	0.21	0.80	2.90	18.36	57.43	13.87	29 550	28 034
1979	4.57	1.31	0.31	0.35	0.49	0.36	0.0	6.18	86.43	23 808	22 720
(*d*) in Stratum 4											
1974	9.88	0.0	1.39	0.55	3.26	0.0	5.16	43.64	36.12	18 296	16 488
1975	11.00	9.50	6.65	5.51	2.64	2.72	4.19	0.0	57.78	6 027	5 364
1976	6.14	7.22	3.32	3.13	3.78	4.07	18.11	39.77	14.46	25 845	24 250
1977	32.66	1.74	2.06	2.72	4.24	10.06	26.18	11.79	8.55	26 369	17 757
1978	0.94	0.0	0.31	0.59	0.30	3.08	14.04	55.91	24.82	26 104	25 859
1979	14.56	17.41	3.09	5.21	6.51	8.04	8.20	8.82	28.16	22 650	19 352
(*e*) in entire survey area											
1974	3.6	0.8	0.9	0.2	1.7	0.6	5.1	29.6	57.5	83 215	80 219
1975	9.8	10.9	2.8	1.6	2.8	2.5	4.0	15.2	50.6	59 079	53 289
1976	6.2	7.1	2.9	2.2	5.7	5.1	14.7	37.0	19.1	97 941	91 869
1977	19.7	4.1	2.8	2.8	4.6	6.3	21.7	17.8	20.3	98 104	78 778
1978	2.0	0.8	0.6	0.5	0.8	2.5	11.7	53.9	27.3	98 144	96 181
1979	10.1	10.5	2.7	2.9	3.9	4.5	8.5	18.1	38.8	81 697	73 446

* Sum of transect areas expanded for regular transect spacing but not for the random sampling fraction.

Table 5
Coefficients of habitat variables entering regressions* of ringed seal density

Year	Cover†	8/8 ice cover	Depth >75 m	Depth >300 m	Sun time >10:00	Sun time >12:00	Sun time >15:00	Sun time >16:00
(*a*) densities in seals/km² total survey area; optional constant								
1974	0.584				–0.210			
1975	0.406						–0.139	
1976	0.263							0.101
1977	0.164	0.130		–0.86		0.082		
1978					0.397			
1979	0.212	0.225	0.217	–0.289				

Year	Constant‡	Cover†	8/8 ice cover	Depth >75 m	Depth >100 m	Depth >400 m	Sun time >10:00	Sun time >12:00	Sun time >16:00
(*b*) densities in seals/km² ice; compulsory constant									
1974	0.511		0.175				–0.227		
1975	0.391								
1976	0.321				–0.111				–0.168
1977	0.090		0.143					0.162	
1978	0.719	–0.678					0.353		
1979	0.190		0.220	0.662	–0.495	–0.291			

Year	Constant§	8/8 ice cover	Depth >50 m	Depth >75 m	Depth >100 m	Depth >300 m	Depth >400 m	Fast ice	Cloud cover >0/10	Cloud cover 10/10	Sun time >10:00	Sun time >12:00	Wind >5knot
(*c*) densities in seals/km² ice; ice type recorded; constant forced													
1977	0.105		0.143			–0.192		0.187		–0.155		0.108	
1978	0.315										0.349		–0.233
1979	0.251	0.207		0.686	–0.444		–0.344		–0.175				

* Regressions were stepwise forward; significance levels 0.005 to enter, 0.01 to leave.
† Continuous variable; all others are binary variables.
‡ Compulsory constant term significant at 0.002 in all regressions.
§ Compulsory constant term significant at 0.001 in 1977–78, 0.05 in 1979.

in 1979. These findings should be free of the effects of ice cover, which was offered simultaneously. We infer that ringed seals prefer water of moderate depth, from 50 or 75 m to perhaps somewhat over 100 m, and avoid the deepest water. No depth preferences were apparent in 1978, probably because seals were more widespread when numbers were high.

The analysis of density with respect to sun time showed few pronounced results, but they are in accordance with what is generally known. For 1977 and 1978, times of 12:00 and 10:00 respectively entered with positive coefficients, and for 1976, 16:00 entered negatively (Table 5*b*). Finley's (1979) data show an increase in the density of visible seals at about 10:00 with a fairly flat peak at about 14:00, which is similar to what we found. Since most of our surveying was done during the maximum haul-out period between 10:00 and 17:00, it is not surprising that we found no time preferences within this period. The anomalous negative coefficient at 10:00 in 1974 (Table 5*b*) is due to the sighting of four or five large groups of over 40 seals, all just before 10:00.

Ringed seal densities showed a negative association with wind speeds greater than 5 knots (9.3 km/h) in 1978 (Table 5*c*), which was in agreement with Finley's (1979) results.

Previous findings on the response of seals to sunny weather are conflicting. Smith (1965) found no response to cloud cover for Weddell seals (*Leptonychotes weddelli*). In our surveys, there were negative coefficients for cloud cover in 1977 and 1979 (Table 5*c*). Ray and Smith (1968) suggested that Weddell seals oriented their bodies at right angles to the sun, presumably to absorb the most warmth, but Finley (1979) reported that ringed seals retreated into the water on sunny windless days. The results obtained from our surveys suggest that, on average, ringed seals prefer to haul out in clear calm weather.

Finley (1976) also used multiple regression to try to elucidate, from survey data, the weather preferences of ringed seals for hauling out. He obtained simultaneous positive coefficients for both cloud cover and temperature and failed to find effects for wind speed or time of day.

The residual densities, after removal of the effect of Table 5*b*, were regressed on a set of binary variables representing the strata (Table 6). Such results as were obtained were consistent with each other: strata 1 and 3 each entered in 2 years with positive coefficients and Stratum 2 entered negatively once. The year (1977) in which Stratum 2, a shallow area, entered negatively, was one for which depth variables were in the regression. In 1974, one of the years in which Stratum 1 entered the regression, high ice cover was in the regression. Stratum 3 may have a positive residual effect because of a generally higher level of biological productivity.

Table 6
Coefficients of stratum binary variables after removal of the effects of Table 5*b**

Year	Stratum 1	Stratum 2	Stratum 3	Stratum 4
1974	0.180			
1975				
1976	0.176			
1977		–0.105	0.143	
1978			0.205	
1979				

* Effects identified by forward stepwise regression; significance levels 0.005 to enter, 0.01 to leave; optional constant never entered.

4. Distribution and abundance of ringed seals

The ice area by stratum and in total, and the estimated visible populations of seals are presented in Table 7. The distributions of the counted ringed seals are shown in Figures 5–8.

Generally, densities were highest in the high-ice-cover areas of strata 1 and 3. It may be that these areas, especially Stratum 3, are more biologically productive. This hypothesis is supported by the fact that the Cape Bathurst polynya, which lies within Stratum 3, is the preferred feeding area for white whales and bowhead whales when they migrate to the eastern Beaufort Sea each summer (Sergeant and Hoek 1974, Fraker 1979). In general, densities of ringed seals were lower in strata 2 and 4, but some of the fast-ice areas of these strata had fairly high densities in spite of the amount of shallow water (less than 75 m), which seems to be less preferred by ringed seals. This may reflect the resident adult population using the fast ice for birth lairs.

The estimated visible population of ringed seals in the study area varied dramatically from year to year (Table 7). Between 1974 and 1975 the estimate fell by about 50% and remained relatively constant until 1977. The highest value for 1975–77 is only 22% greater than the lowest. In 1978, the estimated population suddenly increased by over 250% only to drop again in 1979 by 40% from the previous year. The amount of ice cover on which seals were counted also varied from year to year, but was not the source of the variations in our population estimates since, generally, high populations were associated with high densities rather than with high ice cover (Figs. 7 and 8).

Table 8
Ringed seal counts and densities in Amundsen Gulf

Year	Nelson Head – Holman seals	Nelson Head – Holman seals/km² ice	Holman – Cape Parry seals	Holman – Cape Parry seals/km² ice
1972*	431	1.023	516	1.277
1977	67	0.803	8	0.273
1978	108	1.745	91	1.028
1979	111	0.731	158	0.759

* From Smith 1973*a*.

The transects between Cape Parry and Holman and between Holman and Nelson Head also showed higher densities in 1978 than in 1977 or 1979 but were similar to 1972 (Table 8). In 1978, in contrast to the high cover elsewhere, there was a lot of open water in Amundsen Gulf, and most of the seals counted were on floe ice near Cape Parry and Nelson Head. In 1979, the ice cover was 8/8 over most of both these transects, and, while the counts were higher, the seals were more evenly distributed and the densities lower, as they were elsewhere (Table 8).

Table 7 and Figures 7 and 8 show variations in ice cover, density, and estimated visible population. As visible population is the product of ice area and on-ice density, correlations are expected between these three variables. There are four possible models for their relationships. If total populations are roughly constant, then:

a) the on-ice density remains roughly constant and the estimated population varies with the ice cover, i.e. seals with no ice stay in the water; or,

Table 7
Ice area, densities and population estimates for ringed and bearded seals

Year	Stratum	Ice area* (10^3 km²)	Ringed seal: Density† (seals/km² ice)	Ringed seal: Pop'n‡ (10^3)	Ringed seal: Standard error§	Bearded seal: Density† (seals/100 km² ice)	Bearded seal: Pop'n‡	Bearded seal: Standard error§
1974	1	13.58	0.617(1)	13.39	1.50	0.53(4)	114.3	28.5
	2	21.56	0.462(2)	16.57	2.70	3.91(1)	1403.5	170.5
	3	23.89	0.327(3)	13.36	1.10	2.14(3)	887.5	175.3
	4	13.49	0.227(4)	5.57	0.77	2.74(2)	666.6	252.0
	1–4	72.52	0.403	49.19	3.37	2.48	3071.9	352.4
1975	1	13.17	0.233(3)	4.94	0.59	1.43(4)	301.9	67.2
	2	11.54	0.191(4)	3.68	0.92	2.31(2)	445.0	196.3
	3	13.64	0.540(2)	12.74	2.04	1.81(3)	426.7	143.2
	4	4.15	0.694(1)	4.74	0.94	3.16(1)	215.6	96.6
	1–4	42.48	0.365	26.10	2.50	1.96	1389.2	270.0
1976	1	12.78	0.369(1)	7.54	1.06	0.83(4)	169.4	43.7
	2	19.71	0.231(3)	7.58	0.99	1.63(2)	534.0	138.2
	3	18.84	0.249(2)	8.15	0.91	1.93(1)	631.9	113.1
	4	18.14	0.165(4)	4.94	0.72	1.18(3)	353.3	80.9
	1–4	69.47	0.244	28.21	1.86	1.45	1688.6	200.9
1977	1	14.13	0.183(3)	4.13	0.48	0.25(3)	57.3	42.7
	2	16.85	0.102(4)	2.87	0.52	3.46(1)	971.1	266.1
	3	15.62	0.444(1)	12.01	1.26	0.96(2)	261.1	63.6
	4	12.83	0.195(2)	4.13	0.65	0.10(4)	19.5	20.4
	1–4	59.43	0.231	23.14	1.58	1.31	1309.1	277.7
1978	1	14.30	0.457(2)	10.46	3.20	0.16(4)	37.6	39.8
	2	23.32	0.324(3)	12.62	1.05	5.20(1)	2021.5	455.5
	3	23.77	0.661(1)	27.21	2.46	1.79(2)	736.0	297.1
	4	22.62	0.294(4)	10.97	1.48	0.84(3)	313.9	90.7
	1–4	84.02	0.434	61.26	4.43	2.20	3109.0	552.8
1979	1	10.78	0.273(3)	4.70	0.68	1.31(3)	226.3	19.8
	2	10.92	0.280(2)	5.08	0.88	1.39(2)	252.5	77.7
	3	22.07	0.592(1)	22.65	3.10	3.66(1)	1398.1	299.6
	4	12.50	0.246(4)	5.07	0.84	0.86(4)	178.7	45.1
	1–4	56.27	0.393	37.50	3.40	2.14	2055.6	313.4

* ΣZ_i of equation [3].
† Values in parentheses are the rank (1 highest, 4 lowest) of the stratum density that year.
‡ P_{11} of equation [8].
§ S_p of equation [9].

Figure 5
Distribution each year of ringed seals counted in the survey area

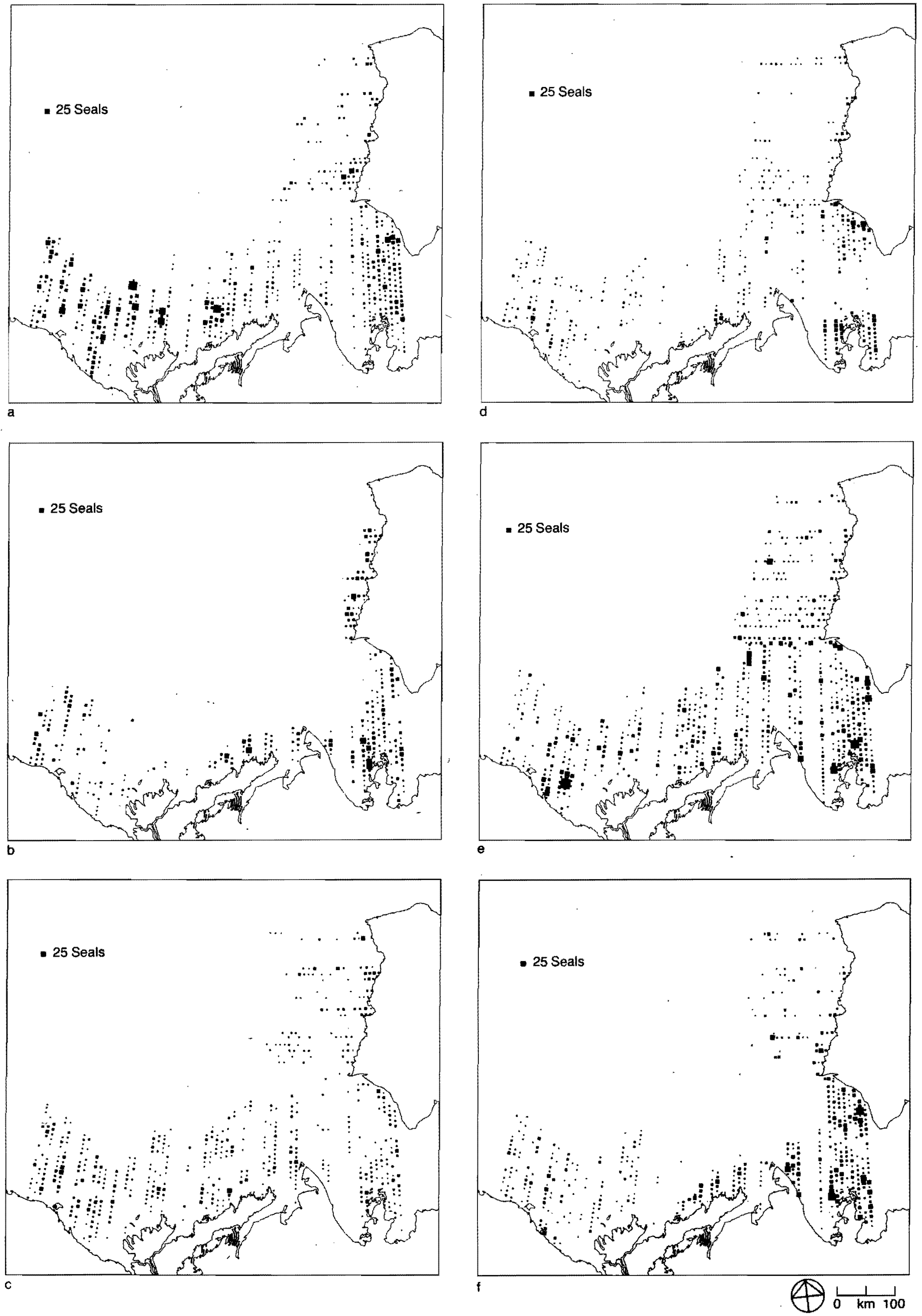


Figure 6
Distribution of ringed seals counted in the survey area 1974–79

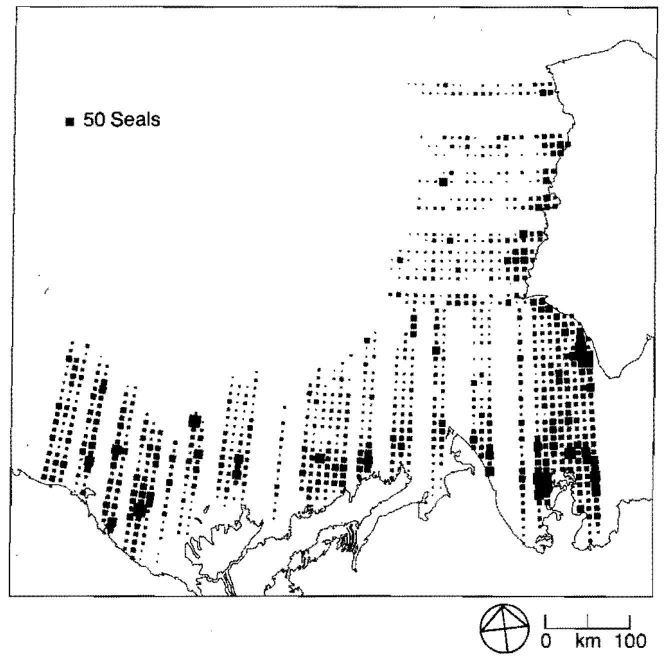


Figure 7
Total numbers of ringed seals, square kilometres of ice and densities of ringed seals in the survey area 1974–79

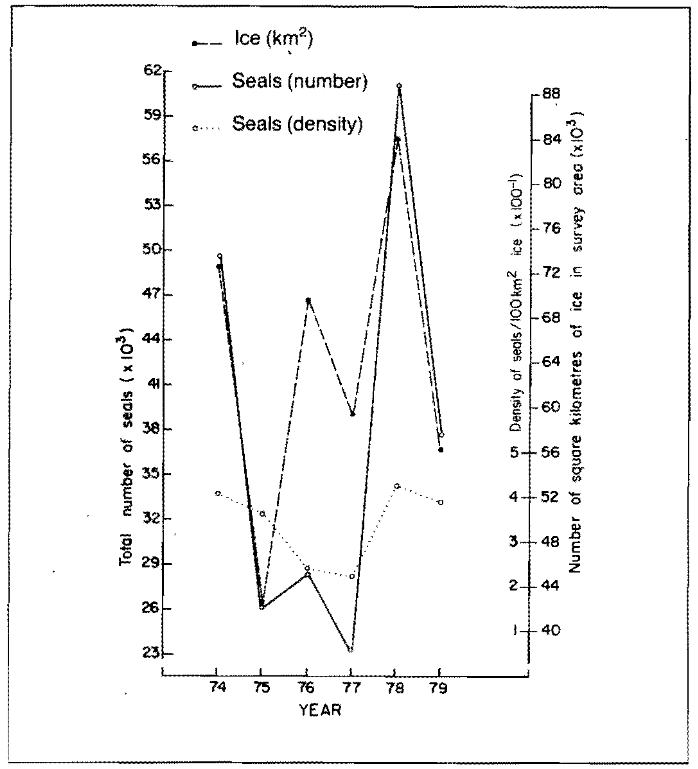
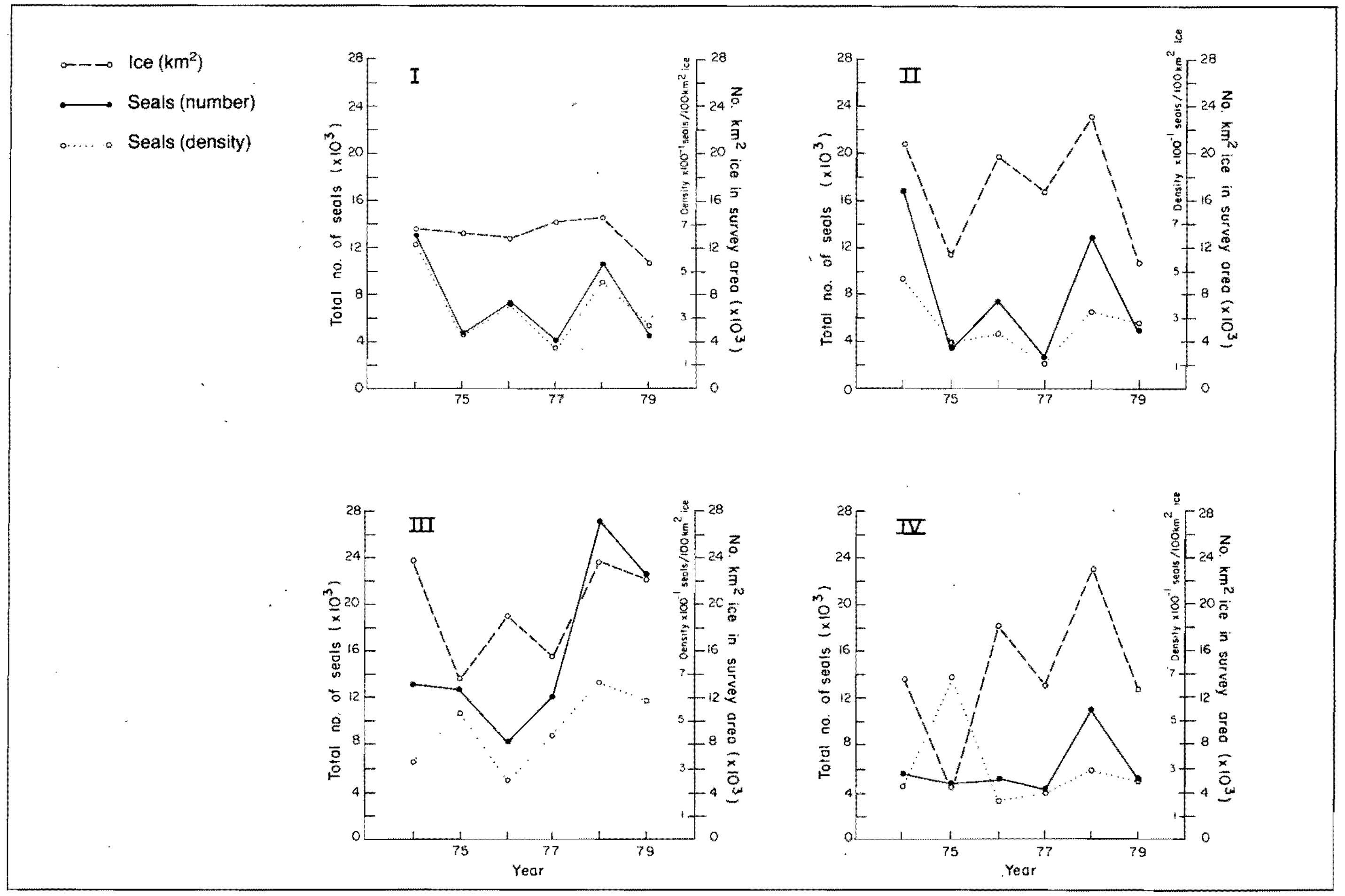


Figure 8
Total numbers of ringed seals, square kilometres of ice and densities of ringed seals in each stratum in the survey area 1974–79



b) the estimated population stays roughly constant and the on-ice density varies inversely with the ice cover, i.e. seals with no ice go and find some.

Intermediate between these models:

c) on-ice density is both negatively correlated with ice cover, and positively correlated with population estimate, i.e. some seals with no ice go and find some while others stay in the water. But if the source of variation was the size of the population and not the ice cover, then

d) the density and the population would show a strong positive correlation, and relationships with ice cover would be masked.

Stratum 4 approximated model b, largely because 1975 had a low ice cover and high density, which combined to yield a normal population estimate (Fig. 8*d*). Amundsen Gulf in all years also approximated model b, which may relate to greater variability of ice cover.

The other three strata and the full results correspond to model d (Figs. 7 and 8*a–c*). There is a small correlation[1] between density and ice area, which happens to be positive, so that estimated population, their product, is positively correlated with both.

Stratum 1 provides the best support for this model (Fig. 8*a*), because its ice area is so nearly constant. The variations in estimated population are therefore almost entirely due to variations in on-ice density, and these variations for Stratum 1 are in step with the total population estimates. These results confirm that the size of the ringed seal population may be quite variable.

The clump factors (Table 9) show that ringed seals are not randomly and independently distributed but rather are very much clumped (see also Stirling *et al.* 1981). Clumpiness increases with population: not only are more groups of seals seen, but the groups are larger. This clumpiness hinders the assessment of habitat preference in the ringed seal by increasing the variability in the counts in the 2-min intervals, and is one reason why our regression results were not more definite.

The ratio c_1/c_2 is a measure of the non-uniformity of distribution between the transects in a stratum. This ratio is not much greater for the total results than for the individual strata, indicating the strata were not very uniform. Again, it appears that stratification was not very effective in improving the precision of the population estimates.

5. Age structure of ringed seals

Our sample sizes are too small to permit a detailed analysis of the age structure of the population. However, from the data available (Table 10), a number of points are clear. In both 1974 and 1975 there were virtually no young of the year in the sample. Thus, although far more pups were born in 1974 than in 1975 (Smith and Stirling 1978), apparently few survived from either cohort. Those cohorts were also almost absent in the samples collected in subsequent years, with the exception of 1976, an anomaly we are unable to explain. This suggests that the conditions that precipitated the decline between 1974 and 1975 had already begun to take effect early in 1974 and were felt first by the young of that year, of which few survived. These results support the conclusion that few young of the year survived from 1974 and 1975. Furthermore, these two missing age classes were not replaced by immigration. A similar pattern was evident in the age structure of ringed seals killed by polar bears (Stirling *et al.* 1977). In 1971–73, 50% (17/34) of those found were young of the year; in 1974 and 1975 none were identified out of a total sample of 57.

In comparison, the ringed seal cohort of 1972 appears strong in all the samples, indicating that was a year of high production and survival of pups. In 1972, young of the year represented 44% of a sample of 292 (Stirling *et al.* 1977). Similarly, in samples of ringed seals collected from apparently healthy populations in other parts of the Arctic, young of the year may make up over 40% of the sample (McLaren 1958*a*, Smith 1973*a*). Thus, from Table 10, ringed seal productivity apparently began to recover in 1976 and returned to normal in 1977.

6. Ovulation rates of ringed seals

The ovulation rates of adult female ringed seals in the eastern Beaufort Sea in 1974 and 1975 were roughly half what they were in 1972, 1977, and 1978 (Table 11), and about half what has been reported from apparently healthy populations from other areas (McLaren 1958*a*, Johnson *et al.* 1966, Smith 1973*a*). The ringed seals in the eastern Beaufort Sea were in poorer physical condition in 1974 than in 1971 and 1972 (Smith and Geraci 1975); presumably that was responsible for the lowered ovulation rates. Judging from the lower ovulation rates and low production of pups in 1975 (Tables 10 and 11), it seems that the seals were still in poor condition that spring as well. Even with the greatly reduced ovulation rates in 1974 and 1975, we expected more young of the year in the 1975 and 1976 samples than we found (Table 10). We do not know if some adult female ringed seals that ovulated did not copulate, did not conceive, or experienced intrauterine mortality. However, Stirling *et al.* (1977) reported that 4 of 130 reproductive tracts examined in 1974 and 1975 showed evidence of pregnancy being terminated prematurely, indicating that at least some copulated and conceived. The samples of reproductive tracts from adult female bearded seals in 1974 and 1975 were small in size but they also showed a similar reduction in reproductive activity.

7. Habitat selection by bearded seals

Regressions of bearded seal densities on habitat factors showed consistent preference between years for shallow water and open ice cover (Table 12). In 4 years (1974 and 1976–78), preferred depths were 25–50 m. This is consistent with the generally reported preference of bearded seals for shallow areas (McLaren 1958*b*, Burns 1967), which would be expected with a demersal feeding habit.

The preference for broken ice areas is shown by a scatter of negative coefficients for various ice cover levels: 2/8 or more in 1975, 7/8 or more in 1976, and any ice cover in 1978. This is in marked contrast to ringed seals, where the preference shown was always for high ice cover.

8. The distribution and abundance of bearded seals

Bearded seals are much less abundant in the Beaufort Sea than are ringed seals. The highest total number estimated was 3072 in 1974 (Table 7). The changes in their total numbers and densities were essentially the same as reported above for ringed seals (Table 7). This similarity is important because, in general, the diets and habitat preferences of the two species are different.

The cumulative observations of bearded seals (Fig. 9) show areas of concentration. The summarized estimates (Table 7) show that Stratum 2 tends to have the highest densities and accounts for a high fraction of the total population. This is probably because Stratum 2 has the largest amount of shallow water, with extensive broken ice. Conversely, Stratum 1, where there is little shallow water, seems to be least preferred by bearded seals.

The clump factors for bearded seals are much lower than those calculated for ringed seals (Table 9), indicating they are less gregarious. However, the highest values occurred in years and strata of high density, showing that the group sizes observed did increase at such times. The lower clumpiness of bearded seals is one reason for the greater consistency and therefore ease of interpretation of their habitat regression results.

[1] Correlations are in general not statistically significant except for those between density and estimated population for strata 1–3.

Table 9
Clump factors for ringed and bearded seals

Year	Stratum	Ringed seals c_1	Ringed seals c_2	Ringed seals c_1/c_2	Bearded seals c_1	Bearded seals c_2	Bearded seals c_1/c_2
1974	1	12.0	8.3	1.45	0.46	0.39	1.17
	2	29.1	22.0	1.32	2.01	1.20	1.68
	3	20.5	4.1	5.00	1.92	1.72	1.12
	4	9.6	5.1	1.88	4.72	4.98	0.95
	1–4	23.2	12.9	1.80	3.04	2.09	1.45
1975	1	10.5	3.7	2.84	1.75	0.65	2.70
	2	26.0	12.5	2.08	4.81	4.81	1.00
	3	14.8	12.5	1.18	2.86	3.46	0.83
	4	7.3	6.9	1.06	1.81	1.86	0.97
	1–4	23.0	10.4	2.21	2.98	3.03	0.98
1976	1	8.3	7.8	1.06	0.82	0.62	1.32
	2	6.2	7.3	0.85	1.84	1.96	0.94
	3	5.6	3.9	1.44	2.86	1.12	2.56
	4	7.0	5.5	1.27	1.19	0.90	1.33
	1–4	8.2	6.3	1.30	1.96	1.28	1.53
1977	1	4.9	3.0	1.63	1.50	1.68	0.89
	2	8.7	4.8	1.81	10.74	3.79	2.84
	3	14.7	6.9	2.13	1.43	0.80	1.78
	4	6.6	3.8	1.74	0.97	1.08	0.90
	1–4	17.6	5.9	2.98	9.20	2.98	3.09
1978	1	59.9	50.4	1.19	2.02	2.24	0.90
	2	6.0	4.6	1.30	8.38	5.50	1.52
	3	16.2	11.7	1.38	6.14	6.02	1.02
	4	20.1	10.7	1.88	1.78	1.33	1.34
	1–4	28.2	16.7	1.69	8.67	4.97	1.74
1979	1	9.2	5.4	1.70	0.33	0.12	2.64
	2	9.9	3.9	2.54	1.17	1.06	1.10
	3	14.8	17.0	0.87	5.09	2.78	1.83
	4	9.3	4.5	2.07	1.12	0.66	1.70
	1–4	23.0	12.1	1.90	3.69	1.89	1.95

Table 10
Number of specimens collected from ringed seals of each age class in the eastern Beaufort Sea

Age class	Age (yr)	1974	1975	1976	1977	1978	1979
Pup	0	[0(0.00)*†	[4(0.02)	14(0.17)	26(0.45)	35(0.48)	43(0.53)
Subadult	1	2	2]	[7	0	9	8
	2	6‡	6	5]	[0	1	10
	3	9	14‡	5	3]	[0	0
	4	0	11	19‡	5	0]	[0
	5	1	5	9	7‡	2	0]
	6	0	4	1	4	6‡	4
	1–6	18(0.30)	42(0.23)	46(0.57)	19(0.33)	18(0.25)	22(0.27)
Adult	7	43(0.70)	140(0.75)	21(0.26)	13(0.22)	20(0.27)	16(0.20)
Total		61	186	81	58	73	81

* The brackets show the cohorts born in 1974 and 1975.
† Proportions of the total are given in parentheses.
‡ Denotes the 1972 cohort.

Table 11
Ovulation rates, determined by the presence of corpora lutea, of adult* female ringed seals in the eastern Beaufort Sea

Year collected	Sample size	Ovulation rate
1972†	27	0.74
1974†	23	0.39
1975†	80	0.49
1977	4	1.00
1978	10	0.90

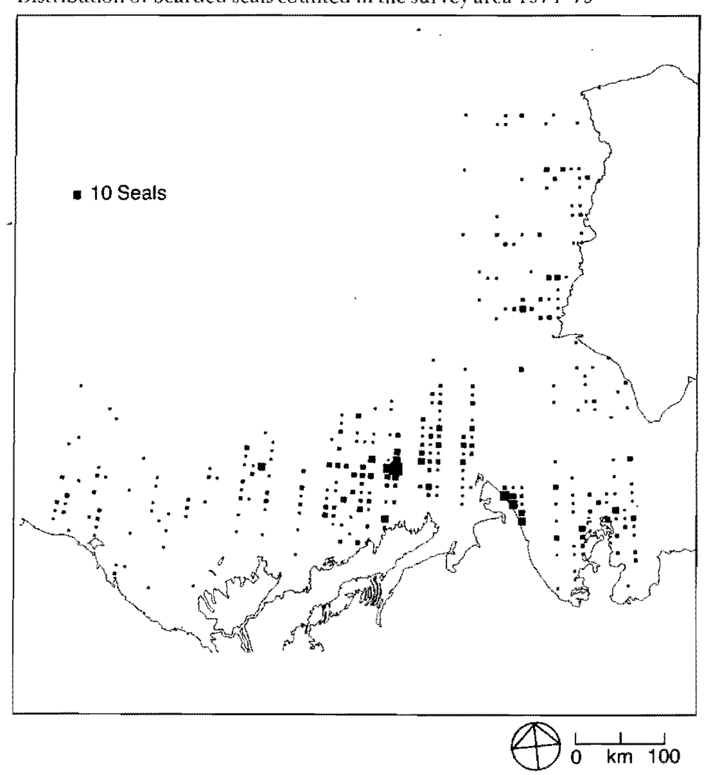
* Six years of age or older (McLaren 1958*a*).
† From Stirling *et al.* 1977.

Table 12
Coefficients of habitat variables entering regressions* of bearded seal density†

Year	Constant‡	Cover§	Ice cover >2/8	Ice cover >7/8	Depth >25 m	Depth >50 m
1974	1.62				5.55	–6.01
1975	1.90		–1.74			
1976	2.49			–1.74	2.71	–3.09
1977	42.15		–42.4		14.73	–16.26
1978	9.83	–9.10			5.89	–6.98
1979	2.25					

* Regressions were stepwise forward with compulsory constant term; significance levels were 0.005 to enter, 0.01 to leave.
† Seals/100 km^2 ice.
‡ Significant at 0.01 in 1974, 0.001 in all other years.
§ Continuous variable, all others binary variables.

Figure 9
Distribution of bearded seals counted in the survey area 1974–79



9. Ecological considerations

Before discussing the ecological considerations, we should briefly review some of the more important points. Our aerial surveys began in 1974, and in 1975 we documented a 50% decline in total numbers. Unfortunately, we have no comparable quantitative survey data from 1972 or 1973, but from the limited data available (Table 8 this paper, Smith and Stirling 1978), it is likely that the total population size and reproductive rates were higher than in 1974. The processes that brought about the decline appear to have begun early in 1974. After 1975, there followed 2 more years of lower numbers, then the population more than doubled. The only estimate of a 'normal' population is the 6-year mean, and six values are barely enough to establish normal values for such a variable quantity. The initial decline from 1974 to 1975, in these terms, is a drop from 30% above normal to 30% below, and the sudden rise in 1978 is to 63% above normal. These changes were far more rapid than have been documented before and the processes involved are of the greatest interest.

There are three possible explanations for the population decline: increased mortality, reduced productivity, and emigration. The normal annual mortality of ringed seals, about 15% (Smith 1973*a*), is not close to the 50% decline recorded. Increased mortality, particularly of subadults (2–5 years), cannot be demonstrated from the data available although we suspect it occurred.

Reduced productivity may have resulted from the seals being in poorer condition in 1974 than in previous years (Smith and Geraci 1975). Although more pups were born in 1974 than 1975 (Smith and Stirling 1978), few survived from either year (Table 10) and ovulation rates were very low in both years (Table 11). Apparently, not only were female seals in poor condition in the spring of 1974, but they did not recover to normal until 1977.

Stirling and Smith (1977) speculated that large-scale movements of ringed seals occur in response to environmental changes and this may have happened to some extent between 1974 and 1975. Smith (1976) reported movements of branded seals from the eastern Beaufort Sea to Point Barrow, Alaska, and Icy Cape, Siberia. Burns *et al.* (1980) reported that densities of seals in the western Beaufort Sea (Barter Island to Barrow) were lower in 1975 than in 1970 and remained low in 1976 and 1977, but were 50% higher farther west in the Chukchi Sea (between Point Barrow and Wainwright) in 1975 than in 1970, then in 1976 and 1977 dropped to levels lower than those of 1970. However, these changes can only be noted without further comment because their direct relationship to our data is not clear.

It is well known locally in the Western Arctic, though poorly documented scientifically, that there is a westward movement of subadult ringed seals along the coast in late summer. This migration is both large and predictable, so net fisheries were well established at several sites in earlier years to catch ringed seals each fall for winter dog food. The size of the fall migration might vary between years, depending on environmental conditions. Also, nothing is known about possible migrations or other movements that might be made by specific age or sex classes of ringed seals.

We cannot be certain what the ultimate factor was that caused this large-scale reduction in numbers. However, we can speculate on the basis of what is known and this may provide a useful point of departure for testing relevant hypotheses. The only major factor that we are aware of was the condition of the sea ice. In the winter of 1973–74 the winds blew predominantly from the northwest and southeasterlies were fewer than usual. As a result, the system of shore leads and polynyas that usually forms along the 20 m depth contour (Cooper 1974, Smith and Rigby 1981) did not occur and the ice was very heavily compacted for many kilometres offshore. Not surprisingly, the sea ice broke up later and to a much lesser extent in 1974 than in most years (Lindsay 1975, 1977).

These unusual sea ice conditions could have affected the seals in two ways. First, it may have been more difficult for the large numbers of ringed and bearded seals that normally occur along the shore lead system to maintain their breathing holes in the exceptionally heavy ice that was continuing to compact through the winter. It seems that a reduction in numbers and reproduction began that was at least coincidental with the heavy ice winter of 1973–74. Smith and Stirling (1978) reported a higher density of ringed seal birth lairs in Prince Albert Sound in 1973 than in 1974, and the densities of ringed seals counted in Amundsen Gulf in 1972 were similar to those of 1978 (Table 8). Polar bears had lower natality rates and were in poorer physical condition in 1974–75 than in 1971–73 (Stirling *et al.* 1976, Kingsley 1979), presumably because of catching fewer seals in the latter years.

Second, Grainger (1975) reported that thicker ice or heavier snow cover reduces the amount of light passing into the water, which could significantly reduce primary productivity. If the ice was thicker in the spring of 1974 and there was less open water, less sunlight would have penetrated the water to warm it and stimulate photosynthesis. Tummers (1980) studied the heat budgets of the southeastern Beaufort Sea in 1974 and 1975. He found that the maximum surface sea temperature was 0.62°C lower in 1974 than in 1975 and that the −1.5°C isotherm was at a maximum of 15 m in 1974 compared to over 50 m in 1975. The major source of heat to the Beaufort Sea is the sun and the net radiation in 1975 was double that of 1974. Clearly, the sea received significantly less sunlight and was colder in 1974; both factors would have reduced biological productivity. Grainger (1975) also noted that the Beaufort Sea supported, at best, a fairly low rate of primary and secondary production and a relatively uncomplicated food chain, so that changes at the lower levels could have rapid and significant effects on higher level species. Thus, it seems likely that the food resources for seals in the winter of 1974–75 were significantly reduced, seals probably entered the winter in poor condition, and productivity remained low in 1975.

An indication that we are dealing with swings in the ecosystem, rather than with isolated effects on one species, is demonstrated by the unexpectedly high correlation (0.968) between the population estimates of ringed and bearded seals. These species have different feeding habits, though both are opportunistic feeders, and, according to the results given earlier, have distinctly different habitat preferences; yet the variations in their populations, over this 6-year period, have been very closely in step. That this correlation is not caused by counting both species on the same varying ice cover is shown by the almost equally high (0.947) correlation in on-ice density.

An aspect that appeared in the data but was not well understood was the relationship between the total area of ice in the survey area, the estimated population, and the density of seals per square kilometre of ice. To recapitulate, except for 1976, there appeared to be a positive correlation between these three factors. For example, density of seals did not drop in 1978 even though the total ice area suddenly doubled. It is curious that total densities did not increase when the total ice area before break-up was less. An hypothesis which may explain this phenomenon is that in the autumn, at the end of the open water period and before freeze-up, the seals establish the densities at which they can overwinter under the sea ice, probably in relation to the available food supply. In fast-ice areas where seals maintain their own breathing holes during the winter, agonistic behaviour probably keeps the densities fairly constant. Smith and Hammill (1981) reported agonistic behaviour between seals hauled out at breathing holes in the fast ice. Densities are probably more variable around shore leads and polynyas where open water recurs during the winter. When the surveys are conducted, in late spring before break-up, the densities would be similar to what they had been during the winter except in areas where new cracks have formed, thus creating new places to breathe or haul out that are not already being maintained or defended by resident seals.

Later in the season, as break-up proceeds, densities of seals may increase in some areas as the amount of ice decreases. Seals move, probably to feed in areas that have not been heavily exploited by winter residents. For example, in the High Arctic, Smith *et al.* (1978) and Finley (1979) reported that densities of seals in Aston Bay and Freeman's Cove increased during July as break-up proceeded in Barrow Strait. Stirling (1969) reported a similar pattern of behaviour in Weddell seals, the Antarctic ecological counterpart of the ringed seal, through the summer in McMurdo Sound.

As discussed earlier, the total ice cover in the survey area rose in 1976 and 1977 but numbers and densities remained low, indicating that the 1975 decline was not observed solely because there was less habitat to survey. The ice cover during the winter and the pattern of break-up in the spring were fairly normal (Lindsay 1975, 1977) but the level of biological productivity is unknown.

In 1978 the estimated populations of seals on the ice and their density more than doubled. Because young of the year could not account for more than 15% of any estimate, increased productivity is almost insignificant when considering possible explanations for an increase of over 250% in the estimates. The amount of ice available to survey was the highest in the 6 years studied, but this did not lower the density. The increase was real and we believe that it could only have occurred as a result of large-scale immigration. In such a circumstance, one might normally expect the bulk of the immigrants to be subadults. However, from the limited data available (Table 10) the proportions of subadults and adults in 1977–79 (when productivity had returned to normal) were quite similar and the missing cohorts of 1974, 1975, and apparently 1976, were not replaced. Thus it appears that if shifts in large portions of the population take place, they affect all age classes. Why this occurred in 1978 is not clear. In 1979, the available ice and the total population decreased although densities did not change appreciably and apparently productivity remained high (Table 10). Because the age structure data indicate that productivity remained high in 1978 and 1979 (Table 10), the population data (Fig. 7) probably indicate the magnitude of variation that may occur within a healthy ringed seal population. In this instance, it was 3 years after the initial decline before productivity returned to normal and 4 years before numbers recovered, apparently largely through immigration. We do not know if these are minimum times for recovery.

Until recently, management of marine mammals in the Canadian Arctic, to the extent that they are managed at all, seems to have been based on the assumption that ecological conditions show little variability. Thus, once populations are counted or quotas are established, little change in population management takes place for long periods. The results of this study have clearly shown that ice conditions in the eastern Beaufort Sea can be highly variable, can influence other ecological parameters, and can cause changes in the distribution and abundance of ringed and bearded seals. We expect that similar variability will be documented in other areas of the Arctic when comparable studies have been completed.

What this means in terms of environmental assessment is that, because conditions are so variable, the consequences of possible man-made detrimental effects will vary depending on the status of the seal population at the time. When the seal population is low, and in poor condition, a similar situation is likely with animals at lower trophic levels. Under these circumstances, it is likely that man-made environmental damage will be considerably more serious and long-lasting in its effect. Although it seems that seal populations are able to recover in only a few years from a 50% decline, apparently with the aid of large-scale immigration, we do not know what determines whether or not this can take place. Could immigration occur in any year or only after a minimum period of time that would allow for the recovery of populations at lower trophic levels? The fact that numbers and densities remained low in 1976 and 1977, even though ice conditions apparently improved, suggests that there is a lag time before productivity and population size can recover.

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