Final Report

Correction Factor for Ringed Seal Surveys in Northern Alaska

by

Brendan P. Kelly*

Juneau Center, School of Fisheries and Ocean Sciences University of Alaska Fairbanks 11120 Glacier Highway Juneau, AK 99801

Assisted by

Orianna P. Harding Mervi Kunnasranta Lori T. Quakenbush Brian D. Taras

February 2005

*Present address: School of Arts and Sciences University of Alaska Southeast 11120 Glacier Highway Juneau, AK 99801 brendan.kelly@uas.alaska.edu

Contact information

e-mail: cmi@sfos.uaf.edu phone: 907.474.7707 fax: 907.474.7204 postal: Coastal Marine Institute School of Fisheries and Ocean Sciences University of Alaska Fairbanks Fairbanks, AK 99775-7220

Table of Contents

List of Tables iv	
List of Figures v	
Abstract 1	
Introduction 1	
Methods	
Study area 3	
Locating seal holes 4	
Spatial and temporal patterns of lair use 5	
Correction factors	
Results	
Locating and capturing seals 7	
Spatial and temporal patterns of lair use	
Correction factors 16	
Discussion 21	
Locating seal holes	
Spatial and temporal patterns of lair use	
Correction factors	
Recommendations	
Survey protocols	
Further research	
Acknowledgements	
Study Products	
References	

List of Tables

Table 1.	Ringed seals captured and telemetrically monitored until 7 June in 1999 and 10 June in 2000	5
Table 2.	Distances between breathing holes and resting locations (lairs and basking sites) used by radio-tagged seals in 1999 and 2000 and home range areas based on minimum convex polygons	10
Table 3.	Daily correction factors (CF) and coefficients of variation (CV) for counts of ringed seals during usual survey dates in the Alaskan Beaufort Sea	18

List of Figures

Figure 1.	The study was conducted on the shorefast sea ice of the Beaufort Sea between Prudhoe Bay, Reindeer Island, and the man-made Northstar Island	4
Figure 2.	Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 1999	8
Figure 3.	Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 2000	9
Figure 4.	Cumulative percent frequency of home range size (minimum convex polygon) for ringed seals radio tracked in 1999 and 2000	10
Figure 5.	Spatial relationships between tracking hydrophones and subnivean lairs and breathing holes used by an adult male ringed seal (LM00) tracked above (by radio transmitter) and below (by ultrasonic transmitter) the ice in April and May 2000	11
Figure 6.	Dates of aerial surveys of ringed seals conducted along the Beaufort Sea coast of Alaska by the Alaska Department of Fish and Game ind by LGL Limited in the search of the	13
Figure 7.	Proportion of radio-tagged seals resting on the ice outside of lairs by time of day	14
Figure 8.	Temperature records from a ringed seal lair (99H014) showing (A) pronounced differences between temperatures inside and outside of the lair and large temperature changes associated with seal occupation in the first week of May 1999, and (B) a less pronounced temperature difference inside and outside of the lair and an example of small temperature changes that may or may not be associated with seal activity	15
Figure 9.	Comparison of the proportions of radio-tagged seals visible and the fraction of the maximal count of seals visible in the study area by date in 2000	16
Figure 10.	Proportion of radio-tagged ringed seals resting on the ice by date in (A) 1999 and (B) 2000	17
Figure 11.	Air temperatures measured at the ice camp (1999 and 2000) and at the Deadhorse airport (1999)	19
Figure 12.	Wind speed measured at the ice camp in 1999 and 2000	20
Figure 13.	The proportion of radio-tagged seals visible on the ice and the diel variation in liquid moisture in the snow (reflected in the diurnal difference in backscatter amplitude) by date in 2000	21

Abstract

The proportion of radio-tagged ringed seals visible on the ice surface from April to June in 1999 (n = 8) and 2000 (n = 10) was used to estimate correction factors for aerial surveys. Radio tracking proved effective for determining when seals were available to be counted; monitoring lair temperatures was less effective for that purpose.

The transition period, defined as the period during which the majority (75%) of the tagged seals began resting outside of lairs, was longer in 2000 (24 days) than it was in 1999 (7 days). The midpoint of the transition period, the day by which 50% of the tagged seals began resting in the open, was 31 May in both years. Only once each year was a lair used subsequent to each seal's first appearance outside of a lair. Changes in the number of seals counted during ground-based, visual surveys of seals resting on the ice corresponded to changes in the number of radio-tagged seals basking. Tagged seals spent approximately 20% of the time out of the water before appearing outside of lairs and approximately 30% of the time out of the water after they began to abandon lairs. The transition from lair use to resting in the open appeared related to measurable characteristics of the snow, and backscatter radar, sensitive to the liquid moisture content of snow, offers promise for remotely determining when seals have abandoned their subnivean lairs.

Aerial surveys underestimated actual ringed seal densities by factors ranging from 2.33 to >13 because the proportion of seals visible during the survey periods changed rapidly from day to day. Interannual comparisons of seal densities based on aerial surveys have been further compromised by a shift in survey dates from mid-June in the 1970s to late May in the 1990s. The proportion of seals visible on the ice was more stable between 12:00 and 18:00 (Alaska Daylight Saving Time [ADT]) than between 10:00 and 16:00, the current standard for aerial surveys of ringed seals in Alaska.

In April, May, and early June, most radio-tagged ringed seals remained close to their capture and release sites, with 88% of their home ranges measuring less than 500 ha in area. One seal, however, had a home range of almost 600 ha and another of almost 3,000 ha.

Introduction

Aerial surveys have been widely used to estimate local densities and, by extrapolation, population size, of ringed seals (*Phoca hispida*) and other pinnipeds [Chapman et al. 1977; Stirling et al. 1977; Harwood and Stirling 1992; Rogers and Bryden 1997; Garner et al. 1999]. Spatial and temporal comparisons typically rest on the assumption (often implicit) that the proportion of animals visible is constant from survey to survey [Caughley 1977; Drummer 1999]. In a few instances, that assumption has been tested in harbor seal (*Phoca vitulina richardsi*) populations using radio telemetry [Withrow and Loughlin 1995, 1996; Huber et al. 2001]. Another recent approach to harbor seal surveys ignored the unseen fraction and analyzed population trends by adjusting counts to standardized conditions based on environmental and temporal covariates [Frost et al. 1999]. The latter approach assumes that the appropriate covariates to predict the peak number of animals potentially visible have

been identified. Further complications are that seasonal peaks in the number of seals out of the water vary by demographic class, and the timing of those peaks may vary from year to year depending on food availability [Green et al. 1995; Daniel et al. 1999; Jemison and Kelly 2001].

Pinnipeds occupying sea ice are especially difficult to count, because they are broadly distributed on an ephemeral, often moving substrate [Green et al. 1995]. Ringed seals, for example, are found in all seasonally ice-covered seas of the northern hemisphere [Scheffer 1958; King 1983]. They likely are the most numerous phocid in the hemisphere [Scheffer 1958; Smith 1987; Kelly 1988], but a reliable worldwide population estimate is lacking due to the difficulties of surveying such an expansive habitat [Kelly 1988]. Nonetheless, regional and local aerial surveys have been used for temporal and spatial comparisons of densities. Assessing the impacts of harvests, ship traffic, and offshore industrial activities on ringed seal populations has depended heavily on analyses of temporal trends in local densities as estimated by aerial surveys. An inherent assumption of that approach is that the proportion of seals visible is constant over time. Surveys of visible seals have been used to test for interannual changes in density within local areas and to compare densities over areas that required several days to weeks to survey. For example, since 1970, the Alaska Department of Fish and Game (ADFG) contrasted densities in several sectors along the Chukchi and Beaufort Sea coasts of Alaska and related the observed differences to habitat features and human activities including industrial activities [Burns and Harbo 1972; Burns and Kelly 1982; Frost and Lowry 1988, 1999; Frost et al. 1988, 1997, 1998]. More recently, LGL Limited¹ used aerial surveys to contrast densities at a much finer scale to assess potential impacts of oil development on ringed seals [Green and Johnson 1983; Link et al. 1999; Moulton and Elliott 1999; Moulton et al. 2000].

In the case of ringed seals, the proportion of the population that is visible during a survey is not only a function of the proportion of seals in vs. out of water (as in other pinnipeds) but also of the proportion under vs. on top of the snow. During winter and much of the spring, ringed seals come out of the water to rest primarily in subnivean lairs excavated above breathing holes in the sea ice [Chapskii 1940; McLaren 1958; Smith and Stirling 1975]. Surveys of ringed seals have been concentrated in late May and early June when some of the seals have abandoned their lairs and are visible resting on the surface of the ice. Adult seals are molting then and regeneration of the epidermis requires that they bask in the sun to elevate skin temperatures [Feltz and Fay 1966; King 1983]. At that time of year, seals partition their time between diving under the ice, where they are not visible, and resting on top of the ice, where they may or may not be visible. Typically, the greatest numbers of seals are visible on the ice "just before the ice break-up in most mid-arctic localities" [Smith 1973a], although Burns and Harbo [1972] recognized that "extensive water on top of the fast ice, from melt and overflow of rivers" reduced the number of seals visible. As a result, "it is difficult to predict when breakup will begin and how long the survey window might be in a particular year" [Frost and Lowry 1999].

¹ LGL Limited is the Canadian parent company. It's Alaska subsidiary is LGL Alaska Research Associates.

Comparisons of local densities of seals visible on the ice have been used to assess the effects of human activities on ringed seals [Frost and Lowry 1988; Kelly et al. 1988; Richardson and Williams 2000]. Frequently, the human activities of concern occurred some months before the surveys were conducted, and the assumption was made that local seal densities had not changed in the interim. Radio tracking and intensive aerial survey efforts, however, indicated that some ringed seals might move away from their winter range when they emerge from their lairs to bask on top of the ice. At least four of thirteen seals tracked telemetrically near Prudhoe Bay in the 1980s "hauled out at new sites ... several kilometers" from those occupied prior to the beginning of snow melt [Kelly and Quakenbush 1990]. Two of ten seals tracked in the Canadian Arctic basked at sites several kilometers from lairs they occupied earlier in the spring [Kelly, unpublished]. The density of seals visible nearshore decreased while the density offshore increased near Prudhoe Bay during intensive aerial surveys conducted over eight days in 1999 [Moulton et al. 2000]. The changes in densities in 1999 were interpreted as a large-scale movement of seals, but no such shift was evident in similar surveys conducted in 2000 or 2001 [M. Williams, pers. comm.]. We do not know what determines whether ringed seals bask at the same breathing holes they used during their months under the ice and snow.

We used radio telemetry to determine where and when in April, May, and early June ringed seals were concealed under the ice, concealed in subnivean lairs, or visible on top of the snow and ice. We simultaneously monitored weather and snow conditions to determine the relationships between environmental variables and the availability of seals for counting. Our objectives were to determine:

- 1. if there is a predictable period when the proportion of seals visible is constant,
- 2. the correction factor(s) necessary to adjust counts of seals visible to yield estimates of population size,
- 3. the environmental conditions that influence the proportion of seals visible, and
- 4. whether the distribution of seals basking in May and June reflects the distribution of seals during winter months.

Methods

Study area

We conducted field studies between 1 April and 7 June in 1999 and 1 April and 9 June in 2000. We monitored on-ice resting bouts by ringed seals in the nearshore Alaskan Beaufort Sea seaward from Prudhoe Bay to just beyond Reindeer Island (Figure 1) in May 1999 and April and May 2000 (Table 1). Shorefast ice covers the area from October to July in most years [Wise and Searby 1977]. Water depths are mostly less than 9 m with a maximum of 15 m. Most of the snowfall occurs during September and October when open water in the Beaufort Sea provides moisture [Dingman et al. 1980; Walker et al. 1980]. Snow is redistributed by winds throughout the winter [Benson et al. 1975], forming areas of shallow snow over smooth ice and drifts on the windward and leeward sides of irregularities in the

ice surface (e.g., pressure ridges). Wind-packed snow, in which ringed seals excavate subnivean lairs, reaches maximal depth in May, averaging 30–40 cm [Benson et al. 1975].



Figure 1. The study was conducted on the shorefast sea ice of the Beaufort Sea between Prudhoe Bay, Reindeer Island, and the man-made Northstar Island.

Locating seal holes

We delayed the intended start of this study by one year in order to train two new dogs to locate ringed seal breathing holes and lairs. The dogs (Labrador retrievers) were trained, using positive reinforcement, to home on the scent of ringed seals and to indicate the source of the odor by digging in the snow [Kelly and Quakenbush 1987]. The principal investigator has trained nine dogs to locate seal holes since learning the method from Thomas Smith and Jimmy Memorana in 1981. Previously, we used experienced dogs to lead those in training to breathing holes and lairs, where they would be positively reinforced. After following the experienced dogs, typically on several dozen searches, the inexperienced dogs would begin to compete with them to reach seal sites first. From then on, the inexperienced dogs could

find seal holes without the aid of other dogs. As no experienced dogs were available to us after 1997, we trained the dogs used in this study to locate seal skin and blubber and then transferred the skill to locating seal holes. The dogs were taught to associate the odor of ringed seals with the command "natchiq", and they practiced locating the seal samples on land weekly in September 1997 through March 1998 before commencing to search for seal holes on the sea ice in April 1998. We focused our field efforts in April and May 1998 on giving the dogs practice at locating seal holes.

Capture date	te Seal ID Sex Minimal age (years)		Minimal age (years)	First observed out of lair	
6 May 1999	RI99	М	6	30 May 1999	
6 May 1999	SW99	F	6	21 May 1999	
13 May 1999	MA99	F	7	28 May 1999	
14 May 1999	VR99	F	6	29 May 1999	
15 May 1999	SM99	М	7	3 June 1999	
21 May 1999	SP99	F	6	-	
23 May 1999	CH99	F	5	3 June 1999	
24 May 1999	OR99	F	5	2 June 1999	
25 April 2000	CS00	М	7	17 May 2000	
27 April 2000	LM00	М	6	10 June 2000	
30 April 2000	CC00	М	6	24 May 2000	
1 May 2000	SL00	М	7	_	
2 May 2000	RA00	F	6	31 May 2000	
3 May 2000	EL00	М	5	<3 May 2000	
6 May 2000	PU00	М	7	5 June 2000	
6 May 2000	OC00	F	4	3 June 2000	
17 May 2000	LS00	F	5	>4 June 2000	
18 May 2000	IS00	М	7	_	

Table 1. Ringed seals captured and telemetrically monitored until 7 June in
1999 and 10 June in 2000. Each seal's minimal age was determined
from counts of annuli on claws of the forelimbs.

Spatial and temporal patterns of lair use

We investigated spatiotemporal patterns of lair use among ringed seals by monitoring lair temperatures and the activity patterns of seals. Trained dogs located subnivean breathing holes and lairs, and we marked those sites with numbered wooden stakes and recorded the locations with global positioning systems.

We measured air temperatures inside and outside of lairs using thermistors and Hobo Temperature Loggers (Onset Computer Corporation). Occupation of lairs by seals was indicated by abrupt temperature changes in the lairs [Kelly et al. 1986; Smith 1987; Kelly 1988; Kelly and Quakenbush 1990; Kingsley et al. 1990]. Ambient and lair temperatures were recorded at 12 lairs in 1999 and another 12 lairs in 2000.

Activity patterns were recorded for radio-tagged ringed seals (8 in 1999 and 10 in 2000). We captured seals in nets that pursed below them when they entered breathing holes [Kelly 1996], and we glued VHF radio transmitters with unique frequencies to the hair on each seal's back. We monitored radio signals hourly from stations equipped with 8-element Yagi antennas on 35-ft high masts and within 5 km of the seal capture sites. We rotated the antenna through 360° while monitoring and recording the direction from which each signal was received. Each time a seal came out of the water, as indicated by the presence of its radio signal, we determined its location using a mobile receiver and hand-held directional antenna array. The directional antenna array consisted of 2 H-antennas communicating with the acoustic receiver by way of a null combiner. Thus, the bearing from the array to a transmitter was indicated by a null surrounded by high amplitude signals. Typically, 5 or more bearings (with an accuracy of approximately $\pm 3^\circ$) from points surrounding a tagged seal were obtained and the seal's position read as the intersection of those bearings. Once the seal's position was determined, we recorded whether it was concealed within a lair or visible on the snow surface.

We glued ultrasonic transmitters (65–75 kHz) to the hair of 3 of the seals radio tagged in 1999 and 6 of the seals tagged in 2000. An array of 4 hydrophones deployed under the ice was used to track the three-dimensional under-ice movements of those seals [Wartzok et al. 1992a, b]. The hydrophones communicated through acoustic receivers with a digital processor that precisely measured the time delays between the arrivals of transmitter pulses at each of the 4 hydrophones. Each seal was tracked for a period of a few hours to 2 weeks.

To assess the impact of our activities on the tagged seals, we counted all seals visible on the ice in an area of approximately 25 km² daily (ca. 16:00 ADT) from 29 May to 10 June 2000. We used binoculars (Leica and Zeiss 10×42) to make the counts from the roof of a building 62 m above the ice at the southern edge of the study area. The number of seals visible in those surveys was compared with the cumulative proportion of tagged seals visible each day to determine whether the tagged population behaved differently than the overall population.

Environmental variables that might influence when seals were visible on the ice were measured in the study area and, for some variables, at the airport in Deadhorse. We recorded air temperature, snow temperature (from ice surface to snow surface at 5 cm intervals), wind speed, and wind direction within the study area every 30 min from 21 April to 8 June 2000. The data were stored on a CR10 data logger and SM192 storage module (Campbell Scientific, Inc.). We examined changes in the distribution of liquid water in the snow pack, snow depth, the size and morphology of snow grains, and the overall snow landscape to monitor the transformation of the snow pack during snowmelt [Liston and Sturm 2002; Sturm and Liston 2003]. We also obtained reports of satellite-borne Ku-band backscatter data for our study area in 2000 from the Jet Propulsion Laboratory in California. The satellite, QuikSCAT, reported active microwave data (14 GHz) from our study area at 06:00 and 18:00 daily. The microwave backscatter is highly sensitive to the amount of liquid

moisture in snow, and the difference in backscatter amplitude between the morning and evening passes of the satellite indicated the degree of diurnal freezing and thawing in the snow cover [Tjuatja et al. 1992; Nghiem et al. 1995].

Correction factors

We used the delta method to calculate the correction factor (and its uncertainty) by which counts of seals should be multiplied to account for unseen seals based on the proportion of tagged seals visible. The delta method finds estimates and standard errors of nonlinear functions of parameter estimates [Cook and Weisberg 1999].

Data from the aerial surveys were acquired from LGL Limited (1999 and 2000) and the Alaska Department of Fish and Game (1999).

Results

Locating and capturing seals

Both dogs readily located ringed seal breathing holes and lairs in their first season on the sea ice; one found her first breathing hole within 0.5 km of the shore on her first ever excursion on the ice. The trained dogs located 86 breathing holes and lairs in 1999 (Figure 2) and 202 in 2000 (Figure 3). An additional 19 and 8 breathing holes and lairs were located by tracking radio-tagged seals in 1999 and 2000, respectively. The overall distribution and density of breathing holes and lairs were similar between years, although there was a greater concentration of breathing holes in the southeastern portion of the study area in 2000. Most of those holes were on an active crack.

We set nets in breathing holes 27 times in 1999 and captured 8 seals 9 times (1 recaptured). In 2000, we set nets 41 times and captured 10 seals 15 times (5 recaptured). We tagged and tracked 2 male and 6 female seals in 1999 and 7 male and 3 female seals in 2000 (Table 1).



Figure 2. Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 1999. Also shown are the minimum convex polygons delineating the home ranges of 8 ringed seals based on on-ice resting sites.

Spatial and temporal patterns of lair use

Home ranges of the seals tracked in 1999 were small and stable throughout the monitoring periods in May and early June (Figure 2). All 8 seals tracked in 1999 remained within 2.1 km of their capture sites and the distances between on-ice resting sites used ranged from 0.4 to 1.6 km (Table 2). Six of those eight seals were tracked to basking sites, all of which remained within these small home ranges. In 2000, 5 of the 10 tracked seals remained within 2.5 km of their capture sites (Figure 3). The other 5 seals, however, rested at sites >2.5 km from their capture sites. Two of those seals moved over 6 km between resting sites. Two lairs occupied by OC00 were 8.6 km apart, and a lair and basking site used by CC00 were 6.8 km apart (Table 2). Minimum convex polygons for 88% of the seals were less than 500 ha in area (Figure 4).



Figure 3. Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 2000. Also shown are the minimum convex polygons delineating the home ranges of 8 ringed seals based on on-ice resting sites. The home ranges of 2 radio-tagged seals were not determined.

Seal ID	Minimal & maximal distances (km) between capture and on-ice resting sites	Maximal distance (km) between on-ice resting sites	Home range (ha)	
RI99	0.4-1.4 1.4		85	
SW99	1.1-1.3	0.4	22	
MA99	0.6-1.3	1.0	40	
VR99	0.9-1.4	0.6	42	
SM99	0.9-1.0	0.7	33	
SP99	1.2-2.1	1.6	101	
CH99	0.7-1.0	0.8	27	
OR99	0.8-1.5	1.1	71	
CS00	1.2-2.4	1.5	104	
LM00	0.2-1.1	1.0	65	
CC00	0.2-6.6	6.8	582	
SL00 4.8-4.8		-	_	
RA00 0.6–1.3		1.0	57	
EL00	2.8-2.8	2.8	_	
PU00	0.5-1.6	1.9	79	
OC00	0.5-8.0	8.6	2924	
LS00	1.5-1.5	1.5–1.5 0.4		
IS00	2.9-4.2	1.4	18	

Table 2. Distances between breathing holes and resting locations (lairs and basking sites) used by radio-tagged seals in 1999 and 2000 and home range areas based on minimum convex polygons.



Figure 4. Cumulative percent frequency of home range size (minimum convex polygon) for ringed seals radio tracked in 1999 and 2000.

Only 1 of the seals tagged with an ultrasonic transmitter was tracked under the ice for an extended period of time. An adult male (LM00) was located (by radio signals) when he was out of the water and tracked in 3 dimensions (by ultrasonic signals) when he was in the water. Between 27 April and 13 May 2000, he used 3 breathing holes and 4 lairs, all within 1.4 km of one another (Figure 5). The greatest distance between 2 lairs used by LM00 was the same (1.1 km) as the greatest distance between 2 of his breathing holes.



Figure 5. Spatial relationships between tracking hydrophones and subnivean lairs and breathing holes used by an adult male ringed seal (LM00) tracked above (by radio transmitter) and below (by ultrasonic transmitter) the ice in April and May 2000.

Aerial surveys of ringed seals in the Alaskan Beaufort Sea have spanned nearly 1 month, with surveys conducted as early as 25 May and as late as 20 June. In the 1970s, surveys were always conducted in June, but in the 1980s and 1990s, surveys were conducted increasingly earlier (Figure 6).

The first radio-tagged seals appeared on the ice outside of lairs on 21 May 1999 and on 3 May 2000. The latter, an adult male (EL00) was captured on 3 May 2000 at a hole already open to the surface and, apparently, began basking there as early as 26 April when a seal was visually observed resting next to that hole. The transition period, defined as the period during which the majority (75%) of the tagged seals began resting outside of lairs, was longer in 2000 (24 d) than it was in 1999 (7 d). The midpoint of the transition period, the day by which 50% of the tagged seals began resting in the open, was 31 May in both years.

Seals spent more time out of the water once they began emerging outside of lairs. The probability of a tagged seal being out of the water increased from 0.18 when seals were using lairs to 0.30 when seals were basking in 1999 and from 0.14 when using lairs to 0.37 when basking in 2000. When basking, the tagged seals showed a strong diel pattern in the proportion of time spent on the ice. Less than 20% of the tagged seals were visible on the ice between 00:00 and 08:00 (ADT), after which the proportion increased rapidly until about 12:00 (Figure 7). The proportion continued to increase slowly until 16:00 after which it declined slowly until about 19:00 and then rapidly until about 03:00. More than 45% of the tagged seals were visible on the ice between 12:00 and 19:00.





Figure 7. Proportion of radio-tagged seals resting on the ice outside of lairs by time of day.

We monitored the temperature in 12 lairs in 1999 and 12 lairs in 2000 for periods ranging from 5 to 47 days. Distinct diurnal patterns were observed in ambient air temperatures, but temperatures inside lairs were stable, as they were heated by the thermally-constant seawater and insulated from atmospheric temperatures by their snow cover. When a seal entered the lair, its body heat produced a marked increase in lair temperature; when the seal left the lair, the temperature dropped quickly. Lair temperatures accurately reflected lair use when ambient air temperatures were well below 0°C in April and early May (Figure 8a), but became more difficult to interpret in terms of lair occupation as ambient air temperature converged with typical lair temperature later in May (Figure 8b).



Figure 8. Temperature records from a ringed seal lair (99H014) showing (A) pronounced differences between temperatures inside and outside of the lair and large temperature changes associated with seal occupation in the first week of May 1999, and (B) a less pronounced temperature difference inside and outside of the lair and an example of small temperature changes that may or may not be associated with seal activity.

Correction factors

To determine if our sample of radio-tagged seals represented the behavior of the population as a whole, we compared, in 2000, the proportion of tagged seals visible with the total number of seals visible in a 25-km² area expressed as a fraction of the maximal count of visible seals (Figure 9). The number of seals visible on the ice in our study area in 2000 ranged from 0 to 19. The cumulative proportion of tagged seals visible on the ice was substantially the same as the cumulative number of all seals (tagged and not tagged) visible in the study area.



Figure 9. Comparison of the proportions of radio-tagged seals visible and the fraction of the maximal count of seals visible in the study area by date in 2000.

In both 1999 and 2000, the proportions of tagged seals visible on the ice increased in late May and early June (Figure 10). Tagged seals began emerging later in 1999 than in 2000, and the proportion visible on the ice increased more slowly in 2000. We observed maximal proportions of 0.41 on 3 and 7 June 1999 and 0.64 on 9 June 2000, but we do not know if those proportions increased after our observations ended on 7 June (1999) and 11 June (2000). Thus, calculated correction factors varied widely from day to day and interannually during the typical aerial survey period in the Alaskan Beaufort Sea (Table 3).



Figure 10. Proportion of radio-tagged ringed seals resting on the ice by date in (A) 1999 and (B) 2000.

	1999		2000			
Date	CF	(CV)	Aerial survey	CF	(CV)	Aerial survey
24 May	>11 ^a			11.00	(0.50)	
25 May	>13 ^a			>11 ^a		
26 May	>13 ^a			11.00	(0.50)	
27 May	>13 ^a			>11 ^a		
28 May	13.00	(0.50)		>11 ^a		
29 May	>13 ^a			>11 ^a		
30 May	4.75	(0.44)		11.00	(0.50)	
31 May	13.00	(0.50)	ADFG	4.00	(0.43)	LGL
1 June	4.75	(0.44)		11.00	(0.50)	LGL
2 June	2.78	(0.37)		>11 ^a		LGL
3 June	2.78	(0.37)		4.00	(0.43)	LGL
4 June	2.78	(0.37)	LGL	4.00	(0.43)	LGL
5 June	4.75	(0.44)	LGL	4.00	(0.43)	LGL
6 June	2.78	(0.37)	LGL	1.63	(0.27)	LGL
7 June	2.78	(0.37)	LGL	4.00	(0.43)	LGL
8 June	No data	-	LGL	2.33	(0.35)	
9 June	No data	-	LGL	2.33	(0.35)	
10 June	No data	_	LGL	4.00	(0.43)	

Table 3. Daily correction factors (CF) and coefficients of variation (CV) for counts of ringed seals during usual survey dates in the Alaskan Beaufort Sea. CFs were calculated based on telemetric observations of 8 seals in 1999 and 10 seals in 2000. Also indicated are dates of aerial surveys conducted in our study area by the Alaska Department of Fish and Game (ADFG) and LGL Limited (LGL).

^aNo tagged seals visible, and CF estimated as greater than the CF calculated when one seal was visible.

Air temperatures, measured on the ice in 1999 and 2000, were mainly between -25 and -5 °C in April, -10 and 0 °C in May, and -5 to +10 °C in June (Figure 11). Air temperatures above 0 °C were recorded frequently in April and May 1999 but rarely during those months in 2000. Daytime temperatures were regularly above 0 °C after 28 May 1999 and after 7 June 2000. Air temperatures measured at the Deadhorse airport showed a similar seasonal pattern (Figure 11). Temperatures at the airport averaged 1.78 ± 0.11 °C lower than on the ice in 1999 and 1.59 ± 0.10 °C higher than on the ice in 2000.



Figure 11. Air temperatures measured at the ice camp (1999 and 2000) and at the Deadhorse airport (1999).

Wind speed (measured on the ice) varied mainly between 0 and 10 m s⁻¹ in 1999 and 2000 (Figure 12). Wind speed measurements at the Deadhorse airport tended to be higher than on the ice, averaging 2.3 m s⁻¹ higher in 1999 and 1.7 m s⁻¹ higher in 2000.



Figure 12. Wind speed measured at the ice camp in 1999 and 2000.

The amplitude of the backscatter signals differed little (<2 dB) between the morning and evening passes of the satellite in May 2000, indicating a more-or-less constant amount of moisture in the snow (Figure 13). In the first week of June, when the proportion of tagged seals visible on the surface was rapidly increasing, the diurnal differential in backscatter amplitude rose sharply to more than 5 dB. That differential indicated that there was substantially more liquid moisture in the snow at 18:00 than at 06:00 each day as a result of thaws during the daytime followed by freezes at night.



Figure 13. The proportion of radio-tagged seals visible on the ice and the diel variation in liquid moisture in the snow (reflected in the diurnal difference in backscatter amplitude) by date in 2000.

Discussion

Locating seal holes

The dogs trained in this study quickly became proficient at finding seal holes despite not having the advantage of training with experienced dogs. Quantifying dog performance is time consuming [Hammill 1987] and peripheral to the objectives of this study. Nonetheless, we judged the dogs to be as proficient as other dogs we have trained and worked with in Alaska and Canada based on the principal investigator's 20 years of experience with such dogs, the speed with which they learned to find seal holes on their own, the number of holes found in the study area each year, and the ratio of holes found by the dogs to holes found by radio tracking tagged seals. We located 86 and 202 seal holes in the study area in 1999 and 2000, respectively. Similar levels of effort with other dogs in the same study area yielded 145 holes in 1982 and 57 holes in 1983 [Kelly et al. 1986, 1988]. In this study, we located seal holes using the dogs and by radio tracking seals to holes. The dogs found 82% of all holes located in 1999 and 96% of all holes located in 2000, rates similar to the 85% success rates that Hammill [1987] achieved in repeated searches of his study area.

Spatial and temporal patterns of lair use

We radio tracked 18 ringed seals in April, May, and early June in 1999 and 2000 and found spatial and temporal patterns in the use and abandonment of lairs that have substantial implications for the interpretation of aerial survey data. We are not certain, however, that 18 seals tracked in two different years adequately capture the variation in behavior between individual animals, and increasing that sample size would be desirable.

We observed that 90% of the seals remained within home ranges less than 500 ha in area. One adult female seal, however, maintained a home range of nearly 3,000 ha, suggesting that home range size is not limited by the availability of breathing holes. The generally small home ranges maintained in winter and early spring have implications for the potential impact of human activities on the ice and for the utility of aerial surveys for counting seals. The surveys, however, are typically conducted in late May to mid-June, not long before the ice begins to deteriorate. Inevitably, the winter/spring home ranges must change when the ice breaks up, but we have yet to track seals long enough into the summer to characterize the changes in home ranges. The degree to which aerial surveys in May and June reflect the distributions and densities of seals in the winter months will depend, in part, on the timing of ice break up.

Home ranges determined by radio tracking necessarily are based only on sites where seals exit the water. While the possibility exists that under-ice home ranges might be underestimated by ranges determined from on-ice resting locations, in this study there was no difference in the under-ice and on-ice ranges of an adult male intensively tracked in three dimensions. Those results were consistent with observations in previous studies we conducted in Alaska and the Canadian Arctic [Wartzok et al. 1992a; Kelly and Wartzok 1996; Simpkins et al. 2001].

Seasonal changes in proportion of time ringed seals spend basking affect the interpretation of aerial survey data. We observed rapid increases in that proportion in the last week of May through the first week of June. Similarly, Frost and Lowry [1999, figure 3F] reported a more than two-fold increase in seal densities within our study area during the last week of May based on a covariate analysis of aerial survey data. Based on the proportions of tagged seals visible, surveys flown on 6 June 1999 would have counted, on average, 40% of the population; however, surveys flown on 29 May 1999 would have counted, on average, 12% of the population. Thus, comparison of densities observed in aerial surveys conducted in 1985–1987 with those observed in 1996–1998 [Frost and Lowry 1999] is confounded by differences in timing. The 1985–1987 surveys took place 1–14 June, while the 1996–1998 surveys were conducted 25 May–2 June. Interannual variability in the duration and timing of the transition period further complicates between-year interpretations of aerial survey data.

Telemetrically monitoring the location of tagged seals at one-hour intervals proved an effective method of determining dates of lair abandonment. Monitoring lair temperatures via thermistors and data loggers proved less useful for determining dates of lair abandonment due to the difficulties of interpreting the records as air temperatures in and out of lairs converged in late spring. Monitoring lair temperatures might still prove useful for determining dates of lair abandonment, but first it would be necessary to acquire extensive,

simultaneous records of lair occupation using an alternative method (such as acoustic monitoring) to calibrate the subtle temperature signals.

Our method of attaching radio transmitters to the seals (gluing to the pelage) is noninvasive and results in a temporary attachment. Nonetheless, as with any study involving handling and tagging, it is important to consider whether the investigators' activities alter the behavior under study. In our case, if handling and tagging the seals caused them to move from their normal home range or to change the frequency or duration of time out of the water, our conclusions about their spatiotemporal patterns of lair use would be compromised. The actions of our tagged seals after we released them suggests that their behavior patterns were not disrupted by our activities. None of the holes at which we captured seals froze over after they were captured and released, indicating continual maintenance of the holes by the seals. Furthermore, all of the tagged seals remained within a few kilometers of their capture site for at least several weeks after their release. The similar proportions of tagged and non-tagged seals visible on the ice by date in 2000 further suggested that the seals' behavior was not altered by handling and tagging.

In an unusual and unfortunate encounter between one of our seal dogs and a seal in 2000, the dog bit the seal, breaking its skin. Nonetheless, the seal's subsequent behavior did not differ notably from that of the others and one month later that seal began a long series of resting bouts on the ice at the breathing hole at which it was captured and released. Notwithstanding, we retired that dog from the project and modified our protocol to ensure separation between dogs and seals.

It has long been recognized that in early summer ringed seals tend to rest on the ice more in the afternoon hours than at other times of day. Burns and Harbo [1972] conducted surveys in Alaska between 10:00 and 16:00 (presumably Alaska Daylight Saving Time) "based on previous general observations" of when the greatest number of seals were expected to be visible. Smith [1973a, b] made repeated counts throughout the day to determine when the maximum number of seals were visible resting on the ice. He concluded that for a site in the eastern Beaufort Sea the optimal survey times were between 09:00 and 15:00 (again, presumably local time). The Alaska Department of Fish and Game adopted a protocol that called for conducting ringed seal aerial surveys between 10:00 and 16:00 local time [Burns and Kelly 1982; Frost et al. 1988, 1998; Frost and Lowry 1999]. An analysis of the effects of covariates on ringed seal density in the Beaufort Sea during surveys in 1996-1998 suggested a nearly three-fold linear decrease in densities between 10:00 and 18:00 local time [Frost and Lowry 1999]. In contrast, our records indicated that the proportion of seals out of the water increased from early morning until about 18:00, with close to half of the seals out of the water between 12:00 and 18:00. It may be that the linear decrease in seal densities suggested by Frost and Lowry's [1999] results is an artifact of their considering the effect of covariates one at a time. A multivariate model could well yield a different relationship between density of seals and time of day. If the decreasing density with time of day holds up, it would suggest that sightability from aircraft is negatively related to time of day.

Previous investigations have found inconsistent relationships between the density of visible ringed seals and air temperature, wind speed, and cloud cover [Kingsley et al. 1985; Stirling

et al. 1977; Burns and Harbo 1972; Burns and Kelly 1982; Frost et al. 1988]. We are exploring the use of temperature of the snow pack (which integrates air temperature, wind speed, and cloud cover) to predict when seals are visible. We observed a longer transition period in 2000 (24 days) than in 1999 (7 days), but the periods were centered on the same date. In both years, the transition periods corresponded to changes in the temperature of the snow near the snow-ice interface. Most of the radio-tagged seals were basking as the temperature of the snow reached 0°C.

It may be possible to use historical records of snow conditions to estimate the transition period for previous years and to correct past surveys for the proportion of ringed seals not visible. Records of snow temperature on the ice are lacking, but it may be possible to use snow temperature records from the tundra as a proxy.

The transition from dry, insulating snow to wet, conductive snow is visible in Ku-band radar backscatter signatures. In collaboration with S.V. Nghiem at the Jet Propulsion Laboratory in California, we obtained Ku-band backscatter images of our study area in spring 2000 and were able to correlate the transition of radio-tagged seals from lair use to basking with the changes in the radar backscatter. The use of the Ku-band backscatter data as an early indicator of snowmelt conditions and as a means to determine (remotely and in real time) when to fly aerial surveys of ringed seals is worthy of further investigation.

Smith [1973b] and Smith and Hammill [1981] presented evidence that ringed seals redistribute themselves in early summer, leading Smith [1987] to speculate that aerial surveys in early summer are not "representative of the resident winter population of the area." We recorded the locations of lairs and basking sites used by 18 seals in 1999 and 2000, and in only one instance did a seal expand the size of his winter home range when making the transition from resting in a lair to basking in the open. Previous observations of radio-tagged seals [Kelly and Quakenbush 1990] and changes in distribution observed during replicate aerial surveys [Moulton et al. 2000] suggested that, in some years, the distribution of resting sites within our study area changed when seals began basking in the open or shortly thereafter. Kingsley et al. [1985] suggested that the "collapse of the winter underwater social structure" might be associated with the "seals opportunistically hauling out at newly available sites." The new sites they referred to were chiefly cracks that opened in the ice as the weather warmed. Ringed seals often aggregate along those cracks in early summer [Burns and Harbo 1972], possibly to minimize the threat of predation by polar bears [Burns et al. 1981; Kingsley and Stirling 1991]. The apparent redistribution of seals observed during aerial surveys in 1999, however, occurred in the absence of extensive crack formation [Moulton et al. 2000]. Nor did cracks form within our study area during our period of observation in 2000. We had proposed to quantitatively examine the influence of predation threat on group size at breathing holes and cracks, but we were unable to do so because of the absence of cracks and because we rarely observed more than one seal at a breathing hole.

The conditions that favor redistribution of seals in early summer remain unknown. Kingsley et al. [1985] suggested that ringed seal distributions might change in early summer in response to changes in prey distribution as well as in response to the seasonal change in seal social structure. Smith [1987] suggested that variation in oceanographic factors might

engender local changes in seal distribution in early summer. If the distribution of ringed seals during early summer indeed reflects winter distribution in some locations and years but not in others, the factors influencing those distributions will need to be understood as part of the assessment of aerial survey data.

Correction factors

Protocols for aerial surveys of ringed seals have assumed that the proportion of seals visible during the surveys is sufficiently constant to permit inter- and intra-annual comparisons of estimated densities [Burns and Harbo 1972; Burns and Kelly 1982; Frost and Lowry 1988; 1999; Frost et al. 1988, 1997, 1998; Green and Johnson 1983; Link et al. 1999; Moulton and Elliott 1999; Moulton et al. 2000]. The correction factors calculated here indicate that during the typical survey periods, the fraction of the population available to be counted is changing rapidly and there appears to be substantial interannual variation in the times when seals abandon their subnivean lairs and start to become visible resting on the ice.

The longer transition from lair use to resting in the open observed in 2000 may reflect the later onset of above-freezing temperatures in that year. When temperatures regularly exceed 0°C, the lairs lose first their thermal advantage and then their structural integrity. Ideally, aerial surveys would not commence until it was known that seals had abandoned their lairs. Lair abandonment can be confirmed by telemetrically monitoring seals or lairs, but abandonment also could be inferred from snow conditions, specifically temperature or liquid moisture content. If the correspondence between the rate of lair abandonment and the diurnal backscatter differential observed in 2000 holds up in future samples, it suggests a convenient method of remotely determining when seal surveys should commence.

We intend to augment our sample size beyond the data collected in 1999 and 2000 to test the hypothesis that the proportion of seals visible during aerial surveys is independent of annual variation in snow depth, weather conditions, and age/sex class. Telemetry data from seals monitored during an additional two to three years will be necessary for robust models of the environmental covariates (including temperature and wind speed) that may influence the proportion of the population visible during surveys.

Recommendations

Survey protocols

- 1. Comparisons of ringed seal densities between regions and between years based on aerial surveys should account for the proportion of the population visible during each survey.
- 2. Surveys in the Alaskan Beaufort Sea should be conducted between 12:00 and 18:00 (ADT).

- 3. Until more is known about factors influencing the proportion of seals visible, aerial surveys should coincide with independent estimates, by telemetric or other means, of the proportion of seals visible.
- 4. Comparisons of ringed seal densities should be limited to appropriate geographic scales. Seals may move several kilometers during the late spring and early summer, and comparison of densities at finer scales may be spurious.

Further research

- 1. The environmental and other variables that influence the proportion of seals visible on the ice during the early summer survey period should be further investigated. Radio telemetry should be used to continue monitoring when and for how long ringed seals rest where they are visible on the ice. At the same time, weather and snow conditions should be monitored. The two years over which such data have been collected and other observations suggest that interannual variation is substantial, and observations are needed over more years. Diel patterns in the proportions resting on the ice are quite regular, but the changes in proportions with date are more erratic. Much of the latter variation may be explainable by covariate models, and we suggest that variables describing snow conditions may be especially informative. Snow condition may be important in explaining the proportion of seals visible for at least two reasons: First, deterioration of the snow in early summer ultimately limits the potential for seals to be concealed in subnivean lairs. Second, snow conditions integrate the effects of other variables suspected of influencing whether seals stay out of the water. Date, air temperature, cloud cover, fog, precipitation, and wind all influence the temperature and melting of the snow cover.
- 2. Alternatives to simultaneous telemetric studies for correcting aerial survey estimates (survey protocol recommendation #1 above) should be investigated. When the factors influencing the proportion of seals visible (further research recommendation #1) are better understood, it may be possible to determine comparable survey times by monitoring local conditions. Such monitoring might require on-ice measurements of weather and snow conditions, or it might be accomplished by remote sensing. The use of satellite-borne, Ku-band backscatter images for determining optimal survey conditions should be further investigated.
- 3. The relationship between winter and summer home ranges needs to be better understood. Additional telemetry studies spanning the transition from winter to summer should be conducted.
- 4. Previous aerial surveys should be re-analyzed in the light of new insights into the proportion of seals likely to have been visible at different survey periods.

Acknowledgements

This project was funded by the UA Coastal Marine Institute (Minerals Management Service and the University of Alaska Fairbanks), the National Marine Mammal Laboratory (National Marine Fisheries Service), and the Natural Resources Fund (University of Alaska). ARCO Alaska, Inc. and Phillips Alaska Inc. (now ConocoPhillips Alaska, Inc.) provided extensive logistic support in the form of snow machines, a generator, fuel, room and board, air transportation of our field crew, and ground transportation of our field gear. Mike Joyce, Linda Allen, Michael Stewman and the crew at ARCO's seawater treatment plant were extremely helpful with logistics in the field. Special thanks to Ole Olsgard and Dennis Wall in the shop for helping us keep everything running. In 1999, Alaska Clean Seas provided two snow machines and the Spill Response Team delivered them directly to our camp. Three undergraduate students from the University of Alaska Southeast—Raychelle Daniel, Shannon Crowley, and Philip Singer—put in many long hours in the field. Three graduate students—Karen Blejwas (University of California, Berkeley) and Michael Simpkins and Jamie Womble (both of the University of Alaska Fairbanks)—also assisted the project in 1999. Doug Wartzok of the University of Missouri provided expertise and assistance in the field. John Bengston and Peter Boveng of the National Marine Mammal Laboratory provided PTTs and excellent help in the field in 1999. We appreciate the efforts of pilots Dave Neel, Arctic Wilderness Lodge, and Sandy Hamilton, Arctic Air Alaska, for flights over our study area in 1999. We are grateful to Matthew Sturm, Cold Regions Research and Engineering Laboratory, for his assistance in establishing the meteorological station and loaning us a portable structure. The U.S. Fish and Wildlife Service; U.S. Geological Survey, Biological Resources Division; the University of Alaska, Institute of Arctic Biology and Alaska Cooperative Fish and Wildlife Research Unit assisted our project by loaning telemetry equipment.

Study Products

Presentations on this project have been delivered in several venues. On 23 February 1999, Oriana Harding presented a seminar on the study at the University of Alaska Southeast, and on the same date Brendan Kelly presented an update to the Coastal Marine Institute. In February 2001, Oriana Harding presented a poster at the American Society of Limnology and Oceanography [Harding et al. 2001], Lori Quakenbush presented an update to the Coastal Marine Institute, and Brendan Kelly presented a paper at an international conference in Switzerland [Kelly 2001]. In April 2001, Brendan Kelly presented on the project at the Minerals Management Service Information Transfer Meeting in Anchorage and at the 16th U.S.–Russia Marine Mammal Project Meeting in Santa Cruz, California. In May 2001, he also presented aspects of the work at the Mountain Film Festival in Telluride, Colorado. A report on the work was presented orally at the 14th Biennial Conference on the Biology of Marine Mammals held in Vancouver, British Columbia [Kelly et al. 2001]. A manuscript is in preparation for submission to the journal, Marine Mammal Science.

References

- Benson, C., B. Holmgren, R. Timmer, G. Weller and S. Parrish. 1975. Observations on the seasonal snow cover and radiation climate at Prudhoe Bay, Alaska, during 1972, p. 12–50. *In J. Brown* [ed.], Ecological Investigations of the Tundra Biome in the Prudhoe Bay Region, Alaska. Biological Papers of the University of Alaska, Special Report No. 2.
- Burns, J.J., and S.J. Harbo. 1972. An aerial census of ringed seals, northern coast of Alaska. Arctic 25(4):279–290.
- Burns, J.J., and B.P. Kelly. 1982. Studies of ringed seals in the Alaskan Beaufort Sea during winter: Impacts of seismic exploration. Unpubl. annual report, OCSEAP Res. Unit 232, to U.S. Dept. Commerce, NOAA Office of Marine Pollution Assessment, Juneau, 57 p.
- Burns, J.J., B.P. Kelly and K.J. Frost. 1981. Habitat use and winter ecology of ringed seals in the Beaufort Sea. Unpubl. annual report, Part 2, OCSEAP Research Unit 232, to U.S. Dept. Commerce, NOAA Office of Marine Pollution Assessment, Juneau, 81 p.
- Caughley, G. 1977. Sampling in aerial survey. J. Wildlife Manage. 41:605-615.
- Chapman, D.G., L.L. Eberhardt and J.R. Gilbert. 1977. A review of marine mammal census methods. Final report to U.S. Marine Mammal Commission for contract MM4AC014.
- Chapskii, K.K. 1940. The ringed seal of western seas of the Soviet Arctic (The morphological characteristics, biology and hunting production). Tr. Vses. Arkt. Inst. (Leningrad) 145:1–72. (Transl. from Russian by Fish. Res. Board Can., 1971, Transl. Ser. 1665, 147 p.)
- Cook, R.D., and S. Weisberg. 1999. Applied Regression Including Computing and Graphics. John Wiley & Sons, New York, 632 p.
- Daniel, R., L. Jemison, G. Pendleton and S. Crowley. 1999. Molting phenology of harbor seals on Tugidak Island, Alaska. 13th Biennial Conference on the Biology of Marine Mammals, Wailea, HI.
- Dingman, S.L., R.G. Barry, B. Weller, C. Benson, E.F. LeDrew and C.W. Goodwin. 1980. Climate, snowcover, microclimate, and hydrology, p. 30–65. *In* J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell [eds.], An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska, U.S./I.B.P. Synthesis Series No. 12. Dowden, Hutchinson & Ross, Inc. Stroudsburg, PA.
- Drummer, T.D. 1999. Planning abundance estimation surveys when detectability is < 1.0, p. 67–73. *In* G.W. Garner, S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald and D.G. Robertson [eds.], Marine Mammal Survey and Assessment Methods. A.A. Balkema Publishers, Rotterdam.
- Feltz, E.T., and F.H. Fay. 1966. Thermal requirements in vitro of epidermal cells from seals. Cryobiology 3:261–264.
- Frost, K.J., and L.F. Lowry. 1988. Effects of industrial activities on ringed seals in Alaska, as indicated by aerial surveys, p. 15–25. *In* W.M. Sackinger, M.O. Jeffries, J.L. Imm and S.D. Treacy [eds.], Port and Ocean Engineering Under Arctic Conditions, Vol. II: Symposium on Noise and Marine Mammals. Geophysical Institute, University of Alaska Fairbanks.

- Frost, K.J., and L.F. Lowry. 1999. Monitoring distribution and abundance of ringed seals in northern Alaska. Interim report, April 1998–March 1999, from Alaska Department of Fish and Game, Fairbanks to Minerals Management Service, Anchorage, 44 p.
- Frost, K.J., L.F. Lowry, J.R. Gilbert and J.J. Burns. 1988. Ringed seal monitoring: Relationships of distribution and abundance to habitat attributes and industrial activities. Final report, OCSEAP Res. Unit 667, U.S. Dept. Commerce, NOAA National Ocean Service, Alaska Office, Anchorage, 101 p.
- Frost, K.J., L.F. Lowry, C. Hessinger, G. Pendleton, D. DeMaster and S. Hills. 1998. Monitoring distribution and abundance of ringed seals in northern Alaska. Interim report, April 1997–March 1998, from Alaska Department of Fish and Game, Fairbanks to Minerals Management Service, Anchorage, 48 p.
- Frost, K.J., L.F. Lowry, S. Hills, G. Pendleton and D. DeMaster. 1997. Monitoring distribution and abundance of ringed seals in northern Alaska. Final interim report, May 1996–March 1997, from Alaska Department of Fish and Game, Fairbanks to Minerals Management Service, Anchorage. MMS cooperative agreement 14–35-0001-30810.
- Frost, K.J., L.F. Lowry and J.M. Ver Hoef. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. Mar. Mammal Sci. 15(2):494–506.
- Garner, G.W., S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald and D.G. Robertson [eds.]. 1999. Marine Mammal Survey and Assessment Methods. A.A. Balkema Publishers, Rotterdam.
- Green, J.E., and S.R. Johnson. 1983. The distribution and abundance of ringed seals in relation to gravel island construction in the Alaskan Beaufort Sea, p. 1–28. *In* B.J.
 Gallaway [ed.], Biological Studies and Monitoring at Seal Island, Beaufort Sea, Alaska 1982. LGL Ecological Research Associates, Inc., Bryan, TX for Shell Oil Co., Houston, TX.
- Green, K., H.R. Burton, V. Wong, R.A. McFarlane, A.A. Flaherty, B.C. Pahl and S.A. Haigh. 1995. Difficulties in assessing population status of ice seals. Wildlife Res. 22:193–199.
- Hammill, M.O. 1987. Ecology of the ringed seal (*Phoca hispida* Schreber) in the fast-ice of Barrow Strait, Northwest Territories. Ph.D. Dissertation. McGill University, Montreal.
- Harding, O.R., B.P. Kelly, L.T. Quakenbush and B.D. Taras. 2001. Importance of snow for ringed seal pups, p. 64. *In* Abstract Book. Aquatic Sciences Meeting, 12–16 February 2001, American Society of Limnology and Oceanography.
- Harwood, L.A., and I. Stirling. 1992. Distribution of ringed seals in the southeastern Beaufort Sea during late summer. Can. J. Zool. 70:891–900.
- Huber, H.R., S.J. Jeffries, R.F. Brown, R.L. DeLong and G. VanBlaricom. 2001. Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. Mar. Mammal Sci. 17(2):276–293.
- Jemison, L.A., and B.P. Kelly. 2001. Pupping phenology and demography of harbor seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. Mar. Mammal Sci. 17(3):585–600.

- Kelly, B.P. 1988. Ringed seal, p. 59–75. *In* J.W. Lentfer [ed.], Selected Marine Mammals of Alaska: Species Accounts with Research and Management Recommendations. Marine Mammal Commission, Washington, D.C.
- Kelly, B.P. 1996. Live-capture of ringed seals in ice-covered waters. J. Wildlife Manage. 60:678–684.
- Kelly, B.P. 2001. Climate change and ice breeding pinnipeds, p. 43–55. In G.-R. Walther, C.A. Burga and P.J. Edwards [eds.], 'Fingerprints' of Climate Change: Adapted Behaviour and Shifting Species' Ranges. Kluwer Academic/Plenum Publishers, New York and London.
- Kelly, B.P., J.J. Burns and L.T. Quakenbush. 1988. Responses of ringed seals *Phoca hispida* to noise disturbance, p. 27–38. *In* W.M. Sackinger, M.O. Jeffries, J.L. Imm and S.D. Treacy [eds.], Port and Ocean Engineering Under Arctic Conditions, Vol. II: Symposium on Noise and Marine Mammals. Geophysical Institute, University of Alaska Fairbanks.
- Kelly, B.P., and L.T. Quakenbush. 1987. Trained dogs and wild seals. Whalewatcher, J. Amer. Cetacean Soc. 21(1):8–11.
- Kelly, B.P., and L.T. Quakenbush. 1990. Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). Can. J. Zool. 68:2503–2512.
- Kelly, B.P., L.T. Quakenbush and J.R. Rose. 1986. Ringed seal winter ecology and effects of noise disturbance. U.S. Dept. Commerce, NOAA, OCSEAP Final Rep. 61(1989):447–536.
- Kelly, B.P., L.T. Quakenbush, B.D. Taras and O. Harding. 2001. Snow conditions predict optimal survey periods for ringed seals. Abstract. 14th Biennial Conference on the Biology of Marine Mammals. Vancouver, BC.
- Kelly, B.P., and D. Wartzok. 1996. Ringed seal diving behavior in the breeding season. Can. J. Zool. 74:1547–1555.
- King, J.E. 1983. Seals of the World, 2nd Edition. Comstock Publishing Associates, Ithaca, NY, 240 p.
- Kingsley, M.C.S., M.O. Hammill and B.P. Kelly. 1990. Detecting ringed seal lairs by the heat they radiate. Mar. Mammal Sci. 6:339–347.
- Kingsley, M.C.S., and I. Stirling. 1991. Haul-out behaviour of ringed and bearded seals in relation to defense against surface predators. Can. J. Zool. 69:1857–1861.
- Kingsley, M.C.S., I. Stirling and W. Calvert. 1985. The distribution and abundance of seals in the Canadian High Arctic, 1980–82. Can. J. Fish. Aquat. Sci. 42:1189–1210.
- Link, M.R., T.L. Olson and M.T. Williams. 1999. Ringed seal distribution and abundance near potential oil development sites in the central Alaskan Beaufort Sea, spring 1998. LGL Report P-430. LGL Alaska Research Associates, Inc., Anchorage, 48 p.
- Liston, G. E., and M. Sturm. 2002. Winter precipitation patterns in arctic Alaska determined from a blowing-snow model and snow-depth observations. J. Hydrometeorol. 3(6):646–659.

- McLaren, I.A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Bull. Fish. Res. Bd. Can. 118, 97 p.
- Moulton, V.D., and R.E. Elliott. 1999. Fixed-wing aerial surveys of seals near BP's Northstar and Liberty sites, 1999, p. 3-1–3-39. *In* W.J. Richardson and M.T. Williams [eds.], Monitoring of Ringed Seals During Construction of Ice Roads for BP's Northstar Oil Development, Alaskan Beaufort Sea, 1999: 90-Day Report. LGL Ltd., King City, Ontario.
- Moulton, V.D., R.E. Elliott and M.T. Williams. 2000. Fixed-wing aerial surveys of seals near BP's Northstar and Liberty sites, 2000, p. 3-1–3-32. *In* W.J. Richardson and M.T. Williams [eds.], Monitoring of Ringed Seals During Construction of Ice Roads for BP's Northstar Oil Development, Alaskan Beaufort Sea, Winter and Spring 1999–2000: 90-Day Report. LGL Ltd., King City, Ontario.
- Nghiem, S.V., R. Kwok, S.H. Yueh and M.R. Drinkwater. 1995. Polarimetric signatures of sea ice, theoretical model. J. Geophys. Res. 190(13):665–679.
- Richardson, W.J., and M.T. Williams [eds.]. 2000. Monitoring of ringed seals during construction of ice roads for BP's Northstar oil development, Alaskan Beaufort Sea, 1999. Report from LGL Alaska Research Associates Inc., Anchorage, AK and Silver Spring, MD, 103 p.
- Rogers, T.L., and M.M. Bryden. 1997. Density and haul-out behavior of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. Mar. Mammal Sci. 13(2):293–302.
- Scheffer, V.B. 1958. Seals, sea lions and walruses. A Review of the Pinnipedia. Stanford University Press, Stanford, CA, 179 p.
- Simpkins, M.A., B.P. Kelly and D. Wartzok. 2001. Three-dimensional diving behaviors of ringed seals (*Phoca hispida*). Mar. Mammal Sci. 17(4):909–925.
- Smith, T.G. 1973a. Censusing and estimating the size of ringed seal populations. Fish. Res. Bd. Can. Tech. Rep. No. 427, 18 p.
- Smith, T.G. 1973b. Population dynamics of the ringed seal in the Canadian eastern arctic. Bull. Fish. Res. Bd. Can. 181, 55 p.
- Smith, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian western Arctic. Can. Bull. Fish. Aquat. Sci. 216, 81 p.
- Smith, T.G., and M.O. Hammill. 1981. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Can. J. Zool. 59:966–981.
- Smith, T.G., and I. Stirling. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Can. J. Zool. 53:1297–1305.
- Stirling, I., W.R. Archibald, and D. DeMaster. 1977. Distribution and abundance of seals in the eastern Beaufort Sea. J. Fish. Res. Bd. Can. 34:976–988.
- Sturm, M., and G.E. Liston. 2003. The snow cover on lakes of the arctic coastal plain of Alaska, U.S.A. J. Glaciology 49:370–380.

- Tjuatja, S., A.K. Fung and J. Bredow. 1992. A scattering model for snow-covered sea ice. IEEE Trans. Geosci. Remote Sensing. 30:804–810.
- Walker, D.A., K.R. Everett, P.J. Webber and J. Brown. 1980. Geobotanical atlas of the Prudhoe Bay Region, Alaska. U.S. Army Corps of Engineers, CRREL Report 80-14. Hanover, NH.
- Wartzok, D., R. Elsner, H. Stone, B.P. Kelly and R.W. Davis. 1992a. Under-ice movements and sensory basis of hole finding by ringed and Weddell seals. Can. J. Zool. 70:1712–1722.
- Wartzok, D., S. Sayegh, H. Stone, J. Barchak and W. Barnes. 1992b. Acoustic tracking system for monitoring under-ice movements of polar seals. J. Acoust. Soc. Am. 92:682–687.
- Wise, J.L., and H.W. Searby. 1977. Selected topics in marine and coastal climatology,
 p. 7–27. *In* W.A. Brower, Jr., H.F. Diaz, A.S. Prechtel, H. Searby and J. L. Wise [eds.],
 Climatic Atlas of the Outer Continental Shelf Waters and Coastal Regions of Alaska.
 Vol. III, Chukchi–Beaufort Sea. Arctic Environmental Information and Data Center –
 University of Alaska Anchorage, Anchorage.
- Withrow, D.E., and T.R. Loughlin. 1995. Haulout behavior and method to estimate the proportion of harbor seals missed during molt census surveys in Alaska, p. 206–244. *In* Annual report to the MMPA Assessment Program, Office of Protected Resources, NMFS, NOAA, 1355 East–West Highway, Silver Spring, MD 20910. [Available from National Marine Mammal Lab, 7600 Sand Point Way, NE, Seattle, WA 98115.
- Withrow, D.E., and T.R. Loughlin. 1996. Haulout behavior and a correction factor estimate for the proportion of harbor seals missed during molt census surveys near Cordova, Alaska, p. 89–116. *In* Marine Mammal Protection Act and Endangered Species Act Implementation Program 1995, Office of Protected Resources, NMFS, NOAA, 1335 East–West Highway, Silver Spring, MD 20910. [Available from National Marine Mammal Lab, 7600 Sand Point Way, NE, Seattle, WA 98115].