MARINE MAMMAL SCIENCE, 22(2): 379–393 (April 2006)

DOI: 10.1111/j.1748-7692.2006.00034.x

SPRING HAUL-OUT BEHAVIOR OF RINGED SEALS (*PUSA HISPIDA*) IN KONGSFJORDEN, SVALBARD

HELEN CARLENS
Norwegian Polar Institute,
N-9296 Tromsø, Norway
and
Department of Zoology, Stockholm University,
106 91 Stockholm, Sweden

CHRISTIAN LYDERSEN
BJØRN A. KRAFFT
KIT M. KOVACS[1]
Norwegian Polar Institute,
N-9296 Tromsø, Norway
E-mail: kit.kovacs@npolar.no

ABSTRACT

Haul-out behavior of ringed seals (*Pusa hispida*) was investigated during the spring molting period of 2003 (May–July) in Kongsfjorden, Svalbard, Norway. Hourly counts were conducted on the land-fast ice in six spatially defined sectors in the inner fjord, from an elevated land-based vantage point from early May through until the ice began to break up in June, from 0600 to 2200 daily (total counts $n =$ 478). Concomitantly, measurements were made of a variety of weather parameters. Multiple regression analyses revealed that time of day ($P < 0.001$) and date ($P <$ 0.001) significantly affected the number of ringed seals hauled out on the ice surface. Other factors influencing the number of seals counted on the ice were air temperature ($P = 0.011$) and wind speed ($P < 0.001$). Daily peaks occurred in the early afternoon between 1300 and 1400 and the seasonal high ($n = 385$) was registered during the first week in June, after which the number of seals on the ice in the fjord declined. In addition to the visual counts, 24 ringed seals were equipped with VHF transmitters, and the haul-out behavior of individuals was monitored from May through July *via* an automatic recording station. The VHF-tagged seals exhibited the same diurnal pattern seen in the total counts, with haul-out most frequent from 1300 to 1400. Pups exhibited short and frequent haul-outs, whereas longer haul-out periods were seen in the older age classes; adult females had the greatest number of haul-out periods that exceeded 24 h. The seasonal peak of haul-out for the tagged seals preceded the peak seasonal counts by approximately 3 wk. This may reflect significant out- and influx of seals from and to the area, a phenomenon warranting further attention because of its implications for assessment studies.

Key words: ringed seal, *Phoca hispida*, VHF-tracking, haul-out, seasonal and diurnal trends.

[1] Corresponding author.

Ringed seals (*Pusa hispida*) occupy a key ecological role in the Arctic ecosystem. They are found in virtually all seas and oceans encircling the North Pole and number in the millions (Reeves 1998). They are the main prey of polar bears (*Ursus maritimus*) (*e.g.,* Smith 1980, Derocher *et al.* 2002) and the most important natural resource for many indigenous people in coastal areas of the circumpolar Arctic. Because of their ubiquitous occurrence, dependence on sea ice (and hence potential to be impacted by the effects of predicted climate change, see Kelly 2001, ACIA 2004, Ferguson *et al*. 2005, Loeng *et al.* 2005) and their importance within the arctic ecosystem, ringed seals have been recommended as high-priority subjects for monitoring of arctic marine systems (*e.g.*, Tynan and DeMaster 1997, Reeves 1998). However, current knowledge of population trends and basic behavioral patterns is sparse for many ringed seal populations.

Ringed seals are broadly distributed during the summer months, but by winter they are found principally in areas with land-fast ice where they maintain breathing holes in the ice and construct lairs in snow above some of their holes for resting and parturition (*e.g.*, McLaren 1958, Smith and Stirling 1975). During the winter and early spring ringed seals are either in the water or in lairs and hence are not available for observation. However, in late spring and early summer, following the breeding season, all age groups of ringed seals go through an annual molt of their hair and outer skin layers. Warm temperatures are beneficial for skin growth (Feltz and Fay 1966) and the seals spend a considerable amount of time hauled out on the surface of the ice during this part of their annual cycle (*e.g.*, Finley 1979). This is the period when most studies of ringed seals are carried out.

Several observational studies of haul-out behavior of ringed seals during the molting period have been conducted in the eastern Canadian Archipelago (Smith 1973, Finley 1979, Smith and Hammill 1981), the Beaufort Sea (Moulton *et al*. 2002), and the Eastern Siberian Sea (Ognetov 1993). Additional behavioral information has been gleaned from aerial survey studies conducted during the molting period (Burns and Harbo 1972, Kingsley and Stirling 1991, Härkönen and Lunneryd 1992, Harwood and Stirling 1992, Moulton *et al.* 2002, Frost *et al*. 2004). In combination, these earlier studies of ringed seals have shown that most seals are visible on the ice during midday, but the midday peak is influenced by wind speed and temperature, with warm periods being preferred for haul-out. In some areas on calm, bright, warm days a drop in the number of seals on the ice has been observed that is thought to reflect an upper thermal tolerance limit of the seals. Additionally, a seasonal pattern has been found, where the highest numbers of seals were on the ice in the late spring just before ice breakup.

The main objective of this study was to investigate local haul-out behavior of ringed seals during the molting period in Svalbard, when aerial surveys for this species are targeted. Long-term population monitoring of this region is planned as part of a Norwegian national environmental monitoring plan. The study was designed to explore broad numerical patterns and the influence of abiotic factors such as weather parameters and temporal trends on haul-out numbers, together with the influence of detailed haul-out behavior of individual seals. This was done using VHF telemetry on a sample of ringed seals covering a broad age distribution, concomitant with ground-based visual counts throughout the molting season.

METHODS

This study was carried out on the land-fast ice in the inner basin of Kongsfjorden (78.6°N, 12.2°E), on the west coast of Svalbard, Norway (Fig. 1). The fjord has a string

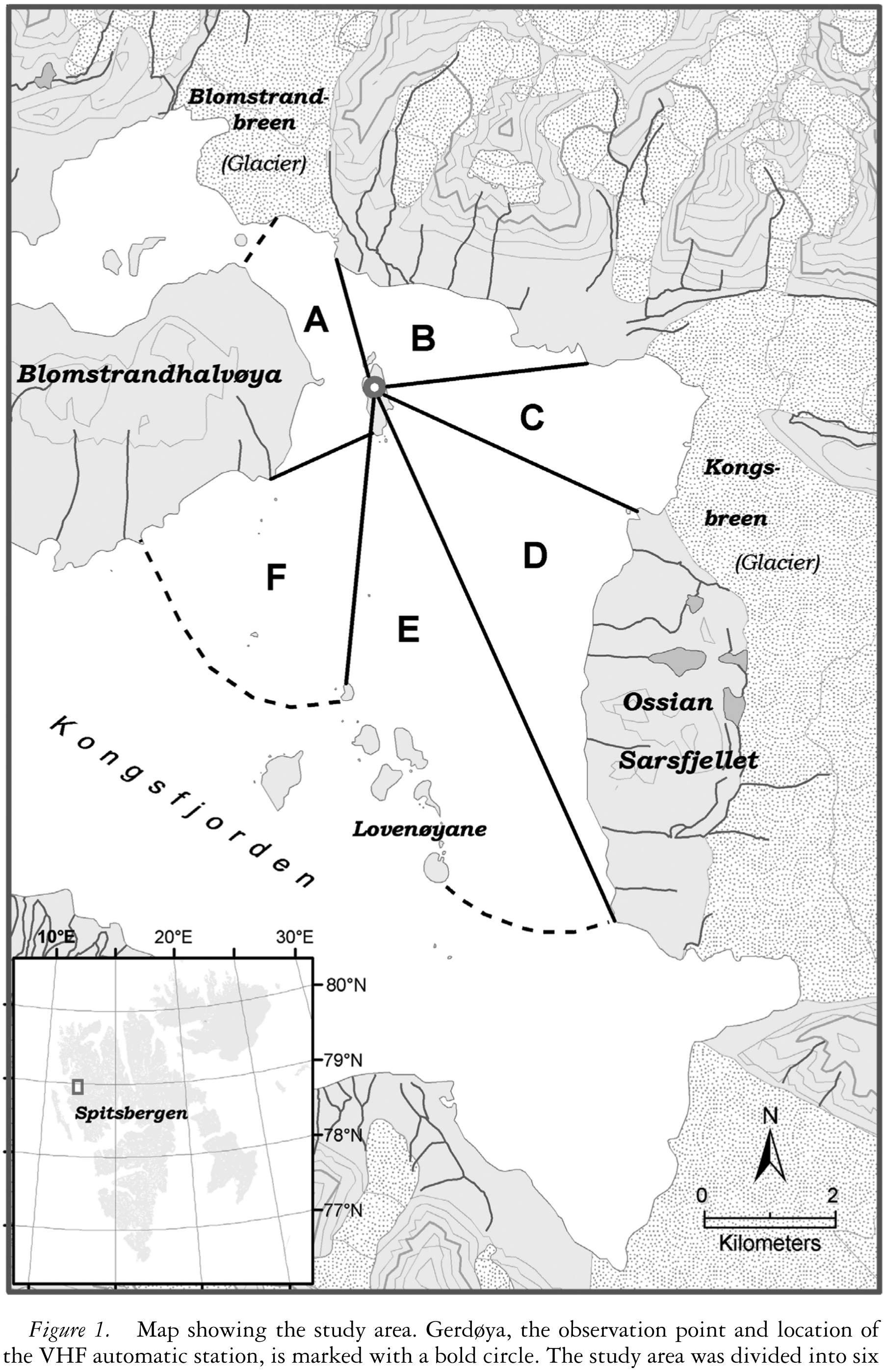

Figure 1. Map showing the study area. Gerdøya, the observation point and location of the VHF automatic station, is marked with a bold circle. The study area was divided into six sectors (A–F), and each was counted separately.

of small islands that protect the ice in its innermost parts from wind and wave action. Hence, the study area retains sea ice late into the season compared with adjacent areas. The mean snow depth in Kongsfjorden is low (20 cm, Svendsen *et al.* 2002). However, a large glacier complex, including several active glacier fronts calving into the fjord make it a suitable ringed seal breeding habitat (Smith and Lydersen 1991), as icebergs from the glaciers become frozen into the sea ice and promote snow drifting. Ringed seals are thought to stay in their breeding areas to haul-out through the molting period, until the break up of the sea ice. The study area experienced 24 h of daylight throughout the whole study period.

Counts of the total number of seals visible on the ice in the study area were conducted hourly between 0600 and 2200 (local time, GMT + 1 h) starting on 12 May, using binoculars (10 × 30) and a telescope (30 × 75). These counts were conducted from Gerdøya, a small island that rises to approximately 30 m above sea level and has a 360° view of the area (Fig. 1). To facilitate counting, the study area was divided into six sectors using easily recognizable landmarks to divide the areas (Sections A–F, Fig. 1). The visibility at the time of each count was estimated on a scale from 1 to 9, with 9 representing clear visibility throughout the study area. Only counts with visibility ratings of 7 or more in at least five of the six sectors were included in the analyses presented herein. The study period for the ground-based visual observations ended on 25 June, at which time the condition of the sea ice precluded safe transportation to and from Gerdøya.

Local wind speed was measured at Gerdøya using a hand-held anemometer at the start of each count. Information on air temperature and air pressure was obtained from a permanent weather station in Ny Ålesund on the south side of Kongsfjorden, approximately 10 km south-west of the observation point. Times of high and low tide were taken from "Tide tables for the Norwegian coast and Svalbard" (Norwegian Mapping Authority, 2003).

VHF transmitters were deployed on 26 ringed seals. The seals were caught using a net trap set at their haul-out holes. One end of a rectangle-shaped piece of nylon netting was secured to the ice with a pair of ice screws next to a breathing hole. An additional pair of ice screws was set on the opposite side of the breathing hole. A piece of string (approximately 100 m) was attached to the corners of the front end of the net and pulled through the front screws to guide the direction of the net pull. The net was then retracted and placed on a sheet of white plastic to prevent it from freezing into the ice; this also left the immediate area around the hole free from net and string. When a seal was hauled out on the ice at a hole with a trap, the net was pulled quickly over the hole, thereby preventing the seal's escape back into the water. Prior to tagging, the seals were weighed, their sex was determined and the degree of molting was assessed for each animal. All females weighing less than 60 kg (except one that had a pup) and all males weighing less than 52 kg and not showing the characteristic black, "tiggak face" of rutting male ringed seals, were considered subadults (Lydersen and Gjertz 1987).

Twenty of the 26 seals that were caught, were equipped with two VHF transmitters, one glued high on the back of the neck (Ringed seal Temple Tag, Model# F1825, Advanced Telemetric Systems, Isanti, MN) and the other on a Roto-style flipper tag that was deployed on a hind flipper (Ringed seal Implant tag, Model# MM420, Advanced Telemetric Systems, Isanti, MN). Four seals were molting heavily at the time of capture so these animals were only equipped with flipper tags. Two seals that showed no sign of molting were equipped with only head tags. The VHF tags sent signals continuously but the signals cannot be detected through salt water. Signals therefore are detected only when the tag is out of the water. The tags all had unique frequencies within the wildlife band (150–152 MHz). Before the animals were released, they were also equipped with plastic identification Rototags through the webbing of each hind flipper. Each animal was also given a color code using marine paint to prevent accidental recapture and to facilitate long distance identification of the individual.

An automatic logging station (TR-5 Telemetry Scanning Receiver, Telonics, Inc., Mesa, AZ) was placed on top of Gerdøya (Fig. 1) to record signals from the VHF transmitters. The logger was programmed using a PC and Parameter Interface Software (TR-5PI, Telonics, Inc., Mesa, AZ). An RA-5A omnidirectional base-loaded whip antenna (Telonics, Inc., Mesa, AZ), mounted on a mast (~3 m high) was linked to the logging station. Each tag's frequency (as well as frequencies ±1 MHz away—in case the frequencies of the tags drifted during the study period) was monitored every 30 min. All frequencies were also tracked manually three times a day, using a hand-held antenna, to test the accuracy of the automatic logger. The tracking station started to log data on 11 May. Data were downloaded (approximately weekly) from the logger to a PC (this was done twice in order to detect possible downloading transmission errors). The two files were compared and cleaned of blank lines or other small anomalies such as premature line- breaks in the data stream. The data set was then put through a pulse period filter such that only intervals around the set period of 1.500 s, [and the double (3.000 s) and triple (4.500 s) values] were retained, in order to eliminate false radio signals recorded by the logger. The station functioned unmanned from the time the field crew departed on 25 June until it was retrieved on 24 July.

Data from flipper tags and head tags were compared in the early stages of analyses. Substantial differences were observed in the records from the two tag placements (these differences will be addressed in a separate manuscript). For the behavioral analyses presented here, flipper tags were selected, with a few exceptions, because they provided the most consistent and complete records of haul-out activity. One adult female record in this study is based on a head tag because this animal was not equipped with a flipper tag and due to the short duration of the records from the flipper-tags in pups, head tags were also used in the analysis of pup behavior ($n = 2$). A haul-out period was defined as at least one signal recorded by the logger in a half hour period.

The data were analyzed statistically using SPSS 11.0 (SPSS, 2003). Initially, univariate plots were constructed for count data *vs.* each potential effect factor to explore the data sets and their variance. Subsequently, multiple regression analyses were performed with the number of seals hauled out entered as the dependent factor, and time of day (TIME), DATE, air temperature (TEMP), air pressure (PRES), wind speed (WIND), and tidal state (TIDE; number of hours away from or toward high tide) entered as independent factors. Residuals were examined. HOUR and DATE showed curvilinear relationships with number of seals hauled out, and therefore a second, (day^2 and time^2) parameter for each of these two variables was added to the regression model. The distribution of all factors was tested for normality. $P < 0.05$ was set as the accepted significance value.

Results

Air temperature varied from a minimum of −6.82°C (2100 on 16 May) to a maximum of 5.18°C (1700 on 22 July) over the study period. The median temperature

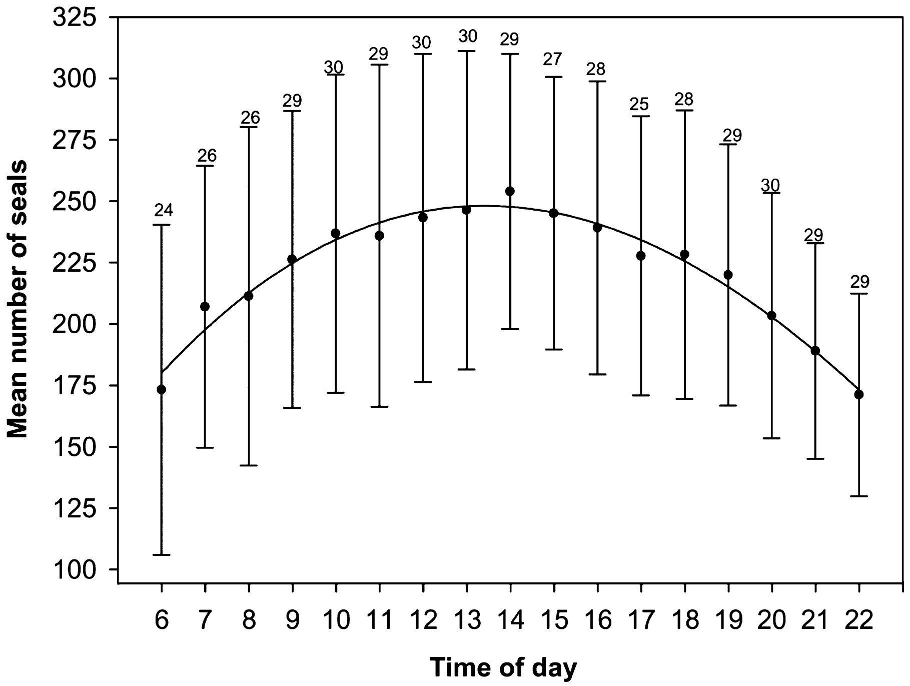

Figure 2. Mean number of seals hauled out per hour ($n = 478$). Vertical bars denote ±1 SD. Numbers on top of variance bars denote the number of usable counts each hour ($\Sigma = 478$).

during the study period was 0.41°C. The animals experienced a maximum wind speed of 11 m/s (1300 on 10 June), but the median wind speed was 0 m/s. Air pressure ranged from 999 hPa to 1,027 hPa with a median of 1,014 hPa.

During 33 d of observations occurring from 12 May until 25 June, a total of 561 counts were conducted. Of these, 478 (85%) had visibility ratings of seven or more, and hence were retained for further analyses. Ringed seals showed a diurnal pattern in numbers hauled out with low numbers out in the morning, building toward a peak in the early afternoon between 1300 and 1400 (Fig. 2, Table 1), and then a decline toward evening. Ringed seals also showed a seasonal trend in their haul-out numbers, with the peak daily maximum numbers occurring in the first week of June ($P < 0.001$, Fig. 3). The highest count during the study period occurred on 2 June at 1200, when 385 ringed seals were counted. Wind speed had a significant negative influence on the number of seals on the ice surface and air temperature had a significant positive influence (Table 1). Air pressure ($P = 0.149$) and tidal state ($P = 0.463$) did not affect the haul-out behavior of the ringed seals (Table 1).

A total of 26 seals were equipped with VHF transmitters—19 adults (10 females and 9 males), 5 subadults (3 females and 2 males), and 2 pups (one female and one male). Contact was lost with one tagged seal immediately after tagging, suggesting that the seal either left the area or (less likely) that both tags failed quickly. Another individual hauled out frequently for the first 3 d of monitoring and then was not recorded again. These two individuals were excluded from the data analyses. The

Table 1. Multiple regression statistics for the number of ringed seals hauled out in relation to time of day, season, temperature, wind speed, air pressure, and tide time. Significant factors ($\alpha = 0.5$) are in bold print. The r^2 value for the model was 0.59.

Factor	t	Significance level
(Time of day)^2	−11.868	**<0.001**
(Time of season)^2	−18.715	**<0.001**
Time of day	10.741	**<0.001**
Time of season	17.405	**<0.001**
Air temperature	2.537	**0.012**
Wind speed	−10.054	**<0.001**
Air pressure	−1.446	0.149
Time to low tide	−0.734	0.463

remaining 24 individuals hauled out frequently from the time of their capture until 25 May. Two battery power failures to the logger station occurred during the study period, each affecting 2 d (parts of 30–31 May and 5–6 June). These 4 d were omitted in the analyses of the VHF data.

By late July, only three of the 24 VHF-tagged individuals still hauled out on a daily basis (Fig. 4). Following 25 May, when about 12 h per day was spent on the ice surface on average, the tagged seals began reducing their haul-out time, coming onto the ice surface more sporadically and for shorter periods (Fig. 5). The time individual seals

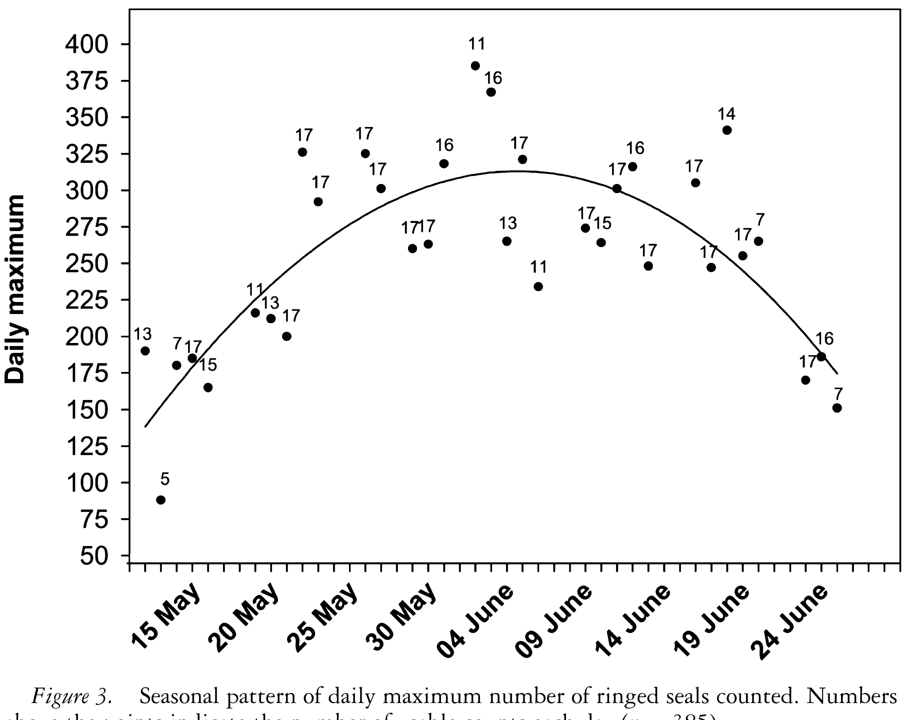

Figure 3. Seasonal pattern of daily maximum number of ringed seals counted. Numbers above the points indicate the number of usable counts each day ($n = 385$).

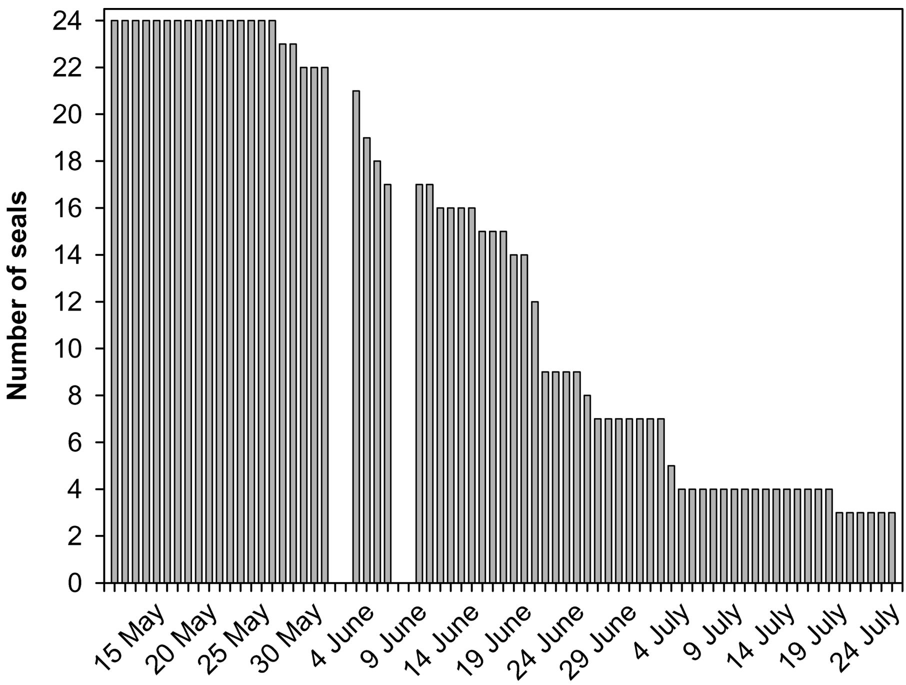

Figure 4. Numbers of VHF-tagged seals hauling out in relation to date. Blank days are due to battery power failures in the logger station.

spent hauled out generally declined as the season progressed beyond 25 May; the few animals that remained in the area in July showed considerable day-to-day variation in the mean number of hours they hauled out each day (Fig. 5, 6). VHF-tagged seals displayed a diurnal trend in their haul-out behavior, similar to the total numbers of seals hauling out through the day. The greatest proportion (approximately 40%) of the tagged animals was present on the ice in the early afternoons, between 1300 and 1400.

Haul-out patterns appear to differ somewhat between age and sex classes (Fig. 6b, 7). Pups hauled out frequently compared with subadults, or adults of either sex (see Fig. 7). More than 50% of the haul-out periods documented for pups were in the shortest sampling interval that was documented by the data logging station and their haul-out periods never exceeded 24 h. One subadult hauled out for a period longer than 24 h (35 h), but 40% of the haul-out periods of the five subadults were less than 60 min in duration. Among the eight adult male records five haul-out periods exceeded 24 h and 35% of their on-ice intervals were shorter than 60 min. Maximum durations of haul-out periods occurred among adult females, including 13 haul-outs that exceeded 24 h and one that lasted 141 h (between 21 May and 25 May). The difference in haul-out behavior between an adult female and her pup is shown in Figure 7. This pup was in and out of the water for short periods from 16 May until 18 July, after which the logging station picked the signal up only once. In contrast, the mother's haul-out behavior was typical of adults, with most on-ice time concentrated in the middle of the day. She ceased hauling out regularly

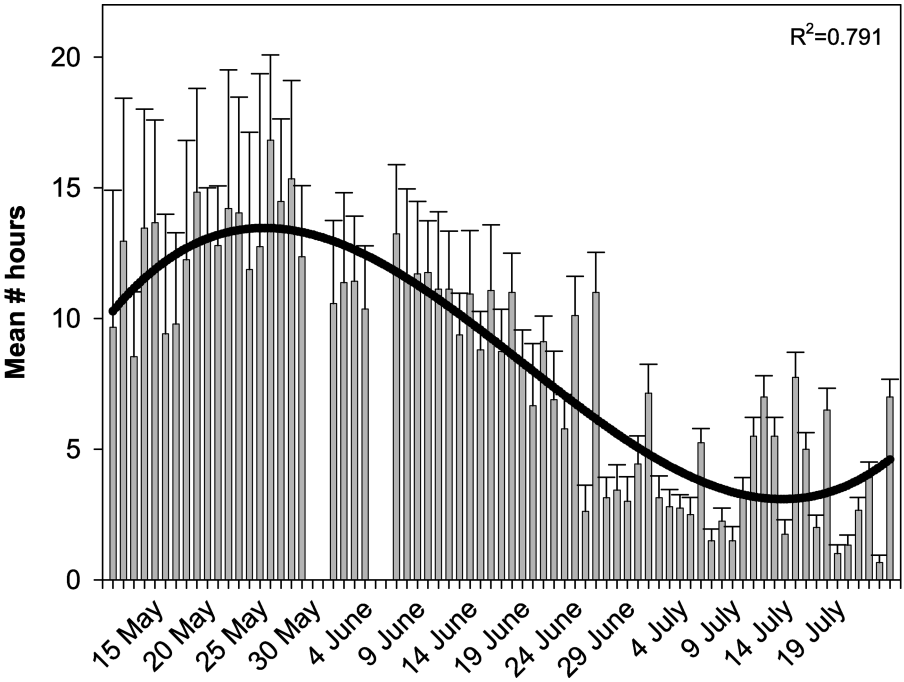

Figure 5. Mean number of hours hauled out per day (±1 SD) by VHF-tagged ringed seals. Blank days are due to battery power failures in the logger station. The upturn at the end of the sampling period is likely an epiphenomenon of the fitting algorithm.

on 10 June, after which she was only detected sporadically for short periods of time.

Discussion

Haul-out behavior of phocid seals that associate with ice is influenced by temporal and meteorological factors as well as other physical parameters. Some of the factors that are known to have influence include date, time of day, amount of solar radiation, cloud cover, temperature, and wind (speed and chill), as well as the physiological status of the seal (reproductive status, stage of molt, *etc.*), (*e.g.*, Finley 1979; Smith and Hammill 1981; Thomas and DeMaster 1983; Lydersen and Kovacs 1993; Haller *et al.* 1996; Moulton *et al.* 2002, 2005). Many of these factors can be intercorrelated and their influence can vary widely based on geographic location (latitude, microclimate influences, *etc.*).

This study evaluated factors influencing spring haul-out behavior of ringed seals during the molt by simultaneously examining haul-out behavior *via* extensive ground-based visual counts in combination with radio-telemetry data from a sample of 24 individuals with broad age- and sex-class coverage. Although both the count and VHF data displayed considerable variation, both data sets clearly demonstrated effects of time of day and date on haul-out behavior. Ringed seals displayed a peak in haul-out just after midday both in the 16 h (daily) visual coverage and the 24 h VHF

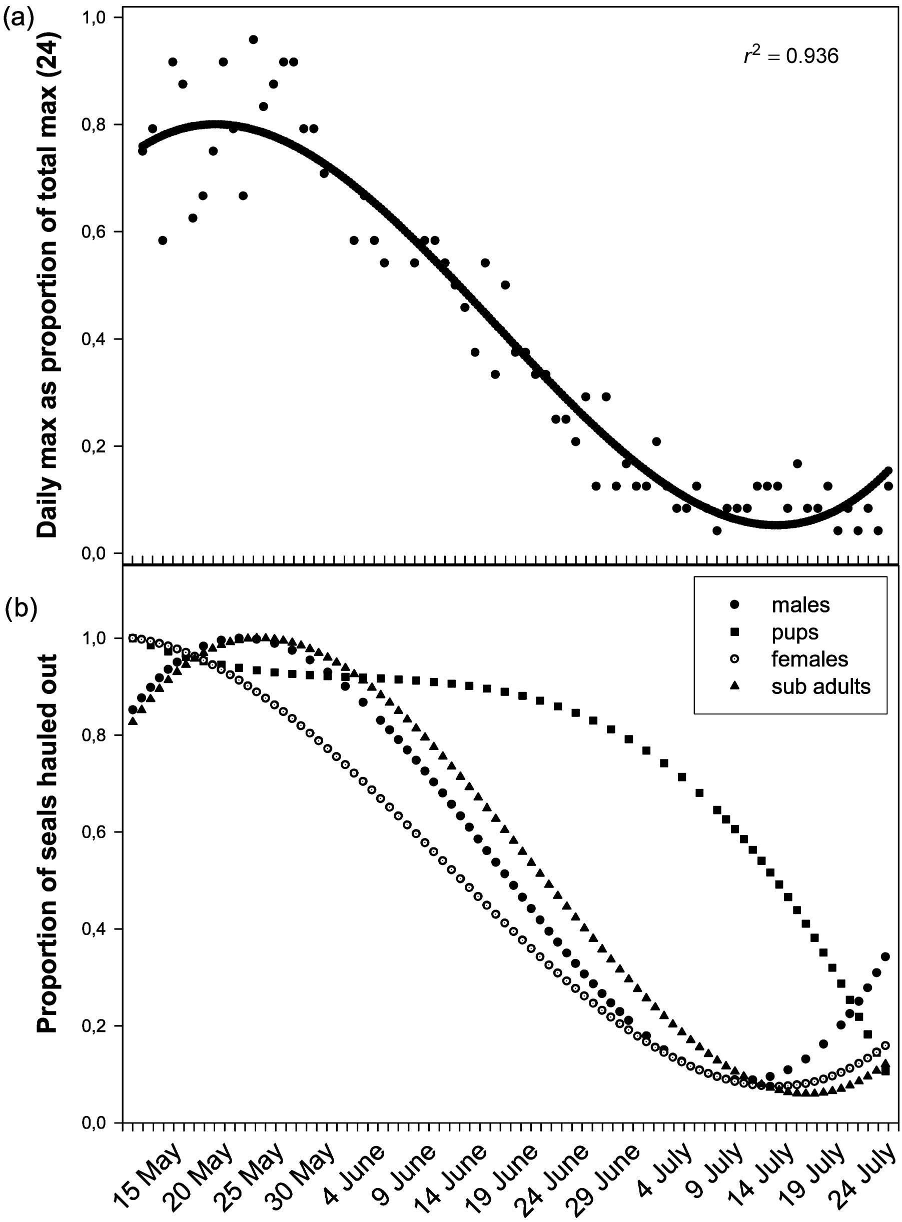

Figure 6. Seasonal pattern in haul-out behavior of VHF-tagged ringed seals. (a) Daily maximum number of seals hauling out, as proportion of the total sample size (n = 24). (b) Proportion of seals hauled out by sex and age categories. The upturns at the end of the sampling period in both (a) and (b) are likely epiphenomena of the fitting algorithm.

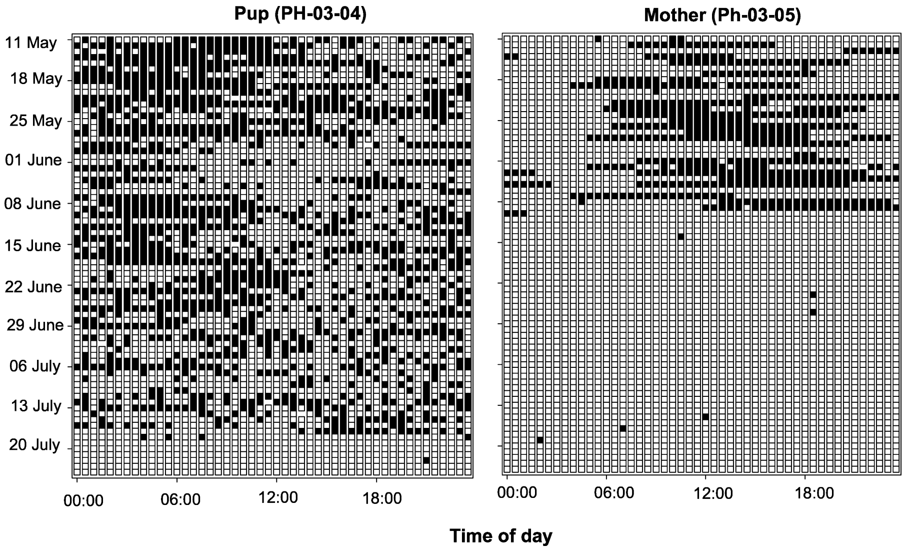

Figure 7. Haul-out behavior in a pup–mother pair. Black squares represent a 30-min period when VHF-signals were detected (indicating that the animal was hauled out on the ice surface). White squares represent a 30-min period when the animal's signal was not detected (*i.e.*, it was in the water). 30 and 31 May and 5 and 6 June are partly affected by battery power failures in the logger station.

records. The precise timing of the diurnal haul-out rhythm in ringed seals appears to vary seasonally. In late winter and early spring, peak haul-out occurs during the evening and early morning (Kelly and Quakenbush 1990, Lydersen and Hammill 1993), but as the season progresses and molting begins, the peak haul-out period shifts to shortly after midday (*e.g.*, Smith 1973, Finley 1979, Smith and Hammill 1981, Kelly *et al.* 1986, Kelly and Quakenbush 1990, this study).

Haul-out behavior in ringed seals exhibits a strong seasonal pattern on a broad scale; only during the molt are large numbers of seals visible on the sea ice. Smith (1973) suggested that the peak season for ringed seal haul-out behavior occurs 2–3 wk before the break up of the land-fast ice. The actual dates of peak haul-out and breakup would therefore be likely to vary geographically. Geographic variations in current, wind, and the physical geography of an area are likely to influence ice conditions. The timing of the seasonal peak of haul-out displayed by ringed seals in Kongsfjorden, compared with the timing of break up of the sea ice in 2003, was very similar to the timing described by Smith (1973). The ice sheet in Kongsfjorden was very stable in 2003 and land-fast ice remained in the area well after the onset of melting. Much of the sea ice was carried out of the fjord in the last days of June and most of the ice that was left after this time was submerged under surface water, unsuitable for haul-out.

The timing of the seasonal peak in haul-out activity (for all sex, and age categories combined) for the VHF-tagged seals preceded peak numbers attained *via* visual counts by about 3 wk. This might reflect some bias toward individuals that molt early in our VHF-tagged animals, although most of the tagged animals showed no, or only slight signs, of commencing the molt at the time of tagging. But, the departure of these animals from the ice, and in all likelihood the area, while seal haul-out numbers were still building toward a peak, suggests that Kongsfjorden might experience a significant out- and influx of ringed seals from adjacent areas as the season progresses. The disappearance of signals from the animals is not tag loss due to molting, because the flipper tags deployed would signal for months, and remain on the animals indefinitely (except for pups, which tend to shed this type of tag after some weeks). Fjords both to the south and north of the study site tend to lose the sea ice before inner Kongsfjorden, so particularly in years when ice cover is poor this fjord may draw animals entering their molt from surrounding areas. This out- and influx theory is similar to suggestions made by Finley (1979) in his comparison of abundance of ringed seals hauling out in two study areas in the Canadian Arctic, and is likely to be a common phenomenon. The VHF data suggest that declining numbers following peak haul-out are due both to animals departing the molting areas, and from decreasing amounts of time spent hauled out by each animal prior to their actual departure from the area. The small increase in average proportion of time hauled out in the final days of data collection is almost certainly an artifact of small sample sizes as only three of the tagged animals were still hauling out in the area. Data from ringed seals satellite tagged late in the molting season in Svalbard confirm that most ringed seals leave the molting area for weeks or in some cases many months upon completion of the molt (Gjertz *et al.* 2000; Lydersen *et al.* 2004; Lydersen and Kovacs, unpublished data).Behavioral data on individual ringed seal's haul-out patterns is scarce. Kelly and Quakenbush (1990) used VHF telemetry successfully to study lair use by 13 ringed seals during the breeding season and into the molting period and Lydersen *et al.* (1993) also used VHF telemetry to study behavior patterns of pups. The latter study reported that pups spent 50% of their time in the water during the molting period and hauled out frequently for short periods, which agrees with our findings where signals for the two VHF-tagged pups were detected an average of 56% of the time with frequent, short haul-outs. Short haul-out periods dominated all age classes. This is in contrast to Kelly and Quakenbush's (1990), findings during the breeding season, when haul-outs shorter than 1 h were uncommon. Similarly, Lydersen and Hammill's (1993) study of pups equipped with time-depth recorders during the nursing period registered a significant number of haul-out periods for pups that were many hours long. Ringed seals of all age classes may tend to be in and out of the water more often during the late spring when they spend time exposed on the ice surface because of a greater feeling of vulnerability compared to when they are hauled out in lairs earlier in the season.

Adult females performed the longest haul-out periods in this study, with a record of 141 h of continuous haul-out by one of the tagged females. The tendency for adult females to spend a lot of time on the surface compared with males or juveniles may be related to an increased need for rest after a demanding nursing period (Lydersen and Kovacs 1999), achieving a fast molt so that they can resume feeding, or it may reflect avoidance of aquatic harassment by males. Kelly and Quakenbush's data (1990) also suggested that females hauled out more of the time than males. Because sample sizes were small and not homogeneous even within groups, definitive conclusions regarding potentially different behavior patterns among age and sex classes, were not possible in this study, beyond noting that pups seem to behave differently than other age groups. The sample of 10 adult females includes individuals that had not reproduced or had lost their offspring at an early stage (fat animals), animals with weaned offspring (very thin animals) and at least one lactating female. Similarly, the adult male sample of eight individuals contained animals in full reproductive condition (tiggaks) and others that were not. Only four subadult VHF-records were obtained.

Air temperature and wind speed clearly influenced the haul-out behavior of ringed seals in this study, similar to the findings of other haul-out studies. Fewer seals are observed on the ice during windy days (Finley 1979, Smith and Hammill 1981). A positive influence of temperature (Smith 1973, Moulton *et al.* 2002) on the number of seals hauled out is likely due at least in part to the fact that efficient molt in pinnipeds is facilitated by warm skin temperatures (Feltz and Fay 1966). It is important for the seals to be able to perfuse their skin with blood at this time, and doing so in the water would result in a much higher heat loss. Basking in the sun is a very cost-efficient way of achieving warm skin, with minimal loss of heat to the environment. At the very high air temperatures observed by Burns and Harbo (1972) and Finley (1979), seal numbers on the ice declined indicating there may be an upper limit where seals have to leave the ice to cool off. Temperatures were never this high in our study.

Results from this study strongly suggest that creating a general model for precisely interpreting aerial survey data for ringed seals in an area such as Svalbard, will be difficult (see Krafft *et al.* 2006, this issue). However, some basic generalizations are possible regarding ringed seal spring haul-out behavior. Ringed seal spring haul-out behavior is influenced by temporal and environmental factors. Both visual observations and telemetric records confirm diurnal and seasonal patterns in haul-out behavior. Air temperature is generally positively correlated with the number of animals hauled and wind speed negatively affects the number of animals hauled out. Differences between seasonal peaks in haul-out timing between VHF-tagged animals compared with total count data in this study, and the departure of many of the tagged animals from the ice, and likely the study area, prior to the timing of peak counting may indicate significant out- and influx of animals during the spring molting season. This possibility warrants further attention because of its implications for assessment studies.

Acknowledgments

All animal handling protocols used in this study were approved by the Norwegian Animal Research Authorities and the Governor (Sysselmannen) in Svalbard. We thank Christian Jørgensen, Aili Lage Labansen, Anna Andersson, and Wojtek Moskal for help in the field, Ellinor Ytterstad (Statistic Department, University of Tromsø) for her help with statistical analyses, and Lori Quakenbush for her helpful editorial comments. This study was funded by The Research Council of Norway and the Norwegian Polar Institute.

Literature Cited

ACIA (Arctic Climate Impact Assessment). 2004. Impacts of a warming Arctic: Arctic climate assessment. Cambridge University Press, Cambridge, UK.

Burns, J. J., and S. J. Harbo, Jr. 1972. An aerial census of ringed seals, northern coast of Alaska. Arctic 25:279–290.

Derocher, A. E., Ø. Wiig and M. Andersen. 2002. Diet composition of polar bears in Svalbard and the western Barents Sea. Polar Biology 25:448–452.

Feltz, E. T., and F. H. Fay. 1966. Thermal requirements *in vitro* of epidermal cells from seals. Cryobiology 3:261–264.

Ferguson, S. H., I. Stirling and P. McLoughlin. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. Marine Mammal Science 21:121–135.

FINLEY, K. J. 1979. Haul-out behaviour and densities of ringed seals (*Phoca hispida*) in the Barrow Strait area, N. W. T. Canadian Journal of Zoology 57:1985–1997.

FROST, K. J., L. F. LOWRY, G. PENDLETON AND H. R. NUTE. 2004. Factors affecting the observed densities of ringed seals, *Phoca hispida*, in the Alaskan Beaufort Sea, 1996–99. Arctic 57:115–128.

GJERTZ, I., K. M. KOVACS, C. LYDERSEN AND Ø. WIIG. 2000. Movements and diving of adult ringed seals (*Phoca hispida*) in Svalbard. Polar Biology 23:651–656.

HALLER, M. A., K. M. KOVACS AND M. O. HAMMILL. 1996. Maternal behaviour and energy investment by grey seals (*Halichoerus grypus*) breeding on land-fast ice. Canadian Journal of Zoology 74:1531–1541.

HÄRKÖNEN, T., AND S. G. LUNNERYD. 1992. Estimating abundance of ringed seals in the Bothnian Bay. Ambio 21:497–503.

HARWOOD, L. A., AND I. STIRLING. 1992. Distribution of ringed seals in the southeastern Beaufort Sea during late summer. Canadian Journal of Zoology 70:891–900.

KELLY, B. P. 2001. Climate change and ice breeding pinnipeds. Pages 43–55 *in* G.-R. Walther, C. A. Burga, and P. J. Edwards, eds. "Fingerprints" of climate change. Kluwer Academic/Plenum Publishers, New York, NY.

KELLY, B. P., AND L. T. QUAKENBUSH. 1990. Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). Canadian Journal of Zoology 68:2503–2512.

KELLY, B. P., L. T. QUAKENBUSH AND J. R. ROSE. 1986. Ringed seal winter ecology and effects of noise disturbance. Pages 447–536 *in* Outer Continental Shelf Environmental Assessment Program (OCSEAP) Final Reports of Principal Investigators No. 61, NOAA, Anchorage, Alaska. OCS Study MMS 89–0026, NTIS PB89–234645.

KINGSLEY, M. C. S., AND I. STIRLING. 1991. Haul-out behaviour of ringed and bearded seals in relation to defence against surface predators. Canadian Journal of Zoology 69:1857–1861.

KRAFFT, B. A., K. M. KOVACS, T. ERGON, M. ANDERSEN, J. AARS, T. HAUG AND C. LYDERSEN. 2006. Abundance of ringed seals (*Pusa hispida*) in the fjords of Spitsbergen, Svalbard, during the peak molting period. Marine Mammal Science 22:394–412.

LOENG, H., K. BRANDER, E. CARMACK, S. DENISENKO, K. DRINKWATER, B. HANSEN, K. M. KOVACS, P. LIVINGSTON, F. MCLAUGHLIN AND E. SAKSHAUG. 2005. Marine systems (Chapter 8) in arctic climate impact assessment. Cambridge University Press, Cambridge, UK.

LYDERSEN, C., AND I. GJERTZ. 1987. Population parameters of ringed seals (*Phoca hispida* Schreber, 1775) in the Svalbard area. Canadian Journal of Zoology 65:1021–1027.

LYDERSEN, C., AND M. O. HAMMILL. 1993. Diving in ringed seal (*Phoca hispida*) pups during the nursing period. Canadian Journal of Zoology 71:991–996.

LYDERSEN, C., AND K. M. KOVACS. 1993. Diving behaviour of lactating harp seals, *Phoca groenlandica*, females from the Gulf of St. Lawrence, Canada. Animal Behaviour 46:1213–1221.

LYDERSEN, C., AND K. M. KOVACS. 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. Marine Ecology Progress Series 187:265–281.

LYDERSEN, C., M. O. HAMMILL AND M. S. RYG. 1993. Differences in haul-out pattern in two nursing ringed seal *Phoca hispida* pups. Fauna norvegica Series A 14:47–49.

LYDERSEN, C., O. A. NØST, K. M. KOVACS AND M. A. FEDAK. 2004. Temperature data from Norwegian and Russian waters of the northern Barents Sea collected by free-living ringed seals. Journal of Marine Systems 46:99–108.

MCLAREN, I. A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Bulletin Fisheries Research Board of Canada, Bulletin Number 118:1–97.

MOULTON, V. D., W. J. RICHARDSON, T. L. MCDONALD, R. E. ELLIOT AND M. T. WILLIAMS. 2002. Factors influencing local abundance and haulout behaviour of ringed seals (*Phoca* *hispida*) on landfast ice of the Alaskan Beaufort Sea. Canadian Journal of Zoology 80:1900–1917.

MOULTON, V. D., W. J. RICHARDSON, R. E. ELLIOTT, T. L. MCDONALD, C. NATIONS AND M. T. WILLIAMS. 2005. Effects of an offshore oil development on local abundance and distribution of ringed seals (*Phoca hispida*) of the Alaskan Beaufort Sea. Marine Mammal Science 21:217–242.

OGNETOV, G. N. 1993. Characteristics of distribution of ringed seals (*Pusa hispida*) on shore ice of the eastern Siberian Sea. Russian Journal of Ecology 24:111–117.

REEVES, R. R. 1998. Distribution, abundance and biology of ringed seals (*Phoca hispida*): An overview. NAMMCO Scientific Publications 1:9–45.

SMITH, T. G. 1973. Censusing and estimating the size of ringed seal populations. Fisheries Research Board of Canada Technical Report 427.

SMITH, T. G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology 58:2201–2209.

SMITH, T. G., AND M. O. HAMMILL. 1981. Ecology of the ringed seal, *Phoca hispida,* in its fast ice breeding habitat. Canadian Journal of Zoology 59:966–981.

SMITH, T. G., AND C. LYDERSEN. 1991. Availability of suitable land-fast ice and predation as factors limiting ringed seal populations, *Phoca hispida*, in Svalbard. Polar Research 10:585–594.

SMITH, T. G., AND I. STIRLING. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology 53:1297–1305.

SPSS. 2003. Statistical package for the social sciences. SPSS Inc., Chicago, IL.

SVENDSEN, H., A. BESZCZYNSKA-MØLLER, J. O. HAGEN, B. LEFAUCONNIER, V. TVERBERG, S. GERLAND, J. B. ØRBÆK, K. BISCHOF, C. PAPUCCI, M. ZAJACZKOWSKI, R. AZZOLINI, O. BRULAND, C. WIENCKE, J.-G. WINTHER AND W. DALLMAN. 2002. The physical environment of Kongsfjorden-Krossfjorden, an arctic fjord system in Svalbard. Polar Research 21:133–166.

THOMAS, J. A., AND D. P. DEMASTER. 1983. Diel haul-out patterns of Weddell seal (*Leptonychotes weddelli*) females and their pups. Canadian Journal of Zoology 61:2084–2086.

TYNAN, C. T., AND D. P. DEMASTER. 1997. Observations and predictions of Arctic climate change: potential effects on marine mammals. Arctic 50:308–322.

Received: 24 January 2005
Accepted: 27 October 2005