

Fall Migration of Ringed Seals (*Phoca hispida*) through the Beaufort and Chukchi Seas, 2001–02

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ABSTRACT. In a study examining the range, distribution, and habitat use of the ringed seal, *Phoca hispida*, in Canada's Western Arctic, eight ringed seals were live-captured, instrumented with satellite-linked (SLTDR-16) transmitters, and released at Cape Parry, Northwest Territories, Canada, on 17–19 September 2001 and 7–8 September 2002. Locations accepted by the filtering process were received from seven of the eight tagged seals (5 subadults, 1 adult female, 1 pup) over periods ranging from 35 to 207 days (mean 99 d, SD 66). Mean rates of travel were 0.91 m/s (SE 0.011, n = 7) in the Canadian Beaufort Sea, 0.92 m/s (SE 0.014, n = 7) offshore of Alaska's North Slope, and 0.79 m/s (SE 0.008, n = 5) in the Chukchi Sea. On average, the seals took 32 days (range 19–56 d) to migrate between Cape Parry and Point Barrow, almost always remaining within 100 km of shore and over the continental shelf or slope, and covering an average migration distance of 2138 km. Dive depths for all groupings were mainly in the 4–80 m range (adult female: 63–73%; subadults: 54–73%; pup: 64–82%), with only the adult female diving deeper than 80 m on occasion, mainly in the Canadian Beaufort Sea (15.1% of her dives). The subadults and pup dove mainly for more than 1 to 5 min (60% and 55%, respectively), while a large proportion of the adult female's dives were longer (34% for > 1 to 5 min; 31% for > 5 to 8 min; 5.4% for > 8 min). The tracks of the westward migrating seals revealed a routing through three political jurisdictions (including oil and gas industry lease areas in all three) over a period of about two months. This pattern highlights the importance of cooperation between the United States, Canada, and Russia in managing this species.

Key words: ringed seal, subadult, Cape Parry, Beaufort Sea, fall migration, diving, Alaska North Slope, Chukchi Sea

RÉSUMÉ. Du 17 au 19 septembre 2001 et les 7 et 8 septembre 2002, dans le cadre d'une étude portant sur le parcours, la répartition et l'utilisation de l'habitat du phoque annelé, *Phoca hispida*, dans l'ouest de l'Arctique canadien, huit phoques annelés ont été capturés en vie, dotés de transmetteurs en liaison avec un satellite (SLTDR-16), puis relâchés au cap Parry, dans les Territoires du Nord-Ouest, au Canada. Des emplacements acceptés par filtrage ont été reçus de la part de sept des huit phoques marqués (5 préreproducteurs, 1 femelle adulte, 1 jeune) sur des périodes variant entre 35 et 207 jours (moyenne 99 d, SD 66). Les taux de déplacement moyens étaient de 0,91 m/s (SE 0,011; n = 7) dans la mer canadienne de Beaufort, de 0,92 m/s (SE 0,014; n = 7) au large du versant nord de l'Alaska et de 0,79 m/s (SE 0,008; n = 5) dans la mer des Tchouktsches. En moyenne, la migration des phoques entre le cap Parry et la pointe Barrow durait 32 jours (écart de 19 à 56 d), et les phoques restaient presque toujours en-dedans de 100 km de la côte et au-dessus de la pente ou du plateau continental. Ils couvraient en moyenne une distance de migration de 2 138 km. La profondeur des plongées de tous les groupements variait entre 4 et 80 m (femelle adulte : 63 % à 73 %; préreproducteurs : 54 % à 73 %; jeune : 64 % à 82 %), et seulement la femelle adulte plongeait à plus de 80 m de profondeur à l'occasion, surtout dans la mer canadienne de Beaufort (15,1 % de ses plongées). Les préreproducteurs et le jeune phoque étaient principalement en plongée pendant plus de 1 à 5 min (60 % et 55 %, respectivement), tandis qu'une grande proportion des plongées de la femelle adulte durait plus longtemps (34 % pour > 1 à 5 min; 31 % pour > 5 à 8 min; 5,4 % pour > 8 min). Les pistes des phoques en migration vers l'ouest révélaient des itinéraires passant par trois compétences politiques (comprenant des concessions de l'industrie pétrolière et gazière dans les trois cas) sur une période d'environ deux mois. Cette tendance fait ressortir l'importance d'une collaboration entre les États-Unis, le Canada et la Russie en matière de gestion de cette espèce.

Mots clés : phoque annelé, préreproducteur, cap Parry, mer de Beaufort, migration automnale, plongée, versant nord de l'Alaska, mer des Tchouktsches

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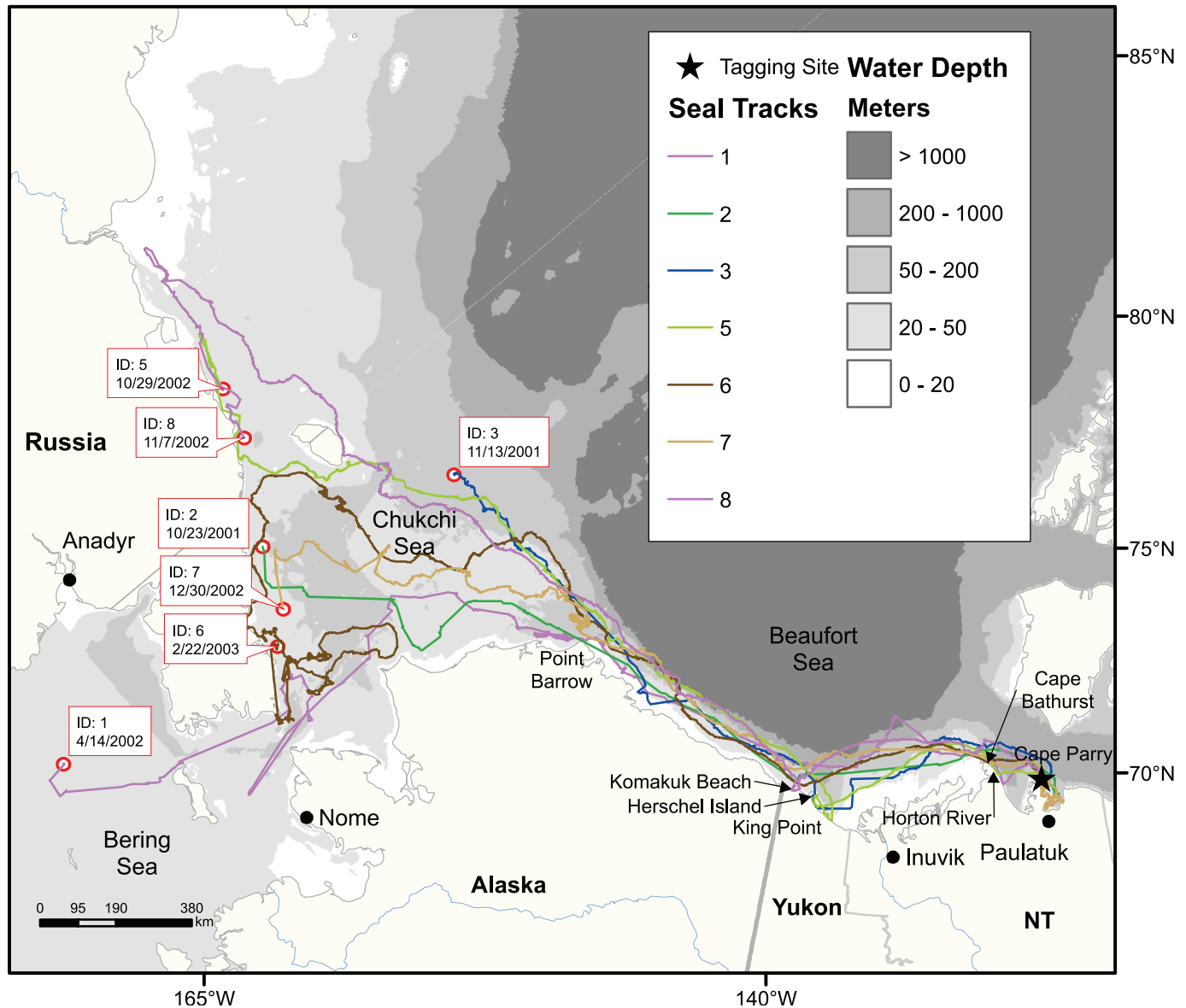


FIG. 1. Map of ringed seal fall migration area, showing locations named in text, ringed seal tagging site (★), seal tracks, and final locations received from seven seals tagged at Cape Parry, Northwest Territories, Canada, on 17–19 September 2001 and 7–8 September 2002.

INTRODUCTION

The ringed seal, *Phoca hispida*, is the most abundant marine mammal species in the circumpolar Arctic. It is important in the subsistence economy of Arctic aboriginal peoples (IRC, 1989; Reeves, 1998; Joint Secretariat, 2003) and the main prey of the polar bear (*Ursus maritimus*) (Stirling, 2002). Ringed seals are highly adapted to their variable polar environment, and they periodically undergo changes in abundance and distribution, apparently in response to changing sea ice conditions (Stirling et al., 1982; Smith, 1987; Kingsley and Byers, 1998). Understanding how this species exists in its environment is especially important in the context of climate change and renewed interest by the hydrocarbon industry throughout much of the ringed seal's assumed range.

Ringed seals feed on arctic cod, *Boreogadus saida*, throughout the western Arctic at all times of the year (Johnson et al., 1966; Lowry et al., 1978, 1980; Bradstreet et al., 1986; Crawford and Jørgenson, 1996). There is evidence that invertebrates are an important diet item in summer and autumn for ringed seals of all age classes, although particularly for subadult animals, which have less experience capturing fish (Lowry et al., 1978, 1980; Smith, 1987; Smith and Harwood, 2001). Satellite tagging studies have shown that adult and subadult ringed seals are far-ranging while feeding during the open water period (Kapel et al., 1998; Teilmann et al., 1999; Freitas et al., 2008a; Kelly et al., 2010).

After extensive summer and fall feeding, adults return to their winter breeding sites just before freeze-up to establish territories (Smith, 1987; Kelly et al., 2010). Subadults,

unconstrained by the need to establish and defend territories, sometimes undertake extensive migrations just prior to freeze-up (Smith, 1987; Heide-Jørgensen et al., 1992; Teilmann et al., 1999; Freitas et al., 2008a), in some cases covering thousands of kilometres (Kapel et al., 1998) or moving to distant ice edges where prey are abundant (Freitas et al., 2008a; J.A. Crawford et al., 2011). These migrations are probably a response to food availability (Smith, 1987; Freitas et al., 2008a); dispersal from core breeding areas has the effect of reducing competition with breeding adults for resources (McLaren, 1958; Smith and Hammill, 1981; Hammill and Smith, 1989; J.A. Crawford et al., 2011). Kelly et al. (2010) provide strong evidence of interannual fidelity to breeding sites among adult Arctic ringed seals, but less is known of the open water movements of subadults.

The specific objective of this study was to enhance our understanding of the timing, location, and characteristics of the westward fall migration of subadult ringed seals in the Canadian Beaufort Sea/Amundsen Gulf region through the use of satellite telemetry and with the assistance of local Inuvialuit harvesters. Knowledge of seal movements is important to understanding the basic ecology of the species, including different strategies and habitats used by the various age class groupings, and to ensuring informed conservation and management practices for this important subsistence species.

METHODS

In September 2001 and September 2002, eight ringed seals were captured, measured, weighed, and tagged with satellite-linked time-depth recorders (SLTDR-16, manufactured by Wildlife Computers Ltd, Redmond, Washington). The tagged seals were released at Brown's Harbour (124°22' W, 70°08' N) near Cape Parry, Northwest Territories, Canada (Fig. 1). The tags were programmed to send data via the Argos system (Harris et al., 1990) and to collect and relay information on movement (geographic positions) and diving behaviour of the instrumented animals.

Following methods of Smith et al. (1973), we captured ringed seals using green, braided nylon nets, with 229 mm (9") stretched mesh, 25 meshes deep and 100 m in length, and a 2.5 cm diameter float line. Nets were secured at the shore and offshore ends by anchors. Nets were deployed for the duration of the operations and monitored on a 24 h basis. We also used monofilament nets of the same configuration.

Age of the seals tagged was estimated in the field by counting claw annuli and measuring axillary girth (to the nearest 1.0 cm) and body mass (to the nearest 1.0 kg) (American Society of Mammalogists, 1967). Live-standard length was estimated as the straight-line distance from nose to tail, with the belly down. The Animal Use Protocol (AUP) administered by Fisheries and Oceans Canada approved all animal-handling procedures used in this study.

The captured seals were restrained as necessary, and the pelage at the tag attachment site was cleaned with rubbing

alcohol. The tags were applied to the middle of the upper back and attached using approximately 150 ml of five-minute epoxy glue. Both the glue and the transmitter were warmed with a hair dryer before deployment to initiate hardening of the glue. Tags deployed in 2001 were duty cycled to conserve battery life, with the on/off cycle of eight days on and two days off. Inuvialuit from the community of Paulatuk, Northwest Territories, participated in the live-capture, tagging, and release of the seals.

The transmitters were cast in epoxy and measured 15 cm × 10 cm × 3.5 cm; their weight was 140 g in seawater and approximately 470 g in air. The transmitters were programmed for up to 500 transmissions per day, with expected battery life of approximately 200 days. The transmission repetition rate was 45 s at sea and 90 s when the seal was hauled out. The tag's saltwater switch ensured that transmissions would occur when the tag was out of the water (when the seal was either surfacing to breathe or hauled out).

The pressure transducer had a resolution of ± 1 m, and an accuracy of ± 1% of the depth reading. Time and pressure (depth) were sampled every 10 sec and stored in 6 h user-defined bins (n = 10 bins in 2001, n = 14 bins in 2002). The type of dive data collected included duration and depth of each dive (sensor capability to 500 m in 2001; 1000 m in 2002). Dive depth bins were 0–4 m, > 4 to 10 m, > 10 to 20 m, > 20 to 40 m, > 40 to 80 m, > 80 to 100 m, > 100 to 150 m, > 150 to 200 m, > 200 to 300 m and > 300 m. Dive duration bins were 0 to 1 min, > 1 to 3 min, > 3 to 5 min, > 5 to 8 min, > 8 to 10 min, > 10 to 14 min, > 14 to 18 min, > 18 to 24 min and > 24 min. The frequency of dives in the different depth and duration categories was plotted in bar graphs for each age class category (pup, subadult, adult) and for the three main areas in which the migration took place (Canadian Beaufort Sea, Alaska North Slope, Chukchi Sea).

Data Analysis

Data on movements, diving behaviour, and transmitter status were collected via the Argos Location Service Plus system (Fancy et al., 1988; Harris et al., 1990). Graphics and analyses were done with ESRI ArcGIS 9.3.1 and ArcGIS Spatial Analyst Extension 9.3.1 (ESRI, 2004) and SAS (SAS Institute Inc., 1990). Dates of freeze-up in the central Chukchi Sea were estimated from National Oceanic and Atmospheric Administration (NOAA) satellite imagery for the two winters (2001–02 and 2002–03).

Location data were collected using the ARGOS system (Harris et al., 1990). Transmitter locations were estimated following uplinks when the transmitter communicated with Argos satellites while the seal was at the surface. All received geographic locations were filtered (Freitas et al., 2008b) in filter R version 2.5.1 (R Development Core Team, 2007), regardless of ARGOS location quality. Locations that indicated unrealistic travel rates (> 2 m/s) were removed when estimating travel rate (Freitas et al., 2008b).

TABLE 1. Sex, claw-band age, size, maximum dive depth, and transmission period for eight ringed seals tagged at Cape Parry, Northwest Territories, Canada, in September 2001 and September 2002. (PTT = Platform Transmitter Terminal.)

ID	PTT	Sex	Maturity ¹	Claw age	Weight (kg)	Approximate standard length (cm)	Axillary girth (cm)	Deployment date	Last signal received	No. days tracked ²	Maximum dive depth (m)
1	2121	female	A	4++	47	115	101	2001 September 19	April 14	207	312
2	5092	male	S	1+	33	108	88	2001 September 17	October 22	35	152
3	11747	male	S	3+	40	110	99	2001 September 19	November 11	53	220
4 ³	5056	female	S	1+	29	100	99	2001 September 19	September 27	8	220
5	5092	male	S	1+	22	91	81	2002 September 07	October 29	54	60
6	23527	male	P	0+	20	88	82	2002 September 07	February 22	168	84
7	23528	female	S	2+ or 3+	30	102	94	2002 September 07	December 30	113	152
8	23529	female	S	2+ or 3+	30	110	88	2002 September 08	November 11	64	132

¹ A = adult, S = subadult, P = pup.

² From first to last signal.

³ Seal excluded from all subsequent analyses because of truncated tracking period (8 d).

Consecutive locations separated by angles of more than 15° (within 2.5 km of the track line) or more than 25° (2.5 to 5 km of the track line) were removed during the filtering process, as were any locations that fell on land.

We used all locations retained by the filtering process to calculate minimum distances travelled (km) and rates of travel (m/s) for each individual seal. Minimum rate of travel was calculated using the minimum horizontal distance between two consecutive, accepted ARGOS locations. Longitude was plotted by date for each tagged animal, to depict and compare the time and location of seal movements.

Dives were linked to location data using the first accepted geographic position in each six-hour time bin of diving data. Dives were summarized for the Canadian Beaufort Sea, the Alaska North Slope, the Chukchi Sea, and the Bering Sea, and separately for the adult female (n = 1), subadults (n = 5) and the pup (n = 1) using SAS (SAS Institute Inc., 1990). Water depth at each accepted location was obtained from the International Bathymetric Chart of the Arctic Ocean (IBCAO) with a resolution of 2 km × 2 km (Jakobsson et al., 2008).

RESULTS

Eight ringed seals (4 males, 4 females, aged 0–4++ y) were captured, tagged, and released (Table 1). Tracking data from one subadult seal (ID 4), which transmitted for only 8 days, have been excluded from all analyses, and the reason(s) for failure of this tag to transmit are unknown. The five subadults averaged 104 cm (SE 6.8) and 30 kg (SE 5.5) (range 22–40 kg; 94–100 cm) (Table 1). We assumed that the largest seal in the sample, a female with 4++ claw bands (weight 47 kg, length 115 cm) was an adult on the basis of a comparison of her weight and length to those of 224 female ringed seals sampled from a nearby subsistence harvest during July 1992–2010, 220 of which were sexually mature (mean weight 46.8 kg, mean length 118 cm) (Harwood et al., 2000; DFO, unpubl. data).

A total of 25 475 locations were received from seven seals, 6455 of which (25.1%) were accepted during the

filtering process (Table 2). This represented a total tracking distance of 23 428 km (mean 3347 km, range 706–6140 km; Table 2). Accepted locations were received over periods ranging from 35 to 207 days (mean 99 d, SD = 66). Seals were located on 80.7% of the tracking days (range 45%–100%) and averaged 922 accepted geographic locations per seal (range 214–2124).

All seven transmitting tagged seals followed a similar westward migration pattern, moving through the Canadian Beaufort Sea, offshore of the Alaska North Slope, and then into the Chukchi Sea (Fig. 1). The mean rates of travel in the Canadian Beaufort Sea (0.91 m/s, SE 0.011, n = 7 seals) and offshore of Alaska's North Slope (0.92 m/s, SE 0.014, n = 7 seals) were both faster than the mean rate of travel in the Chukchi Sea (0.79 m/s, SE 0.008, n = 6) (Fig. 2). The mean rate of travel was 0.75 m/s for the adult (n = 1, SE 0.023), 0.85 m/s (SE 0.008) for the subadults (n = 5), and 0.86 m/s (SE 0.011) for the pup.

Seals took an average of 32 days to migrate between the tagging site at Cape Parry and Point Barrow, Alaska (range 19–56 d), a tracking distance averaging 2138 km (Fig. 1). On average, the seals spent about the same amount of time migrating through the Canadian Beaufort Sea (15.2 d, range 10–29 d) as offshore of Alaska's North Slope (15.0 d, range 4–28 d) (Fig. 2).

The number of days of tracking in the Chukchi Sea was highly variable because the length of time the tags transmitted from this location varied although all transmitting seals passed Point Barrow prior to freeze-up in the central Chukchi Sea (Oct. 30 in 2001; Nov. 20 in 2002). The plot of longitude by date (Fig. 2) illustrates that the seals tagged in September 2000 and September 2001 migrated westward with a similar timing and rate through the Canadian Beaufort Sea and along the Alaska North Slope. Seal ID 7 migrated west approximately 20 days later than other seals tagged in 2002 (IDs 5, 6, 8) but its timing was similar to that of the seals tagged in 2001.

The tag that lasted the longest (207 d) was deployed on the adult female seal that travelled through the Bering Strait (southbound) on 15 December 2001, again on 9 January 2002 (northbound) and finally south again on 26 March

TABLE 2. Accepted positions and minimum distance travelled during periods of open water and ice, for seven ringed seals tagged at Cape Parry, Northwest Territories, Canada, in September 2001 and September 2002.

Seal ID	No. of days with accepted positions	No. of accepted positions	No. of accepted open water positions	Distance tracked by habitat (km)		Min distance travelled (km)
				Open ¹	Ice ¹	
Adult:						
1	93	507	266	1476.6	2225	3702
Subadults:						
2	30	214	196	2304.7	203	2508
3	42	427	127	1476.8	780	2257
5	54	1086	179	2793.6	663	3457
7	97	1898	1031	2251.7	2406	4658
8	62	199	199	705.9	0	706
Pup:						
6	121	2124	1094	2737.3	3403	6140

¹ Freeze-up in the central Chukchi Sea occurred on October 30 in 2001 and November 20 in 2002.

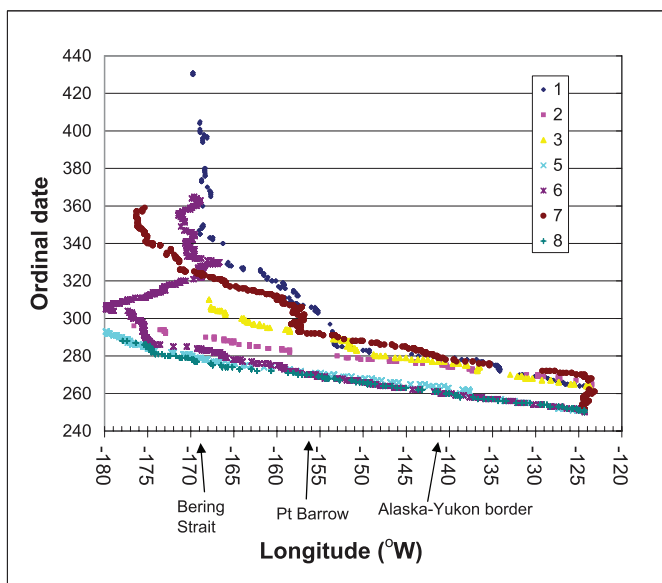


FIG. 2. Longitude vs. ordinal date for seven ringed seals tagged at Cape Parry, Northwest Territories, during their fall migration through the Canadian Beaufort Sea, offshore of the Alaska North Slope, to the Chukchi Sea (September 2001 to April 2002; September 2002 to February 2003).

2002 (Fig. 1). That seal spent the month of April in the Bering Sea; the last signal was received on 14 April 2002, 300 km southwest of St. Lawrence Island (ID 1).

The route used by the tagged seals during migration through the Canadian Beaufort Sea included areas with oceanographic features known to be productive and to concentrate seal prey items (Fig. 1). These included the mouth of the Horton River, offshore of Cape Bathurst, along the Yukon coast near King Point, Herschel Island and Komakuk Beach (Thomson et al., 1986; Harwood and Smith, 2002). The average water depth for tagged seal locations in the Canadian Beaufort Sea was 165 m (range 61–308 m). A polygon encompassing all accepted locations in the Canadian Beaufort Sea had an average water depth of 626 m.

Along the Alaska North Slope, seals moved through waters almost exclusively over the continental shelf, in average depths of 40 m in 2001 and 307 m in 2002. The

westward routes used in 2001 and 2002 were similar; although two seals in 2002 travelled beyond the shelf for part of the migration, they almost always stayed within 100 km of shore. Average distance from shore was 38.9 km (range: 5.1–67.0 km) in 2001 and 60.6 km (range: 13.7–101.5 km) in 2002 (Fig. 1). The average water depth for the tagged seals offshore of the Alaska North Slope was 224 m (range 0–2578 m). A polygon encompassing all accepted locations along the Alaska North Slope had a mean water depth of 1203 m.

All seven transmitting seals arrived in the Chukchi Sea prior to freeze-up of the sea ice and traversed that sea on widely separated routes (Fig. 1), migrating west or southwest across the central Chukchi Sea. Five arrived near the Russian coastline, on average within 28.5 d of passing Point Barrow (range 13–43 d). One stopped transmitting in the Central Chukchi (ID 3) in mid November (Fig. 1). The adult female (ID 1) continued southward into the Bering Sea, while the other five remained along the Chukotka Peninsula, generally within 41 km of the coast (range 24–84 km) until their tags ceased transmitting (on dates ranging from October to February). The average water depth for the tagged seals in the Chukchi Sea was 50 m (range 0–285 m).

Four of the seven tags stopped transmitting at approximately the time of freeze-up in late October and November (ID 2, 5, 8), while three continued to transmit during the ice-covered period, lasting until late December (ID 7), February (ID 6), and April (ID 1) (Fig. 1). On-board battery reserves averaged 6.91 V (range 6.85–6.98 V) at deployment, and 6.75 V (range 6.53–6.85 V) at the final received accepted locations ($n = 7$), all well above the lower limit of battery voltage (5 V) required for SLTDR-16 tags to function.

Diving

We obtained 2160×6 h bins of diving data from the seven transmitting seals. Maximum recorded dive depth was 60 m for the pup, 312 m for the adult female, and ranged from 84 to 220 m for the five subadults. Data were obtained primarily during the open water tracking (79.7%

of 2160; 26.5%, in September, 41.7% in October, and 11.5% in November), and less frequently during ice-covered periods (20.2% of total). Tagged seals were most often located in water that was 40–80 m deep: 47.5% of subadult relocations, 41.2% of those for the adult female, and 67.2% of those for the pup, were in this water depth range.

The subadults and the adult female spent an average of 26% of their time in the upper 4 m of the water column, and the pup spent 42.4% of its time there (Fig. 3). Diving activity was largely limited to four of the depth categories programmed in the tags (> 4 to 10 m, > 10 to 20 m, > 20 to 40 m, > 40 to 80 m) in each of the Canadian Beaufort Sea, the Alaska North Slope, and the Chukchi Sea (adult female: 63%–73%; subadults: 54%–73%; pup: 64%–82%). Only the adult female made more than the occasional dive to depths greater than 80 m, and that was in the Canadian Beaufort Sea (15.1% of her dives). In the Bering Sea, her preferred dive depth category was 20–40 m (33.6%).

The proportion of time seals spent underwater in the 0–1 min category was similar for subadults (30.8%) and the adult female (29.8%) and highest for the pup (39%) (Fig. 4). The five subadults and the pup dove for over 1 to 5 min in 60% and 55% of their dives, respectively, and this pattern held across the Canadian Beaufort Sea, off the Alaska North Slope, and in the Chukchi Sea. A proportion of the adult female's dives were longer than those of the subadults and pup: she dove for > 1 to 5 min in 34% of her dives, for > 5 to 8 min in 31% of her dives, and for more than 8 min in 5.4% of her dives, the latter mainly in the Canadian Beaufort Sea. Diving for longer than 14 min was rare in the adult female (0.2%) and essentially did not occur in the subadults and pup.

DISCUSSION

The most striking finding in this study is that seven of seven transmitting seals undertook a relatively synchronous westward fall migration from the Canadian Beaufort Sea, along the shore of the Alaska North Slope and onward to the Chukchi Sea, over approximately one month. Short (1–5 min) and shallow (4–40 m) dives predominated in all age classes, and the overall mean rate of travel was rapid (0.85 m/s, SE 0.006, n = 7 seals). The one adult tagged in this study provided records of diving for longer than 8 min or deeper than 80 m and did so mainly in the Canadian Beaufort Sea (11.1% exceeded 8 min; 15.1% exceeded 80 m).

The tracking route included (1) oceanographic areas in the Canadian Beaufort Sea known from other studies to be important late summer feeding habitat for seals and bowhead whales (Harwood and Stirling, 1992; Harwood and Smith, 2002), (2) a relatively rapid migration over the continental shelf and slope offshore of the Alaska North Slope, and (3) divergent tracks across the shallower Chukchi Sea to the Russian coast off the Chukotka Peninsula, where the last locations we received were transmitted from five of the seven seals.

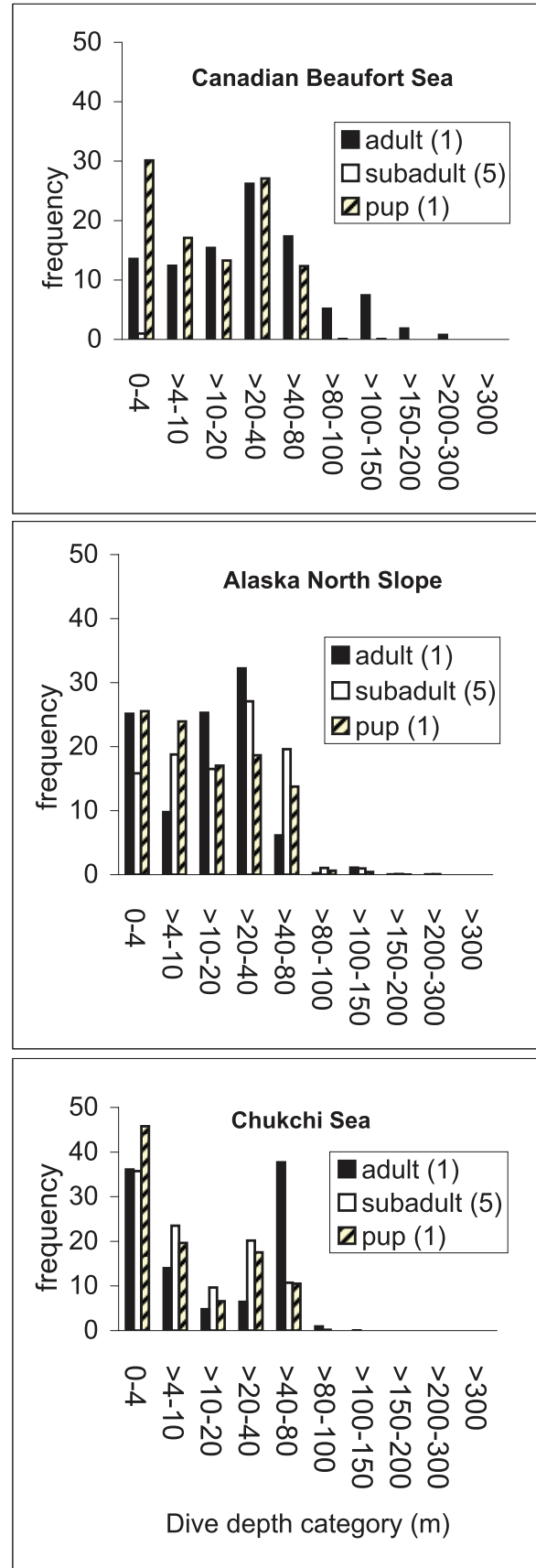


FIG. 3. Dive depth frequencies for tagged ringed seals in the Canadian Beaufort Sea, along the Alaska North Slope, and in the Chukchi Sea.

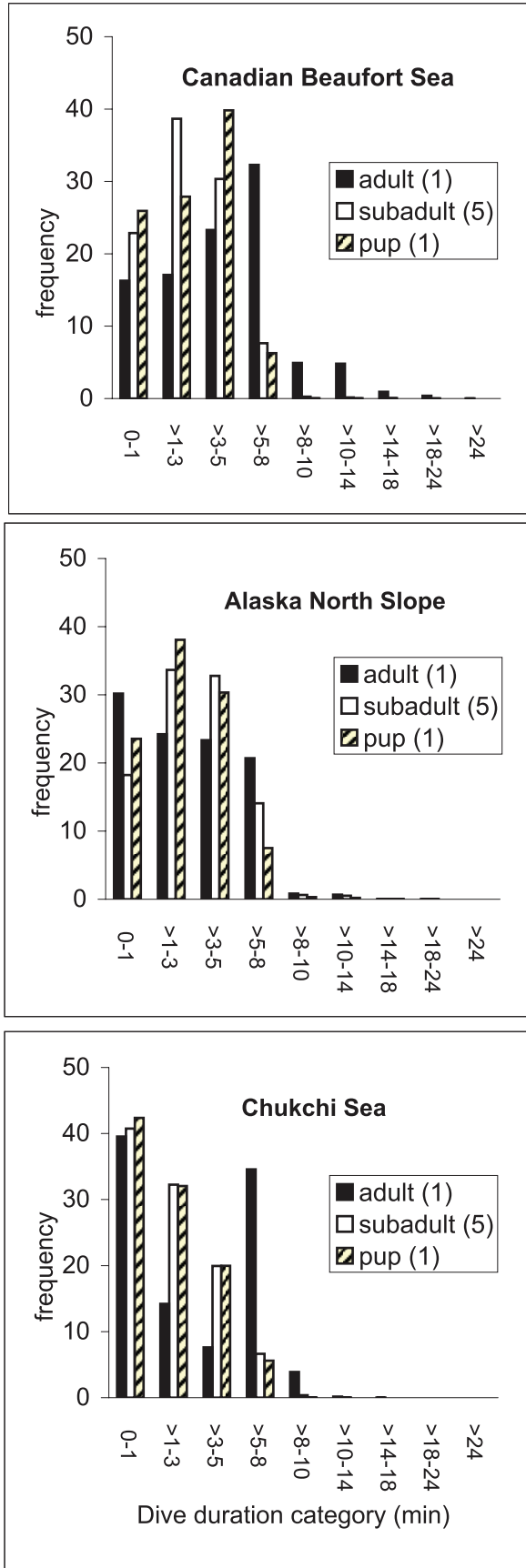


FIG. 4. Dive duration frequencies for tagged ringed seals in the Canadian Beaufort Sea, along the Alaska North Slope, and in the Chukchi Sea.

The disparate proportion of relocations during the open water period (80%) versus the ice-covered period (20%) was similar in our study to that reported by others (e.g., Teilmann et al., 1999). As sea ice forms in the fall, ringed seals initially break the ice with their heads to breathe until the ice thickens and breathing holes must be maintained with their claws (Smith and Stirling, 1975). This change in behaviour from active swimming during open water, to head-up breath-taking during freeze-up and periods of ice cover, is the most plausible explanation for the reduction in uplinks at the time of freeze-up, because during these times the (dorsal) tag is rarely exposed. Battery drain did not appear to be a factor in our study, and a similar conclusion was reported by Teilmann et al. (1999). However, antenna breakage due to ice abrasion or predation by polar bears cannot be discounted.

The late summer feeding areas in the Beaufort Sea mentioned as (1) above that were traversed by tagged seals are characterized by upwelling or bathymetry that concentrates seal and whale planktonic prey items (Thomson et al., 1986; Bradstreet et al., 1987). In addition, recent oceanographic sampling in the Beaufort and Chukchi seas revealed shoals of fish on the Chukchi shelf and at the eastern Chukchi shelf break, and also on the Alaskan and Canadian Beaufort shelves in the upper 20 m at temperatures of 2–5°C. Much larger shoals, purported to be polar cod, were detected within deeper layers of Atlantic Water along the Beaufort continental slope (250–350 m) (R.E. Crawford et al., 2011). These large shoals of cod in deeper, cold Atlantic layers were the probable target of the seal’s dives to deeper depths, particularly those by the adult female who would have been physiologically capable of accessing deeper depths compared with the subadults or pup.

In addition, seals went to the mouth of at least one river known to support a sea-run population of Arctic charr, *Salvelinus alpinus*. The westward migration of all seven tagged seals included portions of offshore oil and gas lease areas in the Canadian Beaufort, which are located over or near the shelf break north of the Mackenzie River estuary (AANDC, 2012).

The mean rate of travel during the entire westward migration (0.85 m/s) was twice that observed in other studies of migrating subadult ringed seals (e.g., 0.43 m/s in the North Water polynya, Teilmann et al., 1999; 0.42 m/s in the Chukchi Sea, J.A. Crawford et al., 2011). The relatively shallow and short dives that we observed in our tagged seals were consistent with findings for subadults in the North Water study (Born et al., 2004), where 92% of the subadult dives in open water were within the upper 50 m of the water column. Similar shallow and short dives, such as we observed in the one adult female in this study, are also reported for adult ringed seals in the Svalbard area (Gjertz et al., 2000).

The tagged seals migrating offshore of the Alaska North Slope followed similar routes in both years. The tendency of tagged ringed seals to remain over the continental shelf or slope makes their route similar to the migratory

path preferred by westward migrating bowhead whales in fall (Quakenbush et al., 2010) and contrasts with the more offshore route preferred by beluga (Richard et al., 2001). Active and possible future locations of oil and gas activity on the shelf offshore of the Alaska North Slope (BOEMRE, 2010a) are situated within the migration route that was used by tagged seals in this study.

The tagged seal's migration across the shallower Chukchi Sea occurred over more divergent routes than were observed in the Canadian Beaufort or off the Alaska North Slope. The Chukchi Sea is a shallow (50 m) shelf sea, north of the Bering Strait and south of the Arctic Ocean. The seal's migration routes initially traversed through Lease Area 193 (BOEMRE, 2010b) presently active in the NE Chukchi Sea. The seals then continued on to coastal waters off Chukotka in the SW Chukchi Sea. This area was attractive to all of the tagged seals in this study, as well as to those in an earlier ringed seal study (Smith, 1987); to bowhead whales, *Balaena mysticetus* (Miller et al., 1986; Moore et al., 1995; Quakenbush et al., 2010); to walrus, *Odobenus rosmarus divergens* (Burns, 1993); and to beluga whales, *Delphinapterus leucas* (Richard et al., 2001). The Long Strait area where seals were last relocated is in the western Chukchi Sea between Wrangel Island and the coast. This area is particularly productive under the buoyant, seasonal influence of the Siberian Coastal Current, being fed by nutrient-rich waters flowing seasonally through the Bering Strait (Woodgate et al., 2005).

Ringed seals in the western Arctic of Canada appear to segregate into adult breeding populations occupying core stable fast ice areas such as Prince Albert Sound and Minto Inlet on western Victoria Island (Smith, 1987). Immature animals undertake a migration to over-wintering areas in the Chukchi Sea or beyond to the Bering Sea. New evidence strongly suggests that adult breeding seals are philopatric (Smith and Hammill, 1981; Kelly et al., 2010). Because our tags operated for less than one year, we do not know how long the animals that we tagged remained in the Chukchi or Bering seas, or whether a significant number of them returned later as breeding seals to areas where they were born.

Future studies combining genetic research to identify breeding stocks, coupled with longer-lasting satellite tags, are needed to define the area necessary to sustain sub-populations of such a mobile species as the ringed seal. Defining this area will be of particular importance if large-scale habitat degradation should occur as a result of climate change, a major offshore oil spill, or other factors.

The tracks and timing of westward fall migrant seals in this study revealed a routing through three political jurisdictions and included present-day oil and gas industry lease areas in all three. This fact points to the importance of cooperation between the United States, Canada, and Russia in the management of this species.

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REFERENCES

- AANDC (Aboriginal Affairs and Northern Development Canada). 2012. Oil and gas rights digital files. <http://www.aadnc-aandc.gc.ca/eng/1100100036298>.
- American Society of Mammalogists. 1967. Standard measurements of seals. *Journal of Mammalogy* 48(3):459–462.
- BOEMRE (Bureau of Ocean Energy Management, Regulation and Enforcement). 2010a. Beaufort Sea – Outer Continental Shelf Lease Ownership. http://alaska.boemre.gov/Maps/2010_bf.pdf.
- . 2010b. Chukchi Sea – Outer Continental Shelf Lease Ownership. http://alaska.boemre.gov/Maps/2010_ck.pdf.
- Born, E.W., Teilmann, J., Acquarone, M., and Riget, F.F. 2004. Habitat use of ringed seals (*Phoca hispida*) in the North Water area (North Baffin Bay). *Arctic* 57(2):129–142.
- Bradstreet, M.S.W., Finley, K.J., Sekerak, A.D., Griffiths, W.B., Evans, C.R., Fabijan, M.F., and Stallard, H.E. 1986. Aspects of the biology of Arctic cod (*Boreogadus saida*) and its importance in Arctic marine food chains. Canadian Technical Report of Fisheries and Aquatic Sciences 1491. 193 p.
- Bradstreet, M.S.W., Thomson, D.H., and Fissel, D.B. 1987. Bowhead whale food availability characteristics in the southern Beaufort Sea: 1985 and 1986. *Environmental Studies* 50. Ottawa: Indian and Northern Affairs Canada. 155 p.
- Burns, J.J. 1993. Epilogue. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press. 745–764.
- Crawford, J.A., Frost, K.J., Quakenbush, L.T., and Whiting, A. 2011. Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. *Polar Biology*, doi:10.1007/s00300-011-1067-1.
- Crawford, R.E., and Jørgensen, J.K. 1996. Schooling behaviour of Arctic cod, *Boreogadus saida*, in relation to drifting pack ice. *Environmental Biology of Fishes* 36(4):345–357.

- Crawford, R.E., Vagle, S., and Carmack, E.C. 2011. Water mass and bathymetric characteristics of polar cod habitat along the continental shelf and slope of the Beaufort and Chukchi seas. *Polar Biology*, doi:10.1007/s00300-011-1051-9.
- ESRI. 2004. ArcGIS 9.3.1. Redlands, California: ESRI. <http://www.esri.com/software/arcgis/eval-help/arcgis-93.html>.
- Fancy, S.G., Pank, L.F., Douglas, D.C., Curby, C.H., Garner, G.W., Amstrup, S.C., and Regelin, W.L. 1988. Satellite telemetry: A new tool for wildlife research and management. Resource Publication 172. Washington, D.C.: U.S. Department of the Interior, Fish and Wildlife Service. 60 p.
- Freitas, C., Kovacs, K.M., Ims, R.A., Fedak, M.A., and Lydersen, C. 2008a. Ringed seal post-moulting movement tactics and habitat selection. *Oecologia* 155(1):193–204.
- Freitas, C., Lydersen, C., Fedak, M.A., and Kovacs, K.M. 2008b. A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science* 24(2):315–325.
- Hammill, M.O., and Smith, T.G. 1989. Factors affecting the distribution and abundance of ringed seal structures in Barrow Strait, Northwest Territories. *Canadian Journal of Zoology* 67(9):2212–2219.
- Harris, R.B., Fancy, S.G., Douglas, D.C., Garner, G.W., Amstrup, S.C., McCabe, T.R., and Pank, L.F. 1990. Tracking wildlife by satellite: Current systems and performance. Fish and Wildlife Technical Report 30. Washington, D.C.: U.S. Department of the Interior, Fish and Wildlife Service. 52 p.
- Harwood, L.A., and Smith, T.G. 2002. Whales of the Inuvialuit Settlement Region in Canada's Western Arctic: An overview and outlook. *Arctic* 55(Suppl. 1):77–93.
- Harwood, L.A., and Stirling, I. 1992. Distribution of ringed seals in the southeastern Beaufort Sea during late summer. *Canadian Journal of Zoology* 70(5):891–900.
- Harwood, L.A., Smith, T.G., and Melling, H. 2000. Variation in reproduction and condition of the ringed seal (*Phoca hispida*) in Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. *Arctic* 53(4):422–431.
- Heide-Jørgensen, M.P., Stewart, B.S., and Leatherwood, S. 1992. Satellite tracking of ringed seals *Phoca hispida* off Northwest Greenland. *Ecography* 15:56–61.
- Gjertz, I., Kovacs, K.M., Lydersen, C., and Wiig, Ø. 2000. Movements and diving of adult ringed seals (*Phoca hispida*) in Svalbard. *Polar Biology* 23(9):651–656.
- IRC (Inuvialuit Regional Corporation). 1989. The Inuvialuit sealing economy: Prospects for development. Ottawa: Inuit Tapirisat of Canada. Available from IRC, Box 2120, Inuvik, Northwest Territories X0E 0T0.
- Jakobsson, M., Macnab, R., Mayer, L., Anderson, R., Edwards, M., Hatzky, J., Schenke, H.W., and Johnson, P. 2008. An improved bathymetric portrayal of the Arctic Ocean: Implications for ocean modeling and geological, geophysical and oceanographic analyses. *Geophysical Research Letters* 35, L07602, doi:10.1029/2008GL033520. <http://www.ngdc.noaa.gov/mgg/bathymetry/arctic/arctic.html>.
- Johnson, M.L., Fiscus, C.H., Ostenson, B.T., and Barbour, M.L. 1966. Marine mammals. In: Wilimovsky, N.J., ed. Environment of the Cape Thompson Region, Alaska. Oak Ridge, Tennessee: U.S. Atomic Energy Commission, Division of Technical Information Exchange. 887–924.
- Joint Secretariat. 2003. The Inuvialuit Harvest Study: Data and methods report 1988–1997. Available from IRC, Box 2120, Inuvik, Northwest Territories X0E 0T0.
- Kapel, F.O., Christiansen, J., Heide-Jørgenson, M.P., Härkönen, T., Born, E.W., Knutsen, L.Ø., Riget, F., and Teilmann, J. 1998. Netting and conventional tagging used to study movements of ringed seals (*Phoca hispida*) in Greenland. In: Heide-Jørgensen, M.P., and Lydersen, C., eds. Ringed seals in the North Atlantic. NAMMCO Scientific Publication 1. Tromsø, Norway: The North Atlantic Marine Mammal Commission. 211–228.
- Kelly, B.P., Badajos, O.H., Kunnasranta, M., Moran, J.R., Martinez-Bakker, M., Wartzok, D., and Boveng, P. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology* 33(8):1095–1109, doi:10.1007/s00300-010-0796-x.
- Kingsley, M.C.S., and Byers, T.J. 1998. Failure of reproduction in ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories, 1984–1987. In: Heide-Jørgensen, M.P., and Lydersen, C., eds. Ringed seals in the North Atlantic. NAMMCO Scientific Publication 1. Tromsø, Norway: The North Atlantic Marine Mammal Commission. 197–210.
- Lowry, L.F., Frost, K.J., and Burns, J.J. 1978. Food of ringed seals and bowhead whales near Point Barrow, Alaska. *Canadian Field-Naturalist* 92(1):67–70.
- . 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 37(12):2254–2261.
- McLaren, I.A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Bulletin 118. Ottawa: Fisheries Research Board of Canada. 97 p.
- Miller, R.V., Rugh, D.J., and Johnson, J.H. 1986. The distribution of bowhead whales, *Balaena mysticetus*, in the Chukchi Sea. *Marine Mammal Science* 2(3):214–222.
- Moore, S.E., George, J.C., Coyle, K.O., and Weingartner, T.J. 1995. Bowhead whales along the Chukotka coast in autumn. *Arctic* 48(2):155–160.
- Quakenbush, L.T., Citta, J.J., George, J.C., Small, R.J., and Heide-Jørgensen, M.P. 2010. Fall and winter movements of bowhead whales (*Balaena mysticetus*) in the Chukchi Sea and within a potential petroleum development area. *Arctic* 63(3):289–307.
- R Development Core Team. 2007. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. www.R-project.org.
- Reeves, R.R. 1998. Distribution, abundance and biology of ringed seals (*Phoca hispida*): An overview. In: Heide-Jørgensen, M.P., and Lydersen, C., eds. Ringed seals in the North Atlantic. NAMMCO Scientific Publication 1. Tromsø, Norway: The North Atlantic Marine Mammal Commission. 9–45.
- Richard, P.R., Martin, A.R., and Orr, J.R. 2001. Summer and autumn movements of belugas of the eastern Beaufort Sea stock. *Arctic* 54(3):223–236.
- SAS (Statistical Analysis System). 1990. SAS Version 8.0. Cary, North Carolina: SAS Institute Inc.

- Smith, T.G. 1987. The ringed seal, *Phoca hispida*, of the Canadian Western Arctic. Canadian Bulletin of Fisheries and Aquatic Sciences 216. 81 p.
- Smith, T.G., and Hammill, M.O. 1981. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. Canadian Journal of Zoology 59(6):966–981.
- Smith, T.G., and Harwood, L.A. 2001. Observations of neonate ringed seals, *Phoca hispida*, after early break-up of the sea ice in Prince Albert Sound, Northwest Territories, Canada, spring 1998. Polar Biology 24(3):215–219.
- Smith, T.G., and Stirling, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology 53(9):1297–1305.
- Smith, T.G., Beck, B., and Sleno, G.A. 1973. Capture, handling and branding of ringed seals. Journal of Wildlife Management 37(4):579–583.
- Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: A synthesis of population trends and ecological relationships over three decades. Arctic 55(Suppl. 1):59–76.
- Stirling, I., Kingsley, M., and Calvert, W. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974–79. Canadian Wildlife Service Occasional Paper 47. 25 p.
- Teilmann, J., Born, E.W., and Acquarone, M. 1999. Behaviour of ringed seals tagged with satellite transmitters in the North Water polynya during fast-ice formation. Canadian Journal of Zoology 77:1934–1946.
- Thomson, D.H., Fissel, D.B., Marko, J.R., Davis, R.A., and Borstad, G.A. 1986. Distribution of bowhead whales in relation to hydrometeorological events in the Beaufort Sea. Environmental Studies Revolving Funds Report 28. Ottawa: ESRF.
- Woodgate, R.A., Aagaard, K., and Weingartner, T. 2005. A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990–91. Deep-Sea Research, Part II, 52(24-26):3116–3149.