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Movements and behavior of satellite-tagged spotted seals (*Phoca largha*) in the Bering and Chukchi Seas

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Abstract Satellite-linked tags were attached to 12 spotted seals (*Phoca largha*) captured at a coastal lagoon in the eastern Chukchi Sea during August 1991–1993. Movements of seals were tracked for 32–298 days using the Argos system. Of 9,651 total location records obtained, 7,268 were usable. Individual seals were located on 41–96% of the days that tags were operational. During August–November, tagged seals alternated haul-outs at coastal sites lasting 1–304 h with trips to sea of 14–901 h. Coastal haul-outs occurred at 14 sites in western Alaska and eastern Russia. On several trips to sea, seals covered distances of more than 1,000 km. Movement southward from the Chukchi Sea generally began in October, with most of the seals passing through the Bering Strait during November. Seals first hauled out on sea ice in October (Chukchi Sea) or November (Bering Sea), and generally moved southward during October–December as sea-ice coverage increased. Seven seals, whose transmitters were still operating, spent December to June in the Bering Sea region between Kuskokwim Bay and Anadyr Gulf, which corresponded to the location of the ice front. The seals made active east-west movements within the ice front. Spotted seals are unlike other ice-breeding seals in that they regularly use coastal haul-outs during summer and autumn. Compared to the closely related Pacific harbor seal (*Phoca vitulina richardsi*), spotted seals make much longer trips to sea and spend longer continuous periods at their haul-outs during summer and autumn.

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Introduction

Spotted seals (*Phoca largha*) are medium-sized pinnipeds of the family Phocidae, occurring principally in the Okhotsk, Bering, and Chukchi Seas (Shaughnessy and Fay 1977). Because of morphological similarities with the Pacific harbor seal (*Phoca vitulina richardsi*), and their adjacent and somewhat overlapping ranges, spotted seals were initially considered to be a subspecies (*Phoca vitulina largha*) (Burns and Fay 1970; Bigg 1981). However, ecological differences in habitat and reproductive biology (Burns 1970) and detailed morphological and craniometric analyses (Shaughnessy and Fay 1977; Burns et al. 1984) confirmed that substantial differences exist between harbor and spotted seals.

Unlike the well-studied harbor seal, the biology of spotted seals is not well described (Quakenbush 1988). Most of the information available has come from studies conducted in the Bering Sea ice front where pupping, breeding and molting all occur from March to May (Burns 1970; Fedoseev 1976; Braham et al. 1984). As the sea-ice cover diminishes and coastal areas become ice-free, spotted seals move to nearshore areas of Alaska and Russia, some of them migrating northward into the Chukchi Sea (Frost et al. 1983a,b; Burkanov 1989; Rugh et al. 1997). During the open-water season, they are commonly seen hauled out on coastal barrier islands, sandbars, rocks and reefs.

Frost et al. (1983a) compiled information on the summer haul-out areas used by spotted seals along the coast of the eastern Chukchi Sea. The most important area identified was Kasegaluk Lagoon (named after the Inupiat word for spotted seal), where 1,000 or more seals were commonly seen hauled out inside the barrier islands. A series of aerial surveys was conducted during

1989–1991 to document spotted seal distribution, abundance, and habitat use in this region (Frost et al. 1993). However, even such detailed surveys did not result in an understanding of the movements and behavior of individual seals. In August 1991, a study was conducted at Kasegaluk Lagoon to assess the feasibility of capturing spotted seals and attaching satellite-linked tags to them (Lowry et al. 1994). This paper describes the results obtained from 12 satellite tags attached to seals at Kasegaluk Lagoon in 1991, 1992 and 1993.

Materials and methods

Spotted seals were caught at Kasegaluk Lagoon (Fig. 1) using nets drifted near entrances to the lagoon at Utukok Pass (70°05′N, 162°28′W) and Akoliakatat Pass (70°18′N, 161°30′W). Seals that became entangled were immediately pulled into a boat, removed from the net, and taken to shore. They were either physically restrained or sedated with a mixture of ketamine (2–4 mg/kg) and diazepam (0.05–0.10 mg/kg) administered intramuscularly (Geraci et al. 1981). Seals were weighed and measured, and a satellite-linked platform transmitter terminal (referred to in this paper as a tag) was glued to the fur of the mid-dorsal surface using a fast-setting epoxy (Fedak et al. 1984; Stewart et al. 1989). After tagging was complete, animals were placed above the tide line near the capture site and left undisturbed until they chose to return to the sea.

In 1991, two types of tags were used: Wildlife Computers (Woodinville, Washington) tags that measured $13.5 \times 12.5 \times 3.8$ cm and weighed 1,050 g, and Telonics (Mesa, Arizona) tags that measured $17.5 \times 10.0 \times 3.5$ cm and weighed 800 g. Both types were powered by four lithium C cells and had 1 W of power output through whip antennas. In 1992 and 1993, only Wildlife Computers tags were used, measuring $14.8 \times 10.0 \times 3.8$ cm and weighing 750 g. Those tags were powered by four lithium C cells and produced 0.5 W of signal output. Tags were equipped with conductivity switches so that they transmitted only when out of water. Wildlife Computers tags operated continuously from the time they were attached, while Telonics tags were duty-cycled and sent data for 7-day periods followed by 7 days of no transmissions.

The tags transmitted on 401.65 MHz to receivers operated by Service Argos on board National Oceanic and Atmospheric Administration polar orbiting satellites. In the area covered by this study there were 20–25 satellite passes per day (depending on the latitude of the seal at the time) and satellites were above the horizon for about 20% of the time (Fancy et al. 1988).

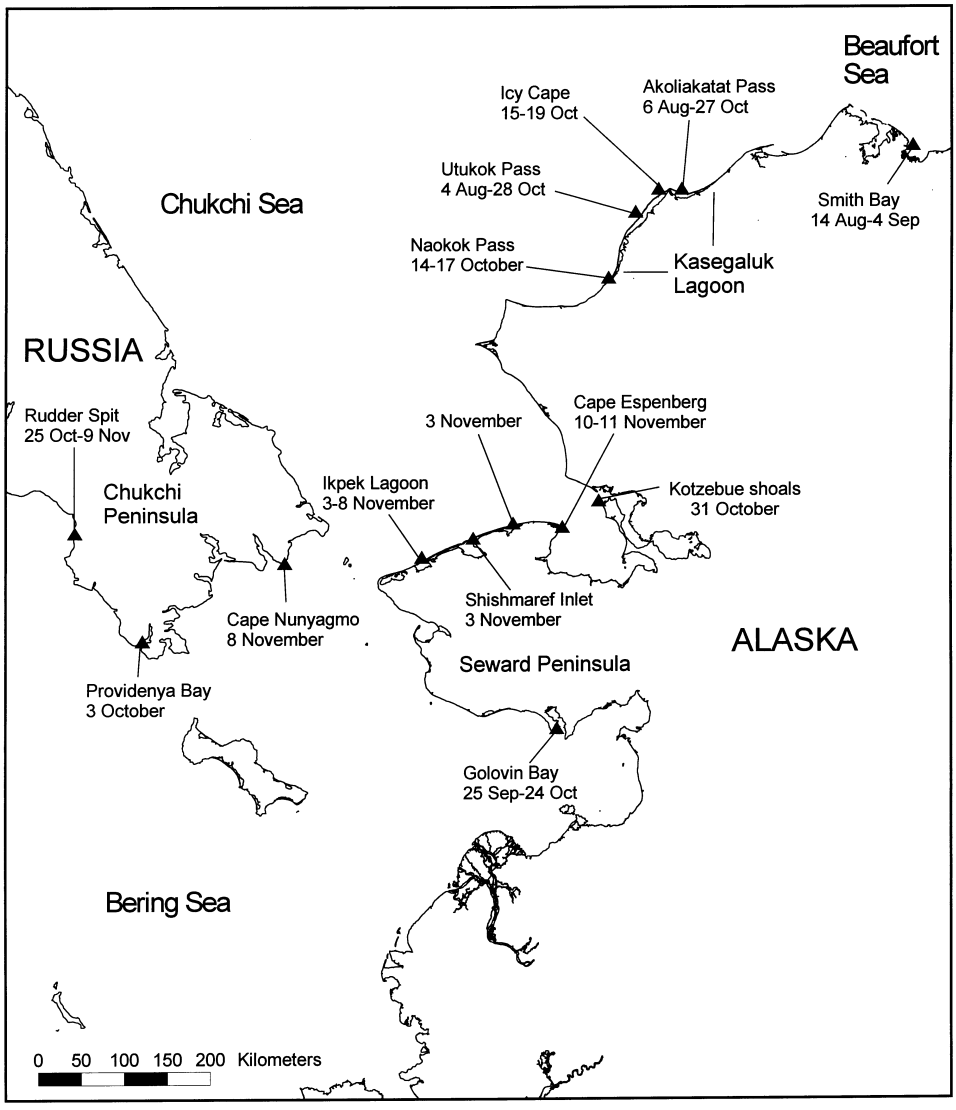

Fig. 1 Map of the Bering, Chukchi, and Beaufort Seas showing the study area and locations used by satellite-tagged spotted seals for on-land haul-outs (*solid triangles*), August to November 1991–1993. The identities of seals using each haul-out are given in Table 2

The Argos data collection and location system recorded the date and time of each signal received by the satellite (termed an "uplink") and calculated a location for the tag based on Doppler shift whenever sufficient uplinks were received during a satellite pass. For analysis and presentation of data, dates and times reported by Argos were converted to true local time from Greenwich mean time by subtracting 11 h. Argos assigns a quality ranking of 3, 2, 1, or 0 to each location, with quality 3 predicted to be the most accurate. Locations that are based on few uplinks or have other potential problems are assigned quality 0. Processing of data to calculate quality 0 locations is an option that we requested only for Wildlife Computers tags. Stewart et al. (1989) and Fancy et al. (1988) provide additional description and analysis of the Argos system.

A multi-stage process was used to screen out erroneous location records. First, records that failed validation tests performed by Argos were deleted from the database. Then, an error index value was calculated for each remaining record according to the equation described in Keating (1994), and all location records that had a value greater than 25 were deleted. Finally, the time, distance, and speed between sequential locations were calculated for all remaining records. Records that indicated apparent speeds greater than 10 km/h [which is slightly more than the likely sustained swim speed of harbor seals (Williams and Kooyman 1985)] were reviewed, and the locations that were most distant from adjacent records were deleted.

Location records and associated data were put into an ArcInfo geographic information system (GIS) and plotted using ArcView. For figures, average daily positions were calculated as the geometric mean of all locations received in each 24-h period starting at midnight local time. Distances moved during trips to sea were calculated by summing the distances between all individual location records received during each trip.

A combination of location and sensor data was used to assess when seals were hauled out. Wildlife Computers tags reported the seals as hauled out or at sea based on the status of conductivity sensors. Because seals at coastal haul-outs often lie in very shallow water where brief immersions of the conductivity switch could result in at-sea readings, location records were inspected and the haul-out duration was considered to include the entire period that the seal was in the vicinity of the haul-out. Because Telonics tags were duty-cycled, durations of haul-out periods were not calculated for them.

To test whether capture location influenced where seals subsequently hauled out, each seal was scored as hauling out more often at Utukok Pass, more often at Akoliakatat Pass, or equally at both locations. The results were analyzed as a 3×2 contingency table.

Differences in behavioral parameters among seals of different genders and size classes were examined using a Student *t*-test with unequal variances, where the random variable was the mean value for each individual seal for a particular parameter. Because of the small sample size, the behavior of animals was tested in only two sizes classes (i.e. <75 kg and >75 kg).

Results

Capture and tagging of seals

Four spotted seals were captured in 1991, one in 1992, and eight in 1993. Seven seals were caught at Utukok Pass and six at Akoliakatat Pass (Fig. 1). Tags were attached to 12 animals (8 males and 4 females) ranging in body mass from 45 to 109 kg. All appeared to be in good physical condition, and none appeared to be injured or unduly stressed by the capture or handling operations. Individual seals will be referred to in this paper by their tag identification number (Table 1).

Tag performance

We received 9,651 location records for all tags combined, of which 2,383 records (25%) were rejected in the screening process. The remaining data set included 3,957 class 0 locations and 3,311 locations of classes 1, 2, or 3. For individual seals the total number of acceptable location records ranged from 48 to 1,538 (mean = 606).

Tags transmitted for 32–298 days after attachment (mean = 166 days; Table 1). Three tags failed prematurely in September–October, four transmitted until January–March, and five transmitted until April–June. Each tag gave an average of 0.6–4.6 fixes of quality 1–3 per operational day. One or more fixes of quality 1–3 were obtained on 16–76% of the days that each tag was operational. When quality 0 locations were included in the data, the percentage of days on which seals were located increased to 41–96%, and the average number of locations per day increased to 1.3–7.8.

Table 1 Summary of tag operation and location data obtained for spotted seals satellite tagged at Kasegaluk Lagoon, August 1991–1993 (*JM* juvenile male; *JF* juvenile female; *AM* adult male; *AF* adult female)

Seal ID	Age/sex	Tag date	Date of last transmission	Total days operational	Days located		Locations/day	
					LQ > 0	all LQs	LQ > 0	all LQs
10919	JM	4 Aug 1991	6 Mar 1992	111	61	–	2.6	–
10920	JM	4 Aug 1991	20 Apr 1992	133	59	–	1.5	–
14098	AF	6 Aug 1991	2 Jan 1992	149	57	109	1.8	4.9
14099	JM	7 Aug 1991	10 Oct 1991	64	15	27	0.8	2.1
2284	AM	27 Aug 1992	19 Apr 1993	236	154	210	2.2	4.9
11041	JM	6 Aug 1993	20 Feb 1994	198	137	191	2.5	7.8
11044	JF	4 Aug 1993	20 May 1994	289	141	230	1.3	3.9
15991	JM	6 Aug 1993	3 Oct 1993	58	44	49	4.6	7.6
15992	AF	6 Aug 1993	3 Jan 1994	152	51	104	0.9	2.7
15993	JF	6 Aug 1993	4 May 1994	270	128	179	1.8	3.3
2281	AM	8 Aug 1993	2 June 1994	298	88	133	0.7	1.3
2286	AM	7 Aug 1993	8 Sep 1993	32	5	13	0.6	1.5

General movements of seals

Movements of individual seals were followed using the GIS. The three seals that were tracked only until September–October remained in the northern Chukchi Sea. Two seals moved southward out of the Chukchi Sea and into the Bering Sea in September, and their activities were then focused near Golovin Bay and the Chukchi Peninsula. The other seven continued to use Kasegaluk Lagoon as a haul-out until the southward migration began.

For presentation of results, the location information was divided into three periods, as follows: (1) the open-water season, including the time between tagging and the last time a seal hauled out at Kasegaluk Lagoon, Golovin Bay, or the Chukchi Peninsula; (2) the southward migration, the autumn period of relatively rapid southward movement as sea ice formed in the Chukchi and northern Bering Seas; and (3) the ice front, the winter and early spring period when seals moved in various directions in the Bering Sea ice pack.

Open-water season

During August–November, satellite-tagged seals alternated haul-outs at coastal sites with trips to sea. Seals hauled out at four areas in Kasegaluk Lagoon and at ten other locations along the coast of northwestern Alaska and the Chukchi Peninsula (Fig. 1, Table 2). The most frequently used haul-out area was Akoliakatat Pass; only seal 14099, whose tag failed on 10 October, did not haul out there. Seven of the seals hauled out one or more times at Utukok Pass. All other haul-out areas except Icy Cape were used by only one individual. The six seals that were tracked throughout the open-water season each hauled out on 3–12 occasions at 2–4 different locations.

There was a significant difference in use of haul-outs at Kasegaluk Lagoon relative to where seals were captured ($\chi^2 = 6.122$, $df = 2$, $P < 0.05$). All five seals captured at Akoliakatat Pass hauled out more times there, while of the seven seals captured at Utukok Pass, two hauled out mostly there, two mostly at Akoliakatat Pass, and three equally at both locations.

The mean amount of time spent at haul-outs during each haul-out period ranged from 15 to 138 h (Table 2). Eight haul-out periods were more than 100 h long, with the longest 304 h.

When they were away from haul-outs, seals were located in both coastal and offshore areas (Fig. 2). The most heavily used region was the eastern Chukchi Sea within about 120 km of the Alaskan coast. Two seals that moved into the Bering Sea in September (11041 and 2281) appeared to stay in nearshore waters.

Characteristics of trips to sea that began from, and ended at, a coastal haulout are shown in Table 3. Trip durations ranged from 14 to 901 h with minimum distances traveled of 28–2,022 km. Calculated average speeds during the trips ranged from 0.4 to 5.2 km/h. Some of the longest trips occurred when seal 11041 moved from Kasegaluk Lagoon to Golovin Bay, seal 2281 moved from Kasegaluk Lagoon to Providenya Bay, and seal 15993 moved from Kasegaluk Lagoon to Smith Bay and back. Long trips were also made by seals that left from, and returned to, Kasegaluk Lagoon (e.g. seal 14098, 410 h and 772 km; seal 14099, 901 h and 1,540 km; seal 11044, 660 h and 1,261 km; seal 15991, 395 h and 827 km; seal 15992, 931 h and 1,254 km).

There were no significant differences in the duration of haul-outs or feeding trips, or the distance covered and speed of movement during feeding trips, for seals of different gender or size class (Table 4). However, sample sizes were small and the statistical power of individual

Table 2 Number, characteristics and locations of spotted seal haul-outs on land in the Beaufort, Chukchi and Bering Seas, August to October 1991–1993 (*AP* Akoliakatat Pass; *UP* Utukok Pass; *IC* Icy Cape; *NP* Naokok Pass)

Seal ID	Capture location	Haul-outs (h)				Kasegaluk Lagoon				Other locations (number of times used)
		N	Mean	Range	SD	AP	UP	IC	NP	
10919	UP	5	–[a]	–[a]	–[a]	1	1	–	1	Cape Espenberg (2)
10920	UP	7	–[a]	–[a]	–[a]	2	2	–	–	Kotzebue Shoals (2) Shishmaref Inlet (1)
14098	UP	6	48	13–114	38	2	4	–	–	
14099	UP	1	46	–	–	–	1	–	–	
2284	UP	3	138	29–304	146	1	1	–	–	West of Cape Espenberg (1)
11041	AP	9	48	2–120	50	2	1	–	–	Golovin Bay (6)
11044	UP	9	18	4–71	22	7	–	1	–	North of Cape Nunyagmo (1)
15991	AP	6	45	2–135	48	6	–	–	–	
15992	AP	5	62	4–179	68	4	–	1	–	
15993	AP	9	36	4–170	57	2	1	–	–	Smith Bay (4) Ikpek Lagoon (2)
2281	UP	12	24	1–97	32	7	–	–	–	Providenya Bay (1) Rudder Spit (4)
2286	AP	3	15	2–38	20	3	–	–	–	

[a] Durations of haul-outs were not calculated because tags were duty-cycled

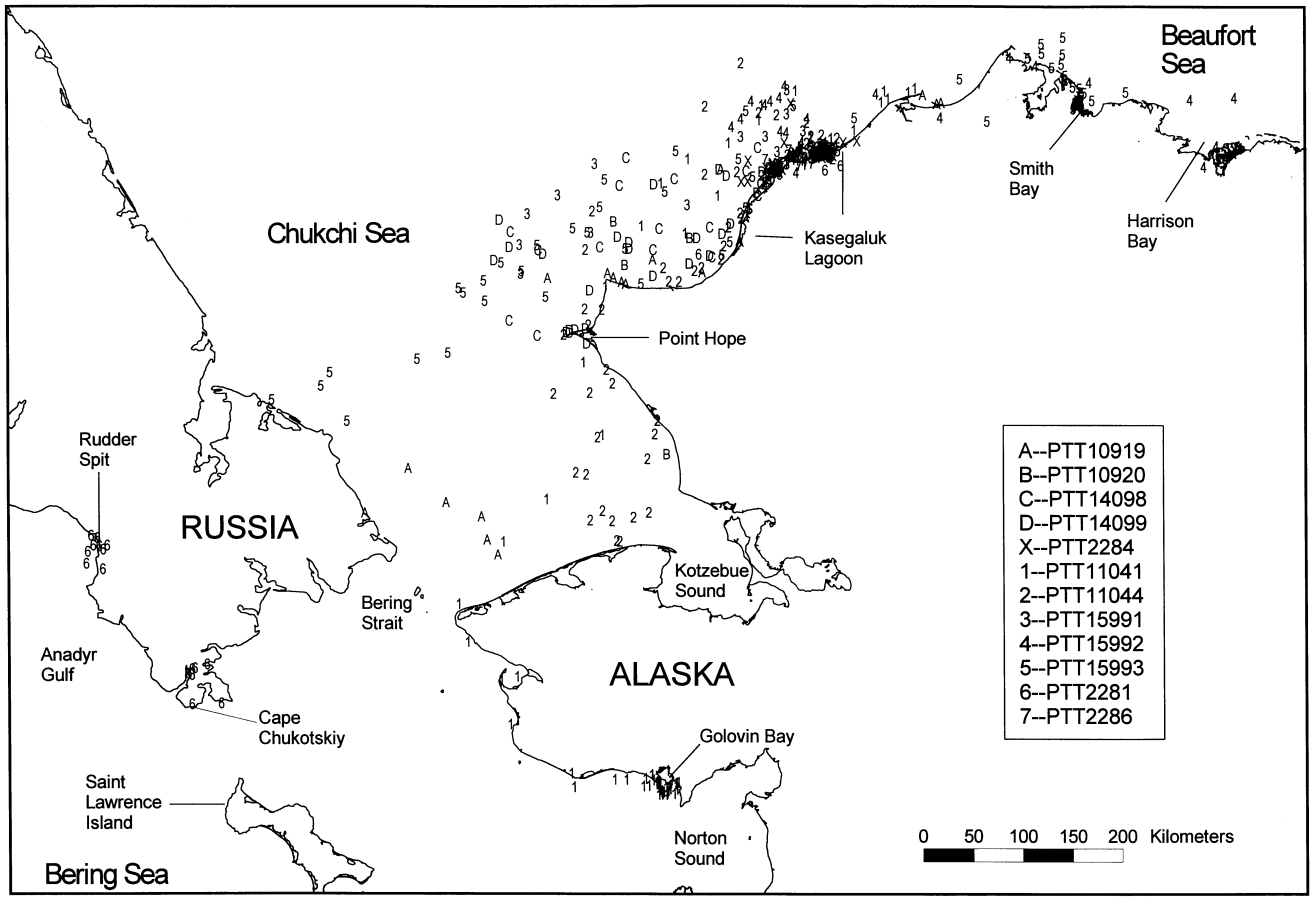

Fig. 2 Map of the Bering, Chukchi, and Beaufort Seas showing average daily at-sea locations of satellite-tagged spotted seals, August to November 1991–1993

Table 3 Characteristics of spotted seal feeding trips during the open-water season in the Beaufort, Chukchi and Bering Seas, August to October 1991–1993

Seal ID	Area	*N*	Duration (h)			Distance (km)			Speed (km/h)		
			Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
14098	Kasegaluk/E. Chukchi Sea	6	184	25–423	193	338	68–772	300	1.8	1.4–5.2	1.5
14099	Kasegaluk/E. Chukchi Sea	2	742	584–901	224	1058	575–1540	683	1.4	1.0–1.7	0.5
2284	Kasegaluk/E. Chukchi Sea	3	263	64–398	176	577	179–865	356	2.2	1.7–2.8	0.6
11041	Kasegaluk/E. Chukchi Sea	3	144	51–202	82	517	146–826	344	3.6	2.9–4.1	0.6
11041	Kasegaluk-Golovin Bay	1	590	–	–	2022	–	–	3.4	–	–
11041	Golovin/N. Bering Sea	5	90	52–144	37	222	120–419	122	2.5	1.5–2.9	0.6
11044	Kasegaluk/E. Chukchi Sea	8	218	17–660	248	567	28–1612	692	2.6	0.7–4.6	1.4
11044	Kasegaluk-Chukotka	1	399	–	–	1260	–	–	3.2	–	–
15991	Kasegaluk/E. Chukchi Sea	6	120	34–395	139	240	66–827	297	2.0	0.7–2.2	0.6
15992	Kasegaluk/E. Chukchi Sea	5	303	82–931	353	604	225–1254	566	1.5	1.3–2.8	0.8
15993	Kasegaluk and Smith Bay/ E. Chukchi and Beaufort Seas	7	247	19–647	265	624	50–1680	703	2.5	0.9–4.6	1.1
15993	Kasegaluk-Ikpek Lagoon	1	152	–	–	712	–	–	4.7	–	–
15993	North of Ikpek Lagoon	1	47	–	–	146	–	–	3.1	–	–
2281	Kasegaluk/E. Chukchi Sea	7	55	14–76	25	47	30–64	15	0.9	0.4–4.2	1.3
2281	Kasegaluk-Chukotka	1	770	–	–	918	–	–	1.2	–	–
2281	Chukotka/N. Bering Sea	4	175	46–530	237	185	97–274	125	0.6	0.5–1.1	0.4
2286	Kasegaluk/E. Chukchi Sea	3	229	63–528	259	97	43–177	71	0.4	0.3–1.1	0.4

Table 4 Summary of contrasts by gender and size for five measures of behavior in seven satellite-tagged spotted seals. Only data from seals whose tags functioned to October and that stayed in the vicinity of Kasegaluk Lagoon were used in tests of differences in haul-out and feeding trip characteristics

Behavioral variable	Gender			Body mass (kg)		
	Male	Female	*P* value	< 75	> 75	*P* value
On-land haul-out duration (h)[a,b]	70	43	0.51	33	68	0.29
Feeding trip duration (h)[b]	154	235	0.33	181	201	0.77
Feeding trip distance (km)[b]	380	503	0.56	542	392	0.34
Feeding trip speed (km/h)[b]	2.2	2.0	0.77	3.1	1.6	0.12
Ice front east-west movement[c]	7.6	8.0	0.75	6.8	10.0	0.02

[a] Includes only haul-outs made at Kasegaluk Lagoon
[b] Sample sizes three males, three females and three small, three large
[c] Maximum difference in degrees longitude during December–June. Sample sizes four males, two females and four small, two large

tests was such that differences would have had to exceed 50% to have been significant.

Southward migration

Two seals last hauled out at Kasegaluk Lagoon on 30 August and 1 September, then moved southward through the Bering Strait. Six other seals last hauled out at Kasegaluk between 29 September and 28 October. As they moved southward, seals spent considerable time in, and to the west of, Kotzebue Sound, along the coast of the Chukchi Peninsula, and in the region between the Bering Strait, Saint Lawrence Island, and the Yukon River delta (Fig. 3).

As they moved southward seven seals used coastal haul-outs on the Seward Peninsula or the Chukchi Peninsula in late October and early November (Table 2; Fig. 1). Seals 14098 and 15992 apparently did not use coastal haul-outs, and spent 42 and 38 days, respectively at sea before first hauling out on sea ice. Seal 2284 first hauled out on ice on 19 October in Kotzebue Sound while the others first hauled out on ice in or south of the Bering Strait between 10 November and 1 December. Two seals passed through the Bering Strait in September and the others sometime between 4 and 27 November.

Ice front

The seven seals whose tags were still operating during December–June spent those months in the Bering Sea. Most locations were in a broad east-west band about 500 km wide extending from Kuskokwim Bay to Anadyr Gulf (Fig. 4).

While in this region, most seals moved a considerable distance from east to west. For example, seal 2284 moved from Kuskokwim Bay to west of Saint Matthew Island and back (round-trip straight line distance of 1,040 km); seal 11041 moved from Saint Matthew Island to Anadyr Gulf (400 km); seal 15993 moved from east of the Pribilof Islands to west of Saint Matthew Island and back (970 km), and seal 2281 moved from Anadyr Gulf to east of Saint Matthew Island and back (950 km). Minimum average rates of travel during several of these trips were 25–28 km/day. Seal 10920 was an exception, and it remained in the vicinity of Saint Matthew Island from December to April.

The maximum amount of east-west movement did not differ between sexes for all seals combined (Table 4). However, the average maximum shift in degrees of longitude from December to June for animals greater than 75 kg was significantly greater than for animals less than 75 kg ($P = 0.02$).

Discussion

Satellite tag performance

Satellite-tagged spotted seals were tracked for periods of up to 10 months. Five tags transmitted into April–June and were probably shed when the seals began their annual molt (Ashwell-Erickson et al. 1986). The reasons why the other tags stopped sending signals are unknown, but could include electronics failure, battery exhaustion, physical damage to or premature shedding of tags, or death of the seal.

The location data we obtained from Service Argos included a number of implausible records (e.g. locations many kilometers inland from the coast, or sequential records that would have required seals to swim at unrealistic speeds). Our screening procedure resulted in deletion of about 25% of the total records received. McConnell et al. (1992) filtered satellite location data from southern elephant seals (*Mirounga leonina*) based on a maximum allowable velocity of 3.5 m/s (12.6 km/h), and rejected 36–48% of the records from three tagged seals.

To minimize problems with location error, some satellite-tag studies have chosen to use only quality 1–3 locations for describing movements (e.g. Heide-Jørgensen et al. 1992; Dietz and Heide-Jørgensen 1995). Using quality 0 location data in this study resulted in a 46% increase in the number of days on which the locations of tagged spotted seals were known.

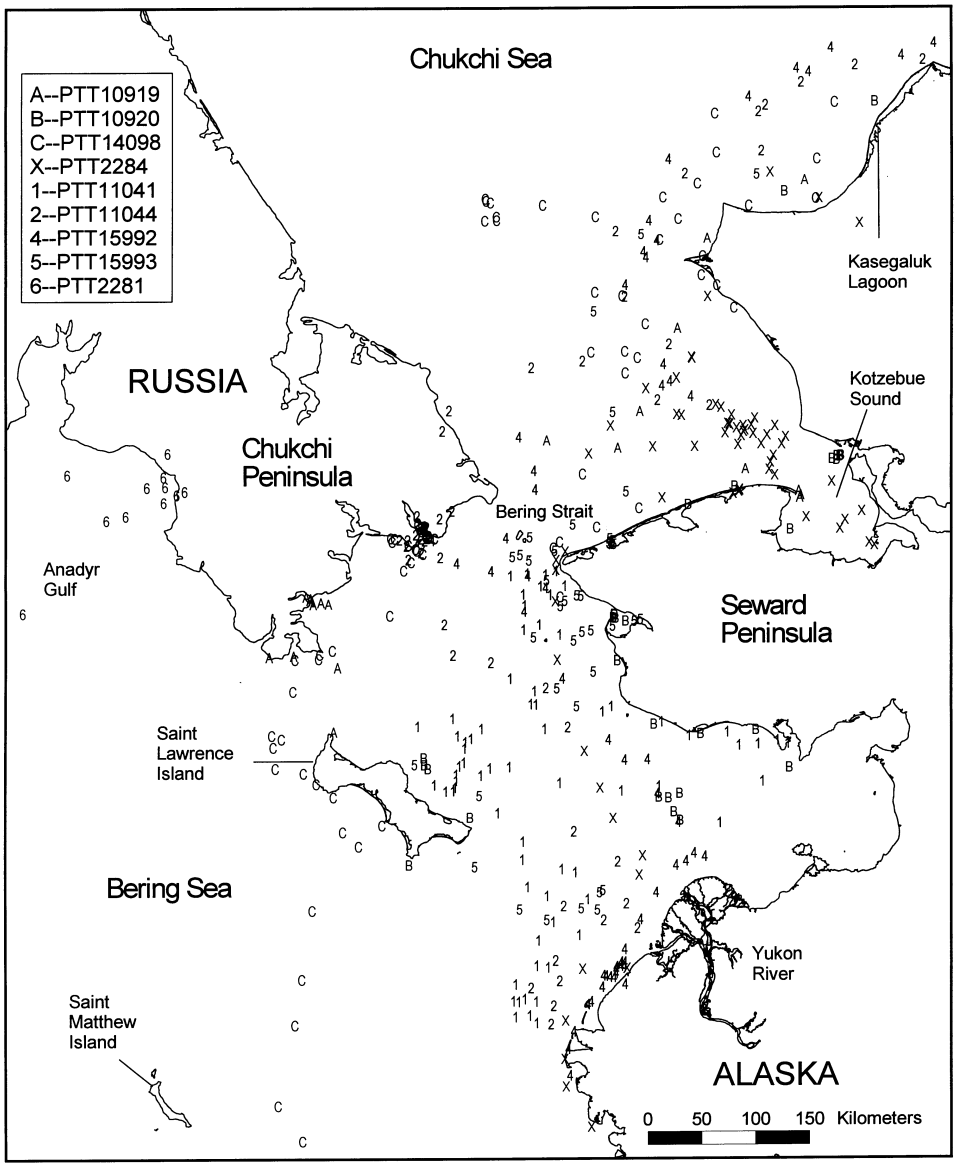

Fig. 3 Map of the Bering and Chukchi Seas showing average daily locations of satellite-tagged spotted seals, October to December 1991–1993

In addition to errors in location data, there are other difficulties inherent in using satellite-linked tags to monitor the movements and behavior of spotted seals. The Argos system uses polar-orbiting satellites, and while satellite coverage was relatively good in our high-latitude study area, tags were not monitored continuously and there was a period of 3–4 h each day during which there was no coverage. Distances moved during trips to sea were calculated from sequential locations and are therefore underestimates because they do not include all the detail of the route followed. Also, it is possible that the lengths of trips to sea were overestimated if seals made brief stops ashore that went unrecorded. We do not think this caused a serious problem because recorded haul-out bouts usually lasted for many hours or even days, and on long trips to sea the seals were many kilometers from land for most of the time.

We cannot evaluate whether the instruments we used might have affected the behavior of the tagged seals. A similiar-sized instrument attached to a captive 35 kg ringed seal (*Phoca hispida*) caused no significant change in surfacing or submergence times (Stewart et al. 1989).

In spite of these limitations, use of satellite-linked tags allowed us to follow in detail the movements of spotted seals. For the ten seals whose tags were not duty cycled and for which we obtained quality 0 locations, at least one useable location was received on 69% of the 1,746 days they were tracked. Locations were received while seals were at coastal haul-outs, while they were at sea in open water, and while they were in sea ice.

Description of spotted seal biology

Previous studies have provided a general description of the distribution of spotted seals, especially when they are in the Bering Sea. This distributional information,

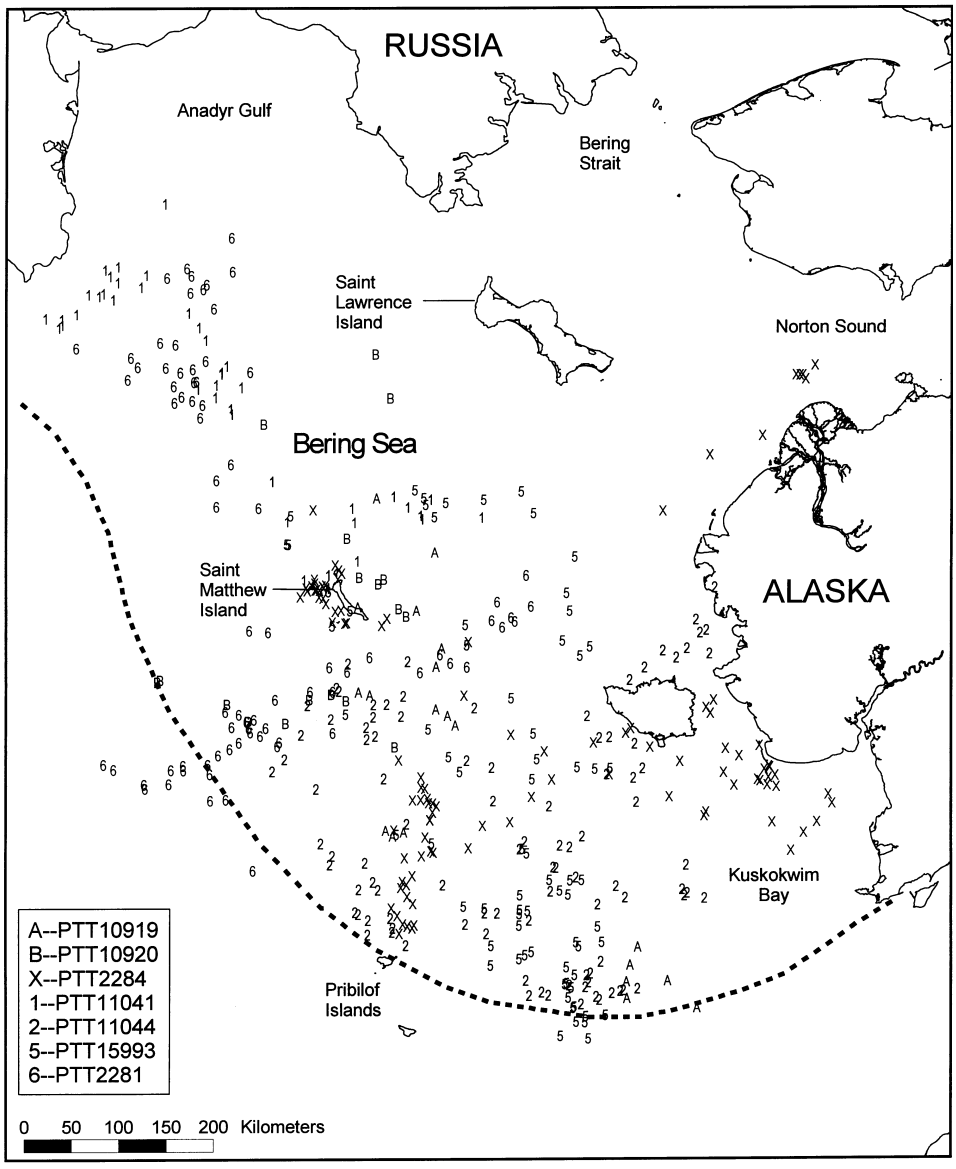

Fig. 4 Map of the Bering Sea showing average daily locations of satellite-tagged spotted seals, December to June 1991–1994. *Dashed line* shows the southern extent of sea ice on 19 April 1994

however, provides little understanding of the movements and behavior of seals. For example, observations of locations and numbers of spotted seals hauled out in Kasegaluk Lagoon have been recorded for many years (Frost et al. 1983a), and repetitive aerial surveys were conducted in 1989–1991 to document use of particular haul-outs and the seasonal variation in seal numbers (Frost et al. 1993). In spite of those studies, it remained unknown whether individual seals used more than one haul-out location, how often they hauled out, whether they fed in and near the lagoon, or traveled to other areas, and when the southward migration began.

Data from this study showed that individuals using Kasegaluk Lagoon haul out at more than one location. Akoliakatat Pass and Utukok Pass were the primary sites, with Akoliakatat Pass more commonly used, perhaps because the sandbar haul-out sites at Utukok Pass are more often submerged by wind-driven-tides than the long spits that make up the Akoliakatat Pass haul-out.

During the open-water season, seals made infrequent, relatively long visits to coastal haul-outs. An individual generally was at a haul-out 2–3 times per month for periods of 1–7 days. The overall average period at a haul-out was 41.6 h and the average period at sea was 214.0 h, which suggests that seals spent about 16% of their time at haul-outs.

While many of the August–November at-sea locations of seals were in the vicinity of Kasegaluk Lagoon, every individual also used offshore waters. On some trips to sea, seals ranged westward to the coast of Russia, south almost to the Bering Strait, and north and east into the Beaufort Sea. Many trips to sea covered in excess of 1,000 km. We presume that the purpose of these trips was to feed. Arctic cod (*Boreogadus saida*) are by far the most abundant fish in this region (Barber et al.

1997), and are an important prey item for spotted seals (L.F. Lowry and K.J. Frost, unpublished data).

Most tagged seals left Kasegaluk Lagoon in October and passed through the Bering Strait in November. During their southward passage seals used several coastal haul-out sites in Kotzebue Sound and along the Chukchi and Seward Peninsulas. Most of the haul-outs used were areas previously known, but the specific sites used on the Chukchi Peninsula and in Shishmaref Inlet and Ikpek Lagoon had not been recorded prior to this study.

Sea ice usually begins to appear in the northern Bering Sea in November, and coverage generally increases until April. After the annual maximum extent is reached the actual location of the edge can vary considerably due to wind direction and other weather conditions (Burns et al. 1981). During this period ice movement is predominantly from north to south at an average speed of about 15 km/day (Muench and Ahlnas 1976), but this is balanced by melting of floes at the southern edge.

Locations of satellite-tagged seals showed a steady shift southward during the months of December and January. During February–May there were relatively short movements both to the north and south that may have served to maintain the seals within their preferred habitat, the ice front and fringe (Burns et al. 1981; Braham et al. 1984). During this period satellite-tagged seals also made extensive and relatively rapid east-west movements. Two concentration areas of spotted seals have been identified in spring aerial surveys (Braham et al. 1984), and it has been suggested that they represent separate breeding populations, one in the region from the Pribilof Islands to Bristol Bay and the other in and south of Anadyr Gulf (Shaughnessy and Fay 1977). Our finding that animals make substantial east-west movements in the ice front suggests that these concentration areas may not be reproductively isolated. The two tagged seals that made the greatest movements were both adult males, which may reflect a breeding structure where mature males are more mobile than other age/sex classes during the breeding season.

Comparison with other seal species

Several other species of northern seals are similar to spotted seals in that they use sea ice during the reproductive season. In the North Pacific, ribbon seals (*Phoca fasciata*) breed in the same general region as spotted seals, but after completing the molt they become pelagic and do not haul out on land or ice until the following winter (Burns 1970). Bearded seals (*Erignatus barbatus*) and ringed seals usually maintain a year-round association with sea ice, and healthy individuals are rarely seen on shore (Burns 1981; Frost and Lowry 1981). An exception is in the Okhotsk Sea, which is completely ice-free during summer, and in that area both ringed seals and bearded seals sometimes haul out on land (Ognev 1935). In the North Atlantic, harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) haul out on sea ice for pupping, breeding, and molting, and both seem to follow the ice and not to use coastal haul-outs at other times of the year (Reeves and Ling 1981; Ronald and Healey 1981).

The closest relative of the spotted seal, the Pacific harbor seal, typically hauls out on land throughout the year, but drifting glacial ice or sea ice may be used in areas where it is available. Harbor seals are generally considered non-migratory although seasonal movements of several hundred kilometers have been reported (Bigg 1981). Recent satellite-tagging studies conducted on harbor seals in Prince William Sound (Gulf of Alaska) have shown that throughout the year the average haul-out frequency ranges from daily to once every 2–3 days (Frost et al. 1996). Most feeding trips made by tagged harbor seals were relatively short, lasting 1 day or less, but occasionally individuals spent periods at sea that were as long as 20 days.

Spotted seals in the Bering and Chukchi Seas are therefore unique among the northern ice-breeding seals in that they haul out on land instead of sea ice during summer and early autumn. The behavior of spotted seals during the open-water season differs from that of harbor seals in that spotted seals leave their haul-outs and spend many consecutive days at sea, returning to coastal haul-outs for periods of several days between feeding trips.

The distributions of harbor and spotted seals overlap to a limited degree, and it is possible that a small amount of interbreeding occurs in those areas (Shaughnessy and Fay 1977). The haul-out and at-sea behavior of spotted seals and harbor seals have not been studied in areas where they co-occur (e.g. Kuskokwim Bay), and such a study would be of great interest.

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