

Ian Gjertz · Christian Lydersen · Øystein Wiig

Distribution and diving of harbour seals (*Phoca vitulina*) in Svalbard

Accepted: 6 October 2000

Abstract The distribution, movements and diving of high-arctic harbour seals (*Phoca vitulina*) were studied in Svalbard, Norway, from 1992 to 1995. A total of 14 seals were equipped with satellite transmitters at Prins Karls Forland (ca. 78°30'N 12°E). These gave data on position, but ten also gave information on dive depths ($N \sim 160,000$) and dive durations ($N \sim 162,000$). Dive-depth frequencies show that ~50% of the diving is shallower than 40 m, and that 95% of the diving is shallower than 250 m. Based on dive-duration frequencies, ~50% of the dives lasted 2–4 min, 90% of the dives lasted less than 7 min, and 97% were shorter than 10 min. All but three seals stayed in the tagging area.

Introduction

Harbour seals (*Phoca vitulina*) are one of the most widely distributed pinnipeds. They are generally considered a shallow-water non-migratory species and are found along the coasts of the northern Atlantic and Pacific Oceans, from temperate waters and north to the Arctic (Bigg 1981). In the North Atlantic with adjacent waters, they are also found in high-arctic areas. Their arctic distribution is believed to be limited by the distribution of fast ice since they do not keep open breathing holes in the fast ice, but they are found in areas with access to open water during the winter (Mansfield 1967).

Their northernmost distribution is at Svalbard, Norway, where a small population, apparently insular, is present throughout the year (Wiig 1989). In this area,

harbour seals have been observed as far north as 80°50'N (Wiig 1989). Harbour seals are not found in Northeast Greenland (Teilmann and Dietz 1994), where ice conditions are more extreme than in Svalbard. The nearest population is therefore found along the coasts of northern Norway and in the Murman region of Russia (Henriksen et al. 1997). The Svalbard population is mainly limited to the area around Prins Karls Forland, the westernmost island in the Svalbard archipelago, where a number of important haul-out sites are found (Prestrud and Gjertz 1990; Gjertz and Børset 1992). Harbour seals have also been observed in the eastern parts of the archipelago (Henriksen et al. 1997). One tagged Svalbard harbour seal has been recaptured in mainland Norway, more than 1,000 km away, indicating that Svalbard seals may not be totally isolated (Henriksen 1996).

Harbour seals are littoral in their distribution and are often seen in the same geographical areas throughout the year (Thompson 1993). They are usually considered sedentary, but may move between different haul-out sites or between favoured haul-out sites and foraging areas at sea (Thompson 1993). The last are usually less than 50 km distant. The use of preferred haul-out sites is therefore an important part of describing the harbour seals' distribution area.

Harbour seals are generally considered to feed close to the sea-bed and at moderate depths (4–200 m) (Härkönen and Heide-Jørgensen 1991; Bjørge et al. 1995; Tollit et al. 1998; Lesage et al. 1999). In Svalbard, most of the haul-out sites are located in areas which include shallow-water shelves less than 200 m deep, but also deep waters down to depths of more than 1,000 m.

The purpose of the present study is, through the use of satellite telemetry, to determine the distribution area of harbour seals in Svalbard. This includes determining if these seals leave their main distribution areas in winter and move either offshore or to the Norwegian mainland. The other aim is to determine at which depths, and for how long, these seals are diving.

I. Gjertz (✉) · Ø. Wiig
Zoological Museum, Sarsgate 1,
0562 Oslo, Norway
e-mail: i.l.b.gjertz@toyen.uio.no

I. Gjertz · C. Lydersen
Norwegian Polar Institute,
9296 Tromsø, Norway

Materials and methods

Harbour seals were caught, using gill nets or a land-fastened seine-net. They were tagged in September 1992, 1993 and 1994 at two closely situated haul-out sites along the west coast of Prins Karls Forland, Svalbard (Fig. 1). September was chosen because the moult would be finished at this time (Thompson and Rothery 1987), which was essential since the transmitters were to be glued on to the seal fur. The seals were physically restrained in a hoop net, weighed to the nearest kilogram, equipped with flipper tags, and some also with transmitters, and then released. Eleven transmitters were glued to the fur using quick-setting epoxy, while three were glued on with silicon paste. The transmitters were glued to the fur of the upper part of the back.

Three different types of transmitters were used. In 1992, three 0.5 W and one 1.0 W Telsonics (Mesa, Arizona) tags were deployed. These four tags only gave position data, and were set for continuous transmission when the built-in salt water switch was dry. In 1993 and 1994, a total of ten 0.5 W Wildlife Computers (Redmond, WA) Satellite Linked Dive Recorders (SLDR) were deployed. The five deployed in 1993 were duty-cycled to transmit every other day, while the ones deployed in 1994 were programmed to transmit 24 h a day every day, whenever the saltwater switch was dry. As long as a conductivity sensor was dry, the SLDR would transmit at 45-s intervals. If ten consecutive transmissions occur without seawater-induced delays, then the transmitter switched to a 90-s transmission interval. If, after a 4-h period, the sensor was still dry, then the SLDR would suspend transmission until the sensor was reactivated by immersion in salt water. (For details on the Argos system, see Fancy et al. 1988; Stewart et al. 1989.)

Apart from transmitting data for position calculation, the SLDRs also transmitted data on diving. The recorders were set to

operate at the manufacturer's deep-depth range option. This means that the instrument measures depths of 0–490 m with a resolution of 2 m. The diving depth data were transmitted as a histogram with each dive registered according to its deepest point. The durations of the dives were also transmitted as histograms. Dives had to be deeper than 4 m to be registered as dives.

Information on dive depth was collected in 14 bins, with lower bin limits set at 10, 20, 40, 60, 90, 120, 150, 200, 250, 300, 350, 400, 450 and > 450 m, while information on dive duration was collected in 10 bins, with lower limits set at 1, 4, 7, 10, 13, 16, 19, 22, 25 and > 25 min. The maximum depth recorded in the previous 24-h period was given in the status messages from the transmitter. (For details on SLDRs, see Burns and Castellini 1998.)

Diving behaviour may be dependant on prey availability. To determine if diving behaviour changed through time, diving was compared between seasons and between years. Since only five SLDRs were deployed each year, and average transmission duration varied between years, comparisons were made only between the time periods in both years when all five transmitters deployed that year were still functioning. Results were compared using Kolmogorov-Smirnov two-sample tests.

Diving behaviour of individual seals (those with transmitters that lasted more than 3 months without the seal leaving the tagging area) was compared for the first full month of data (October) with the last full month of data (December to February). One transmitter lasted until July the following year. For this seal, comparisons were made between diving behaviour in October, January and July. For all seals, monthly diving data were compared using chi-square tests.

Satellite telemetry locations provided by the Argos System were assigned a location quality code of 0–3, representing a presumed level of precision. Precision (i.e. standard deviation of a series of locations of stationary transmitters), as reported by Argos, is 1,000, 350 and 150 m for location qualities 1, 2 and 3, respectively. For location quality 0, the accuracy of the location was not given (Harris et al. 1990). The location quality is dependent on the number of uplinks received by the satellite for each overpass and the pass duration (Harris et al. 1990). There are indications that precision levels are considerably lower than suggested by Argos (Goulet et al. 1999).

A specially constructed SASPC computer program (SAS Institute, Cary, N.C.) compared all daily Argos positions and selected the daily position of highest quality. When several positions had equally high rank, then the first such position of that day was selected. This position was then used to determine where the seal was, and this is indicated on the position maps.

The movements of seals that left the Prins Karls Forland area were compared with ice distribution maps from the Norwegian Meteorological Institute.

Results

Eight male and six female harbour seals were instrumented. The satellite tags transmitted from 7 to 313 days (Table 1).

All but three seals stayed in the Prins Karls Forland area and adjacent offshore waters for the entire duration of the transmitters (Fig. 1). Detailed distribution in the Prins Karls Forland area is indicated in Fig. 2. Near-shore concentrations of locations are centred on haul-out sites.

Seal no. 4 left Prins Karls Forland in late November, before there was any ice. It moved along the coast of Spitsbergen, south to the banks off Hornsund and Sørkapp and stayed there in very open drift-ice (1/10 ice cover) before moving to Bjørnøya in late January,

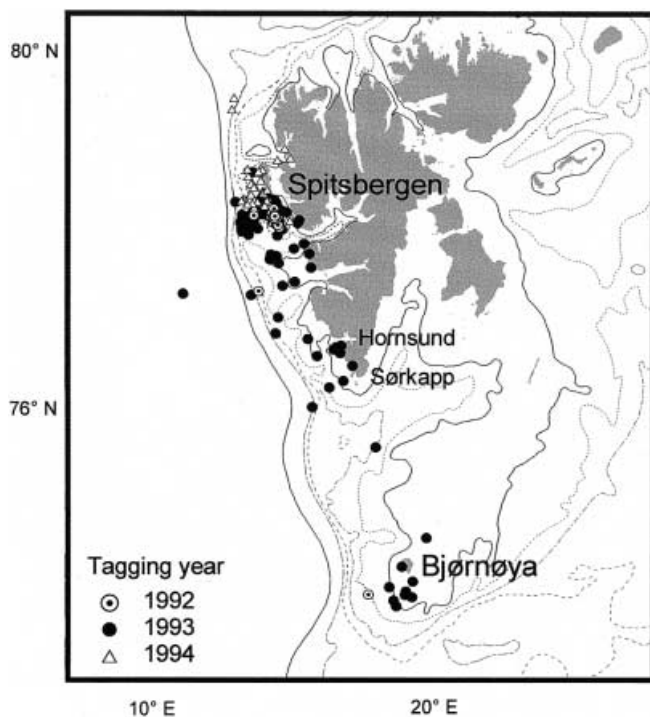


Fig. 1 Map of Svalbard indicating locations of all harbour seal satellite telemetry positions, best position per day location quality > 0, for seals tagged 1992–1994. Symbols reflect year seals were tagged. Isobaths range from 100 to 500 m, and in addition the 1,000 m isobath, which is the westernmost isobath, is given. West of this isobath water depths are greater than 1,000 m

Table 1 Harbour seals tagged with satellite transmitters 1992–1994 in Svalbard

Seal no.	Sex	Length (cm)	Girth (cm)	Weight (kg)	Tagging date	Stopped transmitting	Duration (days)	No. location quality days > 0	Transmitter	Glue	
1	F	120	89	no	920919	920926	7	7	Telonics 0.5 W	Epoxy	
2	F	112	86	no	920919	921105	46	22	Telonics 0.5 W	Silicon	
3	M	121	92	no	920919	920928	8	7	Telonics 0.5 W	Silicon	
4	M	131	88	no	920921	930215	147	34	Telonics 1 W	Silicon	
5	M	125	89	48	930921	940121	122	29	Wildl. Comp 0.5 W	Epoxy	
6	M	136	91	60	930921	940216	148	50	Wildl. Comp 0.5 W	Epoxy	
7	M	125	88	50	930922	931021	29	11	Wildl. Comp 0.5 W	Epoxy	
8	F	123	87	52	930924	940210	139	39	Wildl. Comp 0.5 W	Epoxy	
9	M	148	116	103	930924	940803	313	84	Wildl. Comp 0.5 W	Epoxy	
10	M	142	102	72	940910	950113	124	6	Wildl. Comp 0.5 W	Epoxy	
11	F	139	106	73	940910	941212	92	15	Wildl. Comp 0.5 W	Epoxy	
12	F	132	112	92	940917	941218	98	5	Wildl. Comp 0.5 W	Epoxy	
13	F	136	106	78	940925	941215	95	8	Wildl. Comp 0.5 W	Epoxy	
14	M	126	112	80	940926	950313	184	18	Wildl. Comp 0.5 W	Epoxy	
							Mean ± SD				
							110.9 ± 79.9				
							Range 7–313				

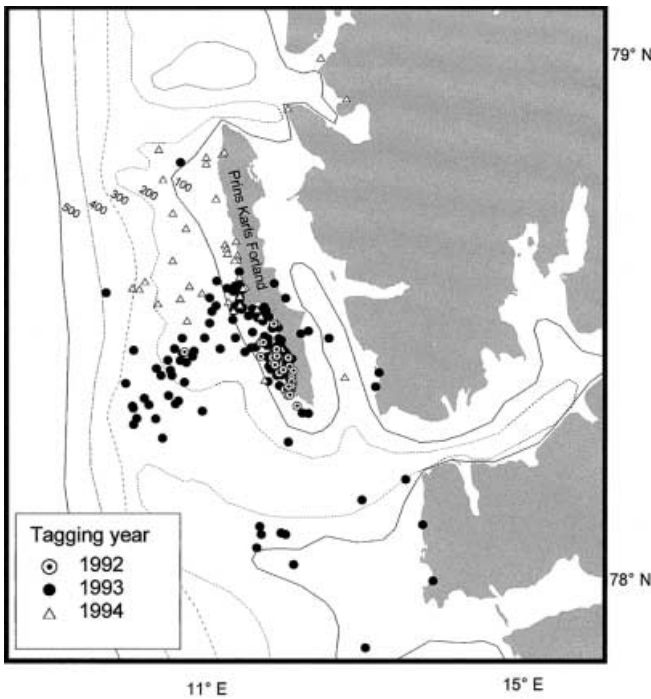


Fig. 2 Close-up bathymetric map of Prins Karls Forland, Svalbard. Harbour seal satellite telemetry positions within the boundaries of the map, daily best position location quality > 0, are given. Symbols reflect year seals were tagged. Isobaths range from 100 to 500 m. Concentrations of positions along shore are centred on haul-out sites. For details of haul-out sites, see Gjertz and Børset (1992)

staying southwest of that island in open water and 1/10 ice cover for the duration of the transmissions. Seal no. 5 left the tagging area in early November when new ice developed and the ice cover was 1/10. It swam south along the Spitsbergen coast to Hornsund where it stayed until 10 December, before going to the offshore banks south of Spitsbergen and west of Hornsund. There it stayed on the open-water side of the drift-ice, which was

4/10 close to land and 1/10 further offshore, for the duration of the transmissions. Seal no. 6 left the Prins Karls Forland area in early January while there was a continuous belt of 1/10 drift-ice along the whole coast of Spitsbergen, with 4/10 drift-ice near Sørkapp. It then moved south to Bjørnøya where it arrived a week later and stayed in open water and 1/10 drift-ice southwest of the island until the transmissions ceased.

Dive depth was recorded from 160,751 dives, and dive durations from 162,434 dives, over a 2-season period for the 10 SLDRs. Total dive-depth frequencies for these seals show that ~50% of the diving is shallower than 40 m, and that 95% of the diving is shallower than 250 m (Fig. 3). Based on dive-duration frequencies, ~50% of the dives lasted 2–4 min, 90% of the diving lasted less than 7 min, and 97% were shorter than 10 min (Fig. 3).

Dive-depth and dive-duration frequencies for the period of both years that all the transmitters were functioning and all seals were still in the tagging area, i.e. 24 September to 18 October, were pooled and tested for differences between years. For 1993, this included records from ~23,000 dives, and for 1994 ~25,000 dives. Diving was found to be significantly different between years (Kolmogorov-Smirnov two-sample test, $d = 0.128$, $P < 0.01$ and $d = 0.289$, $P < 0.01$) with seals diving deeper and longer in 1994.

In 1993, dive-depth frequencies and dive-duration frequencies for seal nos. 5 and 6 were found to be significantly different (Kolmogorov-Smirnov two-sample test, $d = 0.159$, $P < 0.001$, and $d = 0.239$, $P < 0.001$, and Kolmogorov-Smirnov two-sample test, $d = 0.174$, $P < 0.001$ and $d = 0.869$, $P < 0.001$) after these seals moved south, away from the Prins Karls Forland area. Both seals dived deeper and had longer-lasting dives when in the shelf-break areas off southern Spitsbergen.

Diving depths for seals that stayed in the tagging area, i.e. Prins Karls Forland area, varied according to

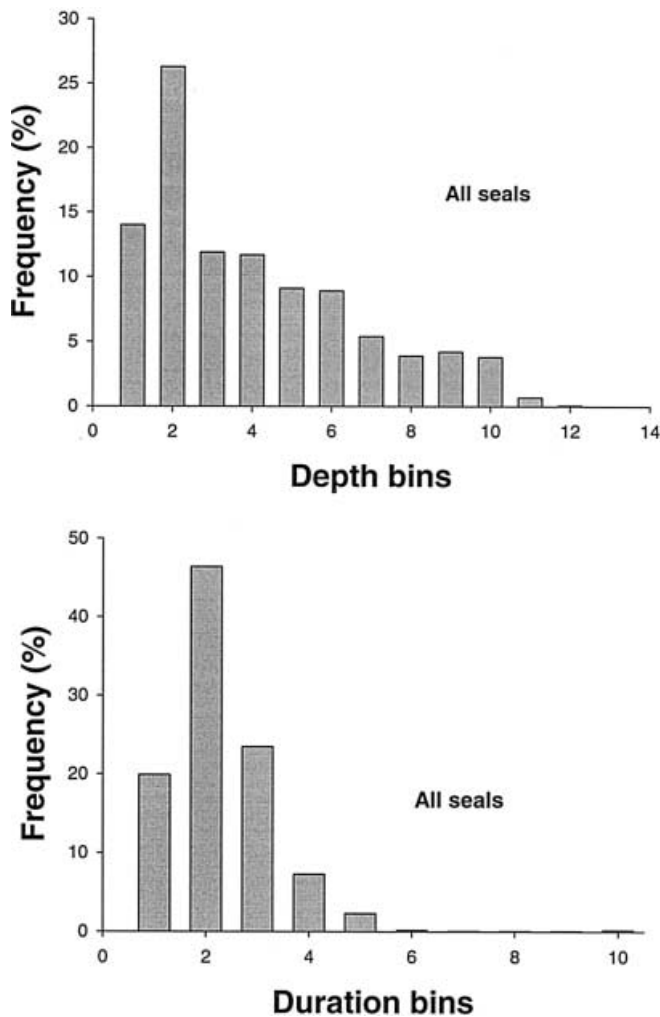


Fig. 3 Frequency distributions of all harbour seal dives in Svalbard, based on Satellite Linked Dive Recorders, according to depth ($n = 160, 751$) and duration ($n = 162, 434$). Depth histogram bin lower limits are: 10, 20, 40, 60, 90, 120, 150, 200, 250, 300, 350, 400, 450 and > 450 m. Duration histogram bin lower limits are: 1, 4, 7, 10, 13, 16, 19, 22, 25 and > 25 min

season. Diving depths and durations for four seals with transmitters that lasted more than 3 months were significantly deeper and longer-lasting in winter (December/February) than in October (chi-square test $P < 0.01$ for all seals). For one seal, both diving depth and duration were similarly found to be significantly deeper and longer-lasting in October than in July (chi-square test $P < 0.01$).

Maximum dive depths recorded for the period of both years that all the transmitters were functioning and all seals were still in the tagging area, i.e. approximately 24 September to 18 October, were similarly compared between years. For 1993 (median 64 m), these were significantly shallower than for those in 1994 (median 112 m) (Mann-Whitney U -test $N = 73$, $W = 5977$, $P < 0.001$).

For seals no. 5 (Mann-Whitney U -test $N = 21$, $W = 670$, $P < 0.001$) and no. 6 (Mann-Whitney U -test

$N = 32$, $W = 199$, $P < 0.05$), daily maximum depths were significantly deeper after they left the Prins Karls Forland area.

Maximum dive depth recorded for the ten seals was 452 m. Maximum dive depths recorded for seals tagged in 1993 (median 122 m) were significantly shallower than for those tagged in 1994 (median 168 m) (Mann-Whitney U -test $N = 283$, $W = 9437$, $P < 0.001$).

Discussion

The transmitters were deployed over a 3-year period. The longevity of all 14 transmitters varied considerably (Table 1). The results from the present study, therefore, only give an insight into what individual seals are doing for parts of the year. Caution should therefore be shown when interpreting these data.

Harbour seals are known to undertake seasonal movements of more than 200 km between haul-out sites (Thompson 1993). It is therefore possible that harbour seals from different areas in Svalbard congregate at Prins Karls Forland for the breeding and moulting season and later return to their specific wintering areas. Such movements are known from other seal species, such as hooded seals (*Cystophora cristata*) (Rasmussen 1960) and grey seals (*Halichoerus grypus*) (Wiig 1991; Hammond et al. 1993). This may be one explanation for the long-distance movements of the three male seals in this study.

Nine of the tagged harbour seals stayed in the tagging area despite the presence of ice. According to Mansfield (1967), fast-ice is a limiting factor for this species. The dense drift-ice that occasionally occurs off the Spitsbergen west coast very rarely becomes fast-ice and should, therefore, not be a limiting factor for the distribution of harbour seals. If necessary, they can leave the heavy drift-ice along the coast and head out to sea for shorter periods where the ice cover is less dense (Vinje 1985).

Deep-diving behaviour depends on a number of external factors, such as local bathymetry and predator and prey ecology (Schreer and Kovacs 1997; Tollit et al. 1998). In the present study, most diving was shallower than 250 m, and half of the dives shallower than 40 m. Deeper and longer-lasting diving occurred further offshore closer to the shelf break. Besides foraging, harbour seals conduct a number of other activities while diving (Bjørge et al. 1995; Suryan and Harvey 1998; Lesage et al. 1999), often concentrated near the haul-out sites (Suryan and Harvey 1998).

Harbour seals are usually believed to dive to moderate depths, but dives of 558 ± 40 m (Kolb and Norris 1982) and 508 m (Schreer and Kovacs 1997) are known. These deep dives were observed when deep waters occurred relatively close to haul-out sites (Tollit et al. 1998). Harbour seal feeding areas are typically located 10–70 km away from their preferred haul-out sites

(Thompson et al. 1991; Bjørge et al. 1995; Tollit et al. 1998; Lesage et al. 1999). In the Prins Karls Forland area, the continental shelf break is only 35 km offshore. The maximum daily depth recordings show that most maximum dives were between 100 and 200 m. For seals that left the Prins Karls Forland area and moved south, maximum dive depths increased. This may be because these seals stayed along the edge of the continental shelf break. The maximum depth recorded in this study, 452 m, is twice what is predicted for harbour seals based on allometry of diving capacity (Schreer and Kovacs 1997).

Dive-duration ability depends on several factors but may, for the sake of simplicity, be related to body mass (Schreer and Kovacs 1997). Harbour seals should, based on results from ringed seals (Lydersen et al. 1992), have an aerobic dive limit of 8.7 min and a maximum breathhold capacity of 25.6 min. The longest harbour seal dive on record is 31 min (Ries et al. 1997). In a number of studies of harbour seal diving, mean dive durations were 1–6 min, with maximum durations 6–15 min, the results reflecting local bathymetry (Boness et al. 1994; Bjørge et al. 1995; Suryan and Harvey 1998; Lesage 1999). In the present study, 97% of the dives were shorter than 10 min, but dives lasting longer than 25 min were recorded. If the extreme duration values in the present study are disregarded, then the results are well within the maximum duration limit calculated according to Schreer and Kovacs (1997).

In the literature, harbour seals are noted as usually feeding at the sea-bed (Härkönen and Heide-Jørgensen 1991; Bjørge et al. 1995; Tollit et al. 1998). Because of the limitations in the accuracy of the SLDRs, it is not known if harbour seals in Svalbard were diving to the sea-bed, but based on the dive-depth frequencies and the bathymetry of the area, this seems likely. The area which is most frequented by Svalbard harbour seals (Fig. 2) stretches from the shore and out to 400 m depth.

At present, only opportunistic feeding data are available on Svalbard harbour seals (I. Gjertz, unpublished data). These seals consume a variety of fish, crustaceans and molluscs, with the most commonly recorded species being cod (*Gadus morhua*).

Several studies have found seasonal changes in harbour seal diet and feeding sites (Härkönen 1987; Thompson et al. 1991; Olsen and Bjørge 1995; Tollit et al. 1997; Hall et al. 1998). Harbour seals seem to feed opportunistically on some prey species, often depending on the relative abundance of the prey (Olsen and Bjørge 1995), but seals are also seen to be selective in their choice of both prey and prey size (Tollit et al. 1997). In an environment such as that along the west coast of Spitsbergen, with large fluctuations between Arctic and Atlantic waters, seasonal dietary changes may be expected. This is especially true if the seals are feeding pelagically (Weslawski et al. 1994). Harbour seals in Svalbard should therefore be expected to show seasonal and interannual variation in their diet. Some harbour seals are believed to specialise on specific prey or for-

aging techniques (Tollit et al. 1998). As the water temperature drops late in the year, cod move south from west Spitsbergen on a feeding migration to the Barents Sea (Gjøsæter et al. 1994). Seals that specialise in eating cod would accordingly have to follow their preferred prey south. Such seasonal movements have also been observed in the Gulf of St. Lawrence (Lesage 1999). This might also explain the southern movements of three of the tagged harbour seals.

The present study has shown that the majority of harbour seals in Svalbard appear to be stationary, and their local distribution at Prins Karls Forland seems little affected by the presence of drift-ice. Apart from favourable ice conditions, the waters off Prins Karls Forland must be a good feeding habitat. The main feeding area stretches offshore out to depths of 400 m.

References

- Bigg MA (1981) Harbour seal *Phoca vitulina* Linnaeus, 1758 and *Phoca largha* Pallas, 1811. In: Ridgeway SH, Harrison RJ (eds) Handbook of marine mammals, vol 2. Academic Press, London, pp 1–27
- Bjørge A, Thompson D, Hammond P, Fedak M, Bryant E, Aarefjord H, Roen R, Olsen M (1995) Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. In: Blix AS, Walløe L, Ulltang Ø (eds) Whales, seals, fish and man. Elsevier, Amsterdam, pp 211–223
- Boness DJ, Bowen WD, Oftedal OT (1994) Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behav Ecol Sociobiol* 34: 95–104
- Burns JM, Castellini MA (1998) Dive data from satellite tags and time depth recorders: a comparison in Weddell seal pups. *Mar Mamm Sci* 14: 750–764
- Fancy SG, Pank LF, Douglas DC, Curby CH, Garner GW, Amstrup SC, Regelin WL (1988) Satellite telemetry: a new tool for wildlife research and management. *US Fish Wildl Serv Res Publ* 172: 1–54
- Gjertz I, Børset A (1992) Pupping in the most northerly harbor seal (*Phoca vitulina*). *Mar Mamm Sci* 8: 103–109
- Gjøsæter H, Godø OR, Ulltang Ø (1994) De viktigste fiskeslagene i Barentshavet (in Norwegian). In: Sakshaug E, Bjørge A, Gulliksen B, Loeng H, Mehlum F (eds) Økosystem Barentshavet. Universitetsforlaget, Oslo, pp 181–197
- Goulet AM, Hammill MO, Barrette C (1999) Quality of satellite telemetry locations of gray seals (*Halichoerus grypus*). *Mar Mamm Sci* 15: 589–594
- Hall AJ, Watkins J, Hammond PS (1998) Seasonal variation in the diet of harbour seals in south-western North Sea. *Mar Ecol Prog Ser* 170: 269–281
- Hammond PS, McConnell BJ, Fedak MA (1993) Grey seals off the east coast of Britain: distribution and movements at sea. *Symp Zool Soc Lond* 66: 211–224
- Härkönen T (1987) Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and the Kattegat. *J Zool Lond* 213: 535–543
- Härkönen T, Heide-Jørgensen MP (1991) The harbour seal *Phoca vitulina* as a predator in the Skagerrak. *Ophelia* 34: 191–207
- Harris RB, Fancy SG, Douglas DC, Garner GW, Amstrup SC, McCabe TR, Pank LF (1990) Tracking wildlife by satellite: current systems and performance. *US Fish Wildl Tech Rep* 30: 1–52
- Henriksen G (1996) Status of grey seal *Halichoerus grypus* and harbour seal *Phoca vitulina* in the Barents Sea region. PhD Thesis, Zoology Institute, Norges Teknisk-Naturvitenskapelige Universitet, Trondheim

- Henriksen G, Gjertz I, Kondakov A (1997) A review of the distribution and abundance of harbor seals, *Phoca vitulina*, on Svalbard, Norway, and in the Barents Sea. *Mar Mamm Sci* 13: 157–163
- Kolb PM, Norris KS (1982) A harbour seal, *Phoca vitulina richardsi*, taken from a sable fish trap. *Calif Fish Game* 68: 123–124
- Lesage V (1999) Foraging ecology of harbour seals, *Phoca vitulina concolor*, in the St Lawrence river estuary, Canada. PhD Thesis, University of Waterloo, Canada
- Lesage V, Hammill MO, Kovacs KM (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Can J Zool* 77: 74–87
- Lyderson C, Ryg MS, Hammill MO, O'Brien PJ (1992) Oxygen stores and aerobic dive limit of ringed seals (*Phoca hispida*). *Can J Zool* 70: 458–461
- Mansfield AW (1967) Distribution of the harbour seal, *Phoca vitulina* Linnaeus, in Canadian arctic waters. *J Mammal* 48: 249–257
- Olsen M, Bjørge A (1995) Seasonal and regional variations in the diet of harbour seal in Norwegian waters. In: Blix AS, Walløe L, Ulltang Ø (eds) Whales, seals, fish and man. Elsevier, Amsterdam, pp 271–285
- Prestrud P, Gjertz I (1990) The most northerly harbor seal, *Phoca vitulina*, at Prins Karls Forland, Svalbard. *Mar Mamm Sci* 6: 215–220
- Rasmussen B (1960) Om klappmyssbestanden i det nordlige Atlanterhav (in Norwegian). *Fisken Havet* 1960: 1–23
- Ries EH, Traut IM, Paffen P, Goedhart PW (1997) Diving patterns of harbour seals (*Phoca vitulina*) in the Wadden Sea, the Netherlands and Germany, as indicated by VHF telemetry. *Can J Zool* 75: 2063–2068
- Schreer JF, Kovacs KM (1997) Allometry of diving capacity in air-breathing vertebrates. *Can J Zool* 75: 339–358
- Stewart BS, Leatherwood S, Yochem PK, Heide-Jørgensen MP (1989) Harbor seal tracking and telemetry by satellite. *Mar Mamm Sci* 5: 361–375
- Suryan RM, Harvey JT (1998) Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. *Mar Mamm Sci* 14: 361–372
- Teilmann J, Dietz R (1994) Status of the harbour seal, *Phoca vitulina*, in Greenland. *Can Field Nat* 108: 139–155
- Thompson PM (1993) Harbour seal movement patterns. *Symp Zool Soc Lond* 66: 225–239
- Thompson PM, Rothery P (1987) Age and sex differences in the timing of moult in the common seal, *Phoca vitulina*. *J Zool Lond* 212: 597–603
- Thompson PM, Pierce GJ, Hislop JRG, Miller D, Diack JSW (1991) Winter foraging by common seals (*Phoca vitulina*) in relation to food availability in the inner Moray Firth, N.E. Scotland. *J Anim Ecol* 60: 283–294
- Tollit DJ, Greenstreet SPR, Thompson PM (1997) Prey selection by harbour seals, *Phoca vitulina*, in relation to variations in prey abundance. *Can J Zool* 75: 1508–1518
- Tollit DJ, Black AD, Thompson PM, Mackay A, Corpe HM, Wilson B, Van Parijs SM, Grellier K, Parlane S (1998) Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *J Zool Lond* 244: 209–222
- Vinje T (1985) Drift, composition, morphology and distribution of the sea ice fields in the Barents Sea. *Nor Polarinst Skr* 179c: 1–26
- Weslawski JM, Ryg M, Smith TG, Øritsland NA (1994) Diet of ringed seals (*Phoca hispida*) in a fjord of west Svalbard. *Arctic* 47: 109–114
- Wiig Ø (1989) A description of common seals, *Phoca vitulina* L. 1758, from Svalbard. *Mar Mamm Sci* 5: 149–158
- Wiig Ø (1991) Demographic parameters for Norwegian grey seals *Halichoerus grypus*. *Fauna Norv Ser A* 12: 25–28