Polar Biol (2000) 23: 559–566

ORIGINAL PAPER

I. Gjertz · K. M. Kovacs · C. Lydersen · Ø. Wiig

Movements and diving of bearded seal (*Erignathus barbatus*) mothers and pups during lactation and post-weaning

Accepted: 31 January 2000

Abstract Eleven bearded seals (*Erignathus barbatus*) were tagged with satellite-linked dive recorders in Kongsfjorden, Svalbard, Norway, in May 1994. These animals included four mother-pup pairs and three single pups. The seals were tracked for 21–258 days. A total of ~207,000 dives were recorded. Bearded seal mothers showed limited movements during the nursing and moulting periods. After weaning, the pups moved out of the tagging area and dispersed coastally. One pup left Svalbard and moved far offshore to Greenland and Jan Mayen. Bearded seal adults displayed a bi-modal dive behaviour, with peaks of activity that were shallower than 10 m or from 50 to 70 m. Most dives for adult seals (97%) were shorter than 10 min. Young pups performed dives that were shallower and shorter in duration than their accompanying mothers, but diving skills improved rapidly with age. Six of the seven pups dived deeper than 448 m by the time they were 2 months old. Analyses of movement data with respect to separation of mother-pup pairs suggest a lactation period of about 24 days.

Introduction

Bearded seals (*Erignathus barbatus*) are large pagophilic phocid seals. They have a wide circumpolar distribution around the Arctic (Burns 1981). Bearded seals prefer open drift ice, but can make and maintain breathing holes in relatively thin ice; they usually avoid regions of continuous, thick land-fast ice (Burns 1981). These seals feed predominantly on benthic prey (Burns 1981), and their distribution is therefore generally restricted to relatively shallow-water areas. Feeding depths down to between 130 and 200 m have been reported (Kosygin 1971 cited in Burns 1981; Kelly 1988), but depths shallower than 100 m, especially in the range 25–50 m, seem to be preferred (Kingsley et al. 1985).

Bearded seals are common in the Svalbard area and the Barents Sea. Svalbard seals are predominantly found in near-shore waters for most of the year, but they are also encountered as far north as 84°N (Nansen 1897; Collett 1911–1912). Their distribution in the northern Barents Sea appears to follow the dynamics of the drifting ice. Relatively high densities of mother-pup pairs are seen near the ice edge in late April to early May (Wiig and Isaksen 1995). The Fram Strait and Greenland Sea are mostly very deep waters, and here single animals are occasionally seen south of 79°N and east of 5°W, but they are more abundant north of 79°N and west of 5°W (Ugland and Ree 1983; Dietz et al. 1985).

Bearded seals in pelagic sea-ice areas are thought to move significant distances during the year with the seasonal advance and retreat of the sea-ice cover (Popov 1975; Burns 1981; Wiig and Isaksen 1995). However, little is known about bearded seals that inhabit coastal areas. According to Vibe (1950), bearded seals are basically stationary in the Thule district in Greenland, but they disperse somewhat during the summer. Krylov et al. (1964) also suggested that bearded seals, in contrast to other Arctic seals, are more or less sedentary and do not undertake lengthy movements. This view was shared by Collett (1911–1912) who classified this species as "relatively stationary".

Bearded seals give birth to their pups between mid-April and mid-May in Svalbard (Lydersen et al. 1994, 1996; Kovacs et al. 1996). The duration of the nursing period is not known, but is thought to be 12–18 days (Burns 1967). There are some indications that pups may remain with their mothers and receive milk for a longer

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

K. M. Kovacs
The University Courses on Svalbard (UNIS), P.B. 156/157, 9170 Longyearbyen, Norway

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

period than this in Svalbard (Lydersen et al. 1996). Burns (1981) claimed that weaning in bearded seals is abrupt, with the pups simply being deserted by their mothers. In contrast, Lydersen et al. (1996) suggested that bearded seal pups may suckle longer than some other phocid pups and that weaning is less abrupt than among other phocid species. A mixture of milk and prey has been recorded in bearded seal pup stomachs (Römer and Schaudinn 1900), which indicates that pups commence foraging while still being nursed. Burns (1981) also suggested that newly weaned pups are active feeders.

Pups of this species normally enter the water within hours of being born (Kovacs et al. 1996), and quickly develop swimming and diving skills (Hammill et al. 1994). By the time they are 4–7 days old they spend half of their time in the water swimming and diving, while being attended by their mothers (Lydersen et al. 1994). Thus, bearded seal pups differ from most other phocids in that they learn to swim and dive at a very young age (Lydersen and Kovacs, in press). Their diving capabilities are not very well developed at first, but they improve quickly on a day to day basis during the nursing period (Lydersen et al. 1994). Bearded seal pups are weaned as skilled divers that are capable of independent feeding and they have some degree of predator avoidance (Lydersen and Kovacs, in press).

The present study had three objectives. The first was to determine the movement patterns of bearded seals in the coastal areas of Svalbard. The second objective was to determine the length of the nursing period and the age at weaning. The final objective was to obtain ecological knowledge about diving skills and diving behaviour of a little-known arctic seal species.

Materials and methods

The fieldwork component of this study was conducted in the Kongsfjorden-Krossfjorden-northern Forlandsundet area (ca. 79°N, 12°E) of Svalbard, Norway (Fig. 1) in May 1994. Pups were captured using a small (4.3 m) aluminium boat and a custom-designed "dip-net" (Lydersen et al. 1994). Once pups were caught, mothers were attracted to the boat, or a nearby ice floe, using the pup as "bait" to draw her toward a fishing net set with floats on the surface (Lydersen et al. 1996). Once in the initial net, the mother was secured using a small, meshed trawl net and both mother and pup were hauled onto an ice floe. Mothers were weighed using a Dillon scale (500 ± 1 kg) suspended from a tripod. Pups were weighed in a similar manner using a Salter spring scale (100 ± 0.5 kg), or with the same scale as for the mothers if pup mass exceeded 100 kg. All seals were tagged with individually numbered plastic tags placed through the webbing of the hind flippers.

A Satellite-Linked Dive Recorder (SLDR) (Wildlife Computers, Redmond, Wash.) was glued to the fur of the upper part of the back of each seal using quick setting epoxy resin. Maximum depth recorded over the previous 24-h period is automatically given in the status message. The 0.5-W-powered SLDRs collected dive-depth data from 0 to 250+ m in 14 intervals (bins) with a precision of 2 m. The maximum depth that can be recorded is 490 m. Dive-duration data were also collected in 14 bins. The dive-depth bins' lower limits were set at 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150,

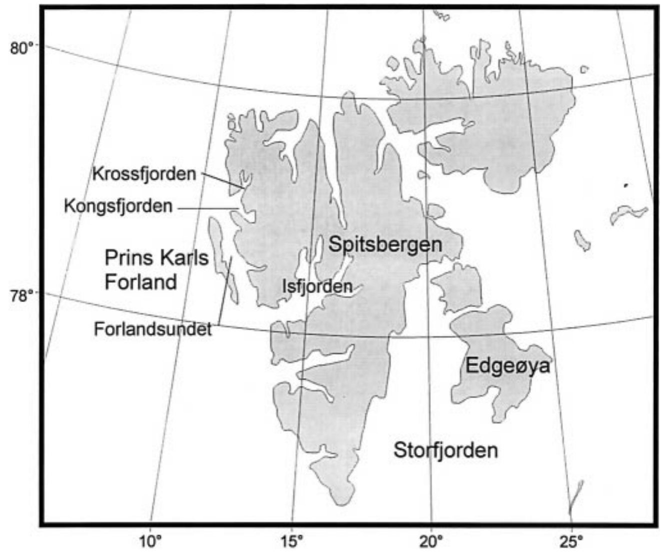


Fig. 1 Map of Svalbard

200, 250 and >250 m. The minimum depth to be recorded as a dive was set at 2 m. The dive-duration bin limits were set at 1, 2, 3, 4, 5, 10, 15, 20, 25, 30, 40, 50, 60 and >60 min.

The SLDRs were programmed to transmit in a continuous mode, i.e. as long as a conductivity sensor was dry the SLDR would transmit at 45-s intervals. If ten consecutive transmissions occurred without seawater-induced delays then the transmitter would switch to a 90-s transmission interval. If, after a 4-hour period the sensor was still dry then the SLDR would suspend transmission until the sensor was reactivated by immersion in salt water.

Telemetry locations provided by the Argos Data Collection and Location System (Argos, Toulouse, France) 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 1000, 350 and 150 m for location quality 1, 2 and 3, respectively. For location quality 0 the accuracy of the location is not given (Harris et al. 1990). The location quality is dependant on the number of uplinks received by the satellite for each overpass, the vertical angle of the satellite, and the pass duration (Harris et al. 1990). Uplinks of poorer quality than 0 are recorded as received, but without being assigned a location quality.

A specially constructed SASPC (SAS Institute, Cary, N.C., USA) computer program compared all daily ARGOS positions and selected the daily position of highest quality. When several positions had equally high rank then the first position of that day was selected for tracking.

Site fidelity was measured for each individual seal by manually determining the shortest swimming distance from the seal's position on the 15th of each month to the tagging site. If no location quality 1 or better existed for the 15th, then the nearest day with such a location quality was chosen.

The ages of pups at the time of capture were estimated by assuming a mean daily mass gain of 3.3 kg (Lydersen et al. 1994) and a newborn body mass of 38 kg (K.M. Kovacs and C. Lydersen, unpublished work).

Location qualities are best when the animals are hauled out, since the transmitter is dry then and transmits continuously, i.e. has a greater chance of obtaining many uplinks per overpass. Since bearded seals haul out to nurse, higher location quality can be expected for periods when the mothers spend more time hauled out and nursing. Following weaning the haul-out periods may be shorter, and if so, location quality should drop. The daily number of location qualities >0 for mothers known to be accompanied by pups, were compared for an equal number of days before and after the weaning dates estimated from the position data. The highest quality position data for mother-pup pairs were manually compared for each day. For position data of quality 1 or better, a difference of 0.0–0.1° latitude (0–11 km) was considered to indicate that the animals were together, i.e. still nursing.

Results

Four mother-pup pairs and three additional pups were equipped with SLDRs (Table 1). The SLDRs transmitted for 24–258 days after attachment (mean 101.8 ± 74.2; Table 1). SLDRs on mothers functioned for 24–47 days (34.3 ± 12.0), while SLDRs on pups transmitted for 58–258 days (140.4 ± 65.8). SLDRs provided a total of 4692 locations; 58% were location quality 0, 24% location quality 1, 7% location quality 2 or better. The rest of the locations were of such poor quality that they were discarded.

Three of the four adult seals stayed within the tagging area, i.e. Kongsfjorden-Krossfjorden-northern Forlandsundet, until the transmissions ceased (Fig. 2). The adult with the most limited movements remained within 40 km of the tagging site. The other adult stayed in the tagging area for 4 days, and then it moved into the inner parts of Isfjorden, a minimum distance of 180 km.

Pup movements were more extensive than those of the adult females (Fig. 2). Pup 2062 performed the longest movements, initially remaining in the tagging area for 8 days, and then moving offshore. On 8 June it moved westward, about 200 km south of the pack ice, turning just 90 km from the Greenland coast (Shannon Ø ca. 75°N, 14°W). Based on the highest quality location selected for each day, the minimum distance this seal swam was 2359 km in a 50-day period, i.e. an average of 47 km a day. The six other pups moved variable distances, but all remained within Spitsbergen's coastal waters (Fig. 2).

One month after tagging the seven pups were 167 ± 176 km (range 40–550 km) away from the tagging sites. After 2 months they were 234 ± 325 km (range 30–960 km) from the tagging sites. After 3 months two transmitters had stopped and the distance from the tagging site had dropped to 90 ± 69 km (10–160 km). After another month an additional transmitter stopped and the distance was 70 ± 60 km (40–160 km); thereafter the distance remained fairly constant even as the transmitters gradually failed.

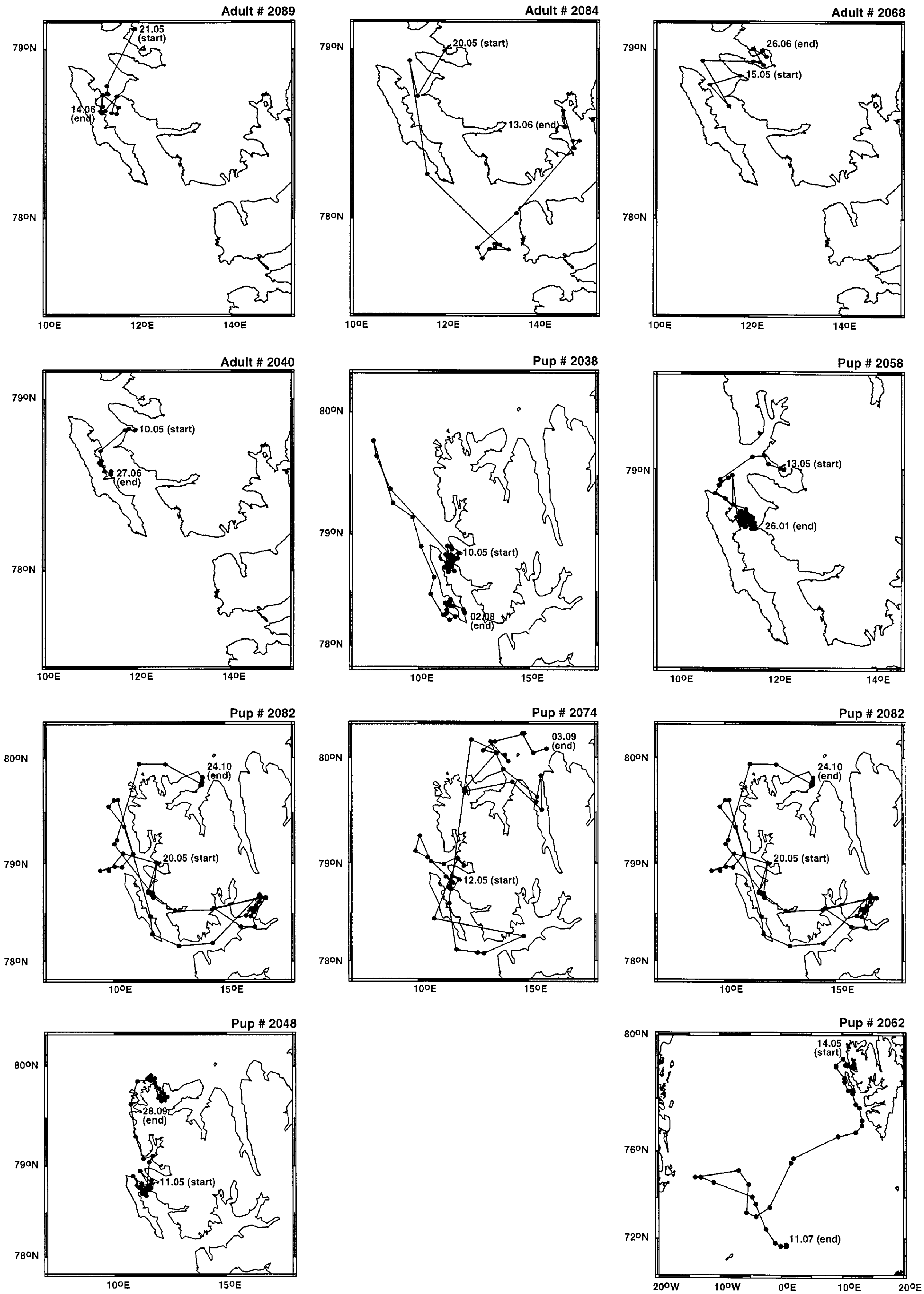
The location data for mothers versus their pups suggest that they separated, and presumably pups were weaned, at an age of ≈24.0 (±2.7) days. Three pups left the tagging area 7–14 days after their estimated weaning dates. Two left on their estimated weaning date, one left 5 days prior to this date and the final pup did not leave. One of the mother-pup pairs separated spatially from 26 to 29 May and then were in the same areas once again, intermittently, until 5 June. This mother and pup were then apart for a week before coming back into the same area(s) for the duration of the adult's transmissions, i.e. 14 days. A second pair displayed a similar pattern, separating on 21 May and coming together intermittently from 25 May until the adult transmitter ceased to function on 14 June.

The number of good-quality locations (location classes 1–3) registered daily for mother 2040 dropped on 26 May, when the pup was 24 days old (Fig. 3). Mother 2068's location quality dropped on 25 May when her pup was 23 days old. The number of good quality locations for both these seals was reduced by ~85% from the time of tagging until weaning compared to an

Table 1 Bearded seals equipped with satellite-linked dive recorders in 1994, Svalbard, Norway

Seal no.	Age	Sex	Mass at capture (kg)	Estimated date of birth[a]	Tagging date	Transmitter stopped	Transmission days	Estimated weaning date[b]	Estimated nursing duration (days)
Mother-pup pairs									
2038	Pup	F	66	2 May	10 May	2 Aug.	84	25 May	24
2040	Adult	F	336		10 May	27 June	47		
2074	Pup	M	82	2 May	15 May	3 Sept.	111	25 May	24
2068	Adult	F	275		15 May	26 June	42		
2082	Pup	M	104	1 May	20 May	2 Nov.	166	22 May	21
2084	Adult	F	252		20 May	13 June	24		
2087	Pup	M	119	27 April	21 May	3 Nov.	166	21 May	25
2089	Adult	F	269		21 May	14 June	24		
Single animals									
2048	Pup	M	90	26 April	11 May	28 Sept.	140		
2058	Pup	F	64.5	5 May	13 May	26 Jan.	258		
2062	Pup	M	70	4 May	14 May	11 July	58		
Mean ± SD									
			Adults 283 ± 37 Pups 85 ± 21				102 ± 74		23.5

[a] Estimated date of birth was back-calculated using an estimated mass gain of 3.3 kg per day (Lydersen et al. 1994) and a newborn body mass of 38 kg (K.M. Kovacs and C. Lydersen, unpublished work)
[b] Weaning date was estimated from satellite transmitter data


Adult # 2089
21.05
(start)
14.06
(end)
79ON
78ON
10OE
12OE
14OE
Adult # 2084
20.05 (start)
13.06 (end)
79ON
78ON
10OE
12OE
14OE
Adult # 2068
26.06 (end)
15.05 (start)
79ON
78ON
10OE
12OE
14OE
Adult # 2040
10.05 (start)
27.06
(end)
79ON
78ON
10OE
12OE
14OE
Pup # 2038
10.05 (start)
02.08
(end)
80ON
79ON
78ON
10OE
15OE
Pup # 2058
13.05 (start)
26.01 (end)
79ON
10OE
12OE
14OE
Pup # 2082
24.10
(end)
20.05 (start)
80ON
79ON
78ON
10OE
15OE
Pup # 2074
03.09
(end)
12.05 (start)
80ON
79ON
78ON
10OE
15OE
Pup # 2082
24.10
(end)
20.05 (start)
80ON
79ON
78ON
10OE
15OE
Pup # 2048
28.09
(end)
11.05 (start)
80ON
79ON
78ON
10OE
15OE
Pup # 2062
14.05
(start)
11.07 (end)
80ON
76ON
72ON
20OW
10OW
0OE
10OE
20OE

◄
Fig. 2 Movements made by all 11 bearded seals, 4 adult females and 7 pups, equipped with radio transmitters in May 1994. The daily location with the highest location quality is given

equal number of days just after the estimated weaning date. Mother 2089 is thought to have left her pup on the day the pair was tagged. The lack of good-quality locations observed for her is further evidence that this may have been the case. The last mother (2084) showed no variance in the quality of locations through the period of study. The weaning dates based on location quality compare favourably with those obtained by estimating the weaning date using location data.

A total of 207,382 dive durations were recorded. The frequency distribution of the total number of dives recorded for each duration bin, for each seal, is given in Figs. 4 and 5. For pups, these frequencies include both nursing and post-weaning time frames. Ninety-nine percent of the total number of dives performed by weaned pups were shorter than 10 min, and the bin with the highest number of dives, bin 5–10 min, contained 41% of the dives. These figures were 97% and 50%, respectively, for adults. Diving performed by pups was significantly different before and after weaning, with shallower and shorter dives before weaning (χ^2, $P < 0.05$ for all pups). Pups and their mothers performed shallower and shorter dives before weaning than for an equal time period immediately following weaning (χ^2, $P < 0.001$ for all animals).

The longest dives recorded for nursing pups were 10–15 min for four different pups. Among all nursing pups, 6% of the dives lasted 5–10 min, and 94% were shorter than 5 min. Adults all occasionally performed dives lasting 15–20 min, and one 20- to 25-min dive was recorded.

Comparisons were made between dive duration for a 1-week period in June (1–7 June) and for a 1-week period as late as possible in the season, to test if dive duration increased with age in pup records. Based on the frequency distribution in the dive-duration bins, diving behaviour was significantly different for those pups with transmitters that lasted more than 4 months, 2058 ($\chi^2 = 33.231$, $d.f. = 5$, $P < 0.001$), 2082 ($\chi^2 = 143.852$, $d.f. = 6$, $P < 0.001$), 2048 ($\chi^2 = 188.866$, $d.f. = 6$, $P < 0.001$) and 2087 ($\chi^2 = 19.236$, $d.f. = 5$, $P < 0.005$). Older pups dived for longer periods.

A total of 192,236 dive depths were recorded. The frequency distribution of the total number of dives recorded for each depth bin, for each seal, is given in Figs. 4 and 5. For individual pups, frequencies of dives shallower than 20 m varied from 34 to 90%, but for all pup dives combined ~80% were shallower than 40 m and 90% were shallower than 60 m. One adult (2089) performed 93% of its diving shallower than 20 m, whereas the other three adults dived deeper, with 35–80% of the dives to depths between 20 and 80 m.

During the nursing period, mothers in pairs 2040/2038 and 2084/2082 dived significantly deeper than their pups, ($\chi^2 = 52.406$, $d.f. = 7$, $P < 0.001$, $\chi^2 = 20.716$, $d.f. = 10$, $P = 0.023$). Pair 2074/2068 did not display a significant difference ($\chi^2 = 13.010$, $d.f. = 10$, $P = 0.223$). No significant correlation could be found between mothers' and their pups' maximum dives during their time together; pair 2038/2040 (Mann-Whitney U-test, $N = 15$, $W = 185$, $P = 0.051$); pair 2074/2068 (Mann-Whitney U-test, $N = 7$, $W = 55$, $P = 0.8$).

One pup dived deeper than 400 m by the time it was 17 days old. Five pups had exceeded depths of 400 m by the time they were 6 weeks old. The remaining two had maximum dives of 336 m and 364 m, respectively. Six of

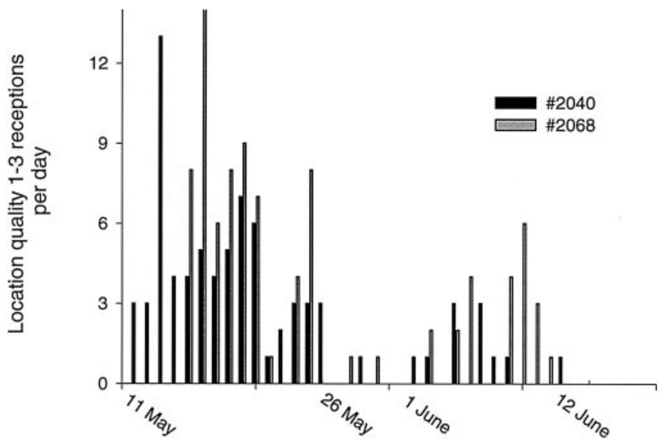


Fig. 3 Number of high-quality receptions per day for bearded seal mothers 2040 and 2068. During nursing the number of receptions per day are expected to be higher than after the pups are weaned. A drop in high-quality receptions indicates weaning. The two other mother-pup pairs in this study split up shortly after tagging, on the day of tagging and after 2 days and are not included in this figure

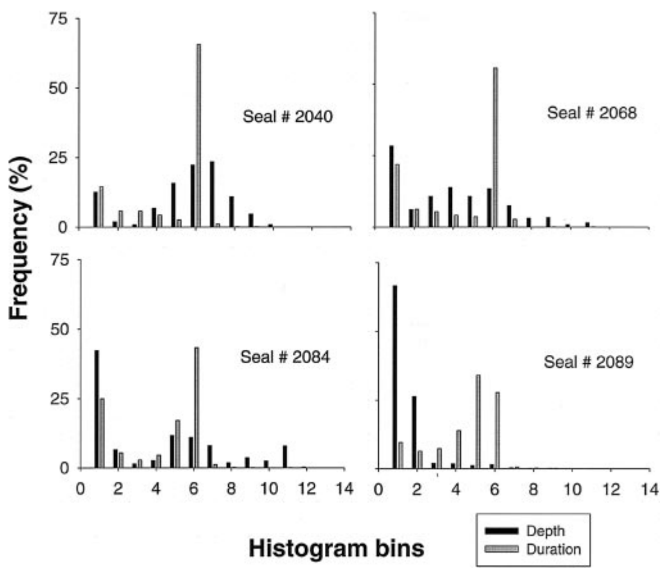


Fig. 4 Frequency of dive durations and dive depths per histogram bin for bearded seal adult females combined over the whole deployment period. The dive-duration bin lower limits were set at 1, 2, 3, 4, 5, 10, 15, 20, 25, 30, 40, 50, 60 and >60 min. The dive-depth bin lower limits were set at 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, 200, 250 and >250 m

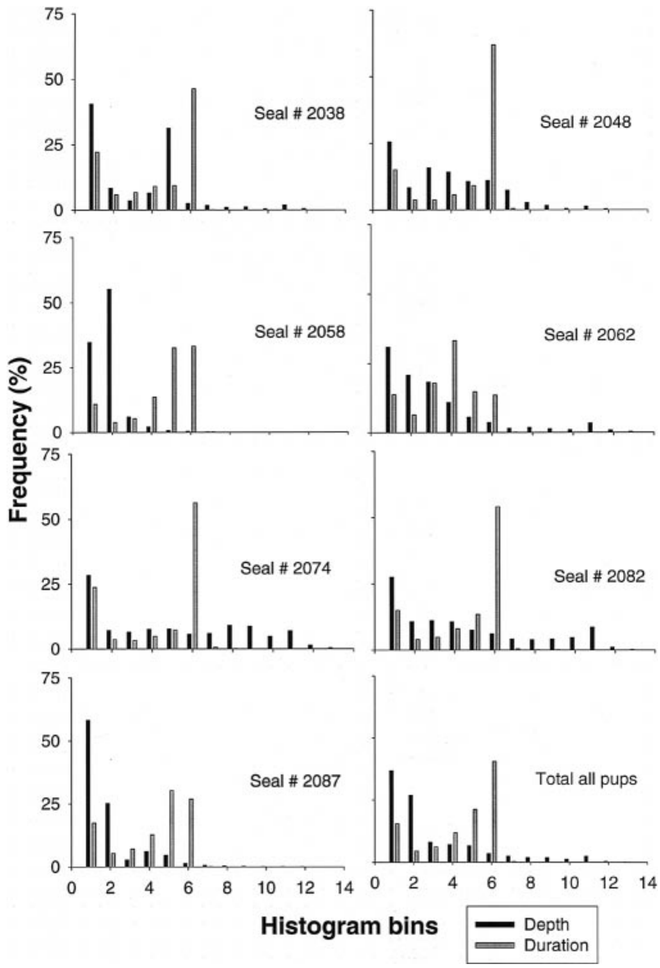


Fig. 5 Frequency of dive durations and dive depths per histogram bin for bearded seal pups combined over the whole deployment period. The dive-duration bin lower limits were set at 1, 2, 3, 4, 5, 10, 15, 20, 25, 30, 40, 50, 60 and > 60 min. The dive-depth bin lower limits were set at 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, 200, 250 and > 250 m

the seven pups dived deeper than 448 m by the time they were 2 months old – the deepest was 480 m. Only one of the adults (2084) dived deeper than 400 m (472 m). Maximum depths for the other three adult females were 284, 236 and 168 m.

Only one seal permanently left the shallow coastal waters of Svalbard. After leaving the Svalbard coast, 92% of pup 2062's dives were shallower than 50 m, compared with 68% while in Svalbard waters. This difference was not statistically significant ($\chi^2 = 18.928$, $d.f. = 11$, $P = 0.062$). Similarly, 79% of dive durations lasted less than 4 min while at sea compared to 50% in Svalbard waters, but this difference was significant ($\chi^2 = 43.713$, $d.f. = 5$, $P < 0.001$). The only other seal to go offshore was pup 2038. It was located in deep, ice-free waters at about 79.7°N 7.5°E from 5–10 June. In this period 77% of the dives were < 70 m but with 14% of the dives at 100–150 m. The pup dived significantly deeper during this period ($\chi^2 = 273.111$, $d.f. = 12$, $P < 0.001$) than during the following 6-day period in shallower water, where 97% of the dives were < 70 m. Dive durations were similar during the two time periods. The only other seals to leave the inshore fjord areas were pup 2074 and adult 2084. Both left the fjords for shorter periods, but remained in the near-shore areas of shallow coastal shelf and banks, areas where the bathymetry was similar to that found in the fjords.

Discussion

The short period for data collection by SLDRs on adults was most probably due to loss of the tags during the moult, which occurs shortly after the lactation period. According to Burns (1981) the moult peaks in May/June, but according to Wollebæk (1907) moulting occurs in June/July for bearded seals in the European Arctic. The latter is more in accordance with our observations of moulting, based on handling of animals and the transmitter failures.

Three of the adult females in this study stayed in the tagging area, moving only an average of 40 km from the tagging sites. One of these animals moved from Forlandsundet into Kongsfjorden, while the other two moved in the other direction and stayed in Forlandsundet. These movements may be partly related to ice drift, as noted by Hammill et al. (1994). The fourth adult bearded seal (2084) weaned her pup 2 days after they were tagged and had the shortest nursing period of the pairs studied. She left the tagging area and travelled to northern Isfjorden (180 km), another large shallow-water area (< 100 m) that has long-lasting land-fast ice. It therefore seems as though bearded seal females stay in shallow-water areas, with access to fast or drifting ice, during the breeding and moulting periods. In addition, the results from the present study indicate that adult females, in May and June, show limited movements.

Two of five adult females tagged in Kongsfjorden in 1994 (the four adults equipped with satellite transmitters and one other female that was only flipper-tagged) were re-captured in the same general tagging area in 1996 and 1997, respectively. Another adult female tagged in 1995 was re-sighted in 1996, and yet another adult female tagged in 1996 was recaptured in 1997, also in the same area (C. Lydersen and K.M. Kovacs, unpublished work). These observations indicate that females show site fidelity at least in the breeding season. Svalbard is largely uninhabited, and for most of the year no observations are made of bearded seals in the tagging area in Kongsfjorden-Krossfjorden-Forlandsundet. Adult females may well stay there year round.

All but one of the bearded seal pups remained in Svalbard. Apart from one trip offshore (2038), three of the pups stayed in the shallow-water areas surrounding Prins Karls Forland. The other three made longer coastal trips and all of these spent some time in a very large shallow-water area along the north coast of Spitsbergen.

Hjelset et al. (1999) found that bearded seals in Spitsbergen's fjords were largely benthic feeders, and that they use a wide variety of prey organisms. However, bearded seals also commonly occur in the pack-ice areas over very deep water (3000 m) in the Fram Strait (Dietz et al. 1985). This may indicate that some bearded seals are sympagic feeders. Pup 2062 moved south of the pack ice making shallow (< 50 m) dives. The speed at which this seal travelled (> 60 km a day) suggests that this seal had little time for feeding. The water depth in this area (~2000–3000 m) indicates that any feeding must have been conducted pelagically.

The innermost parts of Spitsbergen's fjords often offer poor benthic feeding possibilities due to sedimentation of silt from glaciers in the inner basins (Weslawski et al. 1994). These same areas also have limited access for bearded seals for large parts of the year due to virtually continuous fast-ice cover. The results of the satellite telemetry reflect this and show that the seals mainly stay in the outer fjord areas. Here, they have access to large, biologically-rich (Weslawski et al. 1994) shallow-water areas which have a mixture of fast ice, drift ice and open water.

Holsvik (1998) found that the proportion of time female bearded seals spent feeding their pups seemed to remain constant throughout the lactation period. Since these seals haul out when nursing, and haul-out facilitates transmitter to satellite uplinks, it is therefore reasonable to assume that an observed reduction in the haul-out time by the mothers may indicate that the pup has stopped nursing. It may be argued that the change in location quality could be due to circumstances other than weaning. A period of bad weather could give a similar result. However, no drop in location quality was observed in the pup records, suggesting that the change in location quality was not due to weather.

In the present study, mother-pup pairs apparently split up after about 24 days of nursing, which would indicate that the pup's weaning mass should be about 117 kg, based on a daily mass gain of 3.3 kg and a birth mass of 38 kg (K.M. Kovacs and C. Lydersen, unpublished data from more than 100 different nursing bearded seal pups, with individual pups caught several times in the nursing period). However, individual mass gain may vary considerably. This is higher than the 85 kg reported by Burns (1967). However, the lactation period in Burns's study was estimated to be only 12–18 days. Holsvik (1998) observed six bearded seal mothers that attended pups that were 18–22 days old, and thus are in line with those of the present study concerning time of weaning.

Two of the mother-pup pairs studied split up at weaning and then apparently reunited again for long periods of time after weaning was thought to have taken place. This may be an artefact of inaccuracies in the telemetry data. However, there are observations that suggest that adult bearded seals may stay with their pups for a long time (Degerbøl and Freuchen 1935). Local trappers in Svalbard have shot bearded seal mother-pup pairs that were still together as late as September (Lydersen et al. 1996). If the pups are still nursing after estimated weaning then a mixture of milk and prey should be found in young of the year bearded seals after the assumed 24-day lactation period. One example of this has been recorded. In the latter half of June 1898, a 166-cm-long pup, accompanied by its mother, who still had milk in her teats, was killed in Storfjorden, Svalbard (Römer and Schaudinn 1900). The pup's stomach contained milk, two crustaceans and some worms. Another and more likely explanation for observations of mother-pup pairs in late summer and early autumn is that some bearded seals are born much later than the peak pupping season in early May. One newborn bearded seal pup was observed on a floe in Krossfjorden on 15 July 1995 (B. Frantzen, personal communication), and on 3 August 1989 a newborn bearded seal pup was observed on a beach at Edgeøya (F. Mehlum, personal communication).

Our choice of duration bin settings proved to be unfortunate, because important details are obscured in the 5- to 10-min bin. Shorter intervals should have been selected at the low end of the duration range. All of the pups displayed a bi-modal pattern of dive duration, with peaks in bins 1 and either 5 or 6. However, this is due partially to the large time span covered by bin 6.

Since bearded seals are primarily benthic feeders, then most of the dive depths recorded probably reflect the local bathymetry rather than differences in diving behaviour. However, the adult dive-depth data (Fig. 4) showed a bi-modal pattern. This suggests that adult bearded seals in May and June dive shallowly (less than 10 m) or dive to depths of 50–70 m most of the time. The result of the pup diving (Fig. 5) is less clear, since it describes a longer time period than that of the adults, and pup diving ability develops significantly with age.

Based on maximum depths, it is evident that the pups occasionally dive deeper than do their mothers. All pups occasionally dived down to 400 m without the mothers accompanying them to these depths; one explanation for this could be that these are not feeding dives. It may be that this deep diving is exploratory (Bengtson and Stewart 1992; Schreer and Testa 1996). Most of the diving behaviour documented in this study therefore supports Kingsley et al.'s (1985) view that bearded seals prefer depths shallower than 100 m, especially those in the 25- to 50-m range.

References

Bengtson JL, Stewart BS (1992) Diving and haul-out behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. Polar Biol 12: 635–644

Burns JJ (1967) The Pacific bearded seal. Alaska Department of Fish and Game, Juneau

Burns JJ (1981) Bearded seal *Erignathus barbatus* Erxleben, 1777. In: Ridgway SH, Harrison RJ (eds) Handbook of marine mammals, vol 2. Seals. Academic Press, London, pp 145–170

Collett R (1911–1912) Norwegian mammals (in Norwegian). Aschehoug, Oslo

Degerbøl M, Freuchen P (1935) Zoology I. Mammals. Report of the 5th Thule Expedition 1921–1924. Gyldendalske Boghandel, Nordisk, Copenhagen

Dietz R, Heide-Jørgensen MP, Born EW (1985) Marine mammals in East Greenland (in Danish). Report to Råstofforvaltningen for Grønland og Grønlands Fiskeri- og Miljøundersøgelser. Danbiu ApS, Hellerup

Hammill MO, Kovacs KM, Lydersen C (1994) Local movements by nursing bearded seal (*Erignathus barbatus*) pups in Kongsfjorden, Svalbard. Polar Biol 14: 569–570

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: 52

Hjelset AM, Andersen M, Gjertz, I, Lydersen C, Gulliksen B (1999) Feeding habits of bearded seals (*Erignathus barbatus*) from the Svalbard area, Norway. Polar Biol 21: 186–193

Holsvik R (1998) Maternal behaviour and early behavioural ontogeny of bearded seals (*Erignathus barbatus*) from Svalbard, Norway. Thesis, Norwegian University of Science and Technology (NTNU), Trondheim

Kelly BP (1988) Bearded seal. In: Lentfer JW (ed) Selected marine mammals of Alaska: species accounts with research and management recommendations. US Marine Mammal Commission, Washington, DC, pp 77–94

Kingsley MCS, Stirling I, Calvert W (1985) The distribution and abundance of seals in the Canadian High Arctic, 1980–1982. Can J Fish Aquat Sci 42: 1189–1210

Kovacs KM, Lydersen C, Gjertz I (1996) Birth-site characteristics and prenatal molting in bearded seals (*Erignathus barbatus*). J Mammal 77: 1085–1091

Krylov VI, Fedoseev GA, Shustov AP (1964) Pinnipeds of the Far East (in Russian). Food Industry, Moscow

Lydersen C, Kovacs KM (in press) Behaviour and energetics of ice-breeding North Atlantic phocid seals during the lactation period. Mar Ecol Prog Ser

Lydersen C, Hammill MO, Kovacs KM (1994) Diving activity in nursing bearded seal (*Erignathus barbatus*) pups. Can J Zool 72: 96–103

Lydersen C, Kovacs KM, Hammill MO, Gjertz I (1996) Energy intake and utilisation by nursing bearded seal (*Erignathus barbatus*) pups from Svalbard, Norway. J Comp Physiol B 166: 405–411

Nansen F (1897) Fram over Polhavet, vol 2. Aschehoug, Oslo

Popov LA (1975) Status of main ice forms of seals inhabiting waters of the USSR and adjacent to the country marine areas. UN/FAO ACMRR working party on marine mammals ad hoc III status report 33. All-Union Research Institute Marine Fisheries and Oceanography (Vinro), Moscow

Römer F, Schaudinn F (1900) Einleitung, Plan des Werkes und Reisebericht. II. Die Landtiere und die Eistiere. Fauna Arct 1: 1–84

Schreer JF, Testa JW (1996) Classification of Weddell seal diving behavior. Mar Mammal Sci 12: 227–250

Ugland KI, Ree V (1983) Observasjoner av sjøpattedyr på Norsk Polarinstitutts Svalbard-ekspedisjoner 1981 og 1982. Fauna Oslo 36: 105–118

Vibe C (1950) The marine mammals and the marine fauna in the Thule district (Northwest Greenland) with observations on ice conditions in 1939–1941. Medd Grønl 150: 1–115

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, Isaksen K (1995) Seasonal distribution of harbour seals, bearded seals, white whales and polar bears in the Barents Sea. Nor Polarinst Medd 136: 47–59

Wollebæk A (1907) Ueber die biologie der Seehunde und die Seehundjagd in Euroaeischen Eismeer. Rapp PV Reun Cons Perm Int Explor Mer 8: 5–82