

# Diving behaviour of lactating bearded seals (*Erignathus barbatus*) in the Svalbard area

Bjørn A. Krafft, Christian Lydersen, Kit M. Kovacs, Ian Gjertz, and Tore Haug

**Abstract:** This study documents activity patterns and diving behaviour of four bearded seal (*Erignathus barbatus*) mothers during the lactation period. The females spent  $8 \pm 3\%$  (mean  $\pm$  SD) of their time hauled out on the ice and  $92 \pm 3\%$  in the water. Approximately half of their time was spent diving. During the study 15 077 dives were recorded. The duration of dives was  $2.0 \pm 2.3$  min and diving depth was  $17.2 \pm 22.5$  m (maximum 18.7 min and 288 m, respectively). Haulout periods occurred  $3 \pm 2$  times per day (duration =  $44.0 \pm 98.1$  min). The overall distance swum per day was  $48.1 \pm 23.2$  km. Three dive types were differentiated using a combination of hierarchical and *k*-means clustering, one V-shaped grouping and two U-shaped groupings. The most common dive type was  $U_1$ ; these dives were the deepest and longest type (depth =  $28 \pm 32$  m, duration =  $185 \pm 146$  s), and bottom time occupied a significant fraction of the total dive time ( $120 \pm 120$  s). These dives are likely foraging dives. Lactation is energetically demanding for bearded seals, and females do forage while they have dependent pups.

**Résumé :** On trouvera ici les résultats d'une étude sur l'activité et le comportement de plongée de quatre femelles nourricières du Phoque barbu (*Erignathus barbatus*) durant la période de l'allaitement. Les femelles passaient en moyenne  $8 \pm 3\%$  ( $\pm$  écart type) de leur temps au repos sur les glaces et  $92 \pm 3\%$  dans l'eau. Environ la moitié de leur temps était consacré aux plongées. Au cours de l'étude, 15 077 plongées ont été enregistrées. La durée moyenne d'une plongée a été évaluée à  $2,0 \pm 2,3$  min et la profondeur moyenne des plongées, à  $17,2 \pm 22,5$  m (maximum 18,7 min et 288 m). Les phoques sortaient de l'eau  $3 \pm 2$  fois par jour (durée moyenne =  $44,0 \pm 98,1$  min). Dans l'ensemble, les phoques nageaient une distance moyenne de  $48,1 \pm 23,2$  km par jour. Nous avons pu reconnaître trois types de plongées au moyen d'une combinaison de méthodes d'analyses de groupements, méthode hiérarchique et méthode des *k* centroïdes, soit un groupement de plongées en V et deux groupements de plongées en U. Le type le plus commun rencontré était le type  $U_1$ ; les plongées de ce type étaient les plus profondes et les plus longues (profondeur moyenne =  $28 \pm 32$  m, durée moyenne =  $185 \pm 146$  s) et le temps passé au fond constituait une fraction appréciable du temps total de plongée ( $120 \pm 120$  s). La raison d'être de ces plongées est probablement la quête de nourriture. L'allaitement est une activité très exigeante pour les Phoques barbus et les femelles doivent chercher leur nourriture pendant qu'elles ont des petits non sevrés.

[Traduit par la Rédaction]

## Introduction

Bearded seals (*Erignathus barbatus*) have a circumpolar Arctic distribution. Because of their food habits, throughout their range they are generally found in areas of relatively shallow water (Lowry et al. 1980; Burns 1981). They are the largest northern phocid species; adult females normally weigh 300–400 kg (Stirling and Archibald 1979) and are somewhat heavier than adult males of the species. Bearded seals vary widely in density from region to region, but they can be described in a general sense as being nongregarious.

Bearded seals associate closely with drifting sea ice, and hence in some areas they make seasonal migrations that follow the annual movement patterns of sea ice (Burns 1981; Wiig and Isaksen 1995). During their reproductive period, which occurs in the spring, when the ice is both melting and breaking up, they aggregate to some degree in shallow, coastal areas where the loose pack ice that they use as a birthing platform is available (Kovacs et al. 1996). The peak period of birthing in the Svalbard area occurs during the first weeks of May (Lydersen et al. 1994).

Phocid seals have received considerable research attention with respect to patterns of maternal behaviour and lactation energetics because of the variation and the extremes in these features of their life history displayed within this group (Bonner 1984; Kovacs and Lavigne 1986; Oftedal et al. 1987; Bowen 1991; Lydersen and Kovacs 1999). It has been suggested that the duration of the lactation period among phocid seals depends on a variety of factors, including the stability of the breeding habitat. Species breeding in stable habitats, such as land or land-fast ice, have the longest lactation periods, while species breeding on unstable drifting ice have the shortest. Another interesting trait of phocid lactation is the reduced food intake or fasting by mothers during this

Received November 30, 1999. Accepted May 17, 2000.

**B.A. Krafft.** The University Courses on Svalbard (UNIS), N-9170 Svalbard, Norway, and Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway.

**C. Lydersen,<sup>1</sup> K.M. Kovacs, and I. Gjertz.** Norwegian Polar Institute, N-9296 Tromsø, Norway.

**T. Haug.** Norwegian Institute of Fisheries and Aquaculture, N-9005 Tromsø, Norway.

<sup>1</sup>Author to whom all correspondence should be addressed (e-mail: Lydersen@npolar.no).

energetically demanding period of the year. The basic trend among the group is that larger species are able to meet maternal needs and support milk production without feeding, while of the smaller species mothers must feed during lactation (Bowen 1991; Lydersen and Kovacs 1999). However, other features of the breeding environment also play a role in determining the nature of maternal patterns in phocid seals (Lydersen and Kovacs 1999).

Because female bearded seals are so large, and because they give birth in a very unstable habitat, one might hypothesise that this species would have a short lactation period during which females would cover the energetic costs of lactation without additional feeding. However, recent investigations suggest otherwise. Studies of growth in pups and satellite tracking of mother–pup pairs indicate that lactation may last in excess of 3 weeks in this species (Lydersen et al. 1996; Lydersen and Kovacs 1999; Gjertz et al. 2000). That bearded seal pups forage for themselves while they are still attended by their mothers and that mothers also do some foraging during this period have been confirmed by analysing the stomach contents of pups and females, respectively (Burns 1981; Lydersen et al. 1996). However, knowledge of the diving behaviour of bearded seal mothers during the nursing period is sparse and hence it is impossible to describe foraging effort during lactation. It is known that pups spend about 50% of their time in the water (Lydersen et al. 1994), and are usually accompanied by their mother during these periods. Direct observations of bearded seal mother–pup behaviour during the nursing period indicate that mothers spend additional time alone in water when their pups are hauled out on ice (Holsvik 1998). About half of this independent aquatic time is spent at the surface close to the pup, but the other 50% is spent submerged (Holsvik 1998). The purpose of the present study was to quantitatively document the aquatic behaviour of bearded seal mothers and explore the type(s) of dives they are performing during lactation. This was done using time–depth recorders (TDRs). This form of remote sensing provides undisturbed general activity budgets, as well as detailed records of diving activity.

## Material and methods

This study was conducted in the Kongsfjorden/Krossfjorden area (78°55'N, 12°30'E) on the west coast of Spitsbergen, Svalbard, Norway, during May of 1995 and 1996. Daily surveys were conducted using two small aluminium boats to search ice edges and free-floating pack-ice areas within the study area for bearded seal mother–pup pairs. Once a pair was located, attempts were made to capture the pup by means of a custom-built dip net (Hammill et al. 1994). The pup was then used as “bait” to attract the mother for capture. The first approach was to hold the pup on a nearby ice floe. Some mothers readily hauled out and came to their pups and were captured using a hand-held A-frame net. If a female was too wary to haul out, a floating net (25 m long, mesh size 200 mm) was set from the floe edge. The pup was held in the water in the dip net behind the tangle net adjacent to the female’s location. If the mother became entangled, she was brought up onto the surface of the floe and transferred into the A-frame net for restraint and weighing. Adult females were captured and instrumented as early as possible after giving birth.

All captured female bearded seals were weighed using a Dillon dynamometer (500 ± 1 kg) suspended from a portable quadpod on the ice. Pups were weighed in a pole net using a Salter spring scale

(100 ± 0.5 kg). Birth dates (age of pups) were back-calculated on the basis of a newborn body mass of 38 kg (K.M. Kovacs, unpublished data) and an average daily mass gain of 3.3 kg (Lydersen et al. 1994). All captured animals were also tagged using plastic cattle ear tags (Dalton Jumbo Tag, Dalton Supplies, Henley-on-Thames, Oxon, U.K.) through the webbing of each hind flipper. To facilitate recognition at a distance, they were marked with marine paint using individually recognisable patterns. A TDR (MK VI, Wildlife Computers, Redmond, Wash., U.S.A.) was glued onto the mid-dorsal region of females using quick-setting epoxy resin mixed with a small quantity of neon-coloured dye powder to further facilitate recognition. Depth and velocity were recorded at intervals of 10 s, with a depth resolution of 2 m. To locate the pair, a VHF transmitter (Holohill, Ottawa, Ont., Canada) was glued onto the fur in the middorsal region of the pup by means of the same quick-setting epoxy resin used for the TDRs. The handling procedures on the ice usually took less than 20 min for the pair. All animals were handled in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Recapture attempts commenced following a week of deployment. They proved to be very difficult. Although many of the pairs were relocated with relative ease, most females did not haul out and were much more difficult, or impossible, to recapture. A total of 11 lactating female bearded seals were captured and equipped with TDRs. However, only four instruments were retrieved, two in spring 1995 and two in spring 1996.

The data files from the TDRs were extracted using purpose-built software provided by the manufacturer (Dive Analysis, Zero Offset Correction, Minimum–Maximum–Mean, BINEX, and Merge; Wildlife Computers Inc.). A dive was defined as any excursion beneath the surface to ≥4 m depth, which is twice the resolution set for the TDRs. A depth of 4 m was chosen to avoid registering barely subsurface “floating” as diving activity. Female bearded seals spend a lot of time lying in the water next to floes on which their pups are hauled out, and sometimes sink beneath the surface during this activity. Haulout time was registered only if dry readings by the TDR lasted >1 min. One full minute was chosen to minimise the chance of recording floating, during which the TDR was sufficiently high out of the water for the salt-water switch to be dry, as though the animal were hauled out.

Swim-speed data were extracted separately from each dive record following the methods of Lesage et al. (1999). These data were then calibrated following the methods of Blackwell et al. (1999). Dives were split into descent, bottom, ascent, and surface phases following Lesage et al. (1999). Six parameters were calculated: (1) average swim speed at the surface (all activities occurring at <4 m); (2) average swim speed during descent phases; (3) average swim speed during ascent phases; (4) median swim speed during bottom phases; (5) maximum swim speed during bottom phases; and (6) average swim speed during bottom phases.

Swimming distance during descent or ascent phases ( $X_1$ ) was determined by

$$[1] \quad X_1 = V_{\text{hyp}} \times \frac{D_{\text{kat}}}{V_{\text{kat}}}$$

where  $V_{\text{hyp}}$  is average descent or ascent rate (m/s),  $D_{\text{kat}}$  is maximum dive depth (m), and  $V_{\text{kat}}$  is measured average vertical descent or ascent rate (m/s).

Swimming distance at the surface and during bottom phases ( $X_2$ ) was determined by

$$[2] \quad X_2 = T \times V$$

where  $T$  is surface or bottom time (s) and  $V$  is average swim speed (m/s) at the surface or during the bottom phase.

Angles of descent and ascent ( $X_3$ ) were determined by

$$[3] \quad X_3 = \left[ 90 - \cos^{-1} \left( \frac{D_{\text{kat}}}{X_1} \right) \right]$$

Dives with incomplete speed recordings were omitted from these analyses. This included dives involving descent or ascent phases that lasted <10 s (the interval between speed measurements) and dives during which the speed rotor was immobilised by debris or freezing.

Ten variables were selected for input to the dive-classification analyses. Five of them were selected following Schreer and Testa (1995, 1996): (1) bottom time divided by dive duration; (2) bottom time divided by maximum depth; (3) maximum depth divided by dive duration; (4) average calculated ascent rate divided by average calculated descent rate; and (5) average calculated descent rate divided by average calculated ascent rate. The last two variables were selected because they are useful for detecting skewed dives. Five additional parameters were selected following Lesage et al. (1999): (6) maximum dive depth; (7) dive duration; (8) bottom time; (9) median swim speed during bottom phases; and (10) maximum swimming velocity during the bottom phases. None of these variables were found to be normally distributed (using a Kolmogorov–Smirnov test with the option Lilliefors (SYSTAT 7.0, SPSS Inc., Wacker Drive, Chicago, Ill., U.S.A.)). Hence, all of the variables were log-transformed and then adjusted (+1) to eliminate problems associated with zero values (Jongman et al. 1995). Standardising the data (Zar 1996) further reduced discordances of all variables.

Multicollinearity was reduced by introducing the variables into a principal components analysis (PCA; SAS Institute Inc., Box 8000, Cary, N.C., U.S.A.). Only factors having eigenvalues >1 or account for at least 5% of the total variance were retained. The new uncorrelated variables from the PCA were used as input into multivariate clustering techniques (see Schreer et al. 1998; Lesage et al. 1999). Because hierarchical clustering does not tolerate large data sets, a sample of 1000 dives was randomly selected from the PCA results. This sample was introduced into a complete-linkage hierarchical-cluster analysis (SAS Institute Inc.). The TRIM option was used to delete 10% of the points with low estimated probability densities (SAS Institute Inc. 1994). The agglomeration coefficient was used to identify the appropriate number of clusters. The cluster level with the highest percent change in the agglomeration coefficient was chosen. The centroids from each cluster were determined and then used as seed points for further cluster analyses.

The appropriate number of clusters and the initial seed points from the complete-linkage hierarchical-cluster analysis were used to perform *k*-means cluster analysis. The complete data set, with the uncorrelated variables from the PCA, was used in this analysis because *k*-means cluster analysis tolerates large data sets and is not as sensitive to outliers as the hierarchical clustering method (SAS Institute Inc. 1994). The results from the *k*-means cluster analysis contained variables with information about the dives' cluster type. This information was merged with the variables taken directly from the TDRs and the information was computed for dives with complete velocity recordings. The resulting dive classes were labelled according to the "shapes" described by the dives' two-dimensional depth–time profiles (e.g., Hindell et al. 1991; Bengtson and Stewart 1992; Le Boeuf et al. 1992; Slip et al. 1994).

A parametric one-way ANOVA was run to explore patterns in diurnal behaviour and swimming distance. Because homogeneous variance and normal distribution of data are prerequisites for all parametric tests (Zar 1996), the data were tested for normality using a Kolmogorov–Smirnov test with the Lilliefors option (SYSTAT 7.0). The Lilliefors option automatically standardises the selected variables and tests whether the standardised versions follow a normal distribution. If the ANOVA resulted in significant differences by comparing different time blocks, a post hoc Tukey's

test (SYSTAT 7.0) was performed on the variables. Bivariate relationships between dive elements were explored using Spearman's rank correlation coefficient. Values are presented as the mean  $\pm$  SD and  $P \leq 0.05$  was set as the accepted probability value.

## Results

The 4 recovered TDRs were all deployed during May of either 1995 or 1996 (Table 1). The body masses of mothers and pups at the start of the study were  $328 \pm 54$  and  $44.5 \pm 8.4$  kg, respectively. The data records commenced when pups were 0–5 days old (Table 1). The TDR records for the four females yielded 1056 h of activity records (Table 2). During this time the females spent  $92 \pm 3\%$  of the total recorded time in water and  $8 \pm 3\%$  of the total recorded activity time hauled out on the ice (Fig. 1). When they were in the water,  $52 \pm 6\%$  of the time was spent diving, while  $48 \pm 6\%$  was spent at the surface.

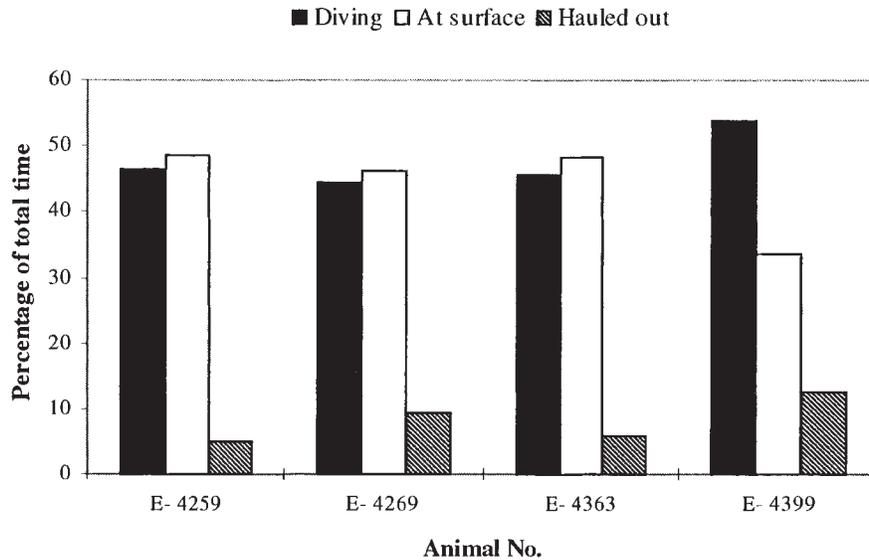
A total of 15 077 dives were recorded for the four females in this study (Table 2, Fig. 2). Most dives were shallow and of short duration, but all of the animals did some diving to >100 m (Table 2, Fig. 3). The maximum dive duration was 18.7 min and the maximum dive depth was 288 m (Table 2). The duration of intervals spent at the surface between dives was  $1.9 \pm 6.9$  min (Table 3). The longest recorded surface interval was 4.7 h. The seals hauled out  $3 \pm 2$  times per day (Table 3), and the duration of each haulout event was  $44.0 \pm 98.1$  min.

Female activities occurred according to a diel rhythm (Fig. 4). The females spent significantly less time diving between 09:00 and 21:00 than between 21:00 and 08:00 (one-way ANOVA,  $F = 44.27$ ,  $P < 0.001$ ). No significant differences according to time of day were found in the amount of time the females spent at the surface (one-way ANOVA,  $F = 0.79$ ,  $P = 0.377$ ). The animals spent more time hauled out on the ice between 09:00 and 21:00 than during the remaining hours in the 24-h cycle (one-way ANOVA,  $F = 9.12$ ,  $P = 0.003$ ).

The speed-recording unit on one TDR (female E-4399) failed a few days before the animal was recaptured. However, 95% of dives in her data set included swim-speed measurements and were included in the analysis. The distance swum by the females, including all phases of diving, was  $48.1 \pm 23.2$  km per day (Table 4). A significant difference was found between the four females in total distance swum per day (one-way ANOVA,  $F = 45.61$ ,  $P = 0.005$ ). Female E-4399 swam significantly longer distances per day than the other three animals (post hoc Tukey's test). Differences in distance swum during descent, bottom, ascent, and surface phases were found (one-way ANOVA,  $F = 6.06$ ,  $P = 0.001$ ). The distances swum during bottom phases over a 24-h cycle were, in total, longer than the distance swum during descent and surface phases over the same time period. The distance swum during ascent phases throughout the day did not differ significantly from that swum during either descent, bottom, or surface phases (post hoc Tukey's test) (Table 4).

The interrelationships between mean maximum depth and (i) dive duration, (ii) descent velocity, (iii) ascent velocity, (iv) angles of descent, and (v) ascent are shown in Table 5. All females increased their dive duration when they increased the depth of their dives. Weak correlations were found

**Fig. 1.** Activity budgets for four lactating bearded seals (*Erignathus barbatus*) from Svalbard in spring of 1995 and 1996.



**Table 1.** Time of capture, duration of TDR deployment, mass of female bearded seals (*Erignathus barbatus*) and their pups at first capture, and estimated age of pups.

Female ID No.	Year of capture	Date of first capture	Duration of TDR record (days)	Mass of female at first capture (kg)	Mass of pup at first capture (kg)	Estimated age of pup (days)
E-4259	1995	May 7	7.8	380	38	0
E-4269	1995	May 10	7.9	266	56.0	5
E-4363	1996	May 8	18.6	300	38.5	0
E-4399	1996	May 18	9.5	365	45.5	2
Mean ± SD			11±5	328±54	44.5±8.4	2±3

**Note:** The data were collected on Svalbard during spring of 1995 and 1996.

**Table 2.** Dive durations and depths recorded from four lactating bearded seals from Svalbard in spring of 1995 and 1996.

Female ID No.	Total recorded activity time (h)	No. of dives	Dive duration (min)		Depth (m)	
			Mean	Max.	Mean	Max.
E-4259	189	2 995	1.8±1.9	9.2	17.2±23.9	176
E-4269	190	3 308	1.5±1.5	9.7	13.4±13.7	110
E-4363	447	6 080	2.0±2.1	16.5	17.7±22.4	162
E-4399	230	2 694	2.7±3.4	18.7	20.7±28.2	288
Total	1056	15 077	2.0±2.3		17.2±22.5	

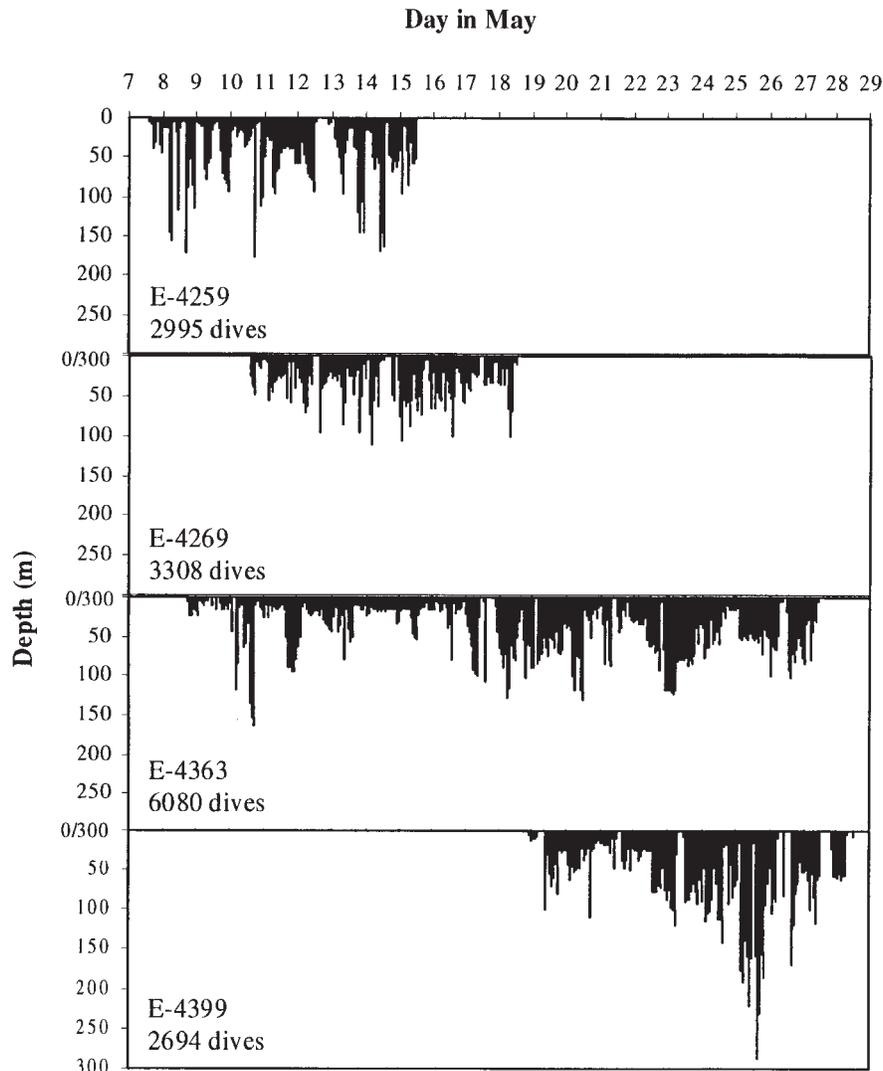
between dive depth and descent velocity and between dive depth and ascent velocity. Modest correlations were found for the relationships between dive depth and angles of descent and ascent for two females (E-4259 and E-4363). The remaining two animals exhibited only weak correlations between these parameters (Table 5).

Dive-classification analyses were conducted on 14 783 dives that were performed to depths >4 m. A PCA run on the 10 selected variables suggested that five factors had sufficient explanatory power to be retained for each of the four females (Table 6). During the hierarchical clustering procedure the

percent change in the agglomeration coefficient from one classification level to the next indicated that three dive cluster types (V, U<sub>1</sub>, and U<sub>2</sub>) were present for two females (Table 7). Only two cluster types (V and U<sub>1</sub>) were present for each of the remaining two females, E-4269 and E-4363 (Table 7).

V-shaped dives were utilised by all four animals. The percentage of dives in this dive category ranged from 27 to 37% among the four females. The percentage of time spent performing dives of this type ranged from 5 to 12% (Fig. 5). These dives were shallow and of short dive duration and included little or no bottom time. Slow swimming speeds

**Fig. 2.** Diving records from four lactating bearded seals from Svalbard in spring of 1995 (E-4259, E-4269) and 1996 (E-4363, E-4399).



were displayed throughout V dives. The angles of ascent and descent were gentle and symmetrical. The time the animals spent at the surface after such dives was  $3 \pm 9$  min. The velocity of swimming at the surface after V dives was  $0.7 \pm 0.4$  m/s (Table 7).

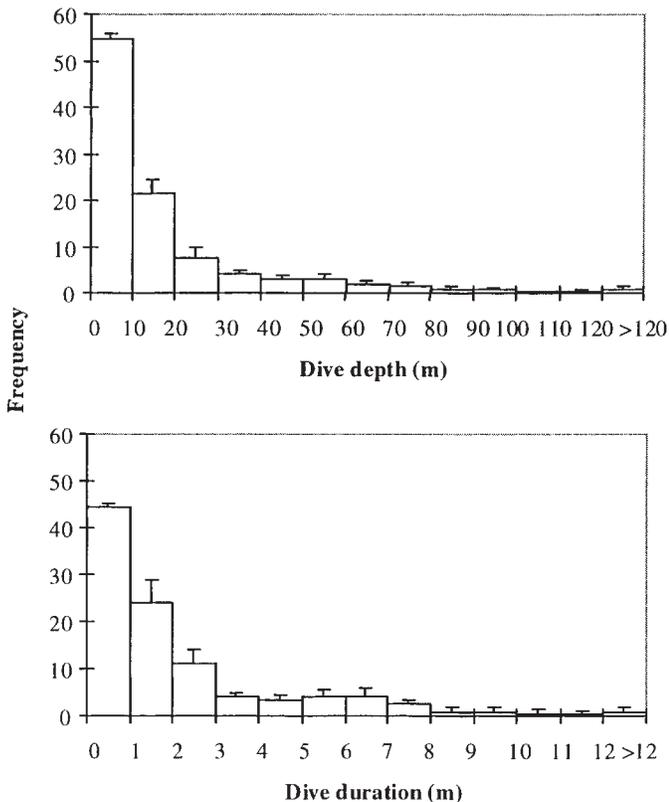
U-shaped dives were characterised by long bottom times (compared with the total duration of dives) and long dive durations, relatively speaking. They had few wiggles, but some were present. Two dive types were recognised within this category. All four females performed  $U_1$  dives. This dive type represents 15–73% of the dives performed by individual females. The four females' diving records showed that time spent doing these dives ranged from 47 to 92% (Fig. 5). These dives were deep and long compared with the other dive types. The mean descent and ascent velocities in this dive type were more rapid than for the other two dive categories. However, the mean bottom velocity remained slow. Bursts of speed occurred during the bottom phases of these dives and average maximum velocities were higher than for the other dive categories. A few wiggles appeared in this dive category for all four females. The mean descent and as-

cent angles were steep in  $U_1$  dives and lightly skewed to the right. After completing  $U_1$  dives the females spent  $3 \pm 10$  min at the surface and the swimming velocity at the surface was low (Table 7).

$U_2$  dives were performed by only two of the females. The percentage of dives of this type was 52% for female E-4259 and 19% for female E-4399. These dives represented 41% of female E-4259's diving time and 10% of female E-4399's diving time (Fig. 5). Like V dives, these dives were shallow and of short duration. Bottom time was intermediate compared with the other two dive types. The mean descent, bottom, and ascent velocities as well as the mean maximum velocity were slow. Wiggles appeared infrequently during the bottom phase in female E-4399's records. These dives were slightly skewed to the right. The post- $U_2$ -dive surface interval was  $2 \pm 10$  min and the velocity at the surface following these dives was slow (Table 7).

No diel patterns were observed in the frequency of use of either V dives (one-way ANOVA,  $F = 0.47$ ,  $P = 0.911$ ) or U dives (both  $U_1$  and  $U_2$ ; one-way ANOVA,  $F = 1.94$ ,  $P = 0.659$ ).

**Fig. 3.** Frequency distributions of dive depths and durations (vertical lines represent SD) of dives ( $N = 15\,077$ ) made by four lactating bearded seals from Svalbard in spring of 1995 and 1996.



## Discussion

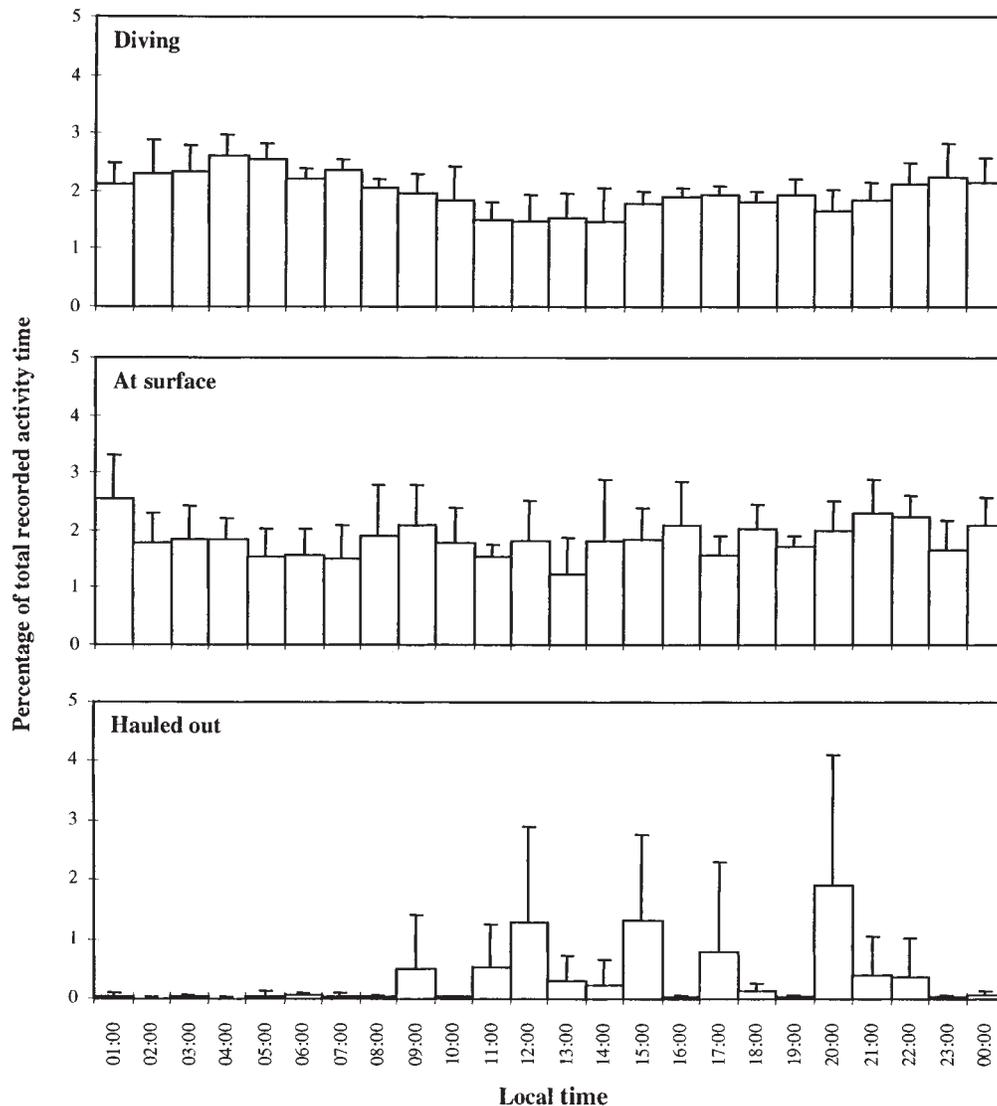
In this study a total of ~44 days (1056 h) of bearded seal maternal activity, including over 15 000 dives, was documented. Unfortunately, these records were collected from only 4 individuals out of the 11 instrumented, despite the fact that a great deal of effort was made to locate and recapture all of the animals. Another shortcoming in the data is that the duration of the TDR records for individual seals was only  $11 \pm 5$  days, although the lactation period of bearded seals is estimated to be approximately 24 days (Lydersen and Kovacs 1999). However, the extreme similarity in activity budgets among the four seals (Fig. 1) suggests that the data are likely representative of the maternal behaviour of this species, at least in this area.

The females in this study were found to spend only 8% of their time hauled out on the ice. The only comparative information for this species comes from an observational study which suggests that bearded seal mothers spend more than 30% of their time hauled out on the ice together with their pup (Holsvik 1998). However, Holsvik noted that her study might have been biased toward overrepresenting haulout time because observation periods only lasted 3 h, and pairs were more easily found if mothers were hauled out at the time of their discovery. The remote-sensing (TDR) data confirm Holsvik's suggestion of bias. Activity budgets for lactating females of other ice-breeding northern phocids document that they spend 20–100% of their time on the ice (Lydersen

and Kovacs 1999). One reason for this large variation is the difference in the degree to which females of the different species feed during lactation. For example, hooded seal mothers spend the entire 4-day lactation period hauled out (Bowen et al. 1985; Kovacs and Lavigne 1992; Lydersen et al. 1997), and consequently fast throughout this period, while ringed seals spend less than 20% of their time hauled out, and feed significantly during the lactation period (Lydersen 1995). One would assume that bearded seal mothers feed during some of the 90+% of the time that they spend in the water (see below). Other factors that may contribute to the small amount of time bearded seal mothers spend on the ice are harsh weather conditions and surface predation. The data from this study can be interpreted to support the idea that mothers might adjust their behaviour according to meteorological conditions. They did haul out significantly more during the day (09:00–20:00) than at night (21:00–08:00). But in other marine-mammal studies this sort of diurnal activity pattern has been attributed to tidal cycles and the diurnal behaviour of prey species, in addition to diel patterns of solar radiation (e.g., Finley 1979; Thomas and DeMaster 1983; Kovacs 1987; Le Boeuf et al. 1988; Feldkamp et al. 1989; Bengtson and Stewart 1992; Watts 1996). Polar bear (*Ursus maritimus*) predation may be a factor that influences females' haulout behaviour. It could be that the large females minimise their time on the ice to make the mother-pup pair less conspicuous to predators.

The female bearded seals in this study spent a total of 92% of the time in the water. This time was divided almost equally into time spent at the surface and time spent submerged. If the sole purpose of aquatic activity were feeding, females would be expected to spend a much greater proportion of their time diving. However, much of the time spent in the water by female bearded seals is dedicated to maternal care. Bearded seal pups spend about half of their time swimming and diving (Lydersen et al. 1994), and when doing so they are almost always accompanied by their mother. Additionally, mothers spend considerable amounts of time in the water resting beside the floes on which pups are hauled out (Holsvik 1998). The small fraction of the day (8%) spent hauled out by mothers must be dedicated primarily to nursing behaviour; the data on females' haulout behaviour in this study suggest that the pups are nursed about 3 times per day (Table 3).

It was not surprising to find that most dives performed by the bearded seal mothers in the present study were shallow and of short duration. Bearded seals are known to be shallow divers (Burns 1981), and most pinniped diving studies show a clear correlation between depth and duration of diving (e.g., Le Boeuf et al. 1988; Boyd and Arnborn 1991; Lydersen and Hammill 1993; McCafferty et al. 1998). Additionally, the water in the study area is quite shallow. Maximum water depths in the outer part of the fjords is ~330 m and depths are generally <100 m in the inner-basin areas. Another important factor affecting diving performance is that when the pup is in the water, which is about 50% of each day (Lydersen et al. 1994), the mother accompanies it. Thus, the diving performance of the mothers during these periods is likely constrained by the pups' aquatic abilities. All these factors lead to bearded seal mothers diving in a rather modest

**Fig. 4.** Diurnal variation in activities (vertical lines represent SD) of four lactating bearded seals from Svalbard in spring of 1995 and 1996.**Table 3.** Durations of surface and haulout intervals recorded from four lactating bearded seals from Svalbard in spring of 1995 and 1996.

Female ID No.	Duration of surface intervals (min) <sup>a</sup>	Max. duration of surface intervals (h)	Duration of haulout periods (min) <sup>a</sup>	Max. duration of haulout periods (h)	Time elapsed between haulout periods (h) <sup>a</sup>	No. of haulouts per 24 h
E-4259	1.8±6.5	2.7	42.3±125.8	7.7	14.2±13.8	2±1
E-4269	1.6±4.6	2.1	107.8±132.6	5.8	18.4±10.7	1±1
E-4363	2.1±7.3	2.9	21.6±56.4	6.1	6.2±5.6	4±3
E-4399	1.7±8.7	4.7	107.3±152.7	8.2	14.4±13.4	2±1
Mean ± SD	1.9±6.9		44.0±98.1		9.2±9.6	3±2

<sup>a</sup>Values are given as the mean ± SD.

fashion compared with predicted maximum capabilities based on their body size.

Three distinct dive types were identified from the TDR recordings in the present study (Table 7). A small proportion of the recorded dive time was spent in V-shaped dives, while the largest fraction of the time spent submerged was devoted

to U-shaped dives. Many studies have discussed the possible functions of V- and U-shaped dives (e.g., Hindell et al. 1991; Bengtson and Stewart 1992; Le Boeuf et al. 1992; Slip et al. 1994). V dives are usually thought to be associated with exploring the environment for possible foraging areas or with transit (Williams and Kooyman 1985; Thompson et al.

**Table 4.** Total mean distances swum per 24 h and distances swum while descending, during the bottom phase, ascending, and at the surface for four lactating bearded seals from Svalbard in spring of 1995 and 1996.

Female ID No.	Total distance swum in 24 h (km)	Total distance (km) swum in 24 h during:			
		descent phase	bottom phase	ascent phase	surface phase
E-4259	39.8±17.4	8.7±4.9	13.6±4.8	10.1±5.0	7.4±3.9
E-4269	43.9±12.6	10.9±4.1	10.1±3.2	12.3±3.8	10.5±2.4
E-4363	42.0±16.6	8.1±3.8	13.3±7.4	9.5±4.8	11.1±3.2
E-4399	70.1±32.7	14.1±7.3	27.3±13.6	19.4±12.3	9.3±4.3
Total	48.1±23.2	10.0±5.3	15.9±10.2	12.2±7.9	10.0±3.6

**Table 5.** Spearman’s rank correlation coefficients ( $r_s$ ) between dive elements: maximum dive depth versus dive duration, descent velocity, ascent velocity, and angles of descent and ascent for four lactating bearded seals from Svalbard in May of 1995 and 1996.

	Female ID No.	$r_s$
Depth vs. dive duration	E-4259	0.88
	E-4269	0.81
	E-4363	0.86
	E-4399	0.87
Depth vs. descent velocity	E-4259	0.27
	E-4269	0.21
	E-4363	0.26
	E-4399	0.24
Depth vs. ascent velocity	E-4259	0.14
	E-4269	0.07
	E-4363	0.32
	E-4399	0.24
Depth vs. angle of descent	E-4259	0.53
	E-4269	0.31
	E-4363	0.59
	E-4399	-0.1
Depth vs. angle of ascent	E-4259	0.51
	E-4269	0.38
	E-4363	0.49
	E-4399	0.11

1991). U dives are usually considered to be foraging dives, especially for benthic feeders (Thompson et al. 1991; Slip et al. 1994; Schreer and Kovacs 1997). By far the most common dive type performed by the bearded seals in this study was the  $U_1$  dive, which was characterised as a deep and relatively long dive with a long bottom time and relatively steep and rapid ascent and descent rates (Table 7). This dive profile exhibits all the characteristics of a foraging dive.  $U_2$  dives, which are shallower and shorter than  $U_1$  dives, may occur when the animals feed in shallower areas. The bottom “burst segments” (see “maximum bottom velocity” in Table 7), which occur during U-shaped dives, are likely associated with the pursuit of prey. The few wiggles that occurred during the bottom phase of some U dives might reflect seals swimming close to an uneven seabed, or chasing prey that swim vertically in an effort to escape. However, speed bursts

and wiggles were rare in the dive records in this study, which might indicate that the bearded seals were feeding on prey that were sedentary or relatively slow moving and probably easy to capture. A study of the diet of bearded seals in this area has shown that much of their food consists of benthic invertebrate prey organisms or fish that tend to be found close to the bottom (Hjelset et al. 1999). A nursing female bearded seal that died during drugging in a study by Lydersen et al. (1996) had a stomach full of a variety of benthic invertebrates. Thus, both indirect evidence (dive profiles) and direct evidence (stomach contents) show that bearded seal mothers feed during lactation. The energy expenditure required to produce a weaned pup for female bearded seals is extremely high (Lydersen and Kovacs 1999). Few data exist on energy losses by females during this period; however, based on mass losses of recaptured animals in the present study, females lose about 4.5 kg daily. This rate of mass loss does not account for the combined energy expenditure of lactation and the female’s own metabolism (Lydersen and Kovacs 1999).

Bearded seal mothers swim a distance of  $48.1 \pm 23.2$  km per day. This distance includes not only surface swimming but movements in all dimensions, i.e., during the ascent, descent, and bottom phases of dives. Only 10 km, on average, is swum at the surface daily, although about half of the seals’ time is spent here. This is because a lot of time at the surface is spent attending the pup (Holsvik 1998), and because mother–pup pairs tend to remain in the same general area for some days at a time (Hammill et al. 1994).

One would expect bearded seals to take the shortest route from the surface to the bottom during foraging sessions, spending the largest portion of the dive at the bottom, where they find food. The seals in this study did swim for significantly longer distances in the bottom phases of dives than in the descent phases (Table 4). However, the distance swum during ascent phases did not differ significantly from that swum during any of the other phases. This indicates that the animals do not necessarily take the shortest route back to the surface. One could expect, given the short duration and shallowness of dives, that the seals could spend a much larger fraction of their diving in the bottom phase than was recorded. Again this is probably due to the fact that a lot of the diving is done with the pup, and these dives reflect the diving capacity of the offspring rather than of the mother.

This study has shown that bearded seal mothers spend most of the time (92%) in the water during the lactation period. The short periods of the day spent hauled out on the

**Table 6.** Principal component factors identified using 10 selected dive characteristics measured from TDRs deployed on four lactating bearded seals in the Svalbard area during May of 1995 and 1996.

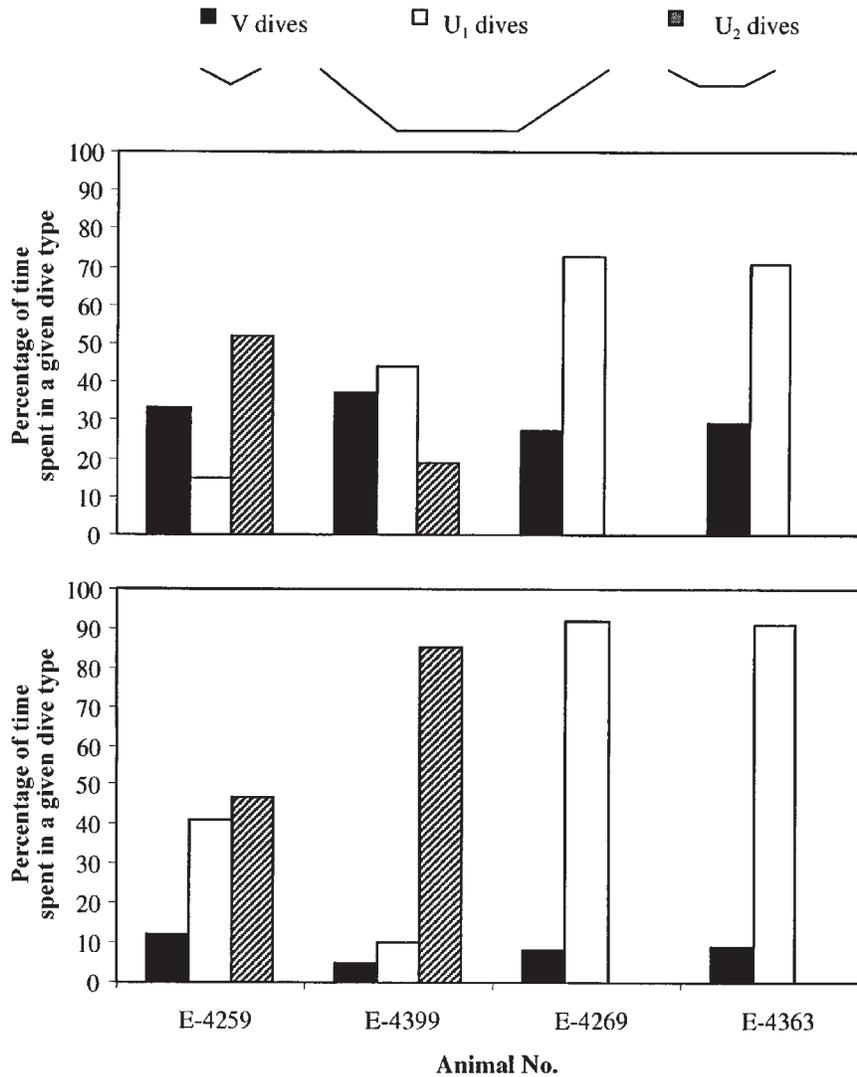
PCA factor	Female E-4259			Female E-4269			Female E-4363			Female E-4399		
	Eigen-value	% of variance explained	Cumulative % of variance	Eigen-value	% of variance explained	Cumulative % of variance	Eigen-value	% of variance explained	Cumulative % of variance	Eigen-value	% of variance explained	Cumulative % of variance
1	<b>3.61</b>	<b>36.1</b>	36.1	<b>4.13</b>	<b>41.3</b>	41.3	<b>4.31</b>	<b>43.1</b>	43.1	<b>4.35</b>	<b>43.5</b>	43.5
2	<b>1.73</b>	<b>17.3</b>	53.4	<b>1.91</b>	<b>19.1</b>	60.4	<b>1.97</b>	<b>19.7</b>	62.8	<b>2.05</b>	<b>20.5</b>	64
3	<b>1.61</b>	<b>16.1</b>	69.5	<b>1.72</b>	<b>17.2</b>	77.6	<b>1.77</b>	<b>17.7</b>	80.5	<b>1.73</b>	<b>17.3</b>	81.3
4	<b>1.47</b>	<b>14.7</b>	84.2	<b>1.28</b>	<b>12.8</b>	90.4	<b>1.06</b>	<b>10.6</b>	91.1	<b>1.05</b>	<b>10.5</b>	91.8
5	0.60	<b>6.0</b>	<b>90.2</b>	0.57	<b>5.7</b>	<b>96.1</b>	0.54	<b>5.4</b>	<b>96.5</b>	0.52	<b>5.2</b>	<b>97.0</b>
6	0.41	4.1	94.3	0.15	1.5	97.6	0.14	1.4	97.9	0.13	1.3	98.3
7	0.25	2.5	96.8	0.13	1.3	98.9	0.13	1.3	99.2	0.09	0.9	99.2
8	0.16	1.6	98.4	0.07	0.7	99.6	0.06	0.6	99.8	0.06	0.6	99.8
9	0.14	1.4	99.8	0.03	0.3	99.9	0.02	0.2	100	0.02	0.2	100
10	0.01	0.2	100	0	0.1	100	0	0	100	0	0	100

**Note:** Principal component factors are as follows: 1, bottom time divided by dive duration; 2, bottom time divided by maximum depth; 3, maximum depth divided by dive duration; 4, average calculated ascent rate divided by average calculated descent rate; 5, average calculated descent rate divided by average calculated ascent rate; 6, maximum dive depth; 7, dive duration; 8, bottom time; 9, median swim speed during bottom phases; and 10, maximum swimming velocity during bottom phases. Values in boldface type represent the appropriate number of factors to extract (i.e., eigenvalue >1 or variance explained >5%), and the cumulative variance explained by these factors.

**Table 7.** Cluster types, proportions (%), and characteristics (mean  $\pm$  SD) of dives (to >4 m depth; types V, U<sub>1</sub>, and U<sub>2</sub>) analysed with a combination of hierarchical and a hard *k*-means cluster analysis of the dive records of four nursing female bearded seals from Svalbard in May of 1995 and 1996.

Cluster	Female E-4259			Female E-4399			Female 4269		Female E-4363		All females		
	V	U <sub>1</sub>	U <sub>2</sub>	V	U <sub>1</sub>	U <sub>2</sub>	V	U <sub>1</sub>	V	U <sub>1</sub>	V	U <sub>2</sub>	U <sub>1</sub>
Number of dives	988	450	1557	888	1056	456	893	2415	1763	4317	4532	2013	8238
Maximum depth (m)	9 $\pm$ 12	59 $\pm$ 37	11 $\pm$ 8	9 $\pm$ 8	37 $\pm$ 36	6 $\pm$ 3	6 $\pm$ 5	16 $\pm$ 15	8 $\pm$ 9	22 $\pm$ 25	8 $\pm$ 8	7 $\pm$ 5	28 $\pm$ 32
Duration (s)	37 $\pm$ 37	352 $\pm$ 86	82 $\pm$ 46	44 $\pm$ 40	317 $\pm$ 218	43 $\pm$ 40	27 $\pm$ 27	116 $\pm$ 97	34 $\pm$ 40	158 $\pm$ 134	32 $\pm$ 35	55 $\pm$ 43	185 $\pm$ 146
Bottom time (s)	8 $\pm$ 14	257 $\pm$ 80	35 $\pm$ 29	6 $\pm$ 8	190 $\pm$ 173	19 $\pm$ 22	0 $\pm$ 1	57 $\pm$ 73	1 $\pm$ 4	95 $\pm$ 105	3 $\pm$ 8	24 $\pm$ 26	120 $\pm$ 120
Descent velocity (m/s)	0.9 $\pm$ 0.4	1.2 $\pm$ 0.2	1.2 $\pm$ 0.3	1.8 $\pm$ 0.6	1.6 $\pm$ 0.4	0.7 $\pm$ 0.4	1.2 $\pm$ 0.5	1.3 $\pm$ 0.5	1.0 $\pm$ 0.4	1.1 $\pm$ 0.4	1.0 $\pm$ 0.5	0.9 $\pm$ 0.4	1.3 $\pm$ 0.4
Bottom velocity (m/s)	0.9 $\pm$ 0.4	0.8 $\pm$ 0.2	1.4 $\pm$ 0.4	2.1 $\pm$ 0.6	1.4 $\pm$ 0.7	0.7 $\pm$ 0.4	1.4 $\pm$ 0.6	1.3 $\pm$ 0.6	1.1 $\pm$ 0.5	1.0 $\pm$ 0.5	1.1 $\pm$ 0.5	1.1 $\pm$ 0.5	1.1 $\pm$ 0.6
Maximum bottom velocity (m/s)	1.0 $\pm$ 0.4	1.7 $\pm$ 0.3	1.6 $\pm$ 0.3	2.3 $\pm$ 0.7	2.2 $\pm$ 0.6	0.9 $\pm$ 0.5	1.5 $\pm$ 0.6	1.7 $\pm$ 0.6	1.3 $\pm$ 0.6	1.5 $\pm$ 0.5	1.2 $\pm$ 0.6	1.3 $\pm$ 0.5	1.7 $\pm$ 0.5
Number of wiggles	0.0 $\pm$ 0.0	0.1 $\pm$ 0.4	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.2 $\pm$ 0.7	0.0 $\pm$ 0.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.2
Ascent velocity (m/s)	0.9 $\pm$ 0.4	1.4 $\pm$ 0.3	1.4 $\pm$ 0.4	2.0 $\pm$ 0.6	1.7 $\pm$ 0.5	0.6 $\pm$ 0.4	1.4 $\pm$ 0.6	1.4 $\pm$ 0.5	1.2 $\pm$ 0.5	1.3 $\pm$ 0.5	1.1 $\pm$ 0.6	1.2 $\pm$ 0.5	1.4 $\pm$ 0.5
Angle of descent (deg.)	36 $\pm$ 17	59 $\pm$ 13	24 $\pm$ 15	17 $\pm$ 13	27 $\pm$ 16	26 $\pm$ 17	23 $\pm$ 16	27 $\pm$ 18	28 $\pm$ 17	36 $\pm$ 20	29 $\pm$ 18	26 $\pm$ 16	36 $\pm$ 20
Angle of ascent (deg.)	37 $\pm$ 19	49 $\pm$ 15	21 $\pm$ 15	16 $\pm$ 11	23 $\pm$ 15	31 $\pm$ 14	19 $\pm$ 14	25 $\pm$ 17	25 $\pm$ 16	34 $\pm$ 19	27 $\pm$ 19	21 $\pm$ 15	33 $\pm$ 18
Postdive surface interval (min)	3 $\pm$ 11	2 $\pm$ 1	1 $\pm$ 1	1 $\pm$ 2	2 $\pm$ 10	2 $\pm$ 13	2 $\pm$ 5	1 $\pm$ 4	2 $\pm$ 8	2 $\pm$ 7	3 $\pm$ 9	2 $\pm$ 10	3 $\pm$ 10
Postdive surface velocity (m/s)	0.6 $\pm$ 0.3	0.4 $\pm$ 0.2	0.7 $\pm$ 0.3	1.0 $\pm$ 0.5	0.6 $\pm$ 0.4	0.5 $\pm$ 0.3	0.8 $\pm$ 0.4	0.7 $\pm$ 0.3	0.7 $\pm$ 0.3	0.6 $\pm$ 0.2	0.7 $\pm$ 0.4	0.6 $\pm$ 0.3	0.6 $\pm$ 0.3

**Fig. 5.** Percentages of dives and percentages of time spent in a given type of dive for four lactating bearded seals. The data were collected on Svalbard during spring of 1995 and 1996. The schematic diagrams at the top represent two-dimensional (time versus depth) plots (“shapes”) of the three classes of dives found in this study.



ice are likely dominated by nursing activity. The lactation period for bearded seals is energetically demanding, and both indirect evidence (dive profiles) and direct evidence (stomach contents) show that bearded seal mothers feed during this period. The time the mothers spend in the water is separated into almost equal fractions spent at the surface and submerged, which reflects a compromise between feeding and attending the pup.

### Acknowledgements

Financial support, equipment, and working facilities were provided by The Norwegian College of Fishery Science at the University of Tromsø, UNIS, The Norwegian Polar Institute, and The Norwegian Research Council. In addition, student grants were awarded to B.A.K. by The Roald Amundsen Centre for Arctic Research and The Polar Research Committee. Thanks are also given to the inhabitants of Ny Ålesund for all their logistic help with this project. Dr. Veron-

ique Lesage of the Department of Fisheries and Oceans, Canada, kindly provided advice on data analyses and also provided custom-developed programming software. Dr. Susanna Blackwell, University of California, Santa Cruz, U.S.A., provided help to calibrate the velocity recordings. Are Edvardsen (The Norwegian College of Fishery Science) wrote software that facilitated data input for swim-speed calibrations.

### References

- Bengtson, J.L., and Stewart, B.S. 1992. Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. *Polar Biol.* **12**: 635–644.
- Blackwell, S.B., Haverl, C.A., Le Boeuf, B.J., and Costa, D.P. 1999. A method for calibrating swim-speed recorders. *Mar. Mamm. Sci.* **15**: 894–905.
- Bonner, W.N. 1984. Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symp. Zool. Soc. Lond. No. 51*. pp. 253–272.

- Bowen, W.D. 1991. Behavioural ecology of pinniped neonates. In Behaviour of pinnipeds. Edited by D. Renouf. Chapman and Hall, London. pp. 66–127.
- Bowen, W.D., Oftedal, O.T., and Boness, D.J. 1985. Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. Can. J. Zool. **63**: 2841–2846.
- Boyd, I.L., and Arnborg, T. 1991. Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. Polar Biol. **11**: 259–266.
- Burns, J.J. 1981. Bearded seal *Erignathus barbatus* Erxleben, 1777. In Handbook of marine mammals. Vol. 2. Seals. Edited by S.H. Ridgway and R.J. Harrison. Academic Press, London. pp. 145–170.
- Feldkamp, S.D., DeLong, R.L., and Antonelis, G.A. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Can. J. Zool. **67**: 872–883.
- Finley, K.J. 1979. Haul-out behaviour and densities of ringed seals (*Phoca hispida*) in the Barrow Strait area, N.W.T. Can. J. Zool. **57**: 1985–1997.
- Gjertz, I., Kovacs, K.M., Lydersen, C., and Wiig, Ø. 2000. Movements and diving of bearded seals (*Erignathus barbatus*) mothers and pups during lactation and post-weaning. Polar Biol. In press.
- Hammill, M.O., Kovacs, K.M., and Lydersen, C. 1994. Local movements by nursing bearded seal (*Erignathus barbatus*) pups in Kongsfjorden, Svalbard. Polar Biol. **14**: 569–570.
- Hindell, M.A., Slip, D.J., and Burton, H.R. 1991. The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). Aust. J. Zool. **39**: 595–619.
- Hjelset, A.M., Andersen, M., Gjertz, I., Lydersen, C., and 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. Cand. Scient. thesis, Norwegian University of Science and Technology, Trondheim.
- Jongman, R.H.G., Ter Braak, C.J.F., and Van Tongeren, O.F.R. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.
- Kovacs, K.M. 1987. Maternal behaviour and early behavioural ontogeny of harp seals *Phoca groenlandica*. Anim. Behav. **35**: 844–855.
- Kovacs, K.M., and Lavigne, D.M. 1986. Maternal investment and neonatal growth in phocid seals. J. Anim. Ecol. **55**: 1035–1051.
- Kovacs, K.M., and Lavigne, D.M. 1992. Mass-transfer efficiency between hooded seal (*Cystophora cristata*) mothers and their pups in the Gulf of St. Lawrence. Can. J. Zool. **70**: 1315–1320.
- Kovacs, K.M., Lydersen, C., and Gjertz, I. 1996. Birth-site characteristics and prenatal molting in bearded seals (*Erignathus barbatus*). J. Mammal. **77**: 1085–1091.
- Le Boeuf, B.J., Costa, D.P., Huntley, A.C., and Feldkamp, S.D. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. Can. J. Zool. **66**: 446–458.
- Le Boeuf, B.J., Naito, Y., Asaga, T., Crocker, D., and Costa, D.P. 1992. Swim speed in a female northern elephant seal: metabolic and foraging implications. Can. J. Zool. **70**: 786–795.
- Lesage, V., Hammill, M.O., and Kovacs, K.M. 1999. Functional classification of harbour seal (*Phoca vitulina*) dives using depth profiles, swimming velocity and an index of foraging success. Can. J. Zool. **77**: 74–87.
- Lowry, L.F., Frost, K.J., and Burns, J.J. 1980. Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walrus. Arctic, **33**: 330–342.
- Lydersen, C. 1995. Energetics of pregnancy, lactation and neonatal development in ringed seals (*Phoca hispida*). In Whales, seals, fish and man. Edited by A.S. Blix, L. Walløe, and Ø. Ulltang. Elsevier Science Publishers B.V., Amsterdam. pp. 319–327.
- Lydersen, C., and Hammill, M.O. 1993. Diving in ringed seal (*Phoca hispida*) pups during the nursing period. Can. J. Zool. **71**: 991–996.
- Lydersen, C., and Kovacs, K.M. 1999. Behaviour and energetics of ice-breeding North Atlantic phocid seals during the lactation period. Mar. Ecol. Progr. Ser. **187**: 265–281.
- Lydersen, C., Hammill, M.O., and Kovacs, K.M. 1994. Diving activity in nursing bearded seal (*Erignathus barbatus*) pups. Can. J. Zool. **72**: 96–103.
- Lydersen, C., Kovacs, K.M., Hammill, M.O., and Gjertz, I. 1996. Energy intake and utilisation by nursing bearded seal (*Erignathus barbatus*) pups from Svalbard, Norway. J. Comp. Physiol. B, **166**: 405–411.
- Lydersen, C., Kovacs, K.M., and Hammill, M.O. 1997. Energetics during nursing and early postweaning fasting in hooded seal (*Cystophora cristata*) pups from the Gulf of St. Lawrence, Canada. J. Comp. Physiol. B, **167**: 81–88.
- McCafferty, D.J., Boyd, I.L., and Taylor, R.I. 1998. Diving behavior of Antarctic fur seal (*Arctocephalus gazella*) pups. Can. J. Zool. **76**: 513–520.
- Oftedal, O.T., Boness, D.J., and Tedman, R.A. 1987. The behaviour, physiology, and anatomy of lactation in the pinnipedia. In Current mammalogy. Vol. 1. Edited by H.H. Genoways. Plenum Press, New York. pp. 175–245.
- SAS institute Inc. 1994. SAS/STAT. User's guide. Version 6. Vol. 1. 4th ed. SAS institute Inc., Cary, N.C.
- Schreer, J.F., and Kovacs, K.M. 1997. Allometry of diving capacity in air-breathing vertebrates. Can. J. Zool. **75**: 339–358.
- Schreer, J.F., and Testa, J.W. 1995. Statistical classification of diving behavior. Mar. Mamm. Sci. **11**: 85–93.
- Schreer, J.F., and Testa, J.W. 1996. Classification of Weddell seal diving behavior. Mar. Mamm. Sci. **12**: 227–250.
- Schreer, J.F., O'Hara Hines, R.J., and Kovacs, K.M. 1998. Classification of dive profiles: a comparison of statistical clustering techniques and unsupervised artificial neural networks. J. Agr. Biol. Environ. Stat. **3**: 383–404.
- Slip, D.J., Hindell, M.A., and Burton, H.R. 1994. Diving behavior of southern elephant seals from Macquarie Island: an overview. In Elephant seals: population ecology, behavior, and physiology. Edited by B.J. Le Boef and R.M. Laws. University of California Press, Berkeley. pp. 253–270.
- Stirling, I., and Archibald, R. 1979. Bearded seal. FAO Fish Ser. **5**: 83–85.
- Thomas, J.A., and DeMaster, D.P. 1983. Diel haul-out patterns of Weddell seal (*Leptonychotes weddelli*) females and their pups. Can. J. Zool. **61**: 2084–2086.
- Thompson, D., Hammond, P.S., Nicholas, K.S., and Fedak, M.A. 1991. Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). J. Zool. (Lond.), **224**: 223–232.
- Watts, P. 1996. The diel hauling-out cycle of harbour seals in an open marine environment: correlates and constraints. J. Zool. (Lond.), **240**: 175–200.
- Wiig, Ø., and Isaksen, K. 1995. Seasonal distribution of harbour seals, bearded seals, white whales and polar bears in the Barents Sea. Norsk Polarinst. Medd. **136**: 47–59.
- Williams, T.M., and Kooyman, G.L. 1985. Swimming performance and hydrodynamic characteristics of harbor seals, *Phoca vitulina*. Physiol. Zool. **58**: 576–589.
- Zar, J.H. 1996. Biostatistical analysis. Prentice Hall Inc., Englewood Cliffs, N.J.