

# Diving behaviour of lactating harbour seals and their pups during maternal foraging trips

W.D. Bowen, D.J. Boness, and S.J. Iverson

**Abstract:** Female harbour seals (*Phoca vitulina*) undertake foraging trips during mid to late lactation. We show that they are accompanied by their pup during many of these foraging trips. Time–depth recorder data were obtained from 20 lactating females and 14 of their pups in 1995 and 1996 at Sable Island, Nova Scotia. Overall, females spent  $55.4 \pm 4.68\%$  (mean  $\pm$  SE) of their time at sea compared with  $39.8 \pm 2.29\%$  for pups. Like those of their mothers, pups' dives occurred in clusters or bouts:  $71.4 \pm 4.4$  dives,  $2.5 \pm 0.15$  h in duration. Bouts of diving by females and pups began 0–3 days post partum. Mean dive duration of pups increased from about 1 to 1.5 min over the course of lactation, but was still shorter than that of adult females (1.5–2.25 min). Both females and pups appeared to dive within their theoretical aerobic dive limits (TADL) of 8.9 and 2.6–3.1 min, respectively. Up to 3.6% of dives by some pups may have exceeded their TADL. Pups appeared to compensate for their lesser diving ability by making more and shorter dives per bout than females, particularly during early lactation.

**Résumé :** Du milieu à la fin de la période d'allaitement, les femelles du Phoque commun (*Phoca vitulina*) entreprennent des excursions de quête de nourriture. Nous démontrons ici que les femelles sont accompagnées de leurs petits au cours de plusieurs de ces déplacements. Des données durée-profondeur ont été obtenues chez 20 femelles nourricières et 14 de leurs petits en 1995 et 1996, à l'île des Sables, Nouvelle-Écosse. Dans l'ensemble, les femelles ont passé  $55,4 \pm 4,68\%$  (moyenne  $\pm$  écart type) de leur temps en mer et les petits,  $39,8 \pm 2,29\%$  de leur temps. Comme leurs mères, les petits avaient tendance à faire des plongées par périodes :  $71,4 \pm 4,4$  plongées pendant  $2,5 \pm 0,15$  h. Les périodes de plongée des femelles et des petits ont commencé 0–3 jours après la parturition. La durée moyenne des plongées des petits a augmenté de 1 à 1,5 min au cours de l'allaitement, mais était toujours plus courte que la durée des plongées des femelles adultes (1,5–2,25 min). La durée des plongées chez les femelles et les petits semblait en-deça des limites théoriques de plongée aérobie (TADL), de 8,9 min chez les femelles et de 2,6–3,1 min chez les petits. Certains petits peuvent avoir outrepassé ces limites au cours de 0–3,6% de leurs plongées. Surtout au début de l'allaitement, les petits semblent compenser leur capacité inférieure à plonger en effectuant des plongées plus fréquentes et plus courtes à chaque période que les femelles.

[Traduit par la Rédaction]

## Introduction

Over the past decade our understanding of the diving behaviour, and by inference the foraging behaviour, of pinnipeds has increased significantly. However, this rapid increase in knowledge is primarily from adults and is often restricted to the breeding season, although this too is changing (e.g., Lydersen and Hammill 1993; Le Boeuf et al. 1996; Burns et al. 1997). Given that diving is essential to the capture of food by pinnipeds, developmental changes in diving behaviour must play an important role in the transition to nutritional independence. This transition is thought to be a critical phase in the early life of pinnipeds, therefore knowl-

edge of the diving behaviour of young seals may provide insight into the effect of ecological variability on the probability of survival.

The diving behaviour of young pinnipeds has received little attention. Early work by Kooyman (1967) showed that newly weaned Weddell seals (*Leptonychotes weddellii*) dived to depths of >90 m. Burns et al. (1997) found that body size of yearling Weddell seals accounted for much of the observed variation in diving behaviour. Le Boeuf et al. (1996) studied the development of diving behaviour in juvenile northern elephant seals (*Mirounga angustirostris*) and found that diving performance increased to 2 years of age (the end of the fourth foraging trip).

Although our understanding of juvenile diving behaviour has increased, little is known of the diving behaviour of pinniped offspring during the lactation period. To a large extent this is a reflection of the fact that nursing pups of many species do not dive to any significant degree until after weaning. However, the pups of several species in the family Phocidae dive during the lactation period: the Weddell seal, the ringed seal (*Phoca hispida*, Lydersen and Hammill 1993), the bearded seal (*Erignathus barbatus*, Lydersen et al. 1994), and the harbour seal (*Phoca vitulina*).

The harbour seal is undoubtedly the most aquatic phocid species from an early age. Harbour seal pups typically enter

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**W.D. Bowen.**<sup>1</sup> Marine Fish Division, Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth, NS B2Y 4A2, Canada.

**D.J. Boness.** Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008, U.S.A.

**S.J. Iverson.** Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

<sup>1</sup> Author to whom all correspondence should be addressed (e-mail: bowend@mar.dfo-mpo.gc.ca).

the sea within hours of birth (Lawson and Renouf 1985) and spend considerable periods in the water each day during the 24-d lactation period, either alone or with their mother. In most harbour seal populations, this aquatic behaviour is necessary because haulout sites are flooded during rising tides. At Sable Island, like other areas with broad beaches, harbour seal behaviour is less affected by the tide cycle (Godsell 1988), but even here pups regularly enter the sea with their mother during lactation.

Adult female harbour seals are among the smallest of phocids and appear to be unable to support the energetic cost of lactation from body stores alone (Bowen et al. 1992). Recent studies have shown that beyond the first week of lactation, most female harbour seals undertake daily foraging trips (Boness et al. 1994; Thompson et al. 1994). VHF telemetry studies on the haulout behaviour of females and their pups (D.J. Boness and W.D. Bowen, unpublished data) at Sable Island suggested that pups did not accompany their mother on most of these foraging trips, as pups were often hauled out when mothers were at sea for many hours. Nevertheless, as both mother and pup are frequently in the water together during the lactation period, the possibility that pups accompany females on some foraging trips remained untested. In the present study, we equipped lactating females and their pups with time–depth recorders (TDRs) to examine the development of diving in neonates and the at-sea relationship between females and their offspring over the course of lactation.

## Materials and methods

The study was conducted in May and June of 1995 and 1996 on Sable Island, a crescent-shaped vegetated sandbar located about 160 km east of Nova Scotia, Canada (43°55'N, 60°00'W). Each day all newborn pups on the north-beach study area were identified with an individually numbered Roto-tag (Dalton, U.K.) to provide accurate information on pup age and hence the lactation stage of the female. We captured females and their pups on the beach as previously described (Bowen et al. 1992). At initial capture, we also Roto-tagged females that had not been previously tagged, and the pair was marked using a fast-drying paint (Lenmar, Baltimore) to permit identification from a distance.

In 1995, 10 mothers were equipped with a Mk3e TDR (Wildlife Computers, 140 g) on the day of birth and 8 of their pups were equipped with Mk5 TDRs (Wildlife Computers, 50 g) at 4–8 d post partum. In 1996, TDRs were deployed on 11 mothers and 8 of their pups on the day of birth. In both years, the combined mass of TDRs and epoxy mounts (300 g in females and 65 g in pups) was <1% of the seal's minimum body mass during the study period. To attach TDRs, mothers and pups were sedated by injection of diazepam at a dose of 0.6 and 0.2 mg/kg i.v., respectively. TDRs were glued to the midback fur of mothers and pups by means of a quick-setting epoxy as described in Boness et al. (1994). We held mothers and their pups for about 30–40 min during which the TDR was fitted and body mass was determined.

TDRs were programmed to sample depth every 10 s once the salinity switch was activated by seawater and to record the sum of the 10-s periods during which the salinity switch was dry. Given the position of the TDR on the seal's back and the relatively rough seas off Sable Island, it is unlikely that the salt-water switch would have become dry while the seals were at sea. Thus, we are quite confident that dry counts measured the time a seal was hauled out on land. TDR data were processed using software from the manufacturer (Wildlife Computers). Hexadecimal files were initially displayed graphically (Strip Chart program) and then corrected for

changes in the calibration of the pressure transducer (zoc program). The DIVE ANALYSIS program was used to estimate parameters of individual dives and time spent at the surface and on land. We used the default definitions of these parameters in the DIVE ANALYSIS program as follows: *dive duration*, the period between surface readings immediately preceding and following a dive minus one sampling interval (i.e., 10 s); *surface time since last dive*, time during which a seal in the water was at or less than the 1 m depth resolution of the TDR; *bottom time*, time spent at  $\geq 85\%$  of the maximum depth of the dive.

Only dives to depths  $\geq 4$  m were used in the analysis because it is only feasible to correct for transducer drift in blocks of dives. Thus, some dives <4 m may be produced by instrument noise. Time spent submerged since the last analyzed dive (i.e., time spent diving to more than the 1 m depth resolution of the TDR but less than 4 m) was used to determine the fraction of time during which mothers and their pups performed shallow dives.

The theoretical aerobic dive limits (TADL) for females and pups were calculated using 2 and 4 times standard metabolic rate (SMR; Lavigne et al. 1986) and estimates of mass-specific oxygen content of seals from Kooyman (1989).

Statistical analyses were conducted using SPSS 6.1 and SYSTAT 7.0 for Windows 95. Although the study was planned as a repeated-measures design, the combination of instrument failure and mortality of pups due to shark predation resulted in uneven sampling over the lactation period (7 pairs in early, 6 pairs to mid, and 3 pairs to late lactation), precluding such an analysis. We nevertheless report changes over the course of lactation, but in most cases we have used confidence intervals (CI) as guides to interpret the results in place of a more complete analysis. The standard error (SE) of the mean is given as the measure of variability.

## Results

Activity (i.e., time spent on land versus time spent at sea) and diving data were obtained from 14 of the 16 pups and 20 of the 21 females (Table 1). In 1995, sharks killed 2 pups. The TDR was lost from one pup, but the TDR from the second pup was recovered along with about 6 days of data. One TDR on a female failed to work. Faulty TDR batteries resulted in truncated data records from another 3 females, so there was no temporal overlap in the data collected from those females and their pups. However, overlapping data were obtained from the other 4 female–pup pairs. In 1996, one recorder was lost when a shark killed the pup. Data were obtained from the 7 other pairs, but shark predation of pups in the first half of the lactation period resulted in abbreviated data from 4 of these pairs (pups' TDRs were recovered from the carcasses).

### Comparison of female and pup behaviour

Although some data on activity budgets were collected from 20 females and 14 pups, the study period in a number of these cases was quite short, raising the possibility that these data might not be representative. Therefore, to compare the overall activity of females and pups we used only individuals that were studied for >6 days. Among these, females ( $n = 12$ ) spent significantly less time on land and a greater percentage of their time at sea than did pups ( $n = 9$ , Mann–Whitney  $U$  test,  $P = 0.02$ ; Table 2). Despite the significantly greater time spent at sea by females, they did not spend a significantly greater percentage of their time diving than pups (Mann–Whitney  $U$  test,  $P = 0.43$ ). Similar results were obtained from the smaller subset of data on 8 pairs for

**Table 1.** Characteristics of adult females and pups studied in 1995 and 1996.

| Year and ID | Initial body mass (kg) |      | TDR record (dpp) |        | Pup |                    |
|-------------|------------------------|------|------------------|--------|-----|--------------------|
|             | Female                 | Pup  | Female           | Pup    | Sex | Status             |
| 1995        |                        |      |                  |        |     |                    |
| J           | 97                     | 10.4 | 0–23             | No TDR | F   | Weaned             |
| K           | 97.5                   | 10.7 | 0–18             | None   | F   | Shark kill, 15 dpp |
| L           | 90.5                   | 11.4 | 0–9              | No TDR | F   | Shark kill, 8 dpp  |
| Y           | 104                    | 12.2 | 0–21             | 7–21   | F   | Weaned             |
| DotE        | 78                     | 12.0 | 0–12             | 8–21   | M   | Weaned             |
| DotF        | 81                     | 10.4 | 1–4              | 8–18   | F   | Weaned             |
| DotG        | 87                     | 11.2 | 0–16             | 7–13   | M   | Shark kill, 13 dpp |
| DotI        | 77                     | 11.7 | 0–22             | 7–22   | M   | Weaned             |
| DotN        | 79.5                   | 12.1 | 0–21             | 6–21   | F   | Weaned             |
| DotO        | 83.5                   | 10.5 | None             | 4–19   | M   | Weaned             |
| 1996        |                        |      |                  |        |     |                    |
| D           | 92.0                   | 12.2 | 0–21             | 0–21   | M   | Weaned             |
| F           | 105.5                  | 13.5 | 0–3              | 0–3    | M   | Shark kill, 3 dpp  |
| L           | 97                     | 11.5 | 0–9              | 0–5    | F   | Shark kill, 5 dpp  |
| M           | 84                     | 11.4 | 0–20             | 0–12   | F   | Weaned             |
| P           | 96                     | 11.2 | 0–7              | None   | M   | Shark kill, 3 dpp  |
| R           | 76.5                   | 12.3 | 0–21             | 0–12   | F   | Weaned             |
| T           | 79.5                   | 11.4 | 0–14             | 0–13   | F   | Shark kill, 13 dpp |
| U           | 87.5                   | 9.7  | 3–9              | 3–7    | F   | Missing, 8 dpp     |
| V           | 90.0                   | 11.4 | 1–8              | No TDR | F   | Shark kill, 5 dpp  |
| Y           | 76.0                   | 10.3 | 0–21             | No TDR | F   | Weaned             |
| X           | 93.0                   | 10.7 | 0–7              | No TDR | F   | Missing, 7 dpp     |

Note: "Dpp" is the number of days post partum.

**Table 2.** Activity budgets of females and pups with TDR records >6 days.

|                                     | Females ( $n = 12$ ) | Pups ( $n = 9$ ) | $p^a$ |
|-------------------------------------|----------------------|------------------|-------|
| Time spent on land (%)              | 44.6±4.68            | 60.2±2.29        | 0.02  |
| Time spent at sea (%)               | 55.4±4.68            | 39.8±2.29        | 0.02  |
| Time spent diving (% of total time) | 8.9±2.89             | 5.4±2.02         | 0.43  |
| Duration of study (d)               | 15.1±1.55            | 11.9±1.15        |       |

Note: Values are given as the mean ± SE.

<sup>a</sup>Mann-Whitney  $U$  test.

which TDR records were available from females and their pups for the same time periods.

Both females' and pups' dives occurred in bouts separated by periods of variable duration when they were hauled out (Fig. 1). The number of bouts varied considerably among pairs, ranging from 0 to 16 (Table 3). Females and pups tended to dive together (6 of 9 pairs had overlapping TDR records). However, females Y, DotI, and T performed 2, 6, and 1 diving bouts, respectively, without their pups. Pups performed diving bouts only when their mothers were also diving (e.g., Fig. 1). Diving bouts occurred at a rate of  $0.6 \pm 0.97$  and  $0.6 \pm 0.92/d$  for females and pups ( $n = 9$  pairs), respectively. In the 5 pairs that were instrumented on the day of birth, the first diving bout occurred between 0 and 3 d post partum (dpp). In another pair studied from 7 to 22 dpp, the pup did not show bout diving until 15 dpp, even though its mother performed 6 bouts prior to this time.

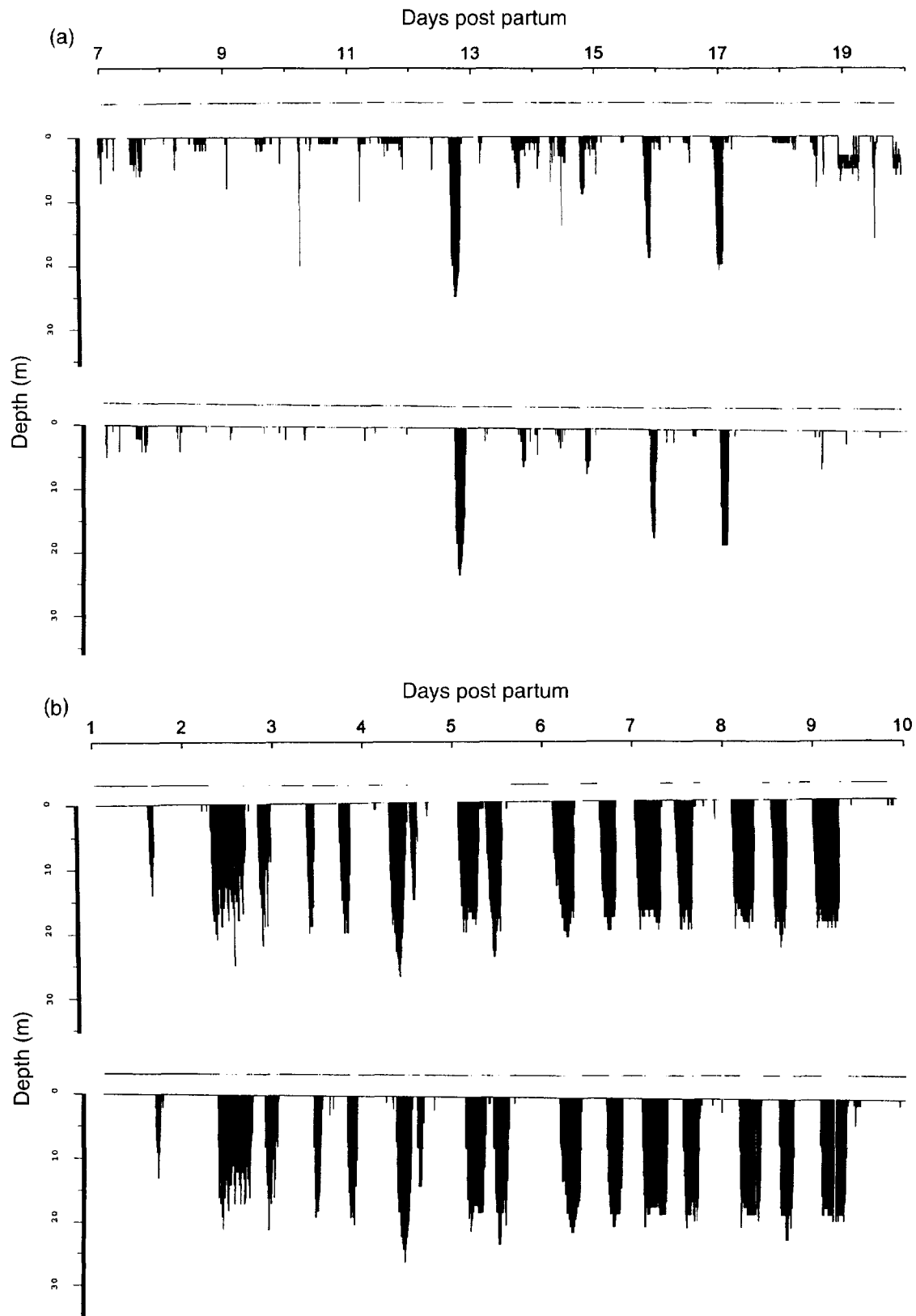
As indicated earlier, missing data prevented us from using a repeated-measures analysis of females and pups as sampling units. We felt that using the bout as the sampling unit

would still shed some light on the behaviour of females and their pups. Bout duration for all individuals ( $2.5 \pm 0.15$  h, range 0.2–9.2 h,  $n = 148$ ) did not differ between females and pups ( $F_{[1,142]} = 0.24$ ,  $P = 0.63$ ) or over the course of lactation ( $F_{[2,142]} = 0.31$ ,  $P = 0.73$ ; two-way GLM). Similarly, the number of dives per bout ( $71.1 \pm 4.4$ , range 5–362,  $n = 148$ ) did not differ between females and pups ( $F_{[1,142]} = 0.08$ ,  $P = 0.78$ ) or over the course of lactation ( $F_{[2,142]} = 1.02$ ,  $P = 0.36$ ; two-way GLM on ln-transformed data).

#### Characteristics of females' and pups' dives

The characteristics of >16 000 dives were measured in 20 females (Table 4) and >7000 dives by 13 pups (Table 5; 1 pup had no dives greater than 3 m depth). Mean rates of both descent and ascent were greater in pups than in females ( $t = 4.1$ ,  $P = 0.001$ , and  $t = 2.26$ ,  $P = 0.03$ , respectively,  $n = 33$ ). Mean dive duration and time spent at the bottom of the dive for pups was 28 and 33% shorter, respectively, than for females ( $t = 3.7$ ,  $P = 0.001$ , and  $t = 2.6$ ,  $P = 0.02$ ). Maximum dive duration of pups was 44% less than that of fe-

**Fig. 1.** Pattern of diving by female Y (top panel) and her pup from 7 to 19 days post partum (dpp) (a) and female R (top panel) and her pup from 1 to 10 dpp (b). Data are compressed so that every 90th and 72nd data points are plotted for females Y and R and their pups, respectively. The broken line above each dive record denotes periods when the TDR was dry and the seal is presumed to have been hauled out on Sable Island.



**Table 3.** Numbers of diving bouts by females and their pups.

| Female ID | Period of study | No. of female bouts | No. of pup bouts | No. of pair bouts (%) | First pair bout (dpp) <sup>a</sup> |
|-----------|-----------------|---------------------|------------------|-----------------------|------------------------------------|
| D         | 0–21            | 13                  | 13               | 100                   | 3                                  |
| DotG      | 7–13            | 0                   | 0                |                       |                                    |
| DotI      | 7–22            | 9                   | 3                | 33                    | 15                                 |
| DotN      | 6–21            | 1                   | 1                | 100                   | 7                                  |
| L         | 0–5             | 5                   | 5                | 100                   | 2                                  |
| M         | 0–12            | 14                  | 14               | 100                   | 2                                  |
| R         | 0–12            | 16                  | 16               | 100                   | 0                                  |
| T         | 0–13            | 10                  | 9                | 90                    | 3                                  |
| Y         | 7–21            | 8                   | 6                | 75                    | 9                                  |

<sup>a</sup>Days post partum.**Table 4.** Mean and maximum values for diving characteristics of female harbour seals during lactation for dives >4 m in depth.

| Year and ID | Study period (dpp) <sup>a</sup> | No. of dives | Rate of ascent (m/s) | Rate of descent (m/s) | Bottom time (min) | Dive duration (min) | Max. dive duration (min) | Total time spent diving (h) | Dive depth (m) | Max. dive depth (m) |
|-------------|---------------------------------|--------------|----------------------|-----------------------|-------------------|---------------------|--------------------------|-----------------------------|----------------|---------------------|
| 1995        |                                 |              |                      |                       |                   |                     |                          |                             |                |                     |
| DotE        | 0–12                            | 92           | –0.8                 | 0.9                   | 0.6               | 1.1                 | 2.5                      | 1.7                         | 11.8           | 27.0                |
| DotF        | 1–4                             | 274          | –0.6                 | 0.7                   | 0.5               | 1.3                 | 3.5                      | 5.7                         | 12.6           | 26.0                |
| DotG        | 0–16                            | 341          | –0.6                 | 0.7                   | 0.8               | 1.5                 | 3.0                      | 8.8                         | 11.7           | 20.0                |
| DotI        | 0–22                            | 800          | –0.7                 | 0.6                   | 1.0               | 1.8                 | 4.5                      | 23.5                        | 11.0           | 52.0                |
| DotN        | 0–21                            | 207          | –0.6                 | 0.7                   | 0.4               | 1.0                 | 2.8                      | 3.3                         | 6.9            | 36.0                |
| J           | 0–23                            | 943          | –0.5                 | 0.5                   | 0.9               | 1.8                 | 4.3                      | 28.7                        | 7.3            | 25.0                |
| K           | 0–18                            | 91           | –0.4                 | 0.5                   | 0.2               | 1.1                 | 17.2                     | 1.6                         | 5.5            | 14.0                |
| L           | 0–9                             | 299          | –0.4                 | 0.4                   | 0.6               | 1.4                 | 4.2                      | 7.2                         | 6.9            | 17.0                |
| Y           | 0–21                            | 477          | –0.6                 | 0.6                   | 0.8               | 1.5                 | 15.7                     | 12.2                        | 10.8           | 25.0                |
| Mean        |                                 |              | –0.6                 | 0.6                   | 0.6               | 1.4                 |                          | 10.3                        | 9.4            |                     |
| SE          |                                 |              | 0.04                 | 0.05                  | 0.09              | 0.10                |                          | 3.22                        | 0.90           |                     |
| 1996        |                                 |              |                      |                       |                   |                     |                          |                             |                |                     |
| D           | 0–21                            | 927          | –0.6                 | 0.6                   | 0.7               | 1.8                 | 6.3                      | 27.1                        | 17.4           | 31.0                |
| F           | 0–3                             | 96           | –0.5                 | 0.6                   | 0.5               | 1.2                 | 2.7                      | 1.9                         | 7.7            | 17.0                |
| L           | 0–9                             | 718          | –0.7                 | 0.7                   | 1.7               | 2.5                 | 5.8                      | 30.1                        | 13.2           | 21.0                |
| M           | 0–20                            | 2 167        | –0.7                 | 0.8                   | 1.1               | 1.9                 | 5.8                      | 69.1                        | 17.8           | 33.0                |
| P           | 0–7                             | 1 207        | –0.5                 | 0.5                   | 0.7               | 1.6                 | 9.0                      | 32.3                        | 10.4           | 27.0                |
| R           | 0–21                            | 5 328        | –0.7                 | 0.7                   | 1.1               | 2.0                 | 8.8                      | 180.8                       | 18.5           | 59.0                |
| T           | 0–14                            | 981          | –0.6                 | 0.6                   | 0.8               | 1.6                 | 6.3                      | 26.5                        | 12.9           | 25.0                |
| U           | 3–9                             | 206          | –0.4                 | 0.4                   | 1.1               | 2.1                 | 6.3                      | 7.3                         | 8.3            | 18.0                |
| V           | 1–8                             | 201          | –0.5                 | 0.5                   | 0.6               | 1.5                 | 5.3                      | 5.1                         | 12.2           | 22.0                |
| X           | 0–7                             | 334          | –0.4                 | 0.4                   | 0.8               | 1.8                 | 6.7                      | 9.8                         | 9.6            | 22.0                |
| Y           | 0–21                            | 694          | –0.6                 | 0.5                   | 0.5               | 1.5                 | 6.3                      | 17.2                        | 14.0           | 49.0                |
| Mean        |                                 |              | –0.6                 | 0.6                   | 0.9               | 1.8                 |                          | 37.0                        | 12.9           |                     |
| SE          |                                 |              | 0.04                 | 0.04                  | 0.10              | 0.11                |                          | 15.44                       | 1.14           |                     |
| Total       |                                 | 16 383       | –0.6                 | 0.6                   | 0.8               | 1.6                 |                          | 25.0                        | 11.3           |                     |
| SE          |                                 |              | –0.03                | 0.03                  | 0.07              | 0.09                |                          | 8.96                        | 0.83           |                     |

<sup>a</sup>Days post partum.

males ( $t = 2.3$ ,  $P = 0.03$ ). Neither mean depth nor mean maximum dive depth differed between females and pups ( $t = 0.67$ ,  $P = 0.51$ , and  $t = 1.11$ ,  $P = 0.28$ , respectively). However, the maximum recorded dive depth for females (59 m) was greater than that for pups (35 m).

Dive duration was positively correlated with dive depth for both females (Pearson's,  $r = 0.54$ ,  $n = 16\,383$ ,  $P = 0.01$ ) and pups (Pearson's,  $r = 0.64$ ,  $n = 7,607$ ,  $P = 0.01$ ); however, pups used only a fraction of the coordinate space used by females (Fig. 2). This pattern suggested that pups faced

greater physiological limitations on their diving behaviour than did females. To investigate this, we plotted two estimates of TADL based on the mean mass of pups near the beginning and end of lactation and compared these with the observed frequency distribution of dive durations for 10 pups with >100 dives (Fig. 3). For a 10- and a 20-kg pup, TADL was estimated at 2.6 and 3.1 min, respectively. Five of these 11 pups with >100 dives had no dives of greater duration than the TADL of 2.6 min, and only 0.2–3.6% of dives of the remaining pups exceeded it. If the TADL were

**Table 5.** Mean and maximum values for characteristics of dives >4 m in depth made by 13 harbour seal pups during lactation.

| Year and mother's ID | Study period (dpp) | No. of dives | Rate of ascent (m/s) | Rate of descent (m/s) | Bottom time (min) | Dive duration (min) | Max. dive duration (min) | Total dive time (h) | Dive depth (m) | Max. dive depth (m) |
|----------------------|--------------------|--------------|----------------------|-----------------------|-------------------|---------------------|--------------------------|---------------------|----------------|---------------------|
| 1995                 |                    |              |                      |                       |                   |                     |                          |                     |                |                     |
| DotE                 | 8–21               | 65           | –0.82                | 1.02                  | 0.87              | 1.64                | 2.83                     | 1.8                 | 19.3           | 31.00               |
| DotF                 | 8–18               | 921          | –0.96                | 1.01                  | 0.53              | 1.10                | 2.83                     | 16.9                | 14.3           | 27.00               |
| DotI                 | 7–22               | 482          | –0.53                | 0.71                  | 0.76              | 1.52                | 2.67                     | 4.6                 | 11.7           | 22.00               |
| DotN                 | 6–21               | 75           | –0.67                | 0.86                  | 0.46              | 0.98                | 1.67                     | 1.2                 | 8.5            | 19.00               |
| DotO                 | 4–19               | 153          | –0.65                | 0.80                  | 0.56              | 1.19                | 2.00                     | 3.9                 | 11.2           | 22.00               |
| Y                    | 7–21               | 493          | –0.60                | 0.73                  | 0.63              | 1.30                | 6.17                     | 10.6                | 10.8           | 25.00               |
| Mean                 |                    |              | –0.7                 | 0.8                   | 0.6               | 1.3                 |                          | 6.4                 | 12.6           |                     |
| SE                   |                    |              | 0.06                 | 0.06                  | 0.06              | 0.10                |                          | 2.53                | 1.52           |                     |
| 1996                 |                    |              |                      |                       |                   |                     |                          |                     |                |                     |
| D                    | 0–21               | 988          | –0.67                | 0.80                  | 0.59              | 1.46                | 3.83                     | 24.1                | 17.9           | 35.00               |
| F                    | 0–3                | 110          | –0.55                | 0.72                  | 0.29              | 0.84                | 1.67                     | 1.5                 | 8.2            | 17.00               |
| L                    | 0–5                | 307          | –0.83                | 0.82                  | 0.29              | 0.83                | 1.83                     | 4.2                 | 11.9           | 20.00               |
| M                    | 0–12               | 896          | –0.59                | 0.67                  | 0.39              | 1.06                | 9.17                     | 15.8                | 11.1           | 33.00               |
| R                    | 0–12               | 2465         | –0.93                | 0.85                  | 0.45              | 1.02                | 6.33                     | 42.0                | 13.6           | 26.00               |
| T                    | 0–13               | 515          | –0.83                | 0.82                  | 0.62              | 1.28                | 4.00                     | 11.0                | 14.7           | 24.00               |
| U                    | 3–7                | 124          | –0.31                | 0.55                  | 0.17              | 0.76                | 1.83                     | 1.6                 | 5.7            | 14.00               |
| Mean                 |                    |              | –0.7                 | 0.7                   | 0.40              | 1.0                 |                          | 14.3                | 11.9           |                     |
| SE                   |                    |              | 0.08                 | 0.04                  | 0.06              | 0.10                |                          | 5.57                | 1.54           |                     |
| Total                |                    | 7607         |                      |                       |                   |                     |                          | 138.4               |                |                     |
| Mean                 |                    |              | –0.69                | 0.80                  | 0.51              | 1.15                |                          | 10.6                | 12.2           |                     |
| SE                   |                    |              | 0.05                 | 0.04                  | 0.05              | 0.08                |                          | 3.30                | 1.05           |                     |

**Note:** One pup had no dives >3 m in depth during the 7- to 13-dpp study period (dpp, days post partum).

3.0 min, 6 pups had no dives that exceeded it, and only 0.2–0.7% of dives of the other 5 pups would have done so. The TADL of females would have been approximately 3 times that of pups (8.9 min for an 80-kg female). Seventeen of the 20 females had no dives that exceeded the TADL. Of the remaining 3 females, the proportion of dives greater than their TADL ranged from 0.1 to 2.2%.

We used local time of sunrise and sunset near the midpoint of the study (7 June) to examine the diurnal pattern of diving of females and their pups. Both females and pups tended to dive more frequently during the night and early morning, until about 09:00, than during the rest of the day (Fig. 4). The mean number of dives per hour was greatest in the early morning for both females and pups. The overall patterns of diurnal diving behaviour of females and pups were similar. Neither dive duration nor dive depth varied significantly as a function of time of day (ANOVA,  $P > 0.9$  for females and  $P > 0.4$  for pups for both variables).

#### Developmental changes in pup diving behaviour over the course of lactation

Dives of females were clearly longer than those of their pups and this difference was greatest early in lactation. To investigate how females and pups coped with their differing diving abilities, we looked at the details of simultaneous diving bouts by females and their pups. Pups typically made a greater number of dives per bout than females, the ratio of pup to female dives averaging 1.3 (95% CL = 1.03–1.64,  $n = 7$ ) between 0 and 6 dpp (one-sample test, ln-transformed data, ratio = 1,  $P = 0.03$ ). Pups appeared to descend with their mother at the beginning of a dive, returned to the sur-

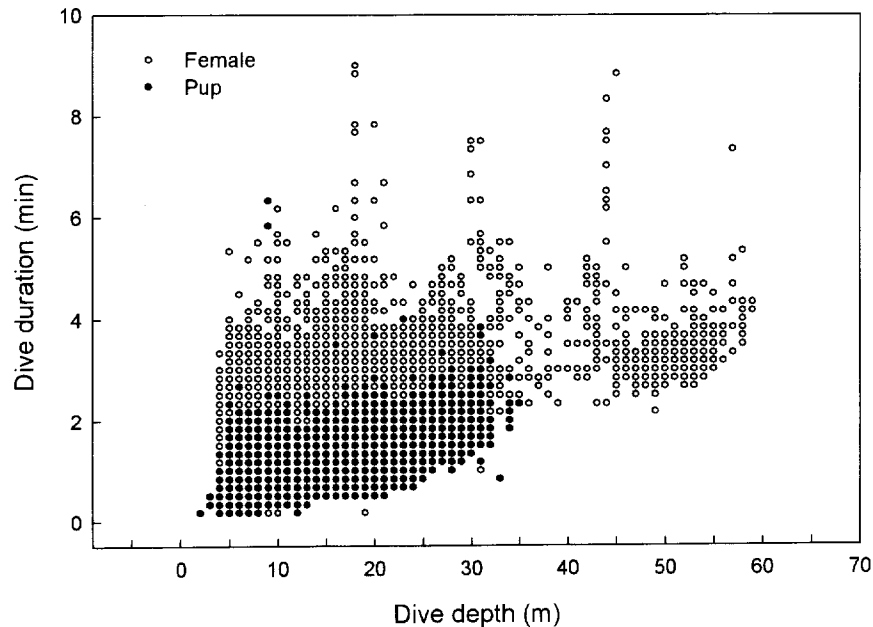
face to load oxygen if the dive exceeded about 1.5 min, and then dived again, presumably to rejoin their mother. During longer dives, females appeared to accompany their pup to the surface and then returned to depth, presumably to continue foraging (Fig. 5). By midlactation, the ratio of pup to female dives declined to an average of 1.1 (95% CL = 1.01–1.26,  $n = 6$ ), but was still greater than 1:1 ( $P = 0.04$ ). By late lactation, however, pups were diving on a one-for-one basis with their mother (ratio = 1.0, 95% CL = 0.93–1.06,  $P = 0.66$ ).

Other aspects of the diving behaviour of females and pups also changed over the course of lactation (Fig. 6). Mean dive depth increased in a similar way in both females and pups over the course of lactation. Dive duration increased during lactation in both females and pups, but the rate of increase and mean duration of dives were greater in females than in pups. Maximum dive duration of pups also increased (Fig. 7). However, surface time between dives showed no significant trend over the course of lactation in either females or pups (Fig. 6). Rate of descent increased in females and pups over the course of lactation (Fig. 6). Females tended to descend more slowly than pups in early and mid lactation, but this difference had disappeared by late lactation. Females also tended to ascend more slowly than pups in early and mid lactation, but again this difference had disappeared by late lactation.

#### Discussion

To our knowledge this is the first study to simultaneously record the diving behaviour of a female pinniped and her de-

**Fig. 2.** Relationship between dive depth and dive duration for females ( $n = 16\ 383$ ) and pups ( $n = 7607$ ) during lactation.



pendent pup over the course of lactation. Harbour seal pups usually accompany their mother into the sea within minutes to hours of birth (Lawson and Renouf 1985). This pattern of daily entry into the sea by mothers with their pups from an early age is thought to be an adaptation to avoid predation by terrestrial carnivores, but is also often a necessary consequence of tidal flooding of the haulout sites of many populations. Although it is common knowledge that females and pups regularly enter the sea together, little is known of the behaviour of pairs at sea. Recent studies have shown that by midlactation, most female harbour seals regularly leave the breeding colony to forage (Boness et al. 1994; Thompson et al. 1994). However, it is not generally known whether pups accompany their mother on these trips and, if so, what they do on such trips.

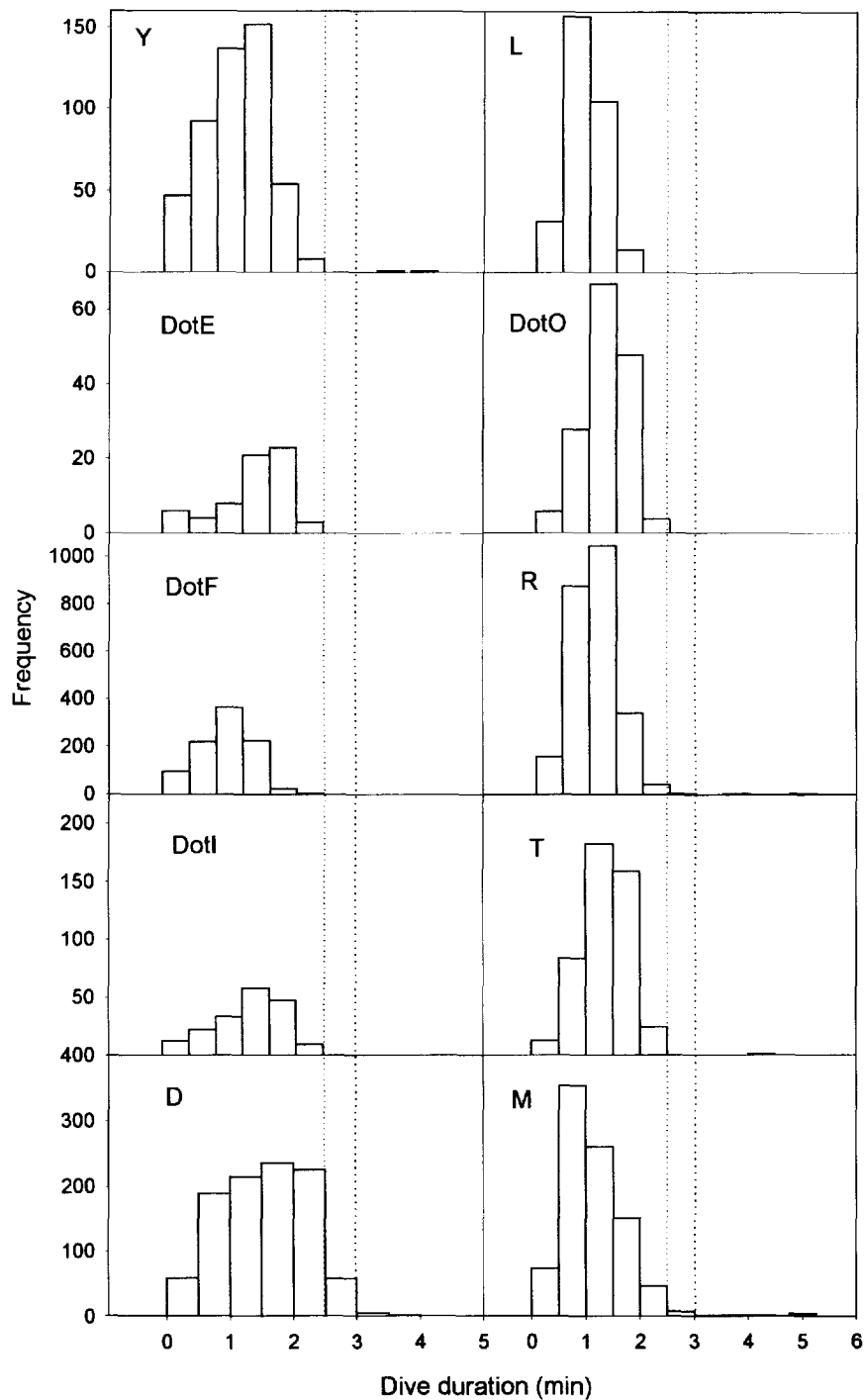
In fact, our earlier behavioural studies of harbour seal females and their pups on Sable Island (D.J. Boness and W.D. Bowen, unpublished data) suggested that females often left their pup on the beach while they went on foraging trips. Evidence for this comes from twice-daily surveys of marked pairs in the study area that were conducted each morning and late afternoon throughout the 6-week breeding season. Data from 25 females and their pups in 1991, as is typical of the late 1980s and early 1990s, indicate that pups were seen alone on the beach in about 40% of the surveys in which females were not seen or both females and their pups were not seen. By comparison, in 1996 the pups of 14 females were seen alone in significantly fewer (6%) of these daily surveys ( $\chi^2 = 26.3$ ,  $df = 2$ ,  $P < 0.001$ ).

The reason for this difference in behaviour is not known, but we speculate that a change in the size of female-pup groups on Sable Island, associated with a dramatic decline in population size, may be partly responsible. Harbour seal production on Sable Island in 1991 was near 600 pups, and females and pups often hauled out in groups ranging from 4 to 25 mother-pup pairs. By 1995 and 1996, when the present study was conducted, production on Sable Island had

fallen to only 175 and 77 pups, respectively, and the size of female-pup groups ranged from only 1 to 11 and from 1 to 3, respectively. Even in 1995, there was only one group in which more than 3 pairs regularly hauled out. It appears that females in larger groups often left their pups onshore while they foraged at sea. These larger groups of females and pups may have provided a reference point for the pup when it entered the water during its mother's absence. Groups also provide greater vigilance and hence increased safety for lone pups. Thus, we suspect that single females and those in small groups may be more likely to take their pups with them to reduce the likelihood of their pups wondering off while they are gone. Premature separation of female and pups can lead to increased pup mortality at Sable Island (Boness et al. 1992). Also, we have evidence from the TDR records recovered from pups killed by sharks that deaths occurred in shallow water, most likely near the beach. Here again, it may be safer for females to take their pups with them than to leave them alone in shallow water near the haulout site.

Although the reasons are uncertain, it is clear that pups usually accompanied their mother to sea during our study. Pups began to accompany their mother and exhibit bouts of diving  $>4$  m from 0 to 3 dpp and continued to dive with their mother over the course of lactation. The bathymetry near Sable Island is such that females and pups would typically need to have traveled between 0.5 and 1.5 km to reach water depths between 10 and  $>20$  m, respectively. Data from underwater video cameras attached to free-ranging adult males showed that harbour seals at Sable Island typically dive to the bottom (D.J. Boness, W.D. Bowen, G. Marshall, and B. Buhleier, unpublished data). Triangulation of the positions of these males at sea, based on VHF telemetry, showed that in 40% of locations where depth was  $>20$  m, seals were beyond 3 km from the beach. All depths between 8 and 12 m were about 1.0–1.5 km offshore. We do not know if females with pups foraged in the same areas as

**Fig. 3.** Histograms of dive durations for 10 pups (identified by the mother's ID) with >100 dives during lactation. The dotted lines represent estimates of TADL for a 10-kg (2.6 min) and a 20-kg pup (3.1 min), respectively.



these adult males, but it seems likely that females and pups often traveled more than 0.5 km offshore and that some pairs regularly traveled more than 1 km (see depths in Fig. 1) to areas where females foraged.

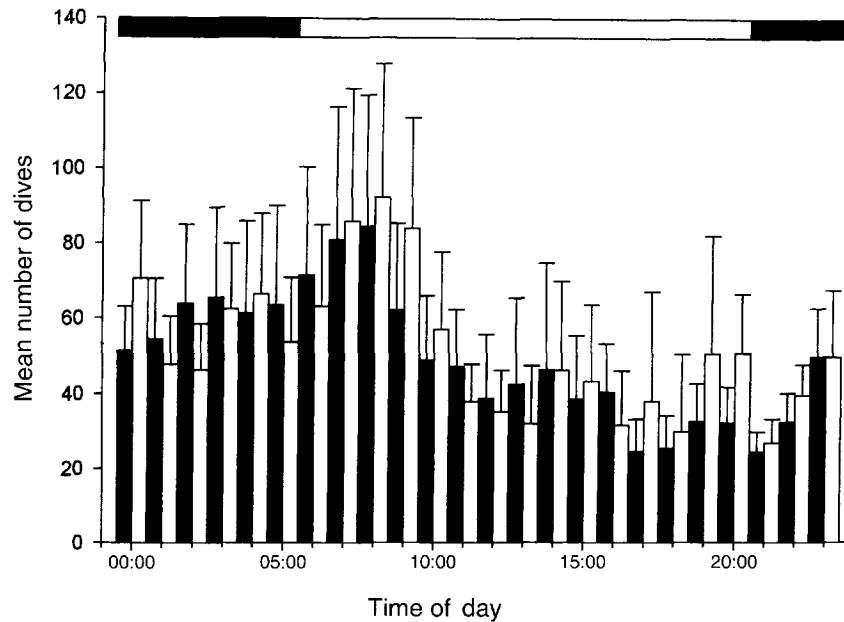
The females in this study both descended and ascended at a lower rate during diving than in our previous study of female diving behaviour on Sable Island (Boness et al. 1994) (*t* test,  $P < 0.01$  for both). However, mean dive duration and time spent at the bottom of the dive did not differ significantly. Pups in our earlier study often did not accompany

their mother. Thus, we suggest that the lower rates of descent and ascent by the females in this study may have been a behavioural response of females to the inexperience of pups early in lactation, when pups had difficulty in anticipating when their mother would dive. By late lactation, rates of ascent and descent of females and pups in this study did not differ from those reported for females in Boness et al. (1994).

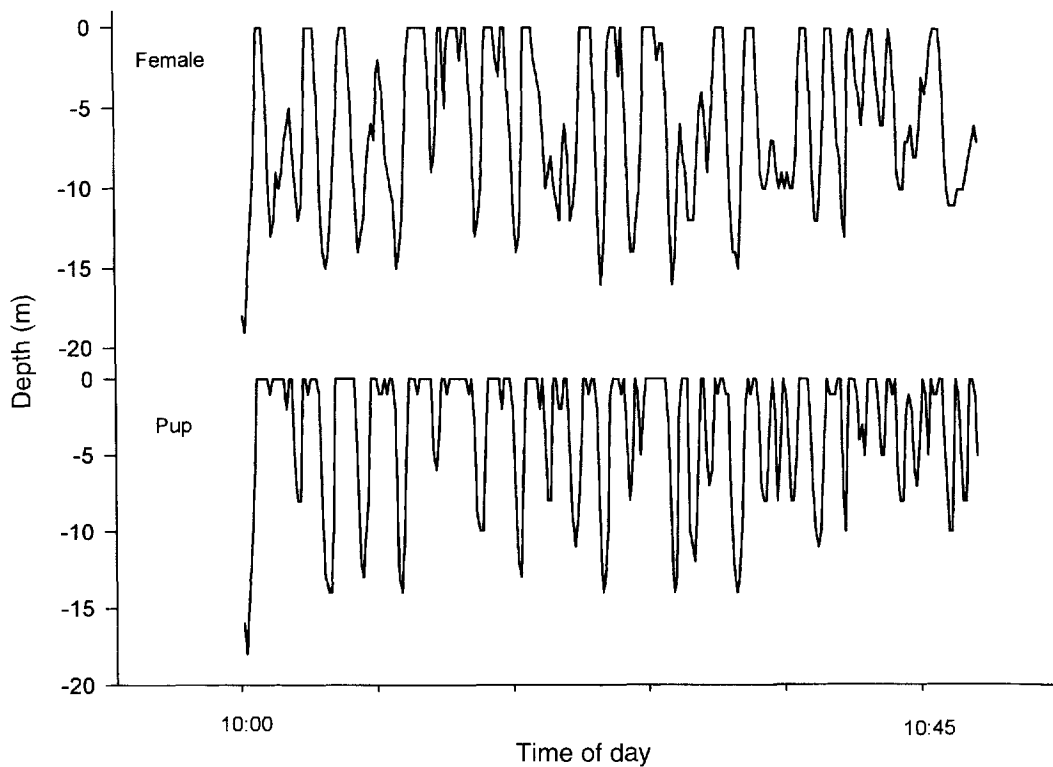
Mean dive duration of both females and pups increased over the course of lactation. Maximum dive duration of pups also increased, again suggesting an increase in diving perfor-



**Fig. 4.** Mean number of dives per hour over a period of 24 h in females (solid bars;  $n = 12$ ) and pups (open bars;  $n = 9$ ) during lactation. Error bars represent 95% CI. The horizontal open bar indicates daylight hours and the solid bars indicate night.



**Fig. 5.** Individual dives made by female R and her pup recorded at the same time between 10:00 and 10:45 on day 1 post partum. Depth was sampled every 10 s for both female and pup.

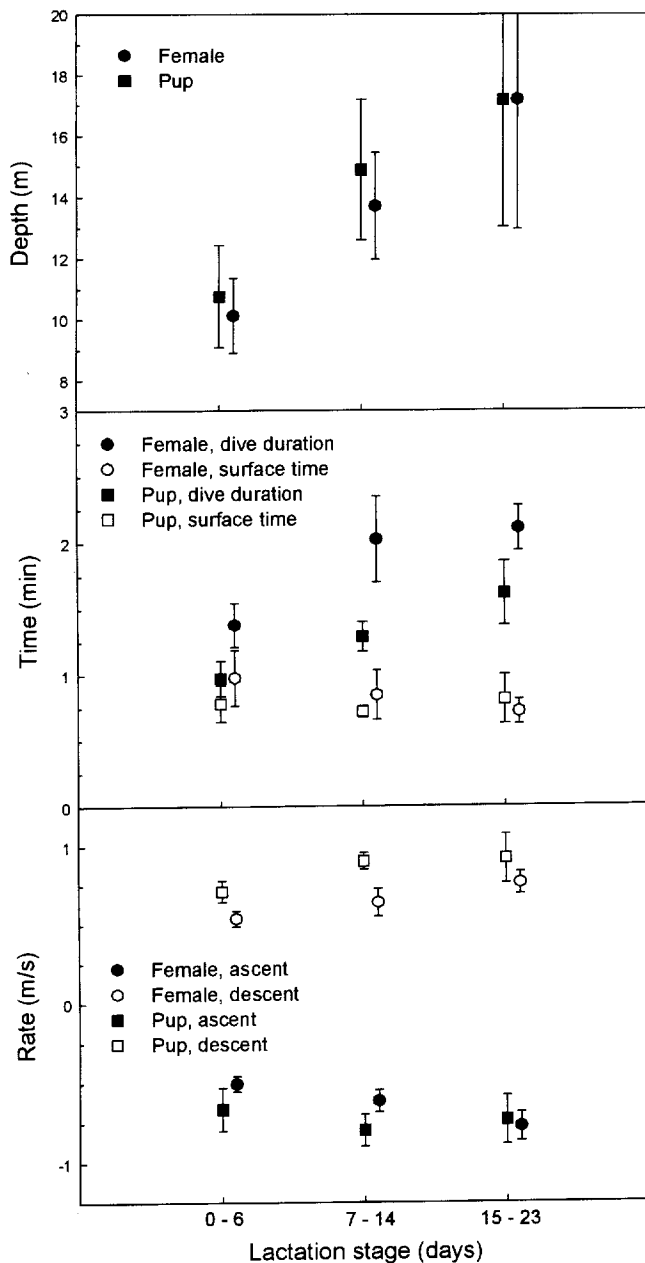


mance of pups. An increase in diving performance of pups over the course of lactation has also been reported in nursing ringed (Lydersen and Hammill 1993) and bearded seals (Lydersen et al. 1994). Diving performance of northern elephant seals also increased with age and experience up to 2 years of age (Le Boeuf et al. 1996). These changes in diving performance are expected, given that the aerobic capacity of

pups should increase at a faster rate than energy expenditure as they grow. Burns et al. (1997) found that about half of the variation in diving performance of yearling Weddell seals could be explained by differences in body size.

The observed increase in dive duration for females may reflect the increasing diving abilities of their pups as well as the increased demand for food energy by females during late

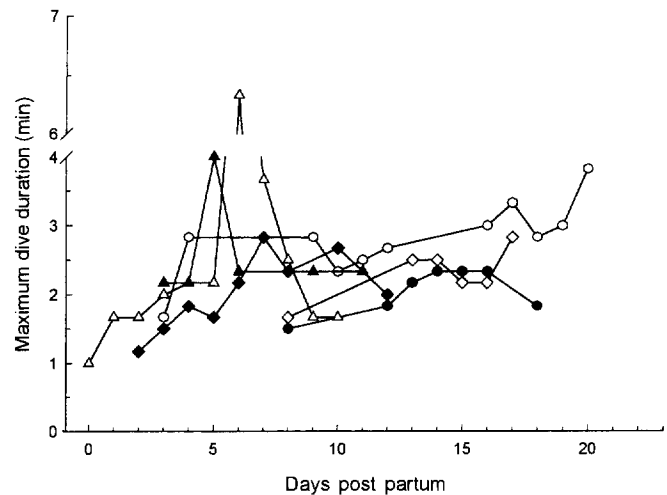
**Fig. 6.** Changes in dive parameters for females and pups over the course of lactation. Error bars represent the 95% CI. Sample sizes of females and pups were 19 and 8 in early lactation, 15 and 8 in midlactation, and 7 and 5 in late lactation, respectively.



lactation (W.D. Bowen, S.J. Iverson, D.J. Boness, and O.T. Oftedal, submitted for publication). Even during early lactation, pups rarely exceeded their estimated TADL; most dives were <2 min in duration. Although our estimate of TADL for these pups should be considered a rough approximation: only one of the pups we studied regularly dived near its TADL. Thus, inexperience, as well as physiology, may play an important role in determining dive duration in these young pinnipeds.

It seems unlikely that pups are attempting to forage during these bouts of diving with their mother. In a study involving extensive stomach lavage, only milk was found in

**Fig. 7.** Changes in maximum dive duration for 6 harbour seal pups over the course of lactation. Each symbol represents a different pup.



the stomach of pups prior to weaning (Muelbert and Bowen 1993). Thus, pups would appear to be diving to maintain contact with their mother, but may also learn where and on what their mother is foraging.

Based on a comparison of the results of this study with our previous work (Boness et al. 1994), we speculate that the foraging efficiency of females that are accompanied by pups may be lower than that of unaccompanied females. Females equipped with TDRs in 1989 and 1990 had diving bouts that were significantly longer (overall mean = 4.8 h; Boness et al. 1994) than those of female-pup pairs in the present study (overall mean = 2.5 h). Pups of the instrumented females studied by Boness et al. (1994) were regularly seen hauled out while their mothers were at sea. Thus, when not accompanied by their pups, females may be able to dive for longer periods. This may result in increased foraging efficiency and greater transfer of milk energy to pups, particularly during late lactation. Of course, it is also possible that differences in prey availability between these two time periods could account for the observed differences in bout duration, but we are unable to test this possibility.

We have suggested that a higher proportion of harbour seal pups accompanying females on foraging trips at Sable Island, where haulout areas are not dependent on tidal cycles, may be a by-product of the reduced size of female-pup groups. Even though pups do not appear to be obtaining direct benefits from solid-food intake, they may be receiving benefits from incidentally learning about foraging locations or food types. In this regard, one direction for future research on the diving behaviour of harbour seal pups would be to investigate the postweaning foraging efficiency of pups that accompany their mother to sea and compare it with the efficiency of those that do not.

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