

Diving Heart Rate Development in Postnatal Harbour Seals, *Phoca vitulina*

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ABSTRACT

Harbour seals, *Phoca vitulina*, dive from birth, providing a means of mapping the development of the diving response, and so our objective was to investigate the postpartum development of diving bradycardia. The study was conducted May–July 2000 and 2001 in the St. Lawrence River Estuary (48°41'N, 68°01'W). Both depth and heart rate (HR) were remotely recorded during 86,931 dives (ages 2–42 d, $n = 15$) and only depth for an additional 20,300 dives (combined data covered newborn to 60 d, $n = 20$). The mean dive depth and mean dive durations were conservative during nursing (2.1 ± 0.1 m and 0.57 ± 0.01 min, range = 0–30.9 m and 0–5.9 min, respectively). The HR of neonatal pups during submersion was bimodal, but as days passed, the milder of the two diving HRs disappeared from their diving HR record. By 15 d of age, most of the dive time was spent at the lower diving bradycardia rate. Additionally, this study shows that pups are born with the ability to maintain the lower, more fully developed dive bradycardia during focused diving but do not do so during shorter routine dives.

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Introduction

Foetal seals demonstrate bradycardia both spontaneously (Bacon et al. 1985) and during maternal dives, a mechanism thought to protect the developing foetus from hypoxia (Elsner 1965; Elsner et al. 1970). However, it remains unclear whether the ability to regulate heart rate (HR) during natural breath hold is well developed in neonates (Castellini et al. 1994b). It has been long accepted that dive bradycardia in young harbour seals generally improves with time (Harrison and Tomlinson 1960; Irving et al. 1963), but exact specifics have not been presented. In addition, the technology has only recently advanced to a point where HR data could be gathered remotely on wild seals.

Specific signs of developing dive bradycardia may include (1) variability of the HR values that declines with age and experience, where the targeted optimum diving bradycardia value may be overshot and/or undershot until later in development, and (2) gradual lowering of the mean bradycardia HR with age, independent of mass-specific and developmental changes in metabolic rate (Rubner 1883; Kleiber 1932; Brody 1945; Stahl 1967; Castellini and Zenteno-Savin 1997). In this study, we set out to quantify this improvement in diving HR with age in free-ranging harbour seals.

The swimming skills of young harbour seals improve during nursing; this trend continues past weaning (Bowen et al. 1999; Bekkby and Bjørge 2000; Jørgensen et al. 2001; Baechler et al. 2002), and there is evidence that even 80-d-old seals do not yet possess the diving ability of adults (Bekkby and Bjørge 2000), probably because of their smaller body size (Burns and Testa 1997; Schreer and Kovacs 1997; Burns 1999). In any case, these early behavioural improvements are vital for the survival of young harbour seals. The objective of this study was to document the development of diving bradycardia in postpartum harbour seal pups. As the pups became older and gained diving experience, we expected diving bradycardia and diving behaviour to become better matched. We built on the established framework that harbour seal pups improve their diving skills in the first months of life (Bowen et al. 1999; Bekkby and Bjørge 2000; Jørgensen et al. 2001) by focusing on whether improved control over HR control coincided with (or preceded) these improvements in dive performance.

Material and Methods

Pups were captured from May to July 2000 and 2001 in the St. Lawrence River Estuary at Métis, Québec (48°41'N,

Table 1: Summary of equipment deployments on harbour seal pups at Métis, Québec, 2000 and 2001

Seal Tag No.	Sex	Mass First Capture ($\pm .5$ kg)	Date First Deployment	No. Deployments ^a	Ages Covered (d) ^b	Time-Depth Recorder Type
3925	F	12.5	May 25, 2001	3	3–8, 17–26	LTD-100
3934	M	13.0	May 27, 2001	4	4–22	LTD-100
3939	F	13.5	May 29, 2001	2	5–10, 18–23	LTD-100
3940	F	14.0	June 1, 2001	4	6–11, 16–30	LTD-100/Mk8
3942	F	12.5	June 25, 2001	1	27–34	LTD-100
3943	M	12.0	June 2, 2001	1	2–7	LTD-100
3945	F	15.0	June 6, 2001	1	8–13	Mk8
3946	F	13.0	June 14, 2001	1	12–15	LTD-100
3948	M	18.0	June 8, 2001	1	13–18	Mk8
3958	M	19.0	June 17, 2001	1	15–20	Mk8
4240	F	11.0	May 25, 2001	1	0–8 ^c	LTD-100
4250	F	11.0	June 14, 2001	3	8–19, 23–42, 43–60 ^c	LTD-100/Mk8
6011	M	16.5	June 2, 2000	1	10–16 ^c	LTD-100
6015	F	15.0	June 4, 2000	1	8–15 ^c	LTD-100
6023	M	18.0	June 11, 2000	1	18–23	LTD-100
6031	F	8.5	June 21, 2000	1	10–16	LTD-100
6038	M	12.0	May 22, 2000	1	2–6 ^c	LTD-100
6049	F	10.0	June 14, 2000	1	19–26 ^c	LTD-100
6050	F	12.0	May 27, 2000	2	2–7, 8–14 ^c	LTD-100
6055	F	13.0	May 31, 2000	2	4–8, 9–17 ^c	LTD-100

^a Only deployments yielding useable data are presented.

^b Age backcalculated from mass at first capture using a mean daily growth rate of 0.54 kg/d and initial birth mass of 11.1 kg (Dubé et al. 2003).

^c Only time-depth recorder data available.

068°01'W) using a modified dip net (2-m aluminum handle, 1-m hoop) and an 8-m inflatable boat with a 30-hp outboard motor. Mass (± 0.5 kg) and sex were noted, a numbered flipper tag was placed in the interdigital webbing of one hind flipper (Jumbo Rototag, Dalton, England), and a numbered pyramid head tag (Dalton, England; Hall et al. 2000) was glued to the fur covering the head (5-Cure Marine Epoxy, Industrial Formulators, or Loctite 422 cyanoacrylate glue and 7452 accelerator, Loctite, Mississauga, Ontario). A VHF radio transmitter (4.0 \times 2.0 cm cylindrical, model A1-2, Holohil, Carp, Ontario, or custom model, Lotek, St. John's, Newfoundland) was also glued caudal to the head tag. The pups were lightly manually restrained in the boat to attach the equipment and then released. Tracking from the boat was done using a portable receiver and Yagi antenna (R2000, ATS, Isanti, MN).

Direct observations of pups at birth were not possible. Therefore, we estimated the age by backcalculation by subtracting a birth mass of 11.1 kg from the mass at first capture and dividing the difference by the daily growth rate (Dubé et al. 2003). A daily growth rate of 0.54 kg/d (SE = 0.14, $n = 194$; Dubé et al. 2003) was used, which is similar to the growth rate of 0.50 ± 0.13 kg/d we obtained from 10 noninstrumented pups in 2000. To minimize error due to nonlinear mass gain (Bowen et al. 2001), all age estimates were made from initial mass values

of less than 20 kg (mean = 13.5 ± 0.5 kg, $n = 20$). Four individuals (20%) were newborn at first capture (≤ 11.1 kg).

Pups were also outfitted with a heart rate recorder (HTR). Sterile electrodes constructed of 1.0 \times 0.25-cm cylindrical, gold RCA-type connectors were implanted subcutaneously via a 1-cm incision (20 mg Lidocaine). These electrodes were attached to waterproof coaxial cables (20 cm) of the HR transmitter unit (Polar Electro Oy, Kempele, Finland, modified for marine mammals by Wildlife Computers, Redmond, WA) using conductive epoxy (Chemtronics, Kennesaw, GA). The R-R intervals were archived by the HTR that was affixed within 10 cm of the transmitter unit. Before deployment, the setup was field tested using a Polar HR receiver watch (Polar Beat).

To monitor diving activity in conjunction with HR, a time-depth recorder (TDR; LTD100, Lotek, or Mk8, Wildlife Computers, maximum total equipment load = 2.0% body weight) was glued to the fur between the scapulae (see Table 1). All equipment was removed (by clipping fur under the attachment site) after final recapture, if no weight gain had occurred, or if the electrode sites appeared infected. The two 1-cm electrode incisions were then irrigated with Betadyne, treated with antibacterial ointment, and left unsutured to allow healing to proceed naturally. To extend observations past weaning (when direct recaptures become unlikely), release mechanism units

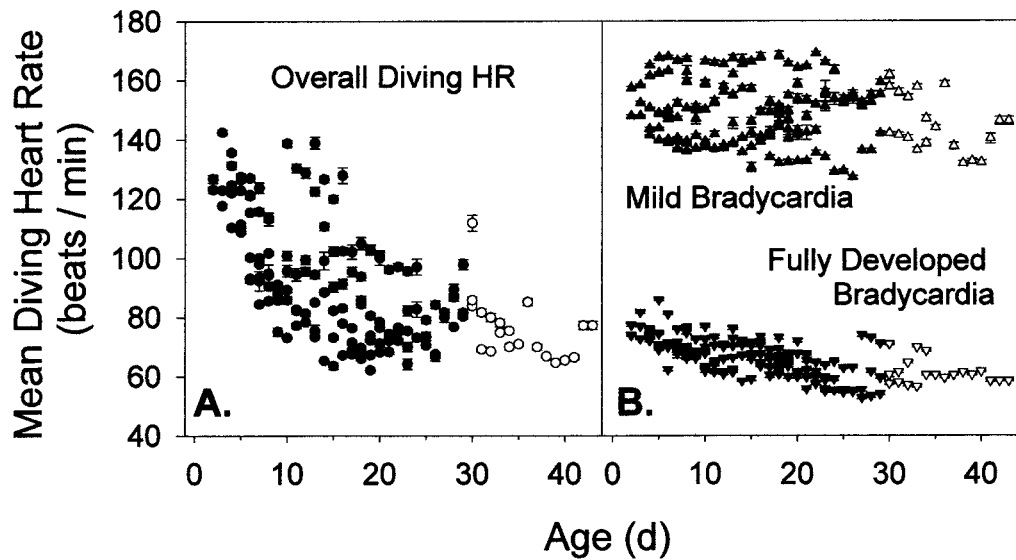


Figure 1. Diving HR of harbour seal pups at Métis, Québec, 2000 and 2001. In A, overall diving HR decreased more sharply with age than either the mild bradycardia or the fully developed bradycardia shown in B. Open symbols represent weaned individuals. $n = 15$ seals, 85,931 dives.

carrying the TDR and HTR (Hammill et al. 1999) were attached to eight seals (>20 kg).

The HTR uses signal processing to interpret raw EKG and produce the R-R interval. The system uses peak voltage to signal a heartbeat. To validate this, we collected raw EKG tracings in the field using a portable EKG and compared them with the R-R value produced by the HTR (Pearson coefficient = 0.72, $P < 0.0001$). False "heartbeats" caused by sudden movement

were recorded either as 207 beats/min or as values >230 beats/min, prompting us to filter these out later during analysis. The HR data was also corrected for instrumental time drift relative to the depth data recorded simultaneously.

A dive was defined as submergence below 1.0 m for more than 5 s. The 1.0-m depth criterion accounted for wave action, differential TDR placement, and body growth. The Wildlife Computers TDR required manual zero-offset correction to re-

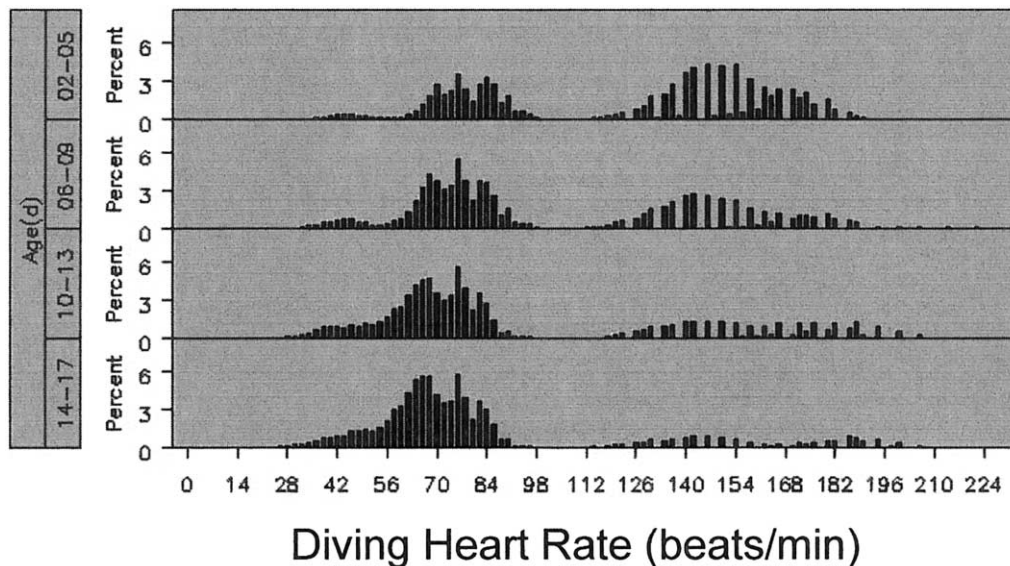


Figure 2. Sample frequency histograms of diving HR of 13 young harbour seal pups aged newborn to 17 d. The unimodal trend continued to 42 d of age (not shown); 533 h of diving HR shown.

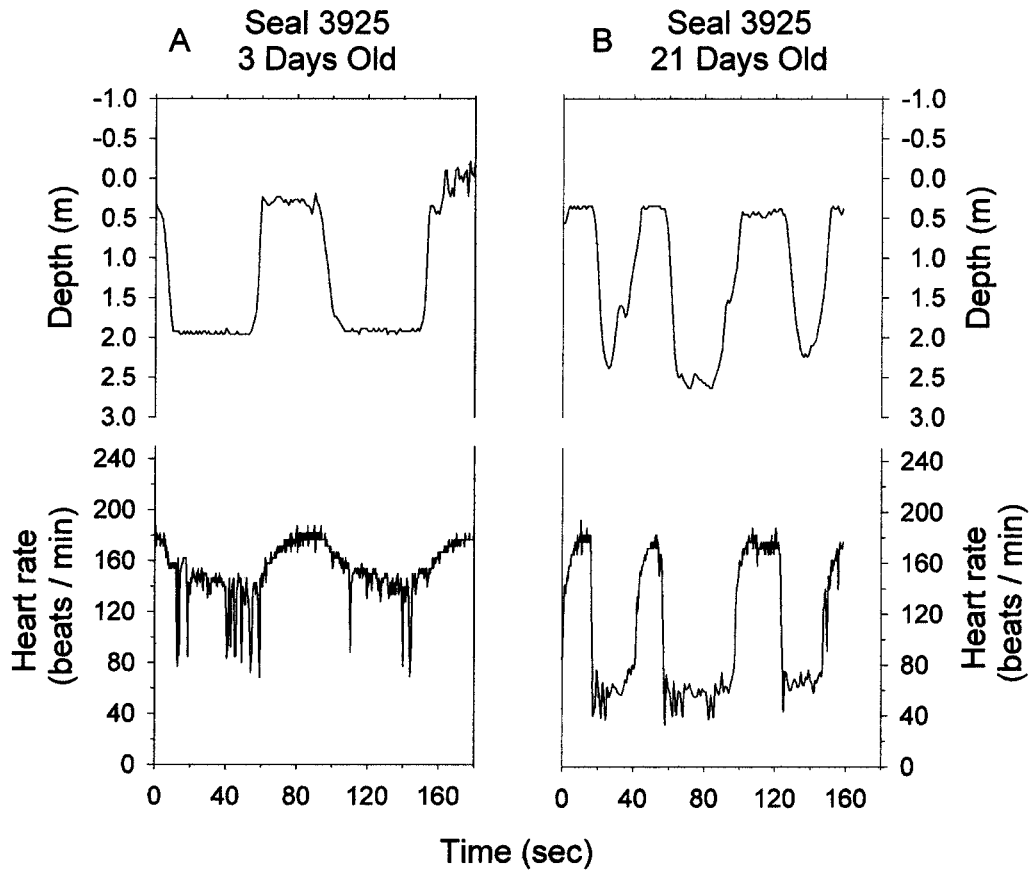


Figure 3. Example of the HR tracing of a free-ranging harbour seal pup while diving (tag 3925). Dive depth (*top*) and corresponding HR (*bottom*) at age = 3 d (A) and 21 d (B).

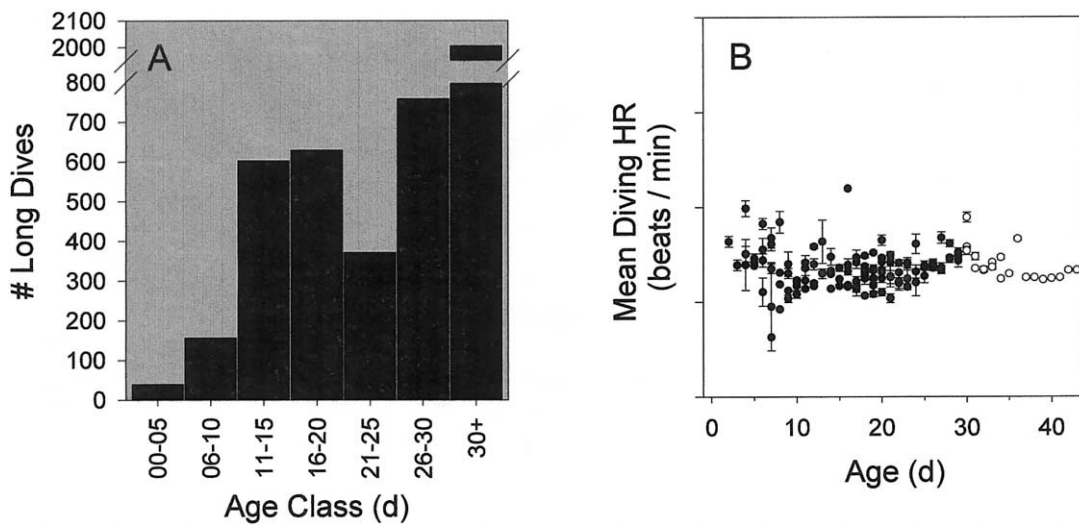


Figure 4. Focused diving in young harbour seal pups. A, Age distribution profile of long dives (>107 s; the top 5%). B, Mean diving HR (+SEM error bars) during focused dives. Open symbols represent weaned pups. $n = 15$ seals, 4,582 long dives.

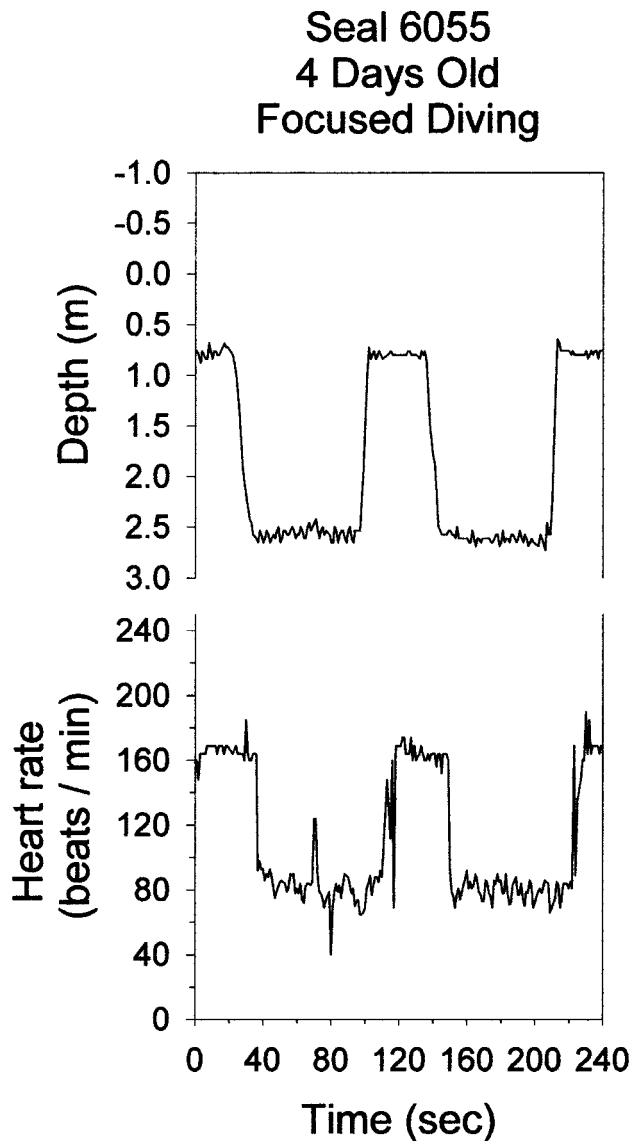


Figure 5. Example of an HR tracing during focused diving from a 3-d-old pup (tag 6055). Dive depth (*top*) and corresponding HR (*bottom*) are shown.

calibrate the pressure transducer. All Mk8 data were manually graphed, and noisy segments were deleted (following Lesage et al. 1999; Jørgensen et al. 2001). The Lotek TDR data required correcting for negative pressure values that occurred sporadically while the instrument was at sea level.

The diving HR was subdivided into mild diving bradycardia and fully developed diving bradycardia on the basis of histograms of diving HR that were constructed for every animal (Fig. 1). An observed node at 100 beats/min consistently divided these two diving HR peaks into mild and fully developed diving bradycardia. Software programs were written in SAS (v. 8.01, SAS Institute) to separate the data set into dives and to

calculate descriptive statistics on the following variables: dive depth, dive duration, proportion of dives by shape, overall diving HR, mild diving bradycardia HR, and fully developed diving bradycardia HR. The daily means presented are the means of each individual seal of the given age.

Dives were classified into four shapes: square (25% of dive time spent in descent, 50% of dive time spent at bottom depth, 25% of dive time spent in ascent), triangle (50% descent, 50% ascent), skewed left (75% descent, 25% ascent), and skewed right-shaped dives (25% descent, 75% ascent; Schreer and Testa 1996; Schreer et al. 2001). Hybrids (intermediate-shaped dives) were not included in the shape analysis (5% or 5,961 of 106,691 dives, following Schreer et al. 2001).

Unpaired *t*-tests (PROC TTEST, $\alpha = 0.05$) were used to test for differences between the following: maximum daily dive depth before and after weaning, mean daily dive depth before and after weaning, maximum daily dive duration before and after weaning, and mean daily dive duration before and after weaning. The *t*-tests of the proportions were used to test the proportion of square dives before and after weaning and the proportion of skewed left-shaped dives before and after weaning. Uneven sampling over the study period prevented a repeated-measures analysis and also regressions of these data. Mean and maximum daily statistics were calculated, but least squares linear regressions could not be made because individual animals provided dependent data spanning several days.

Results

Twenty-four animals were equipped in 2000 and 2001, and 49 deployments were made. Eight deployments did not produce useable HR or depth data because of nonrecovery, data corruption, electrode failure, or cracked/flooded TDRs. Six deployments provided only HR data (because of a lost or damaged TDR) and, without the corresponding depth measurements, were therefore not useable in this study. Only the TDR data were available from seven other deployments, which were included in the analysis of dive behaviour (dive depth, dive duration, and dive shape). The analysis of HR development was completed on 86,931 dives from 15 individuals 2–42 d of age (Table 1). A total of 100,730 (nonhybrid) dives were used in the analysis of depth shape. The analysis of dive behaviour development was then completed on 106,691 dives from 20 individuals spanning in age from newborn to 60 d.

We observed what appeared to be a decline in overall mean diving HR (both modes together) especially in the first 15 d of life (Fig. 1A). However, on closer inspection of the frequency histograms by age, the diving HR in these young harbour seal pups was distinctly bimodal (Figs. 1B, 2; $n = 13$ individuals). That is, during diving, there was a “mild bradycardia” mode that was separate and distinct from a “fully developed bradycardia” mode, separated by a trough at 100 beats/min. Furthermore, the centre values of these two modes did not decline

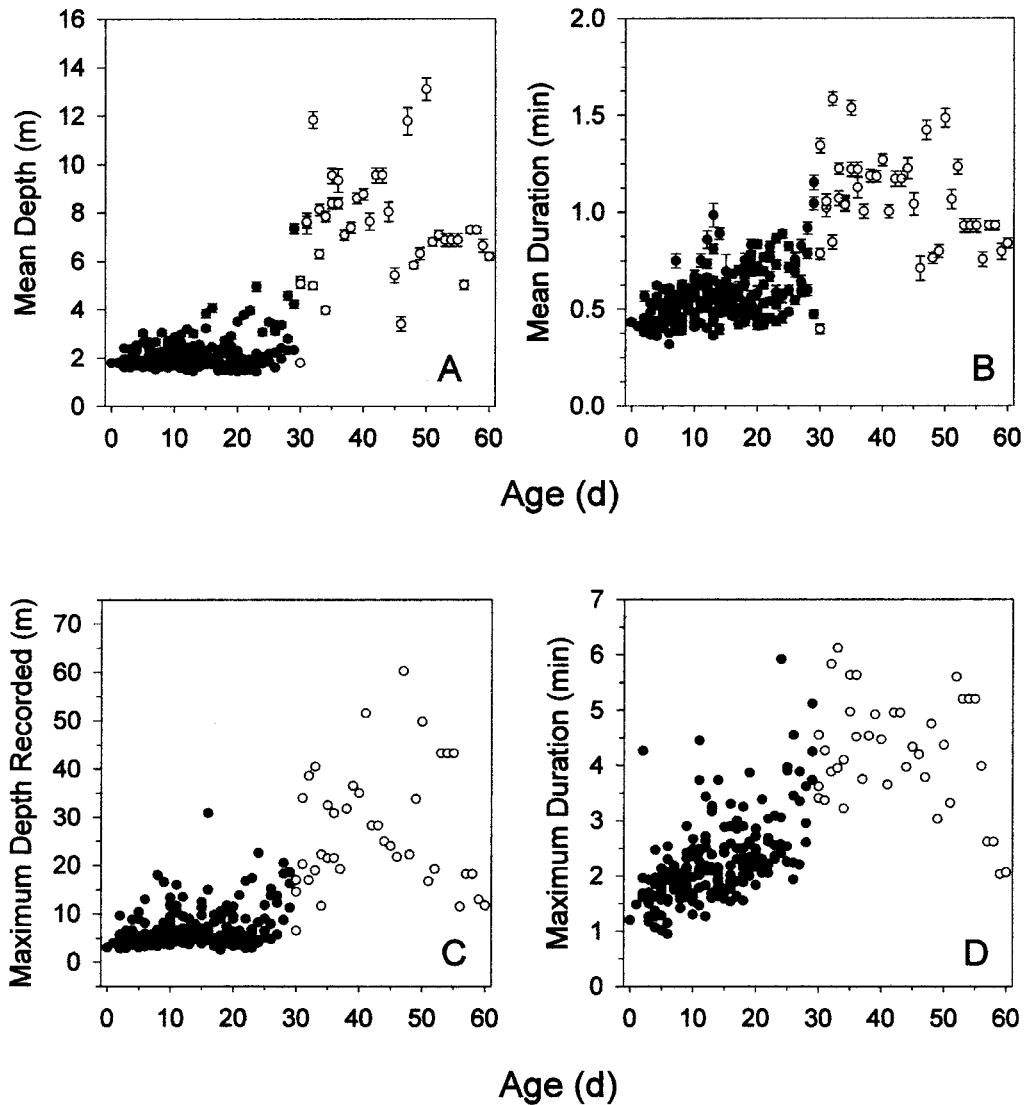


Figure 6. Diving behaviour of harbour seal pups at Métis, Québec, 2000 and 2001. A, Mean dive depth. B, Mean dive duration (+SEM error bars). C, Maximum dive depth. D, Maximum dive duration. Open symbols represent weaned pups. $n = 20$ seals, 106,691 dives.

enough with age to account for the initial observation that overall diving HR decreased. Instead, the “mild bradycardia” mode in the histograms of diving HR gradually decreased in magnitude as the pups aged (Fig. 2). As the pups aged and/or gained diving experience, the heart spent more of the dive beating at the lower of the two rates. An example of a diving HR trace of one individual at 3 d and 21 d is shown in Figure 3. Clearly, the control over HR was refined in the dives made by this pup at 21 d.

To explore diving HR during only the most extremely focused dives, the longest 5% of the dives was separated from the records (≥ 107 s, 4,582 dives, $n = 15$ individuals) and analyzed separately. While relatively few young pups made these longer dives (Fig. 4A), the diving HR was found to be constant re-

gardless of age (Fig. 4B). That is, even the very young pups maintained low HRs during focused dives, similar to older pups. An example of this is shown in Figure 5.

Three indices of dive behaviour were measured: dive depth, dive duration, and dive shape (depth vs. time profiles). Pups exhibited changes in their behaviour that coincided with weaning (at approximately 30 d at this site; Dubé et al. 2003), as indicated by the open circles in Figure 6. However, the small postweaned sample ($n = 3$ individuals; Table 1) kept the focus of this study on trends in the behaviour of nursing pups.

Both the mean dive depth and mean dive duration of dives made by nursing pups remained relatively constant at 2.1 ± 0.1 m and 0.57 ± 0.01 min, respectively (Fig. 6A, 6B). The maximum dive depth recorded by a nursing seal was 30.9 m,



Figure 7. Relative proportion of dive shapes (depth vs. time) as a function of age for harbour seal pups at Métis, Québec, 2000 and 2001. The proportion of square dives significantly decreased after weaning (dashed line), while the proportion of skewed left dives increased (both $P < 0.0001$). $n = 20$ seals, 100,730 dives for all shapes.

and there was very little increase with age (Fig. 6C). The maximum dive duration was 5.92 min and showed no strong upward trend with age (Fig. 6D). A noteworthy 4.27-min dive was recorded from a 2-d-old pup (Fig. 6D). The mean depth and duration values were substantially more conservative than the maximums observed. On average, weaned pups dived significantly longer and deeper than nursing pups, and their maximum dive depths were deeper and their maximum dive durations longer than nursing pups (separate t -tests, all $P < 0.0001$). However, there was considerable individual variability in these behavioural variables ($r^2 \leq 0.5$ in Fig. 6 despite significance, $P < 0.0001$ in all four cases). Nursing pups made 81%–100% square dives (Fig. 7), and the proportion of square dives decreased after weaning while the proportions of skewed left (slow descent) dives increased (t -test of proportions, both $P < 0.0001$). The two remaining shapes (skewed right and triangle) remained $< 11\%$ during the entire sampling period.

Discussion

This study revealed that harbour seals have a remarkable and unexpected developmental strategy for matching diving bradycardia and diving. In very young pups, there are essentially two diving HRs: one mild bradycardia and one much slower and more fully developed bradycardia. Development of HR control continues via a gradual decrease in the amount of time spent at the more rapid rate rather than through changes to the mean.

This result has important implications in terms of the lability of the HR. From this and numerous other studies, it has become apparent that seals functionally exhibit a two-speed heart (Fedak et al. 1988; Butler and Jones 1997). The diving bradycardia and surface tachycardia are separate and distinct (Fedak et al. 1988), and seals show similar haul-out bradycardia and haul-out tachycardia values (Castellini et al. 1994a; Falabella et al. 1999). Furthermore, this bimodality in HR is established before birth. In studies on the HR of foetal harbour seals, a lower HR appears late in gestation that is separate and distinct from the higher HR that had first appeared in the embryonic heart during formation (Bacon et al. 1985). This study documents age-related changes in cardiac control during diving that also adhere to a two-speed heart theme.

A second outcome of this study was the observation that very young pups are capable of controlling their HR with similar success as the older pups but that they do so only during “serious,” long-duration diving. By focusing only on these long dives, we were able to show that harbour seal pups are likely born with the ability to maintain a powerful, sustained dive bradycardia similar to the older pups. Therefore, the mild dive bradycardia we observed was a transient HR seen in only the very young seals during their shorter, routine dives.

Closely associated with the diving HR, several remarkable aspects of diving behaviour were observed. Our analysis of dive shapes suggests that mothers were likely leaving pups behind while foraging during the lactation period. On average, the dives made by these pups were very shallow. This may indicate that pups (1) remained within the shallow whelping patch during nursing while the mother was off foraging, (2) accompanied the mother but remained near the surface as she foraged far below, or (3) accompanied the mother during foraging. The last point is unlikely given the prey items of adult harbour seals. Nearly all of the pups’ dives were square, which was consistent with Baechler et al. (2002), when all nursing pups’ square (or U-shaped) dives are pooled. Shallow, square shapes suggest that the pups were not following the mother during her foraging dives. If this were case, we would expect more triangular-shaped dives as the pup followed the mom for as long as it could and then abruptly ascended as it approached its dive limit. As a result, we suggest the first of these three options was most likely; during this study, pups remained behind while their mothers foraged. The behavioural changes observed with weaning included deeper, longer dives as well as the appearance of skewed left-shaped dives. These behavioural shifts likely indicate exploration outside the whelping patch into nearby areas with deeper bathymetry. Similar improvements in dive duration after weaning have been previously documented (Bekkby and Bjørge 2000).

Given their habit of short, shallow diving combined with the transitory mild dive bradycardia observed here, the nursing pups have much more potential than it would at first appear. Harbour seals have, at a very early age, the physiological ma-

chinery to induce a strong bradycardia during long duration dives. Of course, it is not surprising that the physiological system matured before the dive behaviour changed, but the reason why the strong bradycardia is not used from birth remains unresolved. Nevertheless, should the need arise for “serious” diving, such as predator avoidance, nursing harbour seal pups are able to extend their breath hold capabilities using strong dive bradycardia similar to older pups.

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