

Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped

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Abstract. Aquatically mating male harbour seals, *Phoca vitulina*, must balance the competing demands of foraging and reproduction while at sea during the breeding season. Time-depth recorders (TDRs) were attached to 31 adult male harbour seals to investigate changes in diving behaviour at Sable Island, Nova Scotia, during the 1992–1994 breeding seasons. Male seals were captured, fitted with TDRs and weighed at the beginning of the season in late May, then recaptured for TDR removal and reweighing at the end of June. Males made deep dives (to maximum depths >20 m) more frequently early in the breeding season, then switched to shallow (≤ 20 m) diving later during the mating period. Deep dives (38.8 ± 2.2 m; 4.6 ± 0.1 min) were fairly uniform in shape, appearing flat-bottomed with rapid rates of descent and ascent and long bottom time, but shallow dives (10.5 ± 0.5 m; 3.0 ± 0.1 min) were more variable in shape. Rates of mass loss varied inversely with time spent in deep dives, indicating that deep diving behaviour reflects foraging activity. Males lost mass while making shallow dives associated with mating behaviour later in the breeding season. Deep diving occurred more frequently during daylight hours. Shallow dives were predominant at twilight and at night when females are likely to be departing and returning to the island from foraging trips in late lactation. At Sable Island, males may maximize their encounter rates with oestrous females by ceasing to make offshore foraging trips, and increasing the time spent patrolling home ranges and displaying in shallow water near the breeding colony in late lactation. Relatively larger males may have a competitive advantage since they can afford to spend less time making foraging trips away from the concentration of females and more time displaying in shallow water near the shore.

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Studies of the reproductive behaviour of male pinnipeds usually focus on observable interactions between adult males and females on shore. Among species in which males haul out throughout the duration of the breeding season and mate terrestrially, it is possible to investigate links between body size, reproductive energetic effort, activity patterns and reproductive success through direct observation and serial reweighings of

marked individuals (e.g. Boness 1984; Anderson & Fedak 1985; Deutsch et al. 1990; Boyd & Duck 1991; Tinker et al. 1995).

Many pinniped species mate aquatically. Fifteen of the 18 phocid seals mate exclusively in the water and aquatic copulation occurs frequently in several otariid (i.e. fur seals and sea lions) species (Boness et al. 1993). The mating systems of aquatically copulating pinnipeds have not been studied extensively because of the inherent difficulties in observing reproductive behaviour that occurs at sea. This has been identified as a major gap in our overall understanding of the reproductive strategies of male pinnipeds (Le Boeuf 1991; Boness 1991).

The harbour seal is perhaps the most widely studied aquatically mating pinniped; however,

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most studies of male reproductive behaviour have been limited to observations at the haul-out site (Sullivan 1981, 1982; Davis & Renouf 1987; Godsell 1988; Thompson 1988; Walker & Bowen 1993a, b). Although some authors (e.g. Godsell 1988) suggest that behavioural interactions between males and females onshore may be unrelated to mating strategies of males at sea, such observational studies have provided some important insights into harbour seal mating behaviour. For example, the timing of the appearance of lacerations on the neck and hindflippers of males resulting from intrasexual competition approximately coincides with the presence of increasing numbers of oestrous females (Davis & Renouf 1987; Thompson 1988; Walker & Bowen 1993b), suggesting that males intensify competition for mates in the water towards the latter part of the breeding season. Observations of increased rates of mass loss and the absence of chylomicrons (indicative of recent feeding) in male serum during late lactation (Walker & Bowen 1993a) also suggest that harbour seal males make a transition from foraging activity to aquatic behaviour mainly associated with competition for mates as more oestrous females become available.

Using VHF transmitters, Thompson *et al.* (1989) also observed that males make shorter diving trips during the breeding season, suggesting a reduction in foraging activity near the time of mating. More recently, through VHF telemetry and acoustic recordings, Van Parijs *et al.* (1997) found that male harbour seals reduce their home range size and make shorter dives, which are associated with underwater vocalizations during the mating period of the breeding season. Underwater vocalizations associated with presumed courtship dives appear to be individual-specific, suggesting that they are used in male-male competition and/or as reproductive advertisement to attract females in the water (Hanggi & Schusterman 1994). In the Moray Firth, U.K., Van Parijs *et al.* (1997) also found that males tended to perform these vocalizations at locations where they are likely to intercept females during the breeding season: either on foraging grounds, around haul-out sites or on transit routes between these two areas.

At Sable Island, evidence from time-depth recorders (TDRs) indicates that female harbour seals spend more time in the water as they resume foraging trips during mid-lactation; however, they

return to the beach daily to nurse their pups (Boness *et al.* 1994). These findings suggest that male harbour seals may maximize their encounter rates with potentially oestrous females by discontinuing foraging activity and attempting to intercept or attract females in nearshore waters as females depart from or return to the breeding colony in late lactation and following weaning. We hypothesized that male diving patterns should reflect a transition from offshore, presumably deep diving, foraging activity to shallow dives associated with reproductive behaviour later in the breeding season. Direct observation from underwater video cameras attached to male harbour seals has shown that males predominantly engage in patrolling, making vocalizations, flipper-slapping displays, inter-male aggression and courtship during periods of shallow diving activity during the breeding season (D. J. Boness, W. D. Bowen, G. Marshall & B. Buhleier, unpublished data). Thus, we also predicted an inverse relationship between individual rates of mass loss and deep diving activity, and, conversely, a positive correlation between shallow diving and mass loss throughout the breeding season. Finally, since larger seals start the breeding season with larger absolute energy stores, they should need to spend less time feeding; therefore, we predicted that large males would have different activity patterns from smaller seals, reflecting less effort devoted to foraging and more to reproductive behaviour.

METHODS

The study was conducted during the breeding seasons (mid-May to the end of June) of 1992, 1993 and 1994 on the north beach of Sable Island (43°55'N, 60°00'W), a partially vegetated 40-km-long sand bar, 160 km east of Halifax, Nova Scotia. The waters surrounding Sable Island are fairly shallow with a gradual slope. Depths greater than 20 m are reached approximately 4 km offshore, and seals must travel at least 12 km from the island to reach maximum depths of 50 m or more. Between 300 and 500 harbour seal females gave birth on Sable Island during each year of the study.

Male harbour seals were caught onshore by blocking their access to the sea using all-terrain vehicles (see also Walker & Bowen 1993a, b). Once secured in nets, seals were sedated with

diazepam (approximately 0.2 mg per kg body mass) to minimize stress during handling. Males were weighed by suspension from a 200 ± 0.5 kg Salter spring balance, and a dorsal length measurement (McLaren 1993) was taken. In each season, 12 adult seals with initial mass greater than 85 kg were fitted with a Mk3+ TDR (Wildlife Computers, Woodinville, Washington) containing 256 k of memory. The unit was positioned on the middle of the back as described in Boness et al. (1994). TDRs weighed approximately 300 g, representing about 0.3% (range=0.22–0.35%) of initial body mass. Males were recaptured near the end of the breeding season (range=15 June–1 July) for TDR removal and reweighing.

Analysis of Dive Records

TDRs were programmed to record depth every 10 s. Data from each TDR were processed with software provided by the manufacturer. Data files were initially examined graphically (Strip Chart program) to provide a visual representation of the diving pattern of each male (Fig. 1) and then corrected for changes in the calibration of the TDR's pressure transducer (zero offset correction program) over the data collection period. Corrected files were analysed (dive analysis program) to provide numerical descriptions of individual dive parameters for each record. We used the default definitions found in the dive analysis program to describe the following parameters.

Dive duration: the time between the surface readings immediately preceding and following the dive, minus one sampling interval.

Dive depth: the maximum depth reading that was taken during the dive.

Bottom time: the time between the first and last depth reading equal to or greater than 85% of the maximum dive depth.

Average rate of ascent and descent: the average rate of descent was calculated from the start point of each dive to the beginning of bottom time. The average rate of ascent was calculated from the end of bottom time to the end point of the dive.

Time since last repeated dive: the time since the last dive if the last recorded dive occurred within 10 min. This setting was used to avoid inflating the mean dive interval by including long periods spent at the surface or out of the water.

Deep and shallow dive effort: the proportion of time seals spent in deep or shallow dives,

calculated as the sum of all deep or shallow dive durations divided by the total deployment time for each male, expressed in min/h.

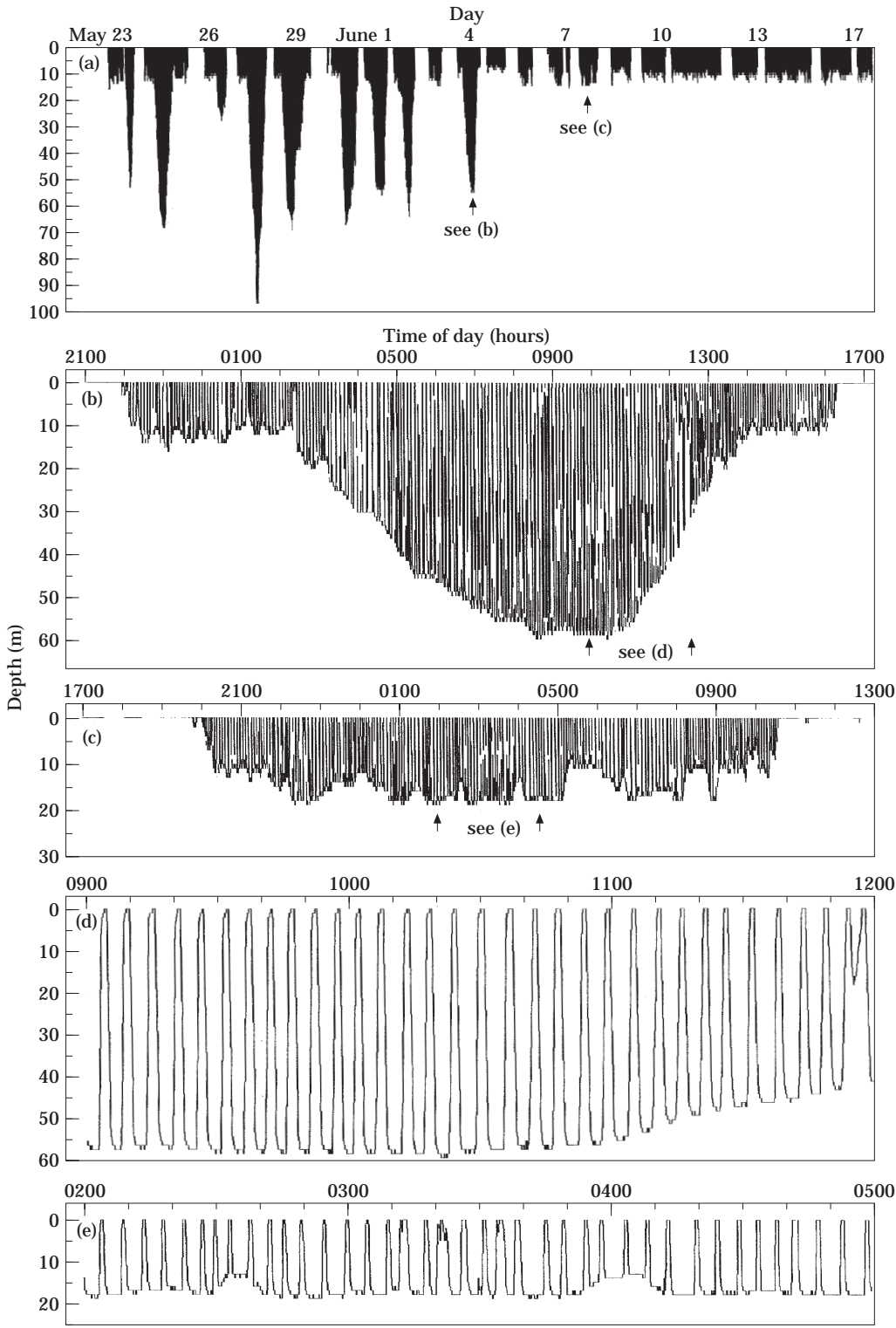
It is only feasible to correct for transducer drift in blocks of dives; therefore dives to 4 m maximum depth or less were not analysed, since instrument noise causing drift slightly greater than 2 m (twice the depth resolution of the TDR) might have been recorded as shallow dives. Approximately 20% of all recorded dives were to 4 m or less maximum depth.

Based on an inspection of the overall dive patterns (Fig. 1), we defined two major classes of dives. Individual dives to depths of no more than 20 m were considered shallow, and dives to maximum depths of over 20 m were considered deep. Bathymetric maps of waters surrounding Sable Island indicate that dives to maximum depths over 20 m must occur at least 4 km offshore, whereas if seals are diving to the bottom at depths of 20 m or less they are relatively close to the breeding colony.

Since diving tended to occur in clusters, or bouts, of dives either 20 m or less, or considerably greater (Fig. 1), we also defined two types of bouts to characterize the temporal aspects of diving patterns. Our operational definition of the onset of a bout was the occurrence of five consecutive dives of 5 m or greater followed by at least five deeper dives. Dive bouts were considered to end when an animal remained at the surface for at least 1 h or returned to land. Visual inspection of graphical representations of some individual bouts suggested that there are two major types of bouts. 'Shallow' bouts tended to start with a small number of dives with increasing depth, then an extended period of repeated diving to a median depth of less than 20 m (Fig. 1c), 'Deep' bouts consisted of clusters of dives with a median depth greater than 20 m, commonly reaching maximum depths of greater than 50 m (Fig. 1b).

Data Analysis

To examine the effect of initial body mass on male diving behaviour and mass change, we divided our sample into two groups based on the median value (108.0 kg) of initial mass measurements. Males with initial mass of 108 kg or less were considered small, and those more massive were classified as large. To investigate the extent to which the diving behaviour of large and small



males differed before and after oestrous females were likely to be present in the colony, we divided the breeding season into a pre-mating and mating period based on similar criteria described in Walker & Bowen (1993a, b). Mating is thought to occur near weaning (Boulva & McLaren 1979; Thompson 1988). On Sable Island, the first pups were born on 15 May, 13 May and 14 May in 1992, 1993 and 1994, respectively. Assuming a mean lactation duration of 24 days (Muelbert & Bowen 1994), oestrous females would have become increasingly numerous after about 8 June in each year (i.e. the median expected date of the appearance of the first weaned pup). We used this date to divide the breeding season into the pre-mating and mating periods.

Most statistical analyses were performed using Minitab Release 10 for Windows. Prior to statistical analyses, all data were checked for normality, transformed if necessary, and in the case of multivariate analyses, converted to a mean of zero and standard deviation of 1. Unless otherwise stated, we set the probability level for significance at $\alpha=0.05$ and give standard errors as the measure of variance about the mean. Regression analyses for changes in dive parameters over time were not performed because of the lack of independence of measures for consecutive days and the variable length of TDR deployment among individuals. Repeated measures ANOVA was used to compare the deep and shallow diving activity of large and small males between the pre-mating and mating periods using SPSS version 6.1.3 for Windows.

RESULTS

We failed to recover data from five TDRs because of loss of the instrument at sea ($N=1$), battery failure ($N=3$) and the infusion of seawater into the unit ($N=1$). Therefore, data from 31 TDRs were used in this analysis (Table I). Deployment duration differed significantly between years (one-way ANOVA: $F_{2,28}=75.17$, $P<0.001$), with a sig-

nificantly longer mean deployment period in each successive year (1992: 22.2 ± 0.2 days; 1993: 26.1 ± 0.8 days; 1994: 33.1 ± 0.8 days). Neither mean body size (length, initial mass and mass loss) nor diving characteristics (dive effort, number of dives, number of bouts, percentage of deep dives; Table I), corrected for the number of days in the deployment period, differed significantly between years (body size MANOVA: $F_{6,52}=1.96$, $P=0.088$; diving characteristics: $F_{8,50}=0.651$, $P=0.731$). Data between years were therefore pooled for all subsequent analyses.

Characteristics of Individual Dives

Although the number of shallow and deep dives per day was variable among males, with coefficients of variation (CV) of 71.6 and 59.5%, respectively, records contained significantly more shallow dives than deep (two-tailed paired t -test: $t_{30}=3.79$, $P<0.001$; Table II). Coefficients of variation were generally higher for shallow dive characteristics than for deep dive characteristics, except for mean dive depth. Deep dives tended to be rather uniform both within records and between seals, with a symmetrical, 'flat-bottomed' shape and similar rates of ascent and descent (Fig. 1). The maximum recorded dive depth was 208 m, and the maximum duration recorded for a single dive was 10.33 minutes. Shallow dives were more variable in shape, particularly with respect to the amount of time spent at the bottom (CV=71.6%). Although many shallow dives appeared to be 'flat-bottomed', there were also many 'V' shaped dives with little time spent at the maximum depth (Fig. 1e). Shallow dives were significantly shorter, had less bottom time and slower average rates of ascent and descent than deep dives (repeated measures MANOVA of standardized parameters: $F_{3,90}=1966.34$, $P<0.001$; $P<0.001$ for each post hoc comparison by univariate repeated measures ANOVA).

The average characteristics of all dives clearly changed over the breeding season in relation to the availability of oestrous females (Fig. 2). In the

Figure 1. An illustration of male harbour seal diving behaviour produced by the strip chart program (Wildlife Computers). (a) The diving pattern of male S6933 (1993) during the entire deployment period of 24 days. Data are compressed such that every 180th sample of depth is plotted. (b) A single deep diving bout; (c) a single shallow diving bout with every sixth sample of depth plotted. Typical shapes of individual dives (i.e. every depth sample plotted) are shown occurring within (d) deep and (e) shallow diving bouts.

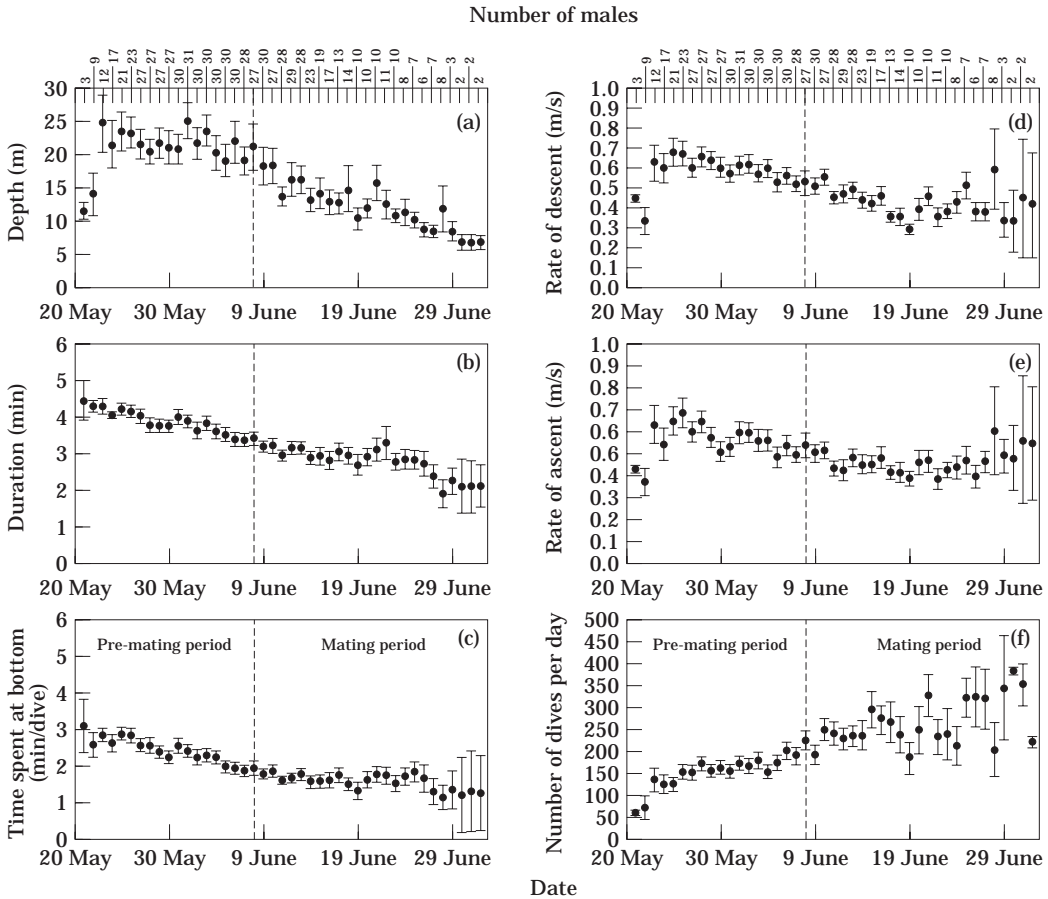
Table 1. Body size and diving characteristics of TDR-fitted adult male harbour seals (N=31)

ID	Year	Length	Initial mass (kg)	Final mass (kg)	Record duration (days)	Number of dives	Number of bouts	Time hauled out (min/h)	Dive effort (min/h)	Dives>20 m (%)
S6853	1992	163.0	115.5	101.0	22	1859	11	9.2	16.04	68.20
S6854	1992	155.0	111.0	101.0	23	6803	11	5.2	41.10	45.11
S6587	1992	151.5	117.0	100.0	24	4951	31	10.5	27.90	26.68
S6856	1992	152.0	115.5	102.0	22	2954	26	13.38	13.38	3.14
S6857	1992	145.0	102.0	91.5	23	4753	18	19.3	29.14	57.94
W116	1992	160.5	114.5	107.0	21	2061	25	12.6	13.26	21.39
S6860	1992	151.5	111.5	98.5	22	4182	20	11.7	28.62	31.90
S6861	1992	152.0	107.0	106.5	22	3636	13	10.2	31.41	81.57
W119	1992	157.5	120.5	113.5	22	3220	16	19.7	24.37	51.35
S6863	1992	153.5	106.5	99.5	22	1535	16	na	11.85	48.73
S6866	1992	150.0	108.0	99.0	22	6484	10	5.8	37.99	19.91
S6864	1992	153.5	108.0	104.0	21	1804	8	na	13.60	61.14
S6921	1993	153.5	103.0	100.0	25	5182	13	5.3	33.06	65.48
3032	1993	150.5	98.5	90.5	24	2615	26	16.7	15.21	58.16
S6920	1993	162.0	111.0	90.0	25	4246	24	14.2	19.12	9.80
S6825	1993	158.0	131.5	111.5	30	7695	22	11.0	32.27	18.90
S6927	1993	148.5	96.5	85.5	24	6429	29	21.2	23.05	11.59
S6928	1993	146.0	112.5	95.0	30	5701	30	19.4	31.29	46.17
J9162	1993	153.5	99.5	90.5	26	2762	24	14.2	16.14	57.13
S6933	1993	144.5	88.5	85.0	25	6167	24	5.8	34.99	16.96
S6945	1993	157.0	127.0	114.5	23	7234	16	1.3	38.38	6.66
S6951	1993	150.0	85.0	74.5	29	4883	18	28.7	24.49	62.37
S6990	1994	154.0	96.0	90.0	38	4800	17	24.1	21.44	65.02
S6862	1994	164.0	110.5	99.5	34	5966	25	10.4	28.01	41.67
S6998	1994	154.5	105.5	91.5	34	5516	24	6.3	29.63	51.27
L11307	1994	153.0	98.0	92.8	32	5512	32	11.8	29.63	27.34
S6577	1994	156.5	111.5	88.5	35	9647	35	9.8	35.49	15.45
L11203	1994	153.5	107.0	88.3	31	4840	31	24.1	28.15	40.50
S6986	1994	153.5	103.5	88.3	30	2060	30	35.4	11.86	71.17
S6958	1994	158.0	111.5	87	32	11 977	32	2.4	34.89	5.86
L11222	1994	166.0	116.5	83	32	10 029	32	1.6	34.69	1.29

Table II. Characteristics of shallow and deep dives made by adult male harbour seals during the breeding season near Sable Island, Nova Scotia ($N=31$)

Parameter	Shallow (<20 m) dives			Deep (>20 m) dives		
	Mean	Range	CV	Mean	Range	CV
Number of dives per day	127 \pm 16	20–353	71.6	61 \pm 7	4–136	59.5
Maximum depth (min)	10.5 \pm 0.5	6.1–17.0	27.6	38.8 \pm 2.2	25.9–78.4	30.9
Duration (min)	3.0 \pm 0.1	1.8–4.4	18.2	4.6 \pm 0.1	3.7–5.6	11.1
Time at bottom (min)	1.6 \pm 0.1	0.8–2.9	71.6	3.1 \pm 0.1	2.4–4.0	12.7
Ascent rate (m/s)	0.42 \pm 0.02	0.24–0.62	22.1	0.90 \pm 0.02	0.61–1.19	14.9
Descent rate (m/s)	0.40 \pm 0.02	0.25–0.65	24.4	0.81 \pm 0.02	0.60–0.98	12.8
Time since last repeated dive (min)	1.31 \pm 0.14	0.55–4.00	58.1	0.98 \pm 0.02	0.75–1.34	12.6

Data are shown as the mean and range of means calculated for each individual male.

**Figure 2.** Changes in average \pm SE (a) dive depth, (b) duration, (c) bottom time, (d) rate of descent, (e) rate of ascent and (f) number of dives per day for male harbour seals ($N=31$) during the breeding season. The numbers at the top of (a) and (d) indicate the number of males represented at each day.

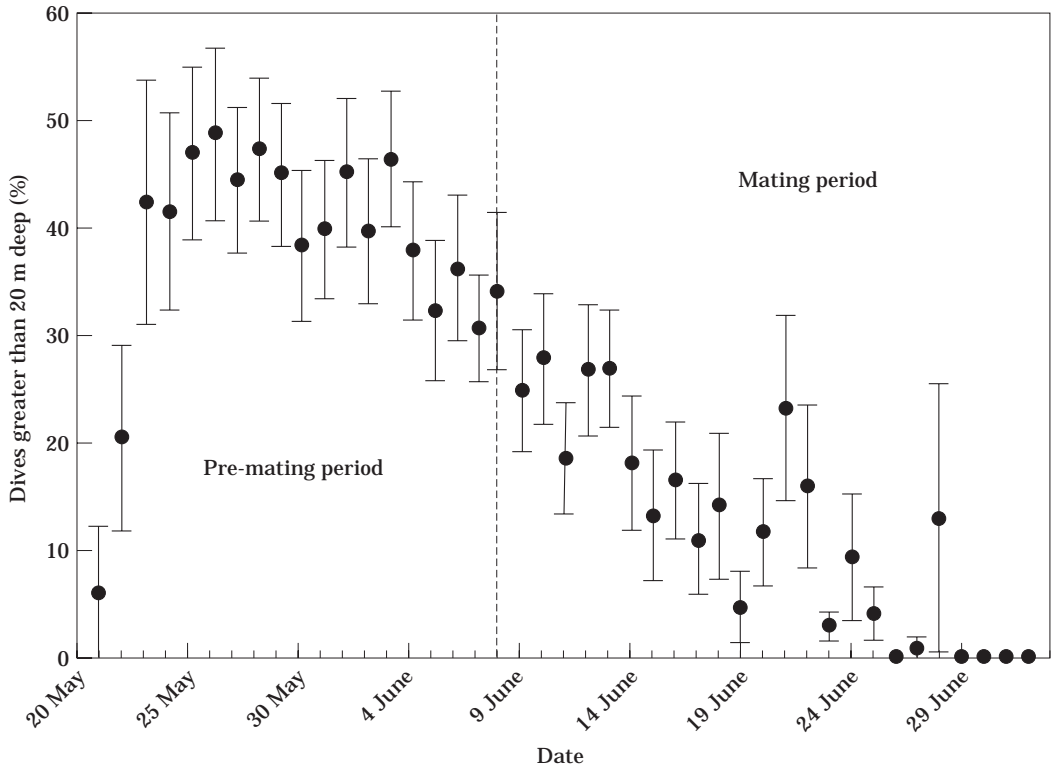


Figure 3. Changes in the percentage of deep (>20 m) dives for male harbour seals ($N=31$) during the breeding season.

mating period, dives generally became shallower (mean dive depth declined from 23.5 ± 1.4 m to 16.6 ± 1.5 m; paired t -test: $t_{30}=5.70$, $P<0.0001$) and shorter (3.9 ± 0.1 versus 3.5 ± 0.1 min; $t_{30}=6.04$, $P<0.0001$), with less time spent at the bottom (2.4 ± 0.1 versus 1.6 ± 0.1 min; $t_{30}=7.20$, $P<0.0001$) and lower rates of ascent (0.65 ± 0.03 versus 0.53 ± 0.02 m/s; $t_{30}=5.45$, $P<0.0001$) and descent (-0.60 ± 0.02 versus 0.50 ± 0.02 m/s; $t_{30}=-5.67$, $P<0.0001$) than they were during pupping in May and early June. Seals also tended to dive more frequently later in the breeding season (mean number of dives per day was 167.2 ± 9.0 versus 228.4 ± 25.6 in the mating period; $t_{30}=-2.83$, $P=0.008$; Fig. 2). The changes in average dive parameters over the breeding season can be mostly attributed to a sharp reduction in the number of deep dives made. The average percentage of dives to depths of greater than 20 m declined from 48.7 ± 4.2 to $24.2 \pm 4.6\%$ in the mating period (paired t -test: $t_{30}=6.32$, $P<0.0001$; Fig. 3).

To determine whether there was a diurnal pattern in diving activity, as has been reported for Scottish male harbour seals (Thompson et al. 1989), we divided the hours of the day into eight equal blocks (Figs 4, 5). The mean percentages of all shallow and deep dives were calculated for each seal for each time block (Fig. 5), and a two-factor repeated measures ANOVA performed over the eight 3-h time blocks. The frequencies of deep and shallow dives differed significantly both with time of day (standardized arcsine square-root transformed variables: $F_{7,420}=49.45$, $P<0.001$) and from each other ($F_{1,60}=13.268$, $P<0.001$). There was a significant interaction between dive depth and time of day ($F_{7,420}=39.48$, $P<0.001$). In general, males made more shallow dives during the dark time periods (2100–0600 hours), but they made more deep dives during daylight hours (0600–1500 hours). The average depth of shallow dives did not vary significantly with time (repeated measures ANOVA: $F_{7,210}=0.032$, $P=0.86$); however, dives to depths greater than 20 m tended

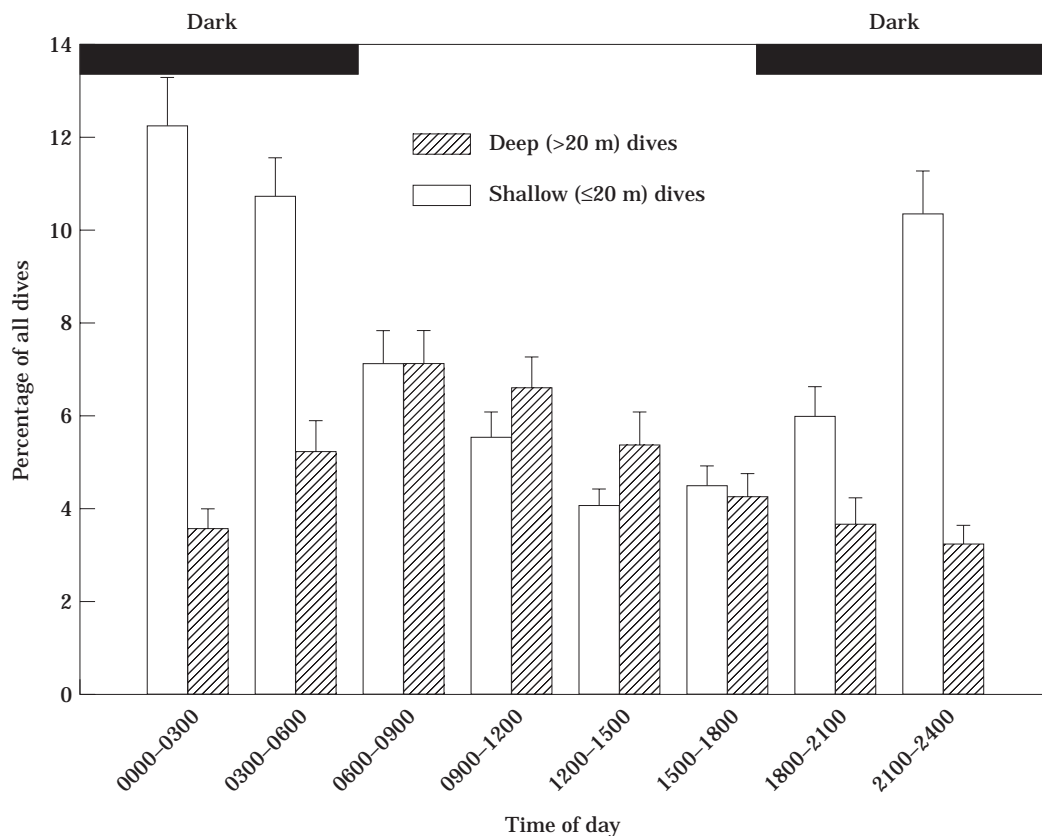


Figure 4. Mean \pm SE percentage of deep and shallow dives of male harbour seals ($N=31$) as a function of time of day.

to be deeper during the daylight hours (Fig. 5) than at night (repeated measures ANOVA: $F_{7,210}=4.36$, $P=0.046$).

Characteristics of Diving Bouts

Graphical representations of dive records (Fig. 1) indicated that male harbour seal dives tended to cluster into two distinct types of bouts distinguished by maximum dive depth: shallow bouts consisting almost entirely of repeated dives to depths less than 20 m, and bouts consisting mainly of considerably deeper dives. When classified by median dive depth, 457 of 642 bouts were thus considered shallow (71.2%) and 185 bouts deep (28.8%; Table III). The characteristics of bout types (bout frequency, dives per bout, time since last bout and bout duration) and of the dives occurring within shallow and deep bouts (average

dive depth, duration, bottom time, rate of ascent, rate of descent and time since last dive) were compared using paired t -tests (Table III). Deep diving bouts occurred less frequently, consisted of more dives, and are longer than shallow diving bouts (Table III). The average parameters of dives occurring within bouts also differed significantly. Dives occurring within deep diving bouts were longer, had longer bottom time, and had greater rates of ascent. There was no significant difference in the mean interval between dives within deep or shallow diving bouts. Except for bout frequency, shallow diving bouts were more variable between males than deep diving bouts, both in the bout characteristics (dives per bout, time since last bout, bout duration, for shallow and deep bouts) and in all dive parameters (Table III). Deep diving bouts occurred more frequently during the pre-mating period (mean percentage of bouts which

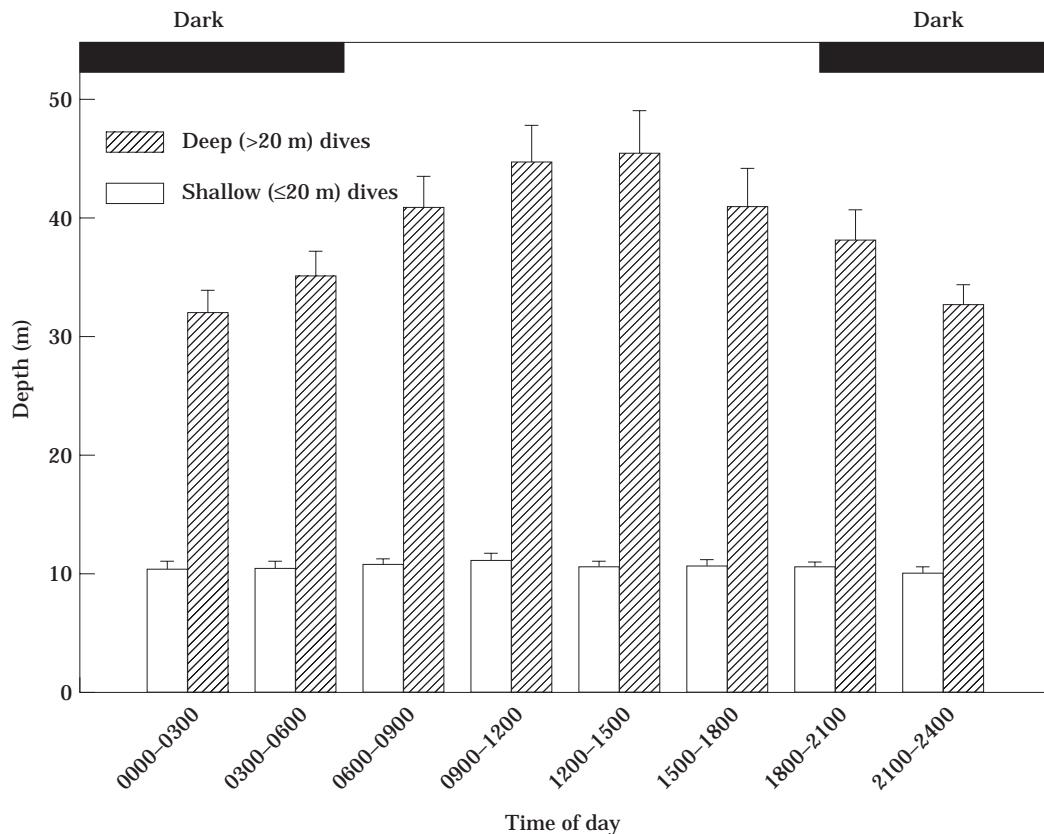


Figure 5. Mean \pm SE depth of deep and shallow dives of male harbour seals ($N=31$) as a function of time of day.

were deep = $37.8 \pm 5.0\%$) than during the mating period ($21.0 \pm 6.3\%$; paired t -test; $t_{30}=2.59$, $P=0.015$; Fig. 6).

Body Size, Mass Change and Diving Activity

The range of initial masses reported here (85–131.5 kg; mean = 108.1 ± 1.8 kg) is comparable to that reported elsewhere for adult male harbour seals on Sable Island (Godsell 1988; Walker & Bowen 1993a). Rates of mass loss (calculated as the difference between the initial and final mass divided by the deployment interval) were variable between individuals (range = 0.02–1.05 kg/day; mean = 0.46 ± 0.04 kg/day; CV = 51.2%). The average mass-specific rate of mass loss for males in this study (calculated as the percentage of initial body mass lost per day) was $0.41 \pm 0.04\%$ day (range = 0.02–0.89%/day; CV = 47.5%).

We postulated that the following variables were related to the rate of mass loss: initial body mass

(positively), deep diving (negatively) and shallow diving (positively). Preliminary univariate analyses (Fig. 7) indicated that the rate of mass loss was significantly correlated with initial mass ($r=0.527$, $N=31$, $P=0.002$), deep dive effort (following arcsine square-root transformation, $r=-0.563$, $N=31$, $P=0.001$) and shallow dive effort (following arcsine square-root transformation, $r=0.491$, $N=31$, $P=0.005$). Initial body mass was not significantly correlated with deep dive effort ($r=0.280$, $N=31$, $P=0.13$) or shallow dive effort ($r=-0.346$, $N=31$, $P=0.06$) over the entire breeding season. Deep and shallow dive efforts were negatively correlated ($r=-0.408$, $N=31$, $P=0.02$). We expected the daily rate of mass loss to be correlated with initial mass since resting metabolic rate increases with body size (Peters 1983); therefore we included initial mass in a step-wise multiple regression analysis on the transformed and standardized dive parameters.

Table III. Characteristics of deep and shallow diving bouts of adult male harbour seals during the breeding season

Parameter	Shallow bouts			Deep bouts				
	N	Mean	Range	CV	N	Mean	Range	CV
Frequency (bouts per day)	31	0.55 ± 0.06	0–1.14	10.7	31	0.23 ± 0.03	0–0.70	14.0
Dives per bout	29	194 ± 33	20–813	92.7	29	421 ± 51	127–1331	64.9
Time since last bout (min)	29	717 ± 106	329–2782	79.5	29	788 ± 76	67–2030	51.8
Bout duration (min)	29	804 ± 117	115–3162	78.1	29	2293 ± 282	684–7202	66.2
Mean dive depth (m)	29	10.4 ± 0.6	5.7–17.4	32.3	29	30.1 ± 1.4	21.0–57.9	24.9
Mean bottom time per dive (min)	29	1.7 ± 0.1	0.5–3.4	35.9	29	2.8 ± 0.1	1.9–3.6	15.3
Mean dive duration (min)	29	3.1 ± 0.1	1.8–4.8	20.1	29	4.3 ± 0.1	3.4–5.3	10.3
Mean rate of ascent (m/s)	29	0.39 ± 0.02	0.23–0.67	25.1	29	0.68 ± 0.02	0.51–0.87	14.2
Mean rate of descent (m/s)	29	0.40 ± 0.02	0.24–0.63	22.8	29	0.76 ± 0.02	0.54–0.93	13.5
Time between dives (min)*	29	1.7 ± 0.3	0.1–8.1	258.6	29	1.2 ± 0.1	0.1–2.2	21.2

*Calculated as the difference between bout duration and the total duration of all dives, divided by the number of dives per bout.

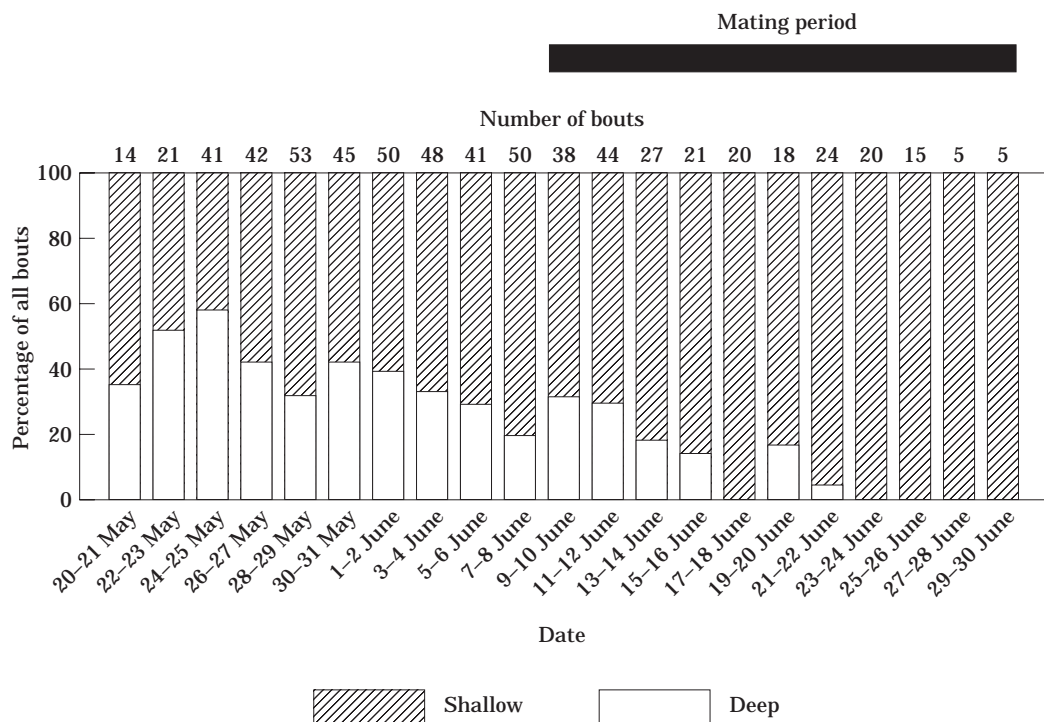


Figure 6. Changes in the percentage of all bouts that were classified as deep and shallow of male harbour seals ($N=31$) during the breeding season. The numbers above indicate the total number of bouts represented in each time interval.

Shallow dive effort was not a significant source of variation in the rate of mass loss when the effects of deep diving and initial body mass were accounted for in the initial multiple regression model ($t_{30} = -0.84$, $P=0.41$). Following the removal of shallow dive effort, mass change varied significantly both with deep dive effort ($t_{30} = -3.13$, $P=0.004$) and initial mass ($t_{30} = -2.79$, $P=0.009$). Together, initial mass and deep dive effort accounted for 46.5% of the variation in individual rates of mass loss ($F_{2,28}=12.16$, $P<0.001$).

Large seals (i.e. with initial masses greater than the median of 108 kg) differed significantly from small males in length ($t_{29} = -3.6$, $P=0.0016$) at the beginning of the breeding season (see Table IV). Large seals lost significantly more of their initial body mass per day, both in absolute terms ($t_{29}=4.50$, $P=0.0001$) and relative to their initial body mass ($t_{29}=3.60$, $P=0.0012$) over the deployment period (Table IV). Over the entire breeding season, large seals made relatively fewer

dives to depths greater than 20 m (t -test of arcsine square-root transformed variables: $t_{29}=3.19$, $P=0.0035$) and their records contained fewer diving bouts which were classified as deep (t -test of arcsine square-root transformed variables: $t_{29}=2.61$, $P=0.0014$).

We used a three-factor, repeated-measures ANOVA model to test for differences in the diving activity (deep and shallow dive effort) of large and small seals between the two periods of the breeding season. The interaction between time period and dive depth was a significant source of variation ($F_{1,27}=39.82$, $P<0.001$), indicating that all males spent significantly more time making shallow dives and less time deep diving in the mating period (Table IV). The interaction between male size and dive depth was also significant ($F_{1,27}=7.94$, $P=0.009$), showing that large males spend significantly more time making shallow dives and less time diving deeply than small males during the breeding season (Table IV). Large males also appear to change their overall diving

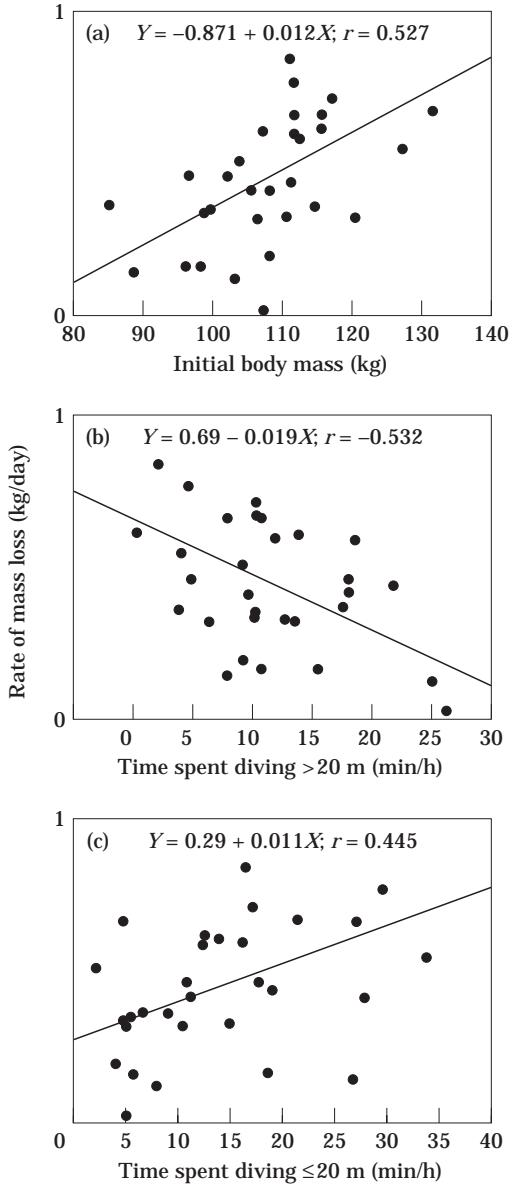


Figure 7. Mass loss as a function of (a) initial body mass, (b) deep dive effort and (c) shallow dive effort for adult male harbour seals ($N=31$) over the breeding season.

patterns earlier than small males. The median day of the last deep diving bout for large males (8 June, the first day of the mating period) occurred significantly earlier in the season than for small males (Mann-Whitney U -test: $N=31$, $Z = -2.18$, $P=0.03$; Table IV).

DISCUSSION

Our results show that adult male harbour seals spend variable amounts of time diving deeply, presumably on feeding trips, during the breeding season at Sable Island. To reach depths of 50 m or greater during these trips, bathymetric maps indicate that males must travel at least 12 km away from the colony. These foraging bouts occurred more frequently during the pre-mating period (Fig. 6). While males were making these foraging trips offshore, females spent most of their time onshore attending their pups (Boness et al. 1994). The likelihood of encountering an oestrous female at sea would therefore be low during this time. Thus, many males apparently continue to forage in relatively deep water offshore prior to the mating period to maintain their body mass, and hence their energy stores, until potentially oestrous females start to make foraging trips in late lactation in the second half of June. This conclusion supports that of Walker & Bowen (1993a), who found that most males maintain or even increase their body mass during the early breeding season.

During the mating period, many males completely ceased deep diving, and most diving activity occurred at depths of less than 20 m (Fig. 3). Most diving bouts were classified as shallow during the mating period (Fig. 6), these bouts sometimes also contained clusters of deep dives. It is possible that some individuals may make brief foraging trips within bouts of predominantly shallow diving or that reproductive behaviour may not be completely restricted to shallow water near the shore (e.g. Scottish harbour seals: Van Parijs et al. 1997). Males also may be feeding opportunistically during periods of shallow dive activity, since deep dive effort and body size accounted for less than 50% of the variation in mass loss. Thus, although there are broad-scale changes in the allocation of time to foraging and reproductive behaviour over the course of the breeding season, our results suggest considerable variation in how individual males allocate time to these behaviours.

The average daily rate of mass loss of male harbour seals in the second half of the breeding season was almost 1 kg/day, representing a mass-specific loss of approximately 0.8% of their initial body mass per day (Walker & Bowen 1993a). Similar rates have been measured in

Table IV. Characteristics of mass loss and diving activity of relatively large and small male harbour seals during the breeding season

Parameter	Large males (<i>N</i> =15)	Small males (<i>N</i> =16)
Standard length (cm)	157.3 ± 1.4	151.4 ± 0.8
Initial mass (kg)	115.8 ± 1.6	100.8 ± 1.7
Mass loss (kg day)	0.61 ± 0.04	0.31 ± 0.04
Mass loss (%/day)	0.53 ± 0.05	0.31 ± 0.04
Deep dives (%)	26.2 ± 5.3	49.8 ± 5.2
Deep bouts (%)	22.8 ± 4.9	42.9 ± 6.5
Pre-mating period		
Shallow diving (min/h)	14.9 ± 1.8	8.7 ± 1.4
Deep diving (min/h)	12.0 ± 1.8	18.7 ± 2.0
Mating period		
Shallow diving (min/h)	24.3 ± 3.0	16.1 ± 3.8
Deep diving (min/h)	5.2 ± 2.2	8.9 ± 2.0
Median day of last deep diving bout relative to June 8*	0 (–16–10)	4 (–9–19)

*Range indicated in parentheses

other male pinnipeds that fast during the breeding season (Anderson & Fedak 1985; Boyd & Duck 1991). Thus, our findings indicate that males generally cease or substantially reduce feeding during shallow diving bouts. Unlike deep diving activity, shallow dives to the bottom in the second half of the breeding season probably occur within 4 km of the breeding colony, given the local bathymetry surrounding Sable Island. In a concurrent study, adult males fitted with VHF transmitters were periodically located at sea throughout the breeding season, and were found within 2 km of shore significantly more frequently in the latter half of the breeding season (D. J. Boness & W. D. Bowen, unpublished data). Evidence from underwater video recordings also shows that during periods of shallow diving activity in the mating period, males are engaged in slow patrolling, agonistic behaviour with other males, and visual and acoustic displays within a more restricted home range near the shore (D. J. Boness, W. D. Bowen, G. Marshall & B. Buhleier, unpublished data). Males vocalize and flipper-slap at the surface, perhaps to attract females or to advertise their presence to other males.

Male diving activity showed a strong diurnal pattern, suggesting that foraging and reproductive behaviours tend to occur at different times of the day (Figs 4, 5). Deeper, foraging dives were more common during daylight hours, when females also tend to forage (Boness et al. 1994). Conversely,

males made approximately twice as many shallow dives during the twilight and dark hours (1800–0600 hours) than during daylight, suggesting that more behaviour associated with acquiring mates occurs during this time. Females generally leave the island in the evening and return from foraging trips in the morning, so males may make many shallow, display dives to maximize their encounter rates during the twilight hours.

Larger males may have a mating advantage over smaller males since, with greater energy stores, they can afford to spend less time foraging during the breeding season. Large seals ceased making deep-diving foraging bouts earlier than small seals, and they spent significantly more time in shallow diving activity near the shore through the breeding season. By behaving in this way, large males may have higher encounter rates with oestrous females, or they may be more likely to establish themselves in a preferential location with respect to predicting female movements at sea. Furthermore, by competing earlier, large males may have access to females that become receptive relatively early in the breeding season, such as non-parturient females. Non-parturient females in captivity come into oestrus 2 weeks earlier than lactating female harbour seals (Reijnders 1990).

Given that males lose up to 1 kg per day in the mating period (Walker & Bowen 1993a), the reproductive behaviour of small males is probably more energetically constrained than that of larger males. Since large seals are significantly longer

than small seals in addition to being more massive, they may also be older. Thus, the differences in the behaviour of large and small males also may reflect differences in experience.

The small body size of harbour seals relative to other pinnipeds has been postulated as an important factor in the evolution of their maternal strategies (Bowen et al. 1992). Larger-bodied phocid females, such as the grey seal and elephant seals, are capable of supporting the entire cost of lactation from their initial body stores; hence they can afford to remain onshore continuously throughout the breeding season. Boness et al. (1994) argued that the constraints of small body size have resulted in the evolution of a maternal foraging cycle in the harbour seal, similar to that seen in otariid females. Since females are energetically forced to spend increasing amounts of time in the water making foraging trips in late lactation as they approach oestrus, small body size may also have helped to maintain aquatic copulation in this species. The results of this study suggest that energetic constraints arising from small body size may also have been important in the evolution of male reproductive strategies. At Sable Island, most males forage during the early stages of the breeding season, then switch to energetically more expensive reproductive behaviour when they can afford to do so, and when it should pay off in terms of mating success.

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