

Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal

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Summary

1. Female mammals increase energy expenditure during lactation to support the high cost of milk production. The extent to which lactation in a small phocid species, the Harbour Seal *Phoca vitulina* L., was fuelled by food vs body stores, how this allocation varied with maternal body mass and the consequences of maternal expenditure on offspring growth were studied.
2. The proportional body composition of 30 females was independent of initial postpartum body mass, but larger females had absolutely more stored energy than smaller ones.
3. Females lost 32% of postpartum body mass and 62% of body energy by late lactation; 97% of energy loss was derived from body fat. Percentage loss of body energy was independent of initial body mass, indicating that females limit their allocation of body stores to offspring by expending a constant proportion of stores rather than a constant amount.
4. Females spent more time diving and individual dives were deeper and longer as lactation progressed. By late lactation, these characteristics of diving were inversely proportional with initial postpartum mass.
5. During early lactation, female expenditures were covered mainly by a reduction in body energy stores. By late lactation, food intake increased six-fold but the extent of this increase varied inversely with postpartum mass.
6. Pup growth rate and weaning mass were positively related to postpartum mass and total daily energy expenditure of females, but were independent of the source of energy used by females during lactation. Pups of heavy females had higher survival than pups of light females.
7. Our results support the hypothesis that maternal body mass is an important determinant of lactation strategies in pinnipeds.

Key-words: Body mass, energetics, Harbour Seal, lactation

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Introduction

Female mammals increase energy expenditure during lactation to support the high demands of milk production (Clutton-Brock, Albon & Guinness 1989; Gittleman & Thompson 1988; Oftedal 1984). Although food intake usually provides most of the energy used to support lactation (Millar 1975; Oftedal 1984), catabolism of maternal tissues also constitutes an important source

of energy exported in milk in some species (Oftedal, Boness & Tedman 1987; Oftedal 1993). These two modes of supporting the energetic costs of lactation (i.e. income and capital breeders) represent either end of a continuum of maternal investment strategies (Stearns 1989). The allocation of time and energy during lactation can affect the fitness of both females and their offspring (Rogowitz 1996). Females face trade-offs because benefits to offspring, such as enhanced growth and survival, may have an associated short-term energetic cost to the female (i.e. excessive loss of body energy stores) that could affect future reproduction and survival (Festa-Bianchet *et al.* 1998; Pomeroy *et al.* 1999). On the other hand, offspring may face increased risk

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through exposure to predation and possibly separation as a result of females foraging during lactation (Boness *et al.* 1992).

Pinnipeds offer an interesting opportunity to study how the timing of energy acquisition and allocation to current reproduction may have affected the evolution of lactation strategies. Females of some species rely exclusively on energy stores, whereas others gather food as the main source of energy during lactation (Bonner 1984). All species give birth to a single offspring, thus removing the confounding effect of litter size in the study of maternal energy expenditure during lactation. Also, maternal postpartum body mass varies by more than 12-fold among species. Until recently (see Boness & Bowen 1996 for review), the two major families of pinnipeds were thought to have dealt quite differently with the need to forage at sea but give birth on land or ice: the Otariidae (fur seals and sea lions) having evolved a 'foraging cycle strategy' and the Phocidae (true seals) a 'fasting strategy' (Bonner 1984; Oftedal *et al.* 1987). Evidence for this phylogenetic dichotomy in maternal lactation strategies comes mainly from comparisons of otariid patterns with those of the larger phocid species (i.e. those >150 kg body mass; Boness, Bowen & Oftedal 1994; Boness & Bowen 1996). However, recent studies on a small phocid species, the Harbour Seal (*Phoca vitulina* L.), show that lactating females exhibit a foraging cycle similar to that observed in otariids (Boness *et al.* 1994; Thompson *et al.* 1994). Bowen, Oftedal & Boness (1992) found that through late lactation Harbour Seal females deplete their body energy stores to a greater extent than other phocid species studied to date. This suggested that in the absence of feeding, lactation could not be sustained and thus food intake might be an important contribution to the energy demands of lactation in this species.

We investigated the extent to which lactation in a small phocid species was fuelled by food intake and how energy allocation and maternal foraging behaviour varied with maternal postpartum body mass. We hypothesized that larger females, with greater energy stores, would spend less time foraging during lactation and more time delivering milk to their offspring than smaller females. In turn, we expected that differences in such patterns of provisioning by mothers would affect the rate of growth and preweaning survival of offspring (Gittleman & Thompson 1988).

Materials and methods

Our study was conducted in May and June on Sable Island, Nova Scotia, Canada (43°90' N, 60°00' W). Thirty Harbour Seal females and their pups were studied; 16 in 1990 and 14 in 1991. Each day all new-born pups were marked with an individually numbered hind-flipper tag. Thus pup age and lactation stage of females were known. Females and pups were weighed at parturition to the nearest 0.5 kg and 0.1 kg, respectively. Maternal age was known for only 6 of the 30 females.

FORAGING EFFORT

Each female was fitted with a MK3 + time-depth recorder (TDR; Wildlife Computers, Redmond, WA, USA) at initial capture to study diving behaviour. Once sedated (0.5–0.7 mg kg⁻¹ of diazepam), the TDR and epoxy mount (about 0.4% of body mass) were glued to the surface of the hair on the lower-back of females using a 5-min epoxy (Boness *et al.* 1994). TDRs were programmed to sample every 10 s. TDRs were recovered near the end of lactation and recorded dive data were analysed as described in Boness *et al.* (1994). Dives to depths ≥4 m were used in the analysis because it is only feasible to correct for transducer drift in blocks of dives. Thus dives <4 m may include instrument noise.

As most diving of Harbour Seal females occurred in clusters or bouts of dives, our analysis of diving behaviour was focused on these bouts, operationally defined following Boness *et al.* (1994). Based on the presence of food in lavage samples of females returning from sea, it was assumed that most bouts of diving represented foraging (Boness *et al.* 1994). Diving effort (DEF) was calculated for each female using the following index:

$$\text{DEF}(\text{m min h}^{-1}) = \frac{\sum_{i=1}^n 2m_i t_i}{T} \quad \text{eqn 1}$$

where m_i is depth in metres and t_i is dive duration in minutes of the i th dive in a set of n dives occurring in T hours of sampling.

TOTAL BODY WATER AND WATER FLUX

Total body water (TBW) and rates of water flux in adult females were estimated using deuterium oxide (D₂O) dilution following the methods described in Oftedal & Iverson (1987). Briefly, a preweighed quantity of D₂O (99.8 atom percentage excess, Atomic Energy of Canada, Chalk River, Ont., Canada) was administered by gastric tube at a dose of approximately 3 g kg⁻¹ body mass on the day of parturition. Two blood samples were taken to establish that equilibration had occurred. Time of the initial sample varied from 3 to 4 h postadministration, with the second sample being taken 20 min later. Females were subsequently weighed and blood sampled every 5–7 days to estimate the fractional turnover rate of body water. To determine late-lactation TBW, females were again weighed and equilibrated with D₂O at 20–21 days postpartum (dpp). Average lactation length in this population is 24 days (Muelbert & Bowen 1993). Although we would have liked to study each female over her entire period of lactation, it was difficult to predict when individual females would finish lactation and leave the colony.

Total water was recovered from serum by heat distillation and assayed for D₂O concentration using infrared spectrophotometry (Oftedal & Iverson 1987). TBW was estimated from isotope dilution space using the equation of Bowen & Iverson (1998). In the absence

of data on adult Harbour Seals, components of body composition were estimated from TBW using the equations in Reilly & Fedak (1990) developed for Grey Seals (*Halichoerus grypus*). An estimate of total body energy (TBE) was calculated based on the energy density of protein (23.6 MJ kg⁻¹) and fat (39.3 MJ kg⁻¹; Blaxter 1989).

Daily fractional water flux (k) of females was calculated from changes in ln (D₂O) concentration over time, corrected for changes in dilution space assuming that changes in TBW were linear during the period of study. Independent two-point estimates of k were calculated for each female during early (0–5 dpp, k_e) and late (14–20 dpp, k_l) lactation. Estimates of average daily total body water flux over lactation (TBWF), and during early (TBWF_e) and late (TBWF_l) lactation, were calculated for each female from the appropriate k and average daily change in TBW (Δ TBW) as:

$$\text{TBWF} = k \times \text{TBW}_{0.5} + \Delta \text{TBW} \quad \text{eqn 2}$$

where TBW_{0.5} represents the estimated TBW at the mid-point of the appropriate period.

TBWF in lactating females represents a combination of water exported directly into milk, free water intake from prey consumption and metabolic water produced from the catabolism of fat and protein for energy metabolism. Daily milk water (MW) exported by each female was estimated from the daily mass gain of her pup (PMG), using the following relationship based on 21 Harbour Seal females and pups previously studied in this population (O. T. Oftedal, W. D. Bowen & D. J. Boness, unpublished data): MW (kg) = 0.22 + 0.37 PMG (kg); $r^2 = 0.53$.

Daily food intake (FI) over the entire study period, and during early and late lactation (as defined above), was estimated using the equation of Oftedal & Iverson (1987), modified to account for MW export and digestible energy losses as follows:

$$\text{FI} = 100 \times \frac{(\text{TBWF} - \text{MW}) + 1.07 \times \Delta \text{F} + 0.42 \times \Delta \text{P}}{\% \text{Wfood} + \text{DE} \times (1.07 \times \% \text{Ffood} + 0.42 \times \% \text{Pfood})} \quad \text{eqn 3}$$

where Δ F = daily change in body fat content, Δ P = daily change in body protein content, %Wfood = percentage of water in food, DE = proportion of digestible energy (0.93; Ronald *et al.* 1984; Lawson, Miller & Noseworthy 1997), %Ffood = percentage of fat in food, and %Pfood = percentage of protein in food. For these calculations, we assumed a diet of sand lance (*Ammodytes* spp.), the major prey (65% of 28 lavage samples containing food) of females during the breeding season, composed of 72.6% water, 7.9% fat, 15.9% protein ($n = 38$, S. J. Iverson & W. D. Bowen, unpublished data). Other foods were shrimp (*Crangon* spp., 20%) and American Plaice (*Hippoglossoides platessoides*, 15%), both having about half the energy density of sand lance (W. D. Bowen,

D. J. Boness & O. T. Oftedal, unpublished data). Although FI estimates are relatively insensitive to the assumption of prey type, the energy intake of the females may have been overestimated in our study. Daily gross food energy intake (FEI) was calculated from FI based on 39.3 MJ kg⁻¹ fat and 23.6 MJ kg⁻¹ protein. FEI was then converted to daily metabolizable energy intake (MEI) assuming metabolizable energy was 85% of food energy intake (Ronald *et al.* 1984; Lawson *et al.* 1997). All females depleted total body energy (TBE) during lactation. Therefore, total daily energy expenditure (DEE) was calculated as DEE = $|\Delta \text{TBE}| + \text{MEI}$.

To account for the serial correlation in our measurements of body mass, mixed-effects repeated-measures linear models (Laird & Ware 1982) were used to estimate rates of maternal mass loss and pup mass gain. Maximum likelihood estimates of parameters were obtained using the implementation in S-Plus 4.0 for Windows. Differences among models were assessed using log-likelihood ratio tests. Other statistical analyses were performed with SPSS 8.0. Non-normally distributed data were transformed as necessary using either log or arcsin square root transformations. The standard error (SE) is reported with means.

Results

Twenty-three of the 30 mother–pup pairs were studied to weaning. Seven females lost their pups before the end of lactation (Table 1). The data from these seven pairs was used only in analyses dealing with early lactation. The TDR records of 16 females covered 70–100% of the lactation period. In another five cases, only 25–40% of lactation was sampled due to premature failure of the TDR battery (Table 1). No data were recovered from the remaining two TDRs.

In 1990 and 1991, average postpartum body mass of females (86.7 ± 2.47 vs 83.8 ± 2.49, respectively) and birth mass of pups (11.1 ± 0.21 vs 10.5 ± 0.27, respectively) did not differ (females, $t = 0.82$, $df = 28$, $P = 0.57$; pups, $t = 1.62$, $df = 28$, $P = 0.42$). New-born male pups (10.9 ± 0.27, $N = 16$) were not significantly ($P = 0.52$) heavier than female pups (10.7 ± 0.22, $N = 14$) in this small sample, but a larger sample collected over 6 years demonstrated that male pups are significantly heavier than female pups in this population (Bowen *et al.* 1994). Pup birth mass was not significantly correlated with maternal body mass at parturition (Pearson $r = 0.28$, $P = 0.14$), again in contrast to a previous study based on a larger sample (Bowen *et al.* 1994).

Survival to weaning of pups born to females greater than the median mass was greater (93.3%) than that of pups born to lighter females (60.0%; Fisher's one-sided exact test, $P = 0.04$). Among the 23 females that completed lactation, duration of lactation varied from 17 to 29 days. Heavier females tended to lactate for longer periods of time than lighter females, but this correlation was not significant ($r = 0.37$, $P = 0.09$).

Table 1. Maternal postpartum body mass, percentage of lactation covered by time–depth recorder data and weaning status of offspring for 30 female Harbour Seals. Females listed in descending order of body mass. Days postpartum = dpp

Female	Postpartum body mass (kg)	TDR record interval (days)	Lactation duration (days)	% lactation sampled by TDR	Pup status
1990					
D190	105.3	0–21	28	78	Weaned
D990	100.2	0–8*	21	38	Weaned
D690	96.5	0–7*	29	28	Weaned
D790	94.4	0–19	27	70	Weaned
D290	94.1	0–20	24	88	Weaned
D890	93.4	None†	20	0	Weaned
D1090	87.0	0–4	–	–	Shark kill, 3 dpp
D590	85.9	0–20	24	88	Weaned
D490	85.2	0–9*	27	41	Weaned
D390	83.2	0–4	–	–	Shark kill, 2 dpp
D1290	81.5	0–6*	27	26	Weaned
D1390	80.3	0–8*	25	36	Weaned
D1590	79.5	0–20	17	100	Weaned
D1690	77.2	0–3	–	–	Missing, 1 dpp
D1490	72.0	0–12	–	–	Missing, 8 dpp
D1190	71.5	0–10	–	–	Missing, 7 dpp
1991					
D191	95.4	0–20	27	74	Weaned
D1291	97.2	0–19	21	90	Weaned
D1391	95.0	0–19	22	86	Weaned
D1091	92.5	0–18	19	95	Weaned
D691	85.0	0–20	22	91	Weaned
D391	84.3	None†	>22	0	Weaned
D1491	84.0	0–14	–	–	Missing after storm, 14 dpp
D491	83.7	0–20	22	91	Weaned
D291	82.0	0–4	–	–	Missing after storm, 2 dpp
D591	81.9	0–20	23	87	Weaned
D891	77.5	0–20	22	91	Weaned
D791	76.5	0–26	19	100	Weaned
D991	71.7	0–20	19	100	Weaned
D1191	65.5	0–19	22	86	Weaned

*Premature battery failure.

†Recorder flooded with sea water.

Table 2. Change in body composition of lactating Harbour Seals during lactation and an estimate of depletion of energy stores. Percentage of postpartum levels lost is given in parentheses. Loss calculated as the difference in composition of 18 females sampled at both times. Days postpartum = dpp

	At birth	Late lactation (20–21 dpp)	Loss
Body mass (kg)	85.3 ± 1.74	58.4 ± 1.51	28.0 ± 1.00 (32.3)
TBW (kg)	43.4 ± 0.92 (50.8)	38.0 ± 0.91 (65.2)	5.9 ± 0.60 (13.1)
Fat (kg)	25.9 ± 0.67 (30.4)	5.5 ± 0.53 (9.23)	20.9 ± 0.80 (79.7)
Protein (kg)	14.2 ± 0.31 (16.6)	13.2 ± 0.32 (22.6)	1.1 ± 0.20 (7.6)
Body energy (MJ)			
Fat (MJ)	1019.3 ± 26.43 (75.2)	214.5 ± 20.89 (39.3)	820.0 ± 30.3 (79.7)
Protein (MJ)	334.2 ± 7.26 (24.8)	311.6 ± 7.46 (60.7)	26.6 ± 4.80 (7.6)
Total (MJ)	1353.5 ± 30.90	526.1 ± 23.40	846.6 ± 29.61 (61.7)
Loss (MJ day ⁻¹)			42.4 ± 1.51
N	30	18	18

CHANGES IN MATERNAL BODY COMPOSITION AND MASS

At parturition, females contained an average of 43.4 kg of body water representing 50.8% of postpartum mass (Table 2). Postpartum females averaged 30.4% body fat and showed little variation (CV = 8.9%) in this

component. Fat accounted for an average of 75.2% and protein for 24.8% of the 1353.5 MJ of TBE.

Estimates of ln TBW scaled linearly with ln postpartum body mass of females with an exponent not significantly different from 1.0 ($b_0 = 0.98$, 95% CL 0.86–1.10, $P = 0.762$). There was no significant difference in the exponents in 1990 and 1991 (1.09, 95% CL

Table 3. Mixed-effects model estimates of mass loss (kg) of 24 Harbour Seal females over the course of lactation

Model	β_0 (SE)	β_1 (SE)	β_2 (SE)	Log-likelihood	<i>P</i>
I Common intercept and slope	86.2 (1.96)	-1.4 (0.05)		-291.55	
II Intercepts differ by pup sex, common slope	F: 86.4 (2.20) M: 86.1 (2.12)	-1.4 (0.05)		-291.54	0.89
III Common intercept and slopes differ by pup sex	87.1 (1.39)	F: -1.4 (0.06) M: -1.4 (0.06)		-335.57	
IV Common intercept and slopes with quadratic term	87.1 (1.95)	-1.76 (0.07)	0.01 (0.003)	-277.83	<0.001

β_0 = intercept, β_1 = slope, β_2 = slope of quadratic term; *P* represents the probability of each model relative to Model I.

0.96–1.22 and 0.90, 95% CL 0.71–1.09, respectively). Heavier females contained more TBE than lighter females on an absolute basis (Pearson $r = 0.91$, $N = 30$, $P < 0.001$); however, the ratio of fat to lean tissue did not vary significantly with initial maternal postpartum body mass (Pearson $r = 0.04$, $P = 0.84$).

During the initial 80% of lactation, females lost 32.3% of their postpartum body mass and expended an average of about 61.7% of their initial TBE (Table 2). Depletion of body fat and protein accounted for 96.9% and 3.1% of this energy loss, respectively. On average, females lost 42.4 MJ day⁻¹ over the first 20 days of lactation. Average daily energy loss from body stores scaled isometrically with postpartum body mass (exponent 1.08, test of exponent = 1.0, $P = 0.676$). Females used almost 80% of their fat stores over the first 20 days of lactation.

A quadratic model described the rate of loss of maternal body mass over this period significantly better than a linear model (Table 3). As the rate of mass loss was lower during late lactation, the rate of fat loss likely also declined during this period. Pup sex had no significant effect on the pattern or rate of female mass loss (Table 3).

MATERNAL DIVING BEHAVIOUR DURING LACTATION

The diving behaviour of females was examined in early (0–6 dpp), middle (7–13 dpp) and late (14–20 dpp)

lactation. The onset of diving bouts varied considerably among females. Only one female (the heaviest at 105.5 kg) that was studied through late lactation had no bouts of diving. Two other females (96.5 kg and 85.2 kg postpartum body mass) also had no bouts of diving, but TDR records for these females were only available in early and mid-lactation. Among the other 21 females (65.5–100.2 initial mass), diving bouts began at an average of 5.4 ± 4.38 dpp (range 1–16 days). Nearly a third of diving bouts lasted less than 1 h, during which it was presumed that relatively little foraging occurred. When these short bouts were removed from the data, the average onset of bouts increased to 8.0 ± 1.29 dpp. Among these 21 females, there was no significant correlation between the day of the first diving bout >1 h and postpartum mass (Pearson $r = 0.16$, $P = 0.46$).

A repeated-measures ANOVA on log-transformed data, with postpartum mass as a covariate, was used to examine changes in the characteristics of dive bouts over the course of lactation (Table 4). The number of bouts per female increased five-fold from early to late lactation. The interaction term with maternal postpartum mass was not significant. The duration of individual bouts increased 10-fold during the same period; however, here there was a significant interaction with maternal postpartum mass ($F_{2,28} = 7.2$, $P = 0.003$). Bout duration was unrelated to maternal postpartum mass during early lactation, but was inversely related to maternal postpartum mass in mid- and late lactation ($r = -0.61$,

Table 4. Characteristics of diving bouts and of individual dives in 16 lactating females over the course of lactation in 1990 and 1991

	Early lactation (0–6 dpp)		Mid-lactation (7–13 dpp)		Late lactation (14–20 dpp)		$F_{2,28}$ *	<i>P</i>
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range		
Number of bouts	1.9 ± 0.64	0.0–8	5.4 ± 1.65	0.0–18	10.0 ± 2.49	0–31	4.2	0.026
Bout duration (h)	0.5 ± 0.18	0.0–2.6	1.7 ± 0.43	0.0–5.3	5.1 ± 0.95	0.0–13.0	11.0	<0.001
Time spent in bouts (%)†	3.0 ± 1.36	0.0–19.0	6.5 ± 1.83	0.0–27.7	26.6 ± 5.24	0.0–57.2	25.2	<0.001
Dive depth (m)	4.9 ± 1.36	0.0–16.1	10.5 ± 1.99	0.0–23.7	15.7 ± 2.78	0.0–32.0	7.9	<0.002
Dive duration (min)	0.5 ± 0.16	0.0–1.7	1.2 ± 0.21	0.0–2.4	1.5 ± 0.24	0.0–2.7	5.4	0.01
Bottom time (min)	0.3 ± 0.09	0.0–1.0	0.7 ± 0.15	0.0–1.7	1.0 ± 0.17	0.0–1.9	6.1	0.01
Time between successive dives (min)	0.9 ± 0.48	0.0–7.8	0.6 ± 0.09	0.0–1.2	0.6 ± 0.09	0.0–0.98	0.4	0.66

*Repeated measures ANOVA with main effects and two-way interaction, maternal mass as covariate.

†Arcsin transformed.

$N = 16$, $P = 0.01$). Percentage of time spent in dive bouts also increased significantly throughout lactation. However, variability among females was large; some females spent no time in diving bouts during late lactation whereas others spent up to 57% of their time in diving bouts.

Characteristics of individual dives within bouts also changed over the course of lactation among the 16 females with full dive records (Table 4). The mean depth, duration and time spent at the bottom of the dive increased significantly from early to late lactation. However, there were significant interactions between maternal postpartum mass and the changes in these dive parameters. For each variable, there was no significant relationship with maternal postpartum mass until late lactation when lighter females made longer dives with more time spent at greater bottom depths than did heavier females. There was no significant change over lactation in the time spent at the surface between dives within a bout.

Mean dive effort of these 16 females increased significantly from $14.0 \pm 11.07 \text{ m min}^{-1}$ ($CV = 316\%$) and $49.6 \pm 19.4 \text{ m min}^{-1}$ ($CV = 156\%$) in early and mid-lactation, respectively, to $678.6 \pm 196.12 \text{ m min}^{-1}$ ($CV = 116\%$) in late lactation (repeated-measures ANOVA on log-transformed data, $F_{2,28} = 6.7$, $P < 0.001$). The interaction term was significant ($P = 0.02$) with maternal postpartum mass being inversely correlated with dive effort only during late lactation (Pearson $r = -0.50$, $P = 0.02$). With few exceptions, females increased diving effort during mid- and, particularly, during late lactation (Fig. 1).

WATER FLUX, ENERGY INTAKE AND ENERGY EXPENDITURE

There were no significant differences between years in the daily TBWF (t -test, $P = 0.33$), FI ($P = 0.23$), depletion of TBE ($P = 0.45$), DEE ($P = 0.86$), or percentage of DEE of lactating females derived from food intake (arcsin-transformed data, $P = 0.20$). Thus, the data from the two years were combined. Over the first 20 dpp, females ingested an average of $12.3 \pm 1.4 \text{ MJ day}^{-1}$, although this varied considerably among individuals (range 0.3 – 25.6 MJ day^{-1}). On average, 19% of DEE was derived from MEI, but again there was considerable variability in this percentage among females (Table 5). Nevertheless, all females were in negative energy balance.

There were significant changes in the sources of energy expended by females between early and late lactation (Table 6). FEI (and thus MEI) increased nine-fold between early and late lactation, while the loss of TBE decreased by 30%. Although DEE did not differ significantly between the two periods, the percentage of DEE derived from MEI increased by more than six times between early and late lactation.

The sources of energy used over the whole of lactation were correlated with postpartum body mass of females. MEI and the percentage of DEE derived from MEI

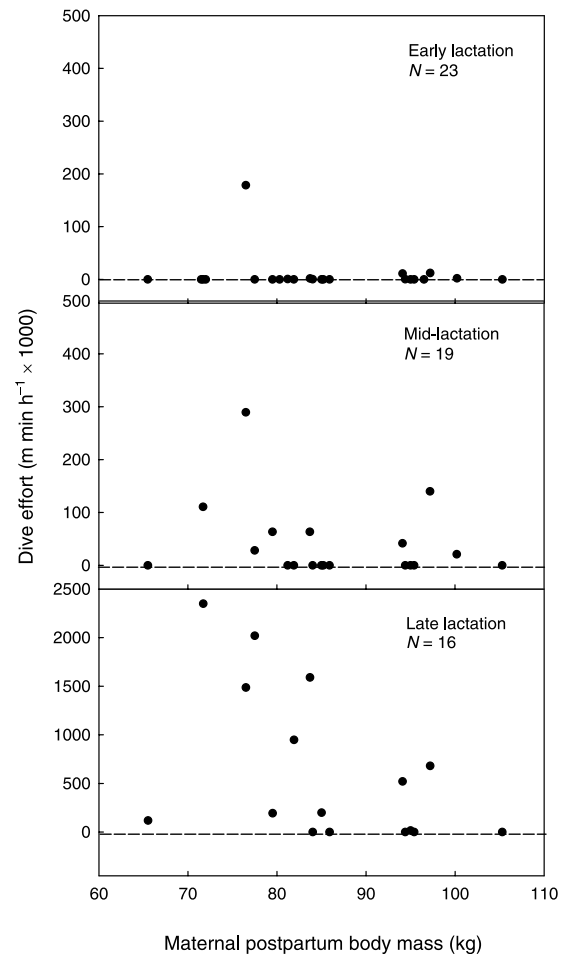


Fig. 1. Diving effort ($\text{m min}^{-1} \times 1000$) of adult female Harbour Seals in early, mid- and late lactation as a function of initial postpartum body mass.

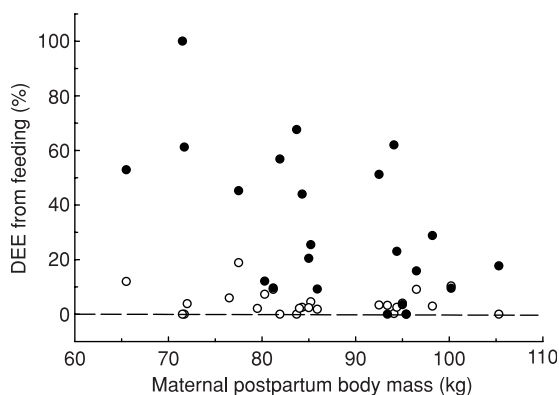
were negatively correlated with postpartum body mass ($r = -0.60$, $N = 21$, $P = 0.004$, and $r = -0.70$, $P < 0.001$, respectively). By contrast, depletion of TBE ($r = 0.76$, $P < 0.001$) and DEE ($r = 0.46$, $P = 0.04$) were both positively correlated with maternal postpartum mass. However, the sources of energy used to support lactation differed between early and late lactation (Fig. 2). In early lactation, neither MEI ($r = -0.16$, $N = 26$, $P = 0.43$) nor the percentage of DEE derived from MEI ($r = -0.19$, $P = 0.34$) was significantly correlated with maternal postpartum mass, while depletion of TBE ($r = 0.42$, $P = 0.03$) and DEE ($r = 0.46$, $P = 0.02$) were only weakly correlated with postpartum mass. Since late lactation energetics might be more related to maternal mass at mid-lactation than at parturition, late lactation variables were compared with maternal mass taken at 14 dpp. During late lactation, MEI ($r = -0.37$, $N = 21$, $P = 0.10$) was not significantly correlated with mid-lactation mass. However, both depletion of TBE ($r = 0.72$, $P < 0.001$) and DEE ($r = 0.63$, $P = 0.002$) were positively correlated with mid-lactation maternal mass, while the percentage of DEE from food ($r = -0.62$, $P = 0.003$) was negatively correlated with mid-lactation mass.

Table 5. Daily body water flux, energy intake and energy expenditure by 21 female Harbour Seals during lactation

	Mean \pm SE	Range	CV
Mid total body water (kg)	41.7 \pm 0.98	32.7–48.8	10.8
Fractional turnover rate (k)	0.08 \pm 0.004	0.05–0.12	25.0
Total body water flux (l day ⁻¹)	3.2 \pm 0.15	2.0–4.6	21.6
Metabolizable food energy intake (MEI, MJ day ⁻¹)	10.4 \pm 1.21	0.2–21.8	53.2
Depletion of body energy (TBE, MJ day ⁻¹)	44.6 \pm 1.68	30.9–55.7	17.0
Total daily energy expenditure (DEE, MJ day ⁻¹)*	55.1 \pm 1.20	47.9–69.6	10.0
Percent of DEE from MEI	19.1 \pm 2.31	0.4–40.3	55.4

*DEE = $|\Delta TBE| + MEI$.**Table 6.** Comparison of body water flux, energy intake and energy expenditure by 21 female Harbour Seals in early and late lactation. Only early and late periods were tested due to non-independence of isotope data in the middle period (i.e. day 6 and 14 samples) from early and late periods

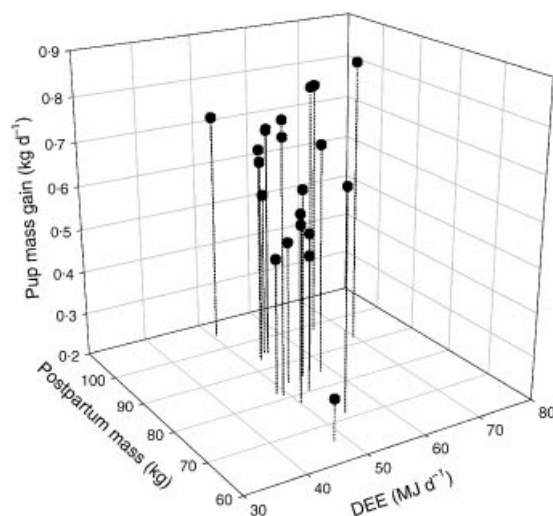
	Early (0–6 dpp)	Late (14–20 dpp)	Paired <i>t</i> -value	<i>P</i>
Total body water flux (l day ⁻¹)	2.1 \pm 0.09	3.9 \pm 0.42	4.3	<0.001
Metabolizable food energy intake (MEI, MJ day ⁻¹)	1.5 \pm 0.66	13.7 \pm 2.63	4.3	<0.001
Depletion of body energy (TBE, MJ day ⁻¹)	53.5 \pm 2.52	37.3 \pm 3.73	3.7	0.001
Daily energy expenditure (DEE, MJ day ⁻¹)*	55.6 \pm 2.25	51.4 \pm 2.77	1.5	0.14
Percent of energy from MEI	4.5 \pm 1.08	29.3 \pm 4.91	4.8	<0.001

*DEE = $|\Delta TBE| + MEI$.**Fig. 2.** Relationships between percentage of DEE derived from food intake during early (○; 0–5 dpp, *N* = 26) and late (●; 14–20 dpp, *N* = 21) lactation and initial postpartum body mass of females.

PUP GROWTH AND MATERNAL ENERGY EXPENDITURE DURING LACTATION

Mass gain of pups over the first 20 days of lactation was linear at an average rate of 0.64 ± 0.03 kg day⁻¹ (*N* = 21, *P* = 0.01). The model fit was not significantly improved by allowing separate intercepts for male and female pups with a common slope (*P* = 0.81) or common intercepts with separate slopes (*P* = 0.33).

To examine the influence of maternal traits on pup mass gain, stepwise regression models were developed for early, late and overall lactation. Initial maternal postpartum mass was the only significant variable, explaining 24% of the variability in pup mass gain in early lactation ($F_{1,24} = 8.9$, *P* = 0.006) and 17% of the variability in late lactation ($F_{1,19} = 4.9$, *P* = 0.038). Over

**Fig. 3.** Daily rate of pup mass gain in relation to initial maternal postpartum mass and maternal DEE for 21 mother–pup pairs.

the whole of lactation, both DEE and maternal postpartum mass were significant predictors of the daily rate of pup mass gain, accounting for 46% of the observed variability ($F_{1,19} = 9.9$, *P* = 0.001; Fig. 3). Variables excluded from these models were MEI, depletion of TBE and percentage of total DEE from MEI.

Pups were weaned at an average of 25.9 ± 0.87 kg (16.0–32.4 kg, *N* = 21). Weaning mass was positively correlated with maternal postpartum mass (Pearson $r = 0.68$, *P* < 0.001). Postpartum mass of females explained 43% of the variability in weaning mass (stepwise multiple regression, $F_{1,19} = 16.2$, *P* = 0.001). Variables excluded from the model were MEI, DEE, depletion of TBE and percentage of total DEE from MEI.

Discussion

Our findings indicate that female body mass in this small phocid species plays a significant role in determining maternal foraging behaviour and energy allocation, and offspring preweaning survival, mass gain and weaning mass. Lighter females spent more time at sea and derived a greater fraction of DEE from food intake, whereas heavier females relied to a greater extent on body energy stores to fuel lactation. Lighter females also had a greater chance of losing their pup prior to weaning. However, despite differences in how females supported lactation, the source of energy allocated to offspring played little role in offspring growth. What mattered was the absolute level of DEE by females, which in turn was determined largely by postpartum body mass. Given the distribution of female body masses among phocid species, it is likely that about half of the 18 species of the Phocidae may forage during lactation (Boness & Bowen 1996; Boyd 1998). Thus, our finding that the degree of foraging by lactating female Harbour Seals is inversely correlated with body mass may have broad significance for understanding phocid lactation strategies.

MATERNAL BODY COMPOSITION

The adult females in our study encompassed the full range in body size observed in this population (Bowen *et al.* 1994). Given that the largest female weighed 1.6 times the smallest, it would be expected that heavier females would have been better prepared (i.e. being both relatively and absolutely fatter) to support lactation than lighter females. However, the percentage of postpartum TBW (and thus fat content) of females was independent of body mass and varied little among females. With a sample of 30 females, the power to detect a moderate correlation between mass and percentage TBW of 0.5 is about 0.9. Thus, on a proportional basis, all females were similarly prepared to support lactation from body stores. Similar findings have been reported in several other phocid species (Bowen, Oftedal & Boness 1987; Fedak, Arnbohm & Boyd 1996; Mellish, Iverson & Bowen 1999). These results suggest that stabilizing selection may place upper limits to fat content and that females that are too lean are less likely to return to the breeding colony to give birth.

Benefits to offspring of maternal transfer of nutrients may have associated maternal costs (Rogowitz 1996). On an absolute basis, the heaviest Harbour Seal females had almost twice the stored energy of the lightest females. Given the difference in absolute energy stores, a small female Harbour Seal might be at greater risk of depleting critical body energy stores to a point where survival or future reproduction would be negatively affected. Conversely, heavier females might spend energy at a faster rate than lighter ones, thus tending to deplete body stores more rapidly than lighter females. Our findings, coupled with those on the Grey Seal (Mellish *et al.* 1999) and the Southern Elephant Seal (*Mirounga*

leonina; Fedak *et al.* 1996), that the relative depletion of body energy stores is independent of postpartum mass of females, does not support this hypothesis. Thus, phocid females appear to deplete a constant proportion of body stores in support of lactation rather than a constant amount (Fedak *et al.* 1996), indicating that females do not respond to the needs of offspring beyond that which might jeopardize their future reproduction. Similar results have been found in Bighorn Sheep (*Orvis canadensis*; Festa-Bianchet & Jorgenson 1998), suggesting that this may be a common feature among large mammals.

FORAGING BEHAVIOUR DURING LACTATION

Previous studies have shown that Harbour Seal females make trips to sea during lactation and that females exhibit bouts of diving during these trips (Boness *et al.* 1994; Thompson *et al.* 1994). Our results demonstrate that these trips are indeed associated with foraging and that some females derive a significant fraction of their DEE from food intake. Harbour Seal females began bouts of diving >1 h at about 8 dpp, but the onset of bouts was independent of postpartum mass, suggesting that most females have ample body stores to support the energetic costs of early lactation. In this respect, Harbour Seal females behave much like otariid pinniped species (i.e. fur seals and sea lions; Boness *et al.* 1994; Boness & Bowen 1996). Our results also suggest that females tend to begin foraging when the benefits to females are greatest in terms of augmenting energy stores and the risks of leaving offspring unattended or taking them on foraging trips are reduced. The risk of losing offspring appears to be greatest for females within the first week of lactation (this study; Bowen, Boness & Iverson 1999). During the first week of life pups cannot match the diving ability of their mothers and therefore are at greater risk of being lost or killed by sharks if the female is diving deeply to forage. Increased foraging by females after the first week of lactation corresponds well with increased diving ability of their pups (Bowen *et al.* 1999).

Unlike most larger species of phocid seals that can be regarded as true capital breeders (Costa *et al.* 1986; Iverson *et al.* 1993; Fedak *et al.* 1996), most lactating Harbour Seal females derived a significant fraction (i.e. $\approx 20\%$ overall) of their energy requirements from feeding. This fraction increased to an average of 29% in late lactation from 4.5% in early lactation. Thus, Harbour Seal females, like many other mammals, used both stored energy (i.e. capital) as well as income derived from feeding to support the energetic costs of lactation. As such, we might expect lactation performance in such species to be influenced by variation in local prey abundance. Although females of all sizes may be influenced by such variability, our results suggest that large females would have an advantage over small females during periods of food shortage as is found in Bighorn Sheep (Festa-Bianchet *et al.* 1998).

CONSEQUENCES FOR OFFSPRING GROWTH
AND SURVIVAL

Among mammals, larger females often produce larger offspring with a greater likelihood of survival (Clutton-Brock 1991). In our study, the pups of heavier Harbour Seal females gained mass at a greater rate and were heavier at weaning than those of lighter females. Maternal postpartum mass and DEE explained about 46% of the variability in rate of pup mass gain. The larger pups of heavier females were also more likely to survive to weaning than those of lighter females. We had expected that the way in which females supported the energetic costs of lactation might also have an impact on offspring growth. Females that foraged more might spend less time nursing their pups. However, the source of nutrients and energy provided to offspring by females was not a significant predictor of pup mass gain or weaning mass. Instead, the most important factors in harbour seals, as in the larger phocid species (Costa *et al.* 1986; Iverson *et al.* 1993; Fedak *et al.* 1996; Mellish *et al.* 1999; Pomeroy *et al.* 1999), was the size of the female and her absolute daily energy expenditure.

Why then do all females not forage during lactation if it has no effect upon offspring growth and weaning mass? There may be several reasons. First, the effects of variation in life-history traits are often only evident during periods of severe environmental conditions such as food shortage (e.g. Ono, Boness & Oftedal 1987; Clutton-Brock *et al.* 1989; Festa-Bianchet 1989; Boyd *et al.* 1994). Our conclusion that the source of energy allocated to offspring does not influence offspring size may apply only during periods of abundant food for females. Both 1990 and 1991 appear to have been good years at Sable Island. Average pup growth rates and postpartum mass of females were at or above average long-term values for this population (Ellis *et al.* 2000). Thus, during years of abundant food, the sources of energy and nutrients used to support lactation may be relatively unimportant as light females can partially compensate for smaller body stores by feeding. However, this compensation is only partial as evidenced by the lower mass gain of the offspring of lighter females compared with those of heavier ones. Thus, heavier females may have an advantage in a poor-food year, as they would be less affected by local food abundance. In such years, lighter females might be unable to rear their pups to a viable weaning mass whereas heavier females may still produce viable offspring.

A second reason is that there may be a trade-off between exposure of the pup to the risk of mortality and time spent feeding by the female. Two important sources of pup mortality are shark predation and separation of pups from mothers during storms (this study; Boness *et al.* 1992). Lighter females spent more time foraging and thus their pups probably spent more time at sea where they were at greater risk from both sharks and storms. Our finding of lower survival rate among the pups of light females provides evidence for such a trade-off.

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References

- Blaxter, K. (1989) *Energy Metabolism in Animals and Man*. Cambridge University Press, Cambridge.
- Boness, D.J. & Bowen, W.D. (1996) The evolution of maternal care in pinnipeds. *Bioscience* **46**, 645–654.
- Boness, D.J., Bowen, W.D., Iverson, S.J. & Oftedal, O.T. (1992) Influence of storms and maternal size on mother-pup separations and fostering in the harbour seal, *Phoca vitulina*. *Canadian Journal of Zoology* **70**, 1640–1644.
- Boness, D.J., Bowen, W.D. & Oftedal, O.T. (1994) Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behavioural Ecology and Sociobiology* **34**, 95–104.
- Bonner, W.N. (1984) Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symposium of the Zoology Society of London* **51**, 253–272.
- Bowen, W.D. & Iverson, S.J. (1998) Estimation of total body water in pinnipeds using hydrogen-isotope dilution. *Physiological Zoology* **71**, 329–332.
- Bowen, W.D., Boness, D.J. & Oftedal, O.T. (1987) Mass transfer from mother to pup and subsequent mass loss by the weaned pup in the hooded seal, *Cystophora cristata*. *Canadian Journal of Zoology* **65**, 1–8.
- Bowen, W.D., Oftedal, O.T. & Boness, D.J. (1992) Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiological Zoology* **65**, 844–866.
- Bowen, W.D., Oftedal, O.T., Boness, D.J. & Iverson, S.J. (1994) The effect of maternal age and other factors on birth mass in the harbour seal. *Canadian Journal of Zoology* **72**, 8–14.
- Bowen, W.D., Boness, D.J. & Iverson, S.J. (1999) Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. *Canadian Journal of Zoology* **77**, 978–988.
- Boyd, I.L. (1998) Time and energy constraints in pinniped lactation. *American Naturalist* **152**, 717–728.
- Boyd, I.L., Arnould, J.P.Y., Barton, T. & Croxall, J.P. (1994) Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology* **63**, 703–713.
- Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*. Princeton University Press, Princeton, NJ.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1989) Fitness costs of gestation and lactation in wild mammals. *Nature* **337**, 260–262.
- Costa, D.P., LeBoeuf, B.J., Huntley, A.C. & Ortiz, C.L. (1986) The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. *Journal of Zoology, London* **209**, 21–33.
- Ellis, S.L., Bowen, W.D., Boness, D.J. & Iverson, S.J. (2000) Maternal effects on offspring mass and stage of development at birth in the harbour seal, *Phoca vitulina*. *Journal of Mammalogy* **81**, 1143–1156.
- Fedak, M.A., Arnomb, T. & Boyd, I.L. (1996) The relation between the size of southern elephant seal mothers, the growth

- of their pups, and the use of maternal energy, fat, and protein during lactation. *Physiological Zoology* **69**, 887–911.
- Festa-Bianchet, M. (1989) Individual differences, parasites and the cost of reproduction for bighorn ewes (*Ovis canadensis*). *Journal of Animal Ecology* **58**, 785–795.
- Festa-Bianchet, M. & Jorgenson, J.T. (1998) Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioural Ecology* **9**, 144–150.
- Festa-Bianchet, M., Gaillard, J.M. & Jorgenson, J.T. (1998) Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist* **152**, 367–379.
- Gittleman, J.L. & Thompson, S.D. (1988) Energy allocation in mammalian reproduction. *American Zoologist* **28**, 863–875.
- Iverson, S.J., Bowen, W.D., Boness, D.J. & Oftedal, O.T. (1993) The effect of maternal size and milk output on pup growth in grey seals (*Halichoerus grypus*). *Physiological Zoology* **66**, 61–88.
- Laird, N.M. & Ware, J.H. (1982) Random-effects models for longitudinal data. *Biometrics* **38**, 963–974.
- Lawson, J.W., Miller, E.H. & Noseworthy, E. (1997) Variation in assimilation efficiency and digestive efficiency of captive harp seals (*Phoca groenlandica*) on different diets. *Canadian Journal of Zoology* **75**, 1285–1291.
- Mellish, J.E., Iverson, S.J. & Bowen, W.D. (1999) Individual variation in maternal energy allocation and milk production in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology* **72**, 677–690.
- Millar, J.S. (1975) Tactics of energy partitioning in breeding *Peromyscus*. *Canadian Journal of Zoology* **53**, 967–976.
- Muelbert, M.M.C. & Bowen, W.D. (1993) Duration of lactation and postweaning changes in mass and body composition of harbour seal, *Phoca vitulina*, pups. *Canadian Journal of Zoology* **71**, 1405–1414.
- Oftedal, O.T. (1984) Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symposium of the Zoological Society of London* **51**, 33–85.
- Oftedal, O.T. (1993) The adaptation of milk secretion to the constraints of fasting in bears, seals, and baleen whales. *Journal of Dairy Science* **76**, 3234–3246.
- Oftedal, O.T., Boness, D.J. & Tedman, R.A. (1987) The behavior, physiology, and anatomy of lactation in the Pinnipedia. *Current Mammalogy* **1**, 175–245.
- Oftedal, O.T. & Iverson, S.J. (1987) Hydrogen isotope methodology for measurement of milk intake and energetics of growth in suckling young. *Approaches to Marine Mammal Energetics* (eds A. D. Huntley, D. P. Costa, G. A. J. Worthly & M. A. Castellini.), pp. 67–96. Allen Press, Lawrence.
- Ono, K.A., Boness, D.J. & Oftedal, O.T. (1987) The effect of a natural environmental disturbance on maternal investment and pup behaviour in the California sea lion. *Behavioural Ecology and Sociobiology* **21**, 109–118.
- Pomeroy, P.P., Fedak, M.A., Rothery, P. & Anderson, S. (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology* **68**, 235–253.
- Reilly, J.J. & Fedak, M.A. (1990) Measurement of the body composition of living gray seals by hydrogen isotope dilution. *Journal of Applied Physiology* **69**, 885–891.
- Rogowitz, G.L. (1996) Trade-offs in energy allocation during lactation. *American Zoologist* **36**, 197–204.
- Ronald, K., Keiver, K.M., Beamish, F.W.H. & Frank, R. (1984) Energy requirements for maintenance and faecal and urinary losses of the grey seal (*Halichoerus grypus*). *Canadian Journal of Zoology* **62**, 1101–1105.
- Stearns, S.C. (1989) Trade-offs in life history evolution. *Functional Ecology* **3**, 329–351.
- Thompson, P.M., Miller, D., Cooper, R. & Hammond, P.S. (1994) Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *Journal of Animal Ecology* **63**, 24–30.

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