

Weaning Mass Affects Changes in Body Composition and Food Intake in Harbour Seal Pups during the First Month of Independence

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ABSTRACT

In phocid seals, the transition to nutritional independence is abrupt, with females abandoning their offspring after weaning and returning to sea. We hypothesized that body size at weaning may play an important role in the nature of this transition. We studied the changes in body composition and water flux of newly weaning harbour seals over the first 4–6 wk postweaning. Thirty-three pups were dosed with deuterium oxide to estimate total body water (TBW) and a subset of 24 was dosed twice to estimate changes in body composition and water flux. All pups lost body mass over the study period, but TBW increased during the period of mass loss, indicating continued lean tissue growth. Combined data from this and our early study indicated that heavy (>median mass) pups were relatively fatter (41.0% vs. 37.1%) and had significantly greater total body energy at weaning than did light (\leq median mass) pups. Percentage TBW declined linearly over time in light pups but was constant in heavy pups for the first 19 d postweaning and then declined linearly. Both the temporal pattern and composition of mass loss differed between light and heavy pups. Estimated food intake increased in the second 2 wk of study compared to the first 2 wk, in both light and heavy pups, reflecting increased foraging success but at levels still insufficient to meet daily expenditures of most individuals.

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Introduction

The transition to nutritional independence is a critical period in the life history of many animals because it often marks the end of the period of parental care (Reiter et al. 1978; Berger 1979; Galef 1981; Martin 1984; Clutton-Brock 1991). During weaning, there are changes in the behaviour, physiology, and nutrition of offspring and in the parent-offspring relationship (Reiter et al. 1978; Collinge 1987; Green et al. 1989; Bøe 1991). In mammals, offspring must replace milk with solid food, often with, but sometimes without, help from their parents (Martin 1984; Oftedal et al. 1987a; Bowen 1991; Clutton-Brock 1991). Although the importance of weaning is broadly recognized (Sauer and Slade 1987; Lee et al. 1991), there are few studies of the foraging energetics of the newly independent mammalian offspring that are weaned abruptly, such as phocid seals (family Phocidae). In these species, offspring are forced to make the transition to nutritional independence without parental assistance (Bowen 1991).

Body size at weaning is likely to be under selection pressure because so many aspects of vertebrate life history are correlated with body size (Blueweiss et al. 1978; Stearns 1983; Janzen 1993). In mammals, there is evidence that juvenile survival is positively correlated with body size at weaning (Van Ballenberghe and Mech 1975; Guinness et al. 1978; Murie and Boag 1984; Sauer and Slade 1987; Wauters et al. 1993). This also appears to be the case among pinnipeds (Baker and Fowler 1992; Arnbom et al. 1993; Baker et al. 1994; Le Boeuf et al. 1994; Hall et al. 2001), but few species have been studied to date.

Lactation strategies of the Phocidae (i.e., true seals) and the Otariidae (i.e., fur seals and sea lions) lead to quite different patterns of pup development and postweaning behaviour (Bowen 1991). Phocid pups are abandoned at weaning with what has been termed an “insurance policy” in the form of blubber. As the absolute size of this policy is correlated with body mass at weaning (Iverson et al. 1993; Muelbert and Bowen 1993; Mellish et al. 1999), it is reasonable to expect that heavy body mass at weaning should confer some selective advantage in these species.

The harbour seal (*Phoca vitulina*) is a phocid species that

exhibits intermediate characteristics of lactation and pup rearing strategies compared to other pinnipeds (Bowen et al. 1992; Boness et al. 1994; Boness and Bowen 1996). Like many other species, harbour seal females give birth and nurse their pups on land. However, females differ from the heavier phocid species by fasting during only the early stage of lactation, thereafter alternating short foraging trips at sea with periods of nursing on land (Boness et al. 1994; Thompson et al. 1994; Bowen et al. 2001a). Harbour seals also differ from many other phocid species in the extent to which pups swim and dive during lactation (Bowen et al. 1999). This activity may increase neonatal energy expenditure and reduce the potential energy stores available to the pup at weaning.

Following weaning, the offspring of many phocid species, including harbour seals, lose body mass for some weeks even after they begin to feed (Bowen 1991), suggesting that the transition to independent feeding is a difficult period. Thus, the body size and the amount of stored energy at weaning may be particularly important in the early development and survival of these species. There is evidence that faster-growing phocid pups are both heavier and relatively fatter at weaning than more slowly growing pups (Iverson et al. 1993). Thus, we predicted that heavier harbour seal pups would be absolutely and relatively fatter at weaning than lighter pups, would have higher rates of daily food intake (i.e., higher foraging success), and thus would use a smaller fraction of body energy stores to support daily energy requirements. We tested this by studying the body composition and subsequent water flux of newly weaned pups over the first month postweaning.

Material and Methods

The study was conducted on Sable Island (43°55'N, 60°00'W), a crescent-shaped, partially vegetated sand bar located approximately 277 km east of Halifax, Nova Scotia. Data were collected from May 17 to August 17 and September 28 to October 3, 1993; from May 20 to August 20, 1994; and from May 18 to June 28, 1995. Daily surveys conducted early in the breeding season ensured that study pups were weighed and tagged in the webbing of the hind flipper with individually numbered Rototags within 24 h of birth. Pups were captured by hand or with hoop nets. Disturbance to mothers and pups typically lasted <10 min. Female pup pairs were observed daily over the course of lactation. A pup was operationally defined as having been weaned when it was seen alone in three consecutive, twice-daily surveys of the colony (Muelbert and Bowen 1993).

Near weaning, body mass (to the nearest 0.1 kg) and standard dorsal length (McLaren 1993) were measured, and a blood sample (≈ 8 mL) was taken from the extradural vein using a 70-mm 18-gauge spinal needle to determine background concentration of deuterium oxide (D_2O). A known quantity (approximately 3 g/kg body mass) of D_2O (99.8 atom % excess; Stable Isotopes Division, ICN Biomedicals, Cambridge, Mass.)

was administered to each pup by gastric intubation. The syringe and the stomach tube were flushed several times with a total of 10 mL of distilled water and 50 mL of air to ensure complete delivery of the isotope. The pup was then placed in a temporary holding pen on the beach to allow the isotope to equilibrate with body water. Previous studies have shown that equilibration is achieved within 1.5 h postadministration (M. M. C. Muelbert, unpublished data). Thus, blood samples were taken from each pup at approximately 1.5 and 2 h postadministration to ensure that equilibration had occurred. Pups were recaptured at 7–10-d intervals to monitor changes in body mass and isotope concentration. At each recapture, pups were weighed and a blood sample was taken. At approximately 3 wk postweaning, we attempted to equilibrate all pups to determine body composition.

All blood samples were collected in Vacutainers without additives. Blood samples were centrifuged and serum was transferred to cryovials and stored at $-20^\circ C$ until analysis. Total water was extracted from sera using heat distillation, and D_2O concentration was determined using a double-beam grating infrared spectrophotometer (Oftedal and Iverson 1987).

Isotope dilution spaces at the initial and final equilibration were estimated as in Oftedal et al. (1987b). As dilution space is known to overestimate total body water (TBW), we corrected dilution space using the equation derived for pinnipeds (Bowen and Iverson 1998). Given that carcass analysis data are not available for harbour seals, body composition was calculated from TBW and body mass using the following regression equations for grey seals (*Halichoerus grypus*; Reilly and Fedak 1990): %TBP = $(0.42 \times \%TBW) - 4.75$; %TBF = $105.1 - (1.465 \times \%TBW)$; TBE (MJ) = $(40.8 \times TM) - (48.5 \times TBW) - 0.4$, where TBP = total body protein, TBF = total body fat, TBE = total body energy, and TM = total body mass.

Fractional water turnover (k) was estimated as the slope of a linear regression of the natural logarithm of the corrected D_2O concentration against time elapsed since the isotope administration. The concentration of D_2O was corrected for changes in dilution space by assuming that changes in TBW were linear during the study period. Overall total body water flux per day (TWF_{over} , kg/d) was calculated as described by Oftedal and Iverson (1987) and Iverson et al. (1993): $TWF_{over} = (k \times TBW_{avg}) - \Delta TBW$, where TBW_{avg} is the average value for TBW during the study period and ΔTBW is the daily change in TBW. To determine whether k changed over time, independent two-point estimates of k were calculated for the initial period (k_i , i.e., the first 2 wk postweaning), and for the final period (k_f , i.e., the second 2 wk postweaning). Estimates of total daily water flux for the initial (TWF_i) and final (TWF_f) periods were calculated for each period using the appropriate k and ΔTBW .

We estimated daily food intake (DFI) from TWF using the

Table 1: Body composition (mean \pm SE) of harbour seal pups at weaning, 21–44 d postweaning (DPW), and approximately 1 yr of age

	Weaning		21–31 DPW (<i>n</i> = 13)	31–44 DPW (<i>n</i> = 11)	1 yr ^a (<i>n</i> = 5)
	Light (<i>n</i> = 8)	Heavy (<i>n</i> = 25)			
Body mass (kg)	20.5 \pm .67	26.3 \pm .68 ^b	21.3 \pm .77	19.6 \pm .74	33.3 \pm 1.28
Total body water (kg)	9.2 \pm .40	11.3 \pm .26 ^b	11.2 \pm .45	11.2 \pm .52	21.2 \pm 1.10
Total body protein (kg)	2.9 \pm .13	3.5 \pm .08	3.7 \pm .15	3.8 \pm .19	7.3 \pm .42
Total body fat (kg)	8.1 \pm .17	11.0 \pm .41	5.9 \pm .33	4.2 \pm .34	3.9 \pm 1.11
Total body energy (MJ)	390 \pm 9.1	522 \pm 17.6	324 \pm 14.5	257 \pm 13.2	307 \pm 38.5
Body water (%)	44.8 \pm .57	43.2 \pm .48 ^c	52.8 \pm .87	56.9 \pm 1.16	63.8 \pm 2.31
Body protein (%)	14.1 \pm .24	13.4 \pm .20	17.4 \pm .36	19.2 \pm .49	22.1 \pm .97
Body fat (%)	39.5 \pm .84	41.9 \pm .71	27.7 \pm 1.27	21.7 \pm 1.70	11.6 \pm 3.39

Note. Light < median > heavy.

^a Sampled in June of the following year.

^b Light versus heavy, nonpaired *t*-test, *P* < 0.001.

^c Nonpaired *t*-test, *P* = 0.06.

equation of Oftedal and Iverson (1987), modified to account for the digestible energy of food:

$$DFI = \frac{100 \times [TWF + (1.07 \times \Delta F) + (0.42 \times \Delta P)]}{W_{\text{food}} + DE \times [(1.07 \times F_{\text{food}}) + (0.42 \times P_{\text{food}})],}$$

where ΔF = daily change in body fat (kg/d), ΔP = daily change in body protein (kg/d), W_{food} = water content of food (%), F_{food} = fat content of food (%), P_{food} = protein content of food (%), and DE = proportion of digestible energy (0.93; Ronald et al. 1984). For these calculations, we assumed a diet of sand lance (*Ammodytes* sp.), a major prey of weaned harbour seal pups at Sable Island (Muelbert and Bowen 1993). Sand lance is composed of 72.6% water, 7.9% fat, and 15.9% protein (*n* = 38; S. J. Iverson and W. D. Bowen, unpublished data). We assumed that 85% of the fat and protein ingested were available. This assumption was based on estimates ranging from 82.7% to 88.7% in which grey and harp seals were fed herring (Ronald et al. 1984; Worthy 1990). DFI was then converted to available food energy ingested (FEL_a), assuming that 1 kg of sand lance contains 6.8 MJ of gross energy and that 85% of the energy from diet was available to pups. Daily energy expended (DEE) was then calculated as the sum of the absolute value of the daily change in total body energy (Δ TBE) and FEL_a. DEE was calculated for the whole study period and also for the early (DEE_e) and late (DEE_l) postweaning periods as described above.

To examine the effects of body mass at weaning on pup energetics, pups were classified as light or heavy based on the median weaning mass in each year of the study. Similar numbers of large males and females were studied, but females dominated the small size class. Although male pups are 7% larger than female pups at weaning, this difference stems from differences in birth mass and not growth rates during lactation (Bowen et al. 2001b). Generally, we did not have a large enough

sample to simultaneously examine both pup sex and size as factors. However, when coupled with data from a previous study, the effect of pup sex on body composition at weaning was considered (see “Discussion”). Statistical analyses were performed using SPSS for Windows (ver. 8.0) and S-PLUS (ver. 6). The standard error is given as a measure of variability about the mean.

Results

Body Mass and Composition

Thirty-three (18 in 1993, 15 in 1994) harbour seal pups were given D₂O at or shortly after weaning. Initial TBW could not be calculated for two pups as the isotope appeared not to have equilibrated. Of the remaining 31 pups, only the 25 pups that were given D₂O within 4 d postweaning were used to estimate body composition at weaning. The other six pups were used to estimate changes in body composition as a function of days postweaning (see below). A second estimate of TBW was obtained 3–4 wk postweaning from 24 of the initial 31 pups, including 22 of 25 pups used to estimate body composition at weaning.

Mean body mass at weaning was about 24 kg and ranged from 17.8 to 32.9 kg (*n* = 25, coefficient of variation [CV] = 15.2%; Table 1). TBW was highly correlated with weaning mass (*r* = 0.95, *P* < 0.001; Fig. 1a). Fat and protein content ranged from 35.5% to 46.7% and 11.9% to 15.2%, respectively. There was little variability in percent fat (CV = 7.1%) and percent protein (CV = 7.7%) among pups. At weaning, pups contained 480 MJ of TBE, ranging from 348 to 696 MJ (CV = 15.3%).

Second equilibrations were performed significantly later in 1994 than in 1993 (33.6 \pm 1.6 d and 27.5 \pm 1.0 d after the initial equilibration, respectively; $F_{1,23}$ = 10.71, *P* = 0.003); consequently, final body mass and composition data were not

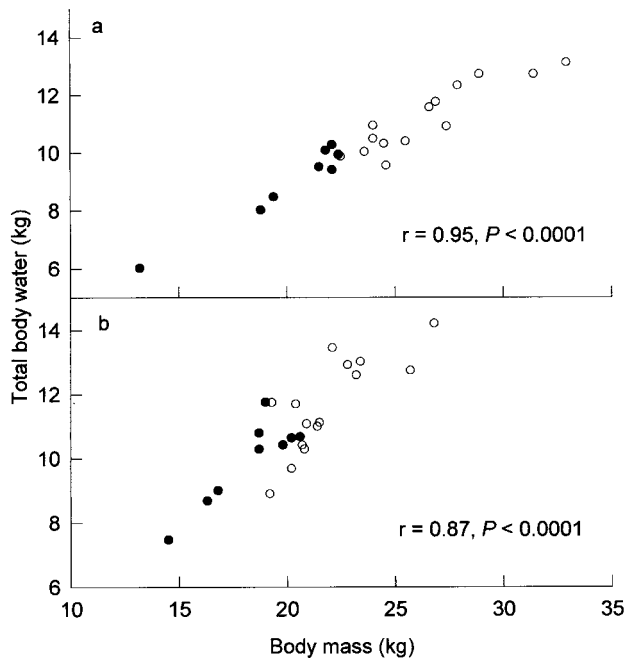


Figure 1. Correlation between total body water and body mass at (a) weaning and (b) 4–6 wk postweaning in light (solid circles) and heavy (open circles) harbour seal pups. Both years of study combined.

compared between years. Again, TBW was highly correlated with body mass ($r = 0.87$, $P < 0.0001$; Fig. 1*b*). The amount of total body protein in pups changed little over the first 21–44 d postweaning; however, the amount of TBF declined from an average of 41.1% to 21.7% (Table 1). By 31–44 d postweaning, pups had depleted 41.6% of TBE.

Five pups born in May 1994 were given D_2O the following June. At approximately 1 yr of age, average body mass had increased by almost 10 kg and total protein mass had doubled, but total fat mass had not changed significantly from that measured at 4–6 wk postweaning (Table 1). As a consequence, percent fat had decreased by half to an average of 11.6% of TM, and TBE was comparable to that estimated in pups at 21–44 d postweaning (Table 1).

Light pups were about 6 kg lighter and also had significantly less TBW, body protein, and body fat than heavy pups (Table 1). Thus, TBE of light pups also was significantly less than heavy pups. However, the percentage body composition of light and heavy pups did not differ significantly (but see “Discussion”). Light pups were significantly shorter (86 ± 1.2 cm) than heavy pups (92 ± 1.0 cm; t -test, $P = 0.002$).

All but one pup lost body mass over the duration of the study. Absolute mass loss varied greatly among pups, ranging from 0.6 to 7.0 kg ($CV = 65.4\%$, $n = 21$). Mass change was negatively correlated with weaning mass ($r = -0.75$, $P < 0.001$). Despite this loss of body mass, TBW increased in 15 of

the 21 pups. The average increase in TBW did not differ significantly between light pups (1.0 ± 0.23 kg, $n = 6$) and heavy pups (1.0 ± 0.22 kg, $n = 9$; ANCOVA with weaning mass as covariate, $F_{1,12} = 1.58$, $P = 0.23$). The body length of pups also increased over the study period at an average rate of 0.1 ± 0.02 cm/d ($n = 18$); however, there was no significant difference in the growth rate of light and heavy pups (t -test, $P = 0.15$).

Differences in weaning mass might affect the use of body fat and protein over the first month of independence. To investigate this, we regressed the percentage of TBW against days postweaning in 64 pups: 31 studied in 1988 and 1989 by Muelbert and Bowen (1993) and a randomly selected single measurement from each of the 33 pups in this study. Percentage TBW of each of the 31 pups from Muelbert and Bowen was recalculated using the equations given above so that both data sets were comparable. A piecewise linear regression was fitted to the percentage TBW (arcsine, square-root transformed) over time for both light and heavy pups (Table 2). In light pups, the break point (i.e., x_0) was not significantly different from zero, indicating that a simple linear model fit the data well. By contrast, the percentage of TBW initially remained constant in heavy pups for an average of 19.2 d before declining linearly (Fig. 2). As percentage body fat and protein are derived from percentage TBW, these components also changed over time, but in the opposite direction.

Energetics

Over the first month of the postweaning period, 21 pups lost an average of about 4 kg (Table 3). During this period, daily

Table 2: Piecewise linear regression models of percentage total body water (TBW) against days postweaning (DPW) in 64 weaned harbour seal pups

Pups	Estimate \pm SE	t	P
Light ($n = 23$):			
b_0	43.1 \pm .81	53.4	<.001
b_1	-.15 \pm .32	-.48	.64
b_2	.38 \pm .32	1.17	.26
x_0	6.0 \pm 4.45	1.35	.19
Heavy ($n = 41$):			
b_0	41.3 \pm .69	59.9	<.001
b_1	.09 \pm .08	1.03	.30
b_2	.29 \pm .12	2.36	.02
x_0	19.2 \pm 5.17	3.71	<.001

Note. Including data from 31 pups studied in 1988–1989 (Muelbert and Bowen 1993) and recalculated using the equations used in this study. Pups classified as light or heavy in relation to median body mass at weaning. The fitted equation: $\arcsin(\%TBW) = b_0 + b_1(DPW) + b_2(DPW - x_0)$ ($DPW > x_0$).

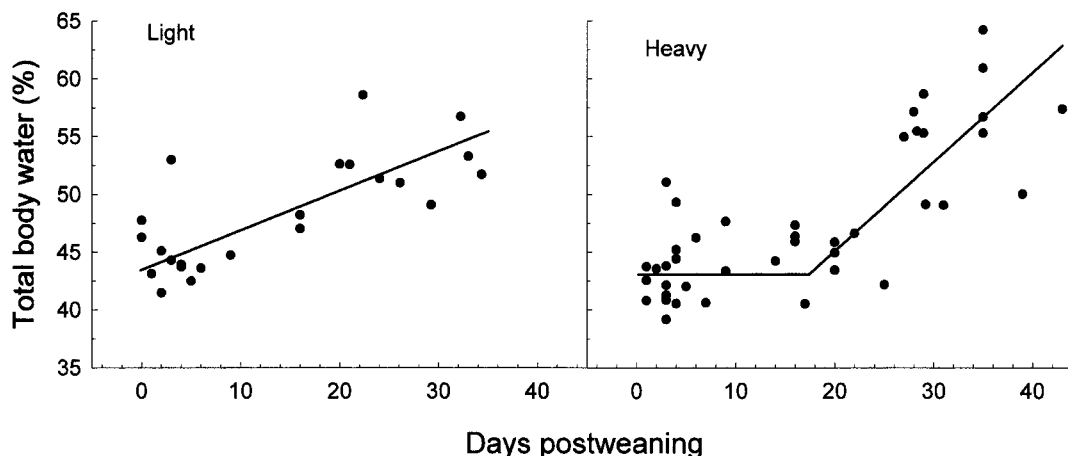


Figure 2. Piecewise linear regressions of percentage total body water against days postweaning in 23 light and 41 heavy weaned harbour seal pups (see Table 2 for regression coefficients).

water flux averaged 1.1 kg/d, and estimated daily food and available energy intakes were 1.0 kg and 7.2 MJ, respectively. Although pups fed during this period, they continued to deplete body energy stores at a rate of 6.4 MJ/d. Pups had an average daily energy requirement of 12.5 MJ. Thus, food intake accounted for more than half of DEE.

Light pups lost significantly less body mass and TBE but had significantly greater daily water flux and hence higher food intake than heavy pups (Table 3). However, total energy expenditure did not differ between light and heavy pups. Heavy pups used a greater fraction of initial TBE ($44.9\% \pm 3.0\%$) during their first month of independence than did light pups ($29.1\% \pm 6.9\%$, Mann-Whitney U , $P = 0.05$).

Rates of mass change, Δ TBE, water flux, FEI, and DEE also differed significantly between the first and second 2-wk periods postweaning in 14 pups, each measured twice (Table 4). Given the small sample size of light pups, we did not use weaning-mass class as a factor in this analysis. Pups lost body mass at

twice the rate during the early postweaning period than they did during the latter period. TWI was significantly higher during the late period than during the early period. FEI more than doubled during the late period compared to the early period, while Δ TBE was reduced by a factor of 3. DEE did not differ significantly between the two time periods (Table 4).

Discussion

Newly weaned offspring face a variety of challenges during the transition to nutritional independence. In the case of most pinnipeds, offspring are abandoned with little or no instruction as to where to find or how to capture food (Bowen 1991). Additionally, first-year mortality is high. In southern elephant seals (*Mirounga leonina*) first-year mortality can be >50% (Hindell 1991), and in grey seals estimates range from 38% in females to 80% in males (Hall et al. 2001). Yet relatively little is known about the postweaning development of pinniped off-

Table 3: Daily loss (mean \pm SE) in body mass, water flux, food and energy intake, and energy expenditure of light and heavy harbour seal pups over the first month postweaning

	Light Pups ($n = 7$)	Heavy Pups ($n = 14$)	P^a
Total mass change (kg)	$-2.4 \pm .43$	$-4.5 \pm .44$.01
Daily mass change (kg/d)	$-.09 \pm .01$	$-.16 \pm .01$.01
Daily water flux (kg/d)	$1.2 \pm .07$	$1.0 \pm .06$.06
Daily food intake (kg/d)	$1.2 \pm .09$	$1.0 \pm .07$.03
Daily food energy intake (FEI _d)	$8.5 \pm .60$	$6.49 \pm .50$...
Daily change total body energy (MJ/d)	$-5.1 \pm .47$	$-7.1 \pm .43$.01
Daily energy expenditure (DEE, MJ/d) ^b	$12.3 \pm .57$	$12.6 \pm .35$.68

^a t -test comparing light and heavy pups.

^b DEE = $|\Delta$ body energy| + MEI (i.e., FEI_d \times 0.85); MEI = metabolizable energy intake.

Table 4: Mean \pm SE body water flux and energy expenditure of 14 weaned harbour seal pups measured over the first 2 wk postweaning (early) and again during the second 2 wk postweaning (late)

	Early	Late	P^a
Mass change (kg)	$-1.7 \pm .18$	$-.5 \pm .31$.001
Daily mass change (kg/d)	$-.2 \pm .02$	$-.04 \pm .03$...
Daily water flux, TWF_{over} (kg/d)	$.8 \pm .08$	$1.4 \pm .13$.005
Daily food intake (kg/d)	$.6 \pm .11$	$1.6 \pm .15$...
Daily food energy intake (FEL_a)	$4.1 \pm .73$	10.7 ± 1.03	.002
Daily change in body energy (MJ/d)	$-9.9 \pm .88$	-2.7 ± 1.17	<.001
Daily energy expenditure (DEE, MJ/d) ^b	$13.4 \pm .60$	13.0 ± 1.33	.739

^a t -test comparing early and late pups.

^b $DEE = |\Delta\text{body energy}| + MEI$ (i.e., $FEL_a \times 0.85$); MEI = metabolizable energy intake.

spring (Bowen 1991), and only recently has this begun to change (e.g., Thorson and Le Boeuf 1994; Burns and Castellini 1996; Burns et al. 1999; Hindell et al. 1999). The reasons for this are not difficult to appreciate because most species' newly weaned offspring spend considerable time at sea where they cannot be easily studied. Our results highlight the difficulties offspring face in becoming nutritionally independent. Harbour seal pups begin to feed within days of weaning but continue to lose body mass for a number of weeks before achieving a positive energy balance (Muelbert and Bowen 1993; this study). When data from our earlier study were combined with our present results, we found that heavier pups were both absolutely and relatively fatter at weaning than lighter pups, as predicted. However, contrary to our predictions, heavier pups had lower daily food intakes and used a greater fraction of stored energy to support metabolic requirements over the first month postweaning than light pups.

Body Mass and Composition at Weaning

Although the weaning masses measured here were similar to our previous data (Muelbert and Bowen 1993), estimates of the body composition differed. The reason for this difference can be explained by the different method used to estimate body composition. Muelbert and Bowen (1993), as in a number of other studies on pinnipeds, assumed that TBW and dilution space were equivalent and thus overestimated TBW and underestimated TBF relative to the data presented here. By correcting dilution space using the relationship between dilution space and TBW (Bowen and Iverson 1998) and using the Reilly and Fedak equations relating TBW to fat and protein, TBF at weaning increased to 37.8% from the 33.2% previously reported for the same pups (Muelbert and Bowen 1993). This revised estimate is not significantly different from that found in this study (41.1%; $t_{37} = 0.73$, $P = 0.23$).

As predicted, heavy pups had significantly more TBE than light pups. They also tended to have a greater percentage of body fat than light pups, but this difference was not significant.

We expected the relatively low number of light pups in our sample ($n = 7$) to affect this conclusion. To test this, we added comparable data on the body composition of recently weaned pups from an earlier study (Muelbert and Bowen 1993). Based on this larger sample, heavy pups had a significantly lower percentage of TBW than light pups ($43.7\% \pm 0.66\%$, $n = 22$ vs. $46.4\% \pm 0.80\%$, $n = 16$; $F_{1,34} = 6.4$, $P = 0.016$) and hence a greater percentage of body fat ($41.0\% \pm 0.97\%$ vs. $37.1\% \pm 1.17\%$). Thus, heavy pups had both a higher energy density and a greater quantity of TBE than light pups. Similar findings have been reported in grey seals (Iverson et al. 1993) and in southern elephant seals (Hindell et al. 1999). This larger "insurance policy" may give heavy pups greater flexibility in learning to forage effectively, which might enhance survival. However, survival probability of weaned harbour seal pups in this population is not known.

This larger sample also enabled us to examine sex effects on body composition at weaning. Although there was no overall sex effect on the percentage of TBW ($P = 0.98$), in addition to the size effect above, there was a significant sex-size interaction ($F_{1,34} = 5.0$, $P = 0.032$), with heavy males having a significantly lower percentage TBW than light males (42.6% vs. 47.4%), whereas heavy and light females did not differ (44.9% vs. 45.2%). Sex differences in body composition at weaning have also been reported in Antarctic fur seals (Arnould and Boyd 1996). However, in contrast to our findings, percentage body fat increased with body mass in both males and females, but males were leaner than females. Although these differences have been interpreted as adaptations associated with male-based body-size dimorphism favoring lean tissue growth in males, the lack of sex differences in body composition at weaning in another highly dimorphic species, the northern elephant seal (Kretzmann et al. 1993), suggests that this explanation may not apply broadly.

Based on their earlier data, Muelbert and Bowen (1993) concluded that recently weaned harbour seals had the lowest energy density of the phocid species studied. However, comparing our revised (from Muelbert and Bowen 1993) and new estimates

Table 5: Estimates of percentage body fat at weaning in phocid species

Species	Weaning Mass (kg)	Body Fat (%)	Method ^a	Source
Northern elephant seal	133.9 (102)	48.4 (24)	ID, DS _c	Kretzman et al. 1993
Southern elephant seal	157.3 (39); 154 (117); 114 (13)	35 (7); 37 (47); 40.8 (21)	ID, DS _c	Hindell et al. 1994; Carlini et al. 2000, 2001
Weddell seal	93.9	37	ID, DS _n	Tedman and Green 1987
Hooded seal	43.7 (12)	44.7 (5)	Carcass analysis	Bowen et al. 1987; Oftedal et al. 1993
Grey seal	38 (12); 41.8 (17)	42.3 (12); 37.1 (17)	ID, DS _c	Reilly 1991; Mellish et al. 1999
Harp seal	38.4 (5)	47.2 (5)	Carcass analysis	Oftedal et al. 1996
Harbour seal	24.8 (14); 24.4 (25)	37.8 (14); 41.1 (25)	ID, DS _c	Muelbert and Bowen 1993; this study
Ringed seal	23.1 (2)	45 (2)	Carcass analysis	Stirling and McEwan 1975

Note. Sample sizes are given in parentheses.

^a ID = hydrogen isotope dilution space; DS_c = dilution space corrected to total body water; DS_n = dilution space not corrected.

in harbour seals with data on other species suggests that Muelbert and Bowen's earlier conclusion was incorrect. Although the estimate of the percentage of body fat of harbour seal pups at weaning falls near the lower range of current estimates, the estimates in the Weddell seal and southern elephant seal are lower or similar to those found in the harbour seal (Table 5). Weddell seal and harbour seal pups are quite active and spend considerable time swimming during lactation (Tedman and Bryden 1979; Bowen et al. 1999). This increased activity and resulting increased energy expenditure may account partly for the somewhat lower fat concentration at weaning in these species than found in species where pups do not usually enter the sea until after weaning and thus are less active. Although ringed seal pups (*Phoca hispida*) also enter the sea during lactation, the percentage of body fat at weaning appears comparatively high. However, only two pups have been measured and thus the estimate may change as more data become available. Low sample size within species, the confounding effect of maternal size on pup body composition (Iverson et al. 1993), and the lack of data on seven of the 15 phocid species currently limit our ability to draw ecological inferences. Nevertheless, we might expect that the body composition of offspring at weaning will reflect the provisioning decisions of females, the storage efficiency of offspring, thermoregulatory requirements, and the distance to and predictability of food, which will determine the length of the time that pups must rely on stored energy during the transition to nutritional independence.

Changes in Body Composition over Time

Harbour seal pups used more than half of their fat stores over the first 4–6 wk postweaning. Nevertheless, these pups continued to grow such that body protein content increased over this period. Similarly, recently weaned captive northern elephant seals that were fed ad lib. gained lean tissue while losing adipose

tissue (Condit and Ortiz 1987). No doubt this increase in protein content reflects the development of body musculature. By 1 yr of age, pups had gained almost 10 kg of body mass relative to weaning mass, and their body composition had changed dramatically, with fat accounting for only 12% of body mass, compared to 41% at weaning, and protein accounting for about 22%, compared to 14% at weaning. Similarly, an increase in the relative proportion of lean tissue has also been reported in both 8-mo-old grey seals (M. Cooper, S. J. Iverson, and W. D. Bowen, unpublished data) and southern elephant seals returning from the first 3–5-mo foraging trip (Bell et al. 1997).

Heavy pups had both an absolute and a relative advantage over light pups in terms of body energy stores at weaning (combined data from this study and Muelbert and Bowen 1993). Our findings also indicate that body size at weaning influenced the substrates used to fuel metabolism during the transition to nutritional independence. Heavy pups lost both lean body mass and body fat at a constant rate for about 19 d before they began to conserve protein and shifted to a reliance on fat as the main fuel for energy metabolism. In contrast, light pups apparently began to use fat as the main source of energy immediately following weaning. Given the importance of maintaining body musculature while learning to dive and forage, this difference between heavy and light pups was unexpected. It is not clear why heavy and light pups should differ in the composition of mass loss, but minimizing heat loss may partly account for our findings. Ryg et al. (1988) showed that heat loss was minimized when body composition of a seal remains constant during a period of mass loss. Thus, heavy pups may be able to reduce metabolic expenditure associated with thermoregulation for a longer period than light pups and thereby gain a further energetic advantage. The switch to a reliance on body fat in both heavy and light pups occurs during a period of increased foraging success, at which point body protein requirements are met through feeding (see below).

Although in terms of absolute energy stores heavy pups appear to have an advantage over light pups, heavy pups used their stores more quickly than light pups. Carlini et al. (2000) reported similar results in southern elephant seal pups during the postweaning fast before undertaking their first foraging trip. Given that most pups lost body energy during this first 4-wk period, we asked if the greater TBE of heavy pups at weaning might confer an advantage by providing a greater period of time to learn to forage effectively. Assuming the daily rates of depletion of TBE in Table 3, both light and heavy pups would have used about 38% of TBE at the end of 4 wk. Thus, because of their larger size, heavy pups appear to retain their energetic advantage over this period (Fig. 2). Although the consequences of this energetic advantage on survival of harbour seal pups is unknown, there is evidence of a positive association between mass at weaning and early survival in several other phocid species (McMahon et al. 2000; Hall et al. 2001).

Water Flux, Food Intake, and Energy Expenditure

Estimates of food intake are relatively robust to the composition of the diet because rather similar amounts of water are produced from catabolism of prey types' differing composition. However, estimates of food energy intake are quite sensitive to the type of food eaten. Muelbert and Bowen (1993) reported that sand lance (*Ammodytes dubius*) was a major prey of weaned harbour seal pups, but American plaice (*Hipoglossus platessoides*), silver hake (*Merluccius bilinearis*), and shrimp (*Crangon* sp.) were also found in stomach lavage samples. As the composition of the diet of the pups we studied was not known and sand lance continued to dominate the diet of adults during the breeding season at Sable Island (W. D. Bowen, unpublished data), we assumed a diet of pure sand lance as the basis of our calculations. However, this assumption would affect our conclusions about differences in energy intake only if the diet of light and heavy pups differed.

In the pups studied in both 2-wk periods, there was clear evidence of improved foraging success. Daily water flux and estimated food intake increased significantly, while the depletion of body energy stores decreased significantly. During the second 2-wk postweaning, catabolism of food accounted for 82% of energy expenditure. By the end of our study, several pups had begun to increase body mass, suggesting that it takes 4–6 wk for newly weaned harbour seals to learn to forage effectively. There are few comparable data from other pinniped species. In southern elephant seals, six pups that were weighed at departure from the colony and again on return from their first foraging trip (averaging 139 d) gained an average of 40.8% of their departure body mass (Hindell et al. 1999). Unlike harbour seals, these elephant seal pups fast for about 3–9 wk before undertaking their first foraging trip (Arnbom et al. 1993). Undoubtedly, young elephant seals continue to lose body mass for some time after setting out to forage for the first time, but they

cannot be reweighed until they return from this 4.5-mo trip. Despite having gained mass, most pups returning from their first months at sea weighed little more than they did at weaning (Bell et al. 1997).

The quantity of stored body energy at weaning is only one of several factors that may affect the survival of newly independent pinniped pups. Nevertheless, our findings indicate that energy content at weaning does influence the early transition to nutritional independence. Our findings also have implications for understanding of female reproductive strategies, as there are strong maternal effects on offspring size and condition at weaning in pinnipeds (Fedak et al. 1996; Mellish et al. 1999; Bowen et al. 2001b). It is generally assumed that variation in energy investment in offspring has fitness consequences for females. Our results on the early foraging energetics of harbour seal pups and data on the survival advantage of large offspring in other species provide some support for this assumption. Nevertheless, studies on other species and over longer periods of time are needed to fully understand the consequences of weaning mass and body composition on offspring and maternal fitness.

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