Mass transfer from mother to pup and subsequent mass loss by the weaned pup in the hooded seal, *Cystophora cristata*

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We studied the components of mass transfer from mother to pup during the lactation period and weight loss by fasting pups postweaning in the hooded seal, *Cystophora cristata*. Measurements were taken from 33 mother–pup pairs and 69 weaned pups. Mean body weight of mothers declined from an average of 179 kg at the beginning of lactation to 150 kg for mothers nursing fat pups near the end of lactation. Over 80% of this weight loss was from the sculp (i.e., skin and blubber). Pup weight doubled during the 4 days of lactation, with about 70% of this weight gain in the form of blubber. Fasting pups lost 29% or 13 kg of their body weight between weaning and mid to late April when feeding begins. Sculp and core weight accounted for 51% and 49%, respectively, of total weight loss during this fasting period. Hooded seal mothers invest a smaller portion of their stored fat (33%) in their pup than do grey seals (85%) and northern elephant seals (58%). Our hooded seal data are consistent with the hypothesis that the abbreviation of lactation allows a reduction in overhead costs and more efficient transfer of nutrients from mother to pup.

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Nous avons étudié le transfert de masse de la mère au petit au cours de la période de lactation, puis la perte de masse chez les petits au cours du jeûne qui suit le sevrage chez le Phoque à capuchon, *Cystophora cristata*. Les paramètres ont été mesurés chez 33 paires mère–petit et chez 69 petits sevrés. La masse moyenne des mères est passée de 179 kg au début de la période de lactation à 150 kg vers la fin de la lactation chez les mères qui nourrissaient des bébés gras. Plus de 80% de la perte de masse s'est faite dans la couche supérieure (i.e., peau et lard). La masse des petits a doublé au cours des 4 jours de lactation et 70% de cette augmentation de masse était due à l'accumulation de lard. Les petits ont perdu 29% de leur masse totale, ou 13 kg, au cours du jeûne entre le sevrage et la mi-avril ou la fin d'avril, moment où a commencé l'alimentation. De cette perte de masse, 51% était due à la perte de masse dans la couche supérieure et 49% à la perte de masse dans la couche centrale. Les mères investissent une plus petite portion de leurs réserves de graisses chez le Phoque à capuchon (33%) que chez le Phoque gris (85%) ou l'Eléphant de mer (58%). Ces données sur le Phoque à capuchon confirment l'hypothèse selon laquelle le raccourcissement de la période de lactation permet une réduction des coûts totaux et un transfert plus efficace des éléments nutritifs de la mère au petit.

[Traduit par la revue]

Introduction

Phocid seals generally have a short lactation period of less than 4 weeks (Bonner 1984; Bowen et al. 1985). It has been suggested that this abbreviation of lactation may reduce the risk of predation for mothers or their pups during nursing, or premature separation of mother and pup brought about by the unpredictable and unstable nursing habitat used by ice-breeding members of this family (Bonner 1984; Bowen et al. 1985). It has also been suggested that a short lactation period reduces the maintenance costs of both mother and pup, thereby reducing "metabolic overhead" and maximizing the efficiency of nutrient transfer from maternal stores to pup tissues (Fedak and Anderson 1982). This reduction in overhead may have been particularly important in the evolution of lactation length in phocids because mothers fast during the nursing period and thus must support the demands of lactation solely from stored energy. At 4 days, the hooded seal, *Cystophora cristata*, has the shortest lactation period of any mammal (Bowen et al. 1985) and hence this species offers an ideal opportunity to test the hypothesis that an abbreviated nursing period results in an increase in the efficiency of energy transfer from mother to pup.

In this paper we examine the components of mass gain by pups and of mass loss by mothers during the nursing period and by fasting pups postweaning.

Previous work on this species has been limited. D. E. Sergeant (Arctic Biological Station, Ste-Anne-de-Bellevue, Quebec, personal communication) collected total and sculp weights of hooded seal pups taken in the commercial harvest at Newfoundland in March and April 1953. Rassmussen (1960) reported the mean length of pups taken from the hunt at Jan Mayen. In both cases, the age of pups was unknown. More complete data on the size and condition of pups are reported by Shepeleva (1973), although even here complete records of standard morphometric data were not taken and no attempt was made to describe the components of neonatal weight gain from birth to weaning. To our knowledge, morphometric data of nursing mothers have not been previously reported.

Materials and methods

Our research was conducted at whelping concentrations of hooded seals on the ice floes approximately 100 and 180 km off northeastern Newfoundland in March 1983 and 1984, respectively, and near the seaward edge of the ice pack in these same areas in April of each year. In March, the seal herd was initially located by fixed-wing aerial survey. Subsequently, Hughes 500D helicopters based on a research vessel were used to ferry investigators to the study area and between

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TABLE 1. Hooded seals collected off northeastern Newfoundland in March and April 1983 and 1984 (number of known-age pups given in parentheses)

Year	Month	Dates	Mothers	Dependent pups	Weaned pups	Total
1983	March	22–25	11	11(6)	11	33
	April	18–21	—	—	17	17
1984	March	18–24	22	22(16)	5(5)	49
	April	18–29	—	—	36	36
Total			33	33(22)	69(5)	135

sites within this area daily. In 1983, our work was severely hampered by unpredictable movements of the ice pack and reduced visibility during inclement weather. As a result, with the exception of newborn pups, we were forced to work with pups of unknown age. In 1984, LORAN-C navigational equipment on board the helicopters and radio transmitters (frequency 148.50 to 148.95 MHz, range about 30 km; Telonics, Mesa, Arizona) placed on the ice permitted relocation of the study area despite unpredictable ice movements and poor weather. However, even in 1984 extensive periods of fog limited our sampling of known-age pups and mothers toward the end of lactation. In both years, dye (DAY-GLO, Series Z, Pigment Chemical Company, Montreal, Quebec) placed on pups or on the ice nearby was used to facilitate the relocation of tagged animals.

On 18 and 19 March 1984, 69 hooded seal pups on a consolidated floe of several square kilometres were tagged on the day of birth with Dalton Jumbo Rototags (Dalton Supplies Ltd., Henley-on-Thames, Oxon, England). Orange and blue streamers (3 × 20 cm) made of vinyl cloth were attached to these hind-flipper tags to distinguish day of birth and enable rapid aerial identification. Changes in pelage colouration and body form were noted for these known-age pups at each recapture to allow more precise estimation of the age of pups collected in 1983.

Animals were collected under an experimental sealing permit issued by the Canadian Department of Fisheries and Oceans, St. John's, Newfoundland. Adult females were shot at close range using a high-powered rifle, whereas pups were killed by several hard blows to the cranium as prescribed by Canadian Sealing Regulations. Instantaneous death was confirmed by the examination of eye reflexes. In reporting weights, no allowance has been made for blood loss. A total of 135 hooded seal neonates, mothers, and weaned pups were collected (Table 1).

Standard morphometric data (American Society of Mammalogists 1967) were taken from all animals with the modification that sternal blubber thickness was defined as the depth of blubber only rather than the combined thickness of blubber and skin. Sculp weight, defined as the weight of skin and attached blubber minus the anterior and posterior flippers, was also taken. Core weight was estimated by subtracting sculp weight from total body weight. Pups were weighed to the nearest 0.2 kg on a 50-kg scale (Salter Model 235, Salter Industrial Measurements Ltd., West Bromwich, England). The weight of mothers was determined to the nearest 2 kg on a 500-kg scale (Chatillon Model WT-12, Chatillon & Sons, New York). Both scales were calibrated before and after use in the field.

The stomachs of mothers and pups were examined in the field for the presence of food. Pup stomachs collected in April were individually labelled and stored in 70% ethyl alcohol for later examination.

The age of adults was estimated by counting growth layer groups in the dentine and cementum of a lower canine tooth (Bowen et al. 1983; Laws 1962). A single transverse section (200–250 μm), cut at the greatest diameter of the tooth root, was examined under transmitted light using a 6 to 50 × binocular microscope. All ages were estimated by the same individual based upon a single examination of each section.

Results

Maternal weight loss

To examine the change in condition of lactating females, standard morphometric measurements were taken from 22

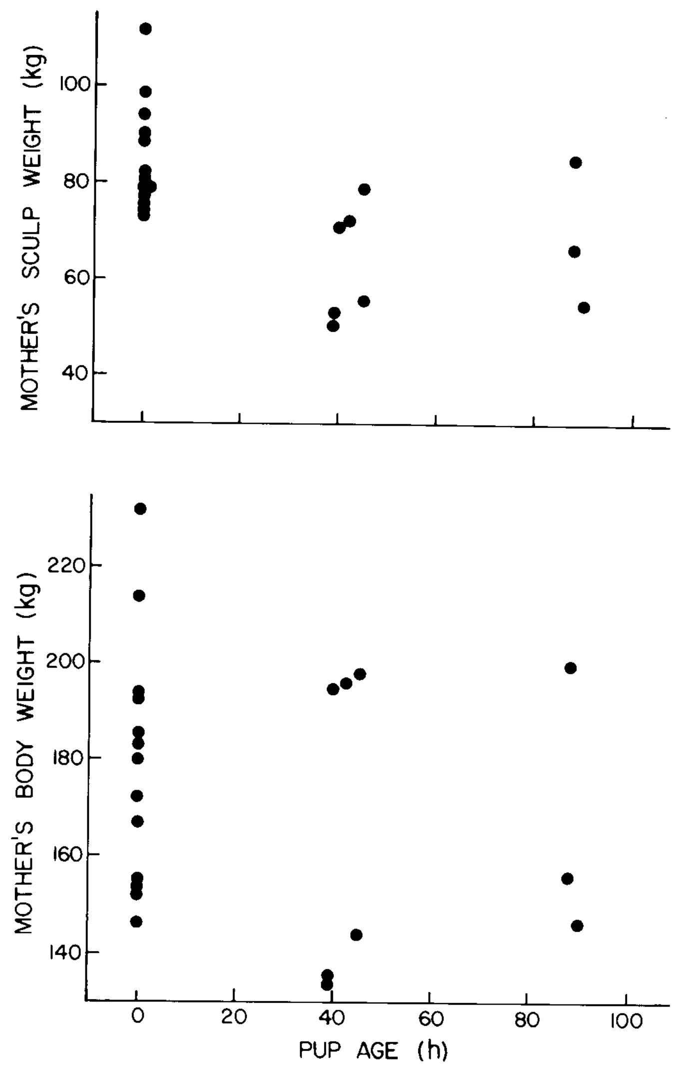

FIG. 1. Body and sculp weight of hooded seal mothers plotted against age of their nursing pups.

mothers with pups that were newborn or had been marked shortly after birth and were therefore of known age. Data were also obtained from 11 mothers with pups whose approximate age was estimated by comparison of the pelage colour and fatness with those of known-age pups (Table 1). Total body weight and sculp weight of mothers at known stages of lactation are given in Fig. 1. There was considerable individual variation in total body weight among females at comparable stages of lactation and no clear relationship is apparent. Although the situation is somewhat clearer in the case of sculp weight, with a trend toward decreasing sculp weight with advanced stage of lactation, in both cases these data are insufficient to reliably

TABLE 2. Changes in morphometric measurements (mean ± SE) of hooded seal mothers and their pups during lactation

	Stage of lactation		
	Beginning	Intermediate	Late
Mothers			
Body wt. (kg)	179±7.0	156±10.7	150±8.2*
Sculp wt. (kg)	85±3.1	62±4.0	61±3.5***
Core wt. (kg)	94±4.4	94±7.3	89±5.1ns
Length (cm)	195±2.8	187±3.7	192±2.5ns
Axillary girth (cm)	140±2.4	132±3.3	128±3.0**
Anterior flipper (cm)	29±0.9	29±1.0	29±0.5ns
Posterior flipper (cm)	38±0.8	36±0.6	39±0.7ns
Sternal blubber depth (cm)	4.5±0.3	3.8±0.2	3.7±0.2*
Age (years)	8±0.8	7±1.0	8±0.8ns
Pups			
Body wt. (kg)	21.5±0.9	29.7±1.3	43.7±1.9***
Sculp wt. (kg)	7.8±0.4[a]	14.5±0.9	23.3±1.2***
Core wt. (kg)	13.4±0.6[a]	15.2±0.7	20.3±0.9***
Axillary length (cm)	103±2.2	108±2.0	111±1.5*
Girth (cm)	65±1.6	78±1.8	91±2.0***
Anterior flipper (cm)	20±0.3	20±0.2	19±0.6*
Posterior flipper (cm)	26±0.4	26±0.4	26±0.4ns
Sternal blubber depth (cm)	1.4±0.1	2.9±0.1	4.0±0.2***
Sample size	13	8	12

NOTE: *, significant at $P < 0.05$; **, significant at $P < 0.01$; ***, significant at $P < 0.001$; ns, not significant ($P > 0.05$).
[a]$n = 12$.

TABLE 3. Relationship between standard morphometric measurements and age (days) of known-age hooded seal pups collected in March 1983 and 1984

	Regression parameters[a]					
	a	b	SE_b	r^2	n	F
Body wt. (kg)	20.8	6.5	0.62	0.85	21	113.1***
Sculp wt. (kg)	7.5	4.6	0.29	0.93	21	241.5***
Core wt. (kg)	13.3	1.9	0.36	0.60	21	29.1***
Length (cm)	103.0	2.4	1.2	0.18	22	4.28ns
Axillary girth (cm)	65.3	8.2	0.86	0.82	22	91.3***
Sternal blubber thickness (cm)	1.5	0.7	0.05	0.93	22	248.4***

NOTE: ***, highly significant at $P < 0.001$; ns, not significant ($P > 0.05$).
[a]Based on the linear model $y = a + bx + \epsilon$.

estimate either total weight loss or the components of weight loss by mothers during lactation.

An approximate measure of the impact of lactation on maternal energy stores may, nevertheless, be determined with available data. In the field, all 33 mothers in our cross-sectional sample were placed into one of three classes based on the developmental stage of their pups: newborn, thin blueback, and fat blueback. These developmental stages are known to represent the beginning, the approximate middle, and the late stages of lactation, respectively, based on observations of known-age pups (Hay et al. 1985). A one-way analysis of variance was used to test for significant differences among stages of lactation of each morphometric character measured on mothers and their pups (Table 2). There was no significant variation in the mean age of mothers in each pup-stage class.

The mean body weight of mothers declined from 179 kg at the beginning of lactation to 150 kg for mothers nursing fat pups near the end of lactation (Fig. 2). This is equivalent to a loss of about 16% of body weight in somewhat less than 4 days. As expected, most measurements that serve as a proxy for stored fat (i.e., sculp weight, axillary girth, and blubber depth) were significantly less for mothers with fat pups than for those with newborn pups (Table 2). There was no significant decline in core weight (Fig. 2), although mothers with fat pups tended to have lighter core weights than those with newborn pups. Of the 29 kg of weight lost, almost 83% was lost from the sculp (i.e., skin and blubber), while the remaining 17% was lost from the core. Measures of skeletal size (standard length and flipper size) of lactating mothers, as expected, did not vary with stage of lactation (Table 2).

No food or food remains such as otoliths were found in any of the 33 stomachs examined from lactating females.

Growth of suckling pups

Morphometric data from 13 newborn pups are presented in Table 2. These pups, determined to be newborn by the presence

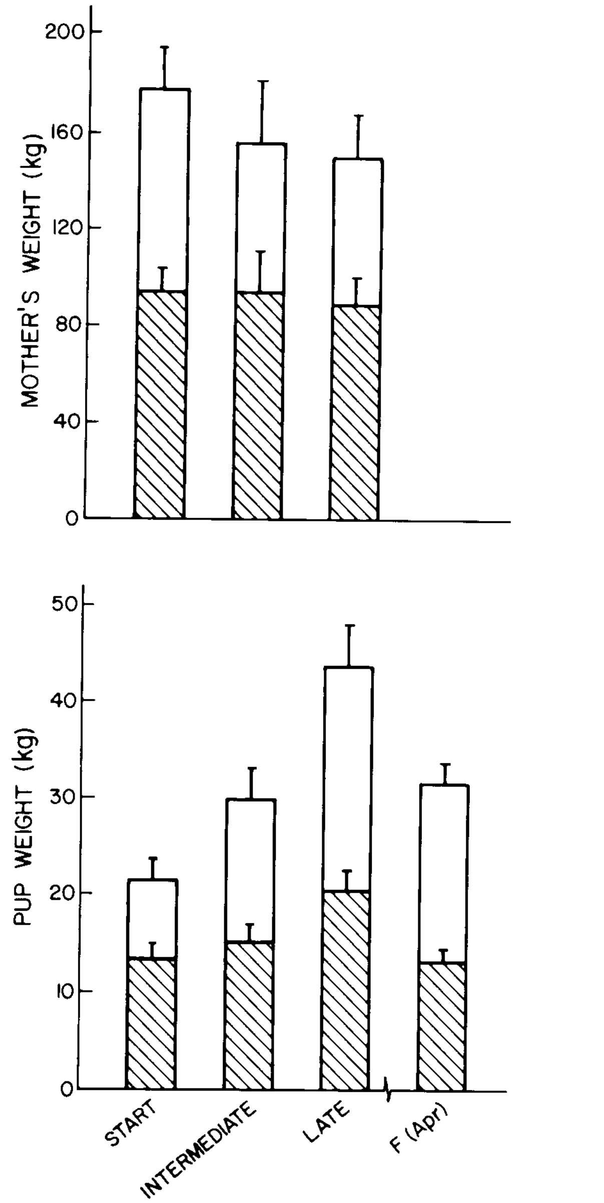

FIG. 2. Components of weight loss by mothers and weight gain by their pups throughout lactation. Bars are mean values and vertical lines represent 95% confidence limits. Open bars, sculp; hatched bars, core; F(Apr), fasting pups sampled in April.

of fresh placentas, the thin or wet appearance of pups, and fresh blood on the ice and pups, weighed an average of 21.5 ± 0.9 kg and were 103 ± 2.2 cm in length.

Using the three developmental stages to indicate the stage of lactation, we see that pup weight doubled to an average of 43.7 ± 1.9 kg during late lactation approximately 4 days postpartum (Table 2). Most (70%) of the weight gained by suckling pups was in the form of blubber (Fig. 2). This is reflected in the change in the ratio of sculp to total body weight, which increases from 0.37 ($n = 12$) at birth to 0.53 ($n = 6$) at weaning.

A more accurate picture of the composition of pup weight gain is obtained using only data from known-age pups. The relationships between standard morphometric measurements of these pups and days postpartum are given in Table 3. From birth to weaning at approximately 4 days, body weight increased linearly at a rate of 6.5 kg/d, sculp weight at a rate of 4.6 kg/d, and core weight at a rate of 1.9 kg/d. During this same period,

TABLE 4. Standard morphometric data ($\bar{x}$ ± SE) of almost weaned or newly weaned hooded seal pups in March 1983 and 1984 and weaned pups in April 1983 and 1984 combined

	Combined March 1983 and 1984 ($n = 19$)	Combined April 1983 and 1984 ($n = 53$)
Body wt. (kg)	44.5±1.25	31.7±0.74***
Sculp wt. (kg)	25.0±0.78	18.5±0.45***
Core wt. (kg)	19.5±0.68	13.2±0.40***
Length (cm)	111.7±1.27	106.4±0.86ns
Axillary girth (cm)	93.7±1.05	79.2±0.74***
Anterior flipper (cm)	19.5±0.23	19.0±0.20ns
Posterior flipper (cm)	25.6±0.32	25.5±0.24ns
Sternal blubber thickness (cm)	4.2±0.11	3.4±0.07***

NOTE: Nonpaired t-test; ***, significantly different $P < 0.001$; ns, not significantly different ($P > 0.05$).

axillary girth and blubber depth increased at rates of 8.2 and 0.7 cm/d, respectively. There was no significant increase in average body length or the length of anterior (20 ± 1.2 cm) and posterior flippers (26 ± 1.3 cm).

Significant weight loss immediately follows weaning. Five pups that were weighed shortly after weaning at 4 d of age lost an average of 1.2 kg (range 0.8 to 1.5 kg) from day 4 to day 5. However, this initial rate of weight loss was not maintained until pups began to feed. In both 1983 and 1984, measurements were taken from a sample of weaned pups in mid to late April (Table 1). There were no significant differences between years in any of the weight measurements and therefore these April samples were pooled. Nineteen almost weaned or newly weaned pups were available for comparison. Measurements of standard body length and flipper length in April were not significantly different from those taken in March. However, there was a significant decrease in body weight, sculp weight, core weight, axillary girth, and blubber depth (Table 4). Approximately 29% or 13 kg of body weight was lost between weaning and mid to late April when pups were around 30 days of age. Reduction in sculp and core weight accounted for 51% and 49%, respectively, of the total weight loss. At about 4 weeks of age, the core weight of fasting pups had dropped to that of newborns (Fig. 2). These data indicate an average rate of weight loss of about 0.4 kg/d, if we assume a birth date of 17 March and that feeding at least to a maintenance level does not begin before 15 April.

This assumption is consistent with the limited available information on feeding by pups. In April 1983, only 5 of 17 pup stomachs contained food, but in each case the food had been greatly digested allowing it to be identified only as shrimp. All five stomachs containing food were taken between 1600 and 1700 on 18 April, suggesting that feeding had occurred earlier that day. An average of 141 ± 117 g ($\bar{x}$ ± 1 SD) of shrimp was present in these stomachs. In 1984, only 1 of 37 stomachs contained any trace of food. Twelve pups were killed on 18 April, 22 on 19 April, and 1 on 20 April. Only the pup taken on 20 April had food in its stomach, in this case, 2.5 g of the hyperiid amphipod, *Parathemisto compressa*. The high proportion of empty stomachs in both years may indicate that pups had only recently begun to feed.

Discussion

As in all phocids, the postnatal care of young is the sole responsibility of the mother in hooded seals. Evidence from the examination of stomachs and behavioural observations during the nursing period which suggest that females do not leave their pups indicate that hooded seal mothers do not feed during lactation. Shepeleva (1973) reached this same conclusion. Thus hooded seal mothers must support both milk production and their own maintenance requirements using only stored nutrients. This pattern appears to be characteristic of phocids, although in a few species some ingestion of food occurs (Oftedal et al. 1986).

Hooded seal mothers suffer a significant loss in weight, primarily from the blubber layer, during the 4 days of lactation. This weight loss, representing 16% of the female's body weight at the beginning of lactation, is significantly less than the estimated loss by lactating grey seals (38%), Weddell seals, *Leptonychotes weddelli* (46%), Hawaiian monk seals, *Monachus schauinslandi* (34%), and northern elephant seals, *Mirounga leonina* (42%) (Table 5). Harp seal mothers are reported to lose about 22% of their body weight during lactation (Stewart and Lavigne 1984), a value close to that estimated for the hooded seal in this study.

Weight loss during nursing may be estimated by sequential measurements on the same mothers (for example the grey, Weddell, and northern elephant seal studies in Table 5) or by single measurements on samples of mothers taken at various stages during the lactation period. This latter method was used to estimate weight loss by harp seal mothers and by hooded seals in our study. Cross-sectional sampling will yield an unbiased estimate only when the birth dates of pups are independent of maternal size. However, M. A. Fedak and S. S. Anderson (personal communication) have found that in grey seals the largest (i.e., heaviest) mothers tend to give birth early in the pupping season and thus cross-sectional sampling of mothers will underestimate weight loss during lactation because larger mothers will be associated with older pups, while smaller females will tend to have younger pups. The extent to which this effect may have biased the estimated weight loss of harp seals reported by Stewart and Lavigne (1984) cannot be determined with available information.

Our estimate of weight loss during lactation is imprecise and likely conservative, since we did not know how close mothers with fat pups were to the end of lactation. Also, our sample of maternal data toward the end of lactation is too small to yield confident estimates. Nevertheless, it seems unlikely that our estimate of weight loss is in error by a factor of two, which would be necessary for data on hooded seals to be consistent with that on other phocid seals. More accurate estimates of weight loss could have been obtained by sequential weighing of the same mothers at the start and end of lactation, as was done, for example, by Fedak and Anderson (1982). Unfortunately, in attempting to immobilize hooded seals with fentanyl citrate for this purpose, we found that hooded seal mothers abandoned their pups upon recovery from the drug.

Fedak and Anderson (1982) estimated that female grey seals use about 84% of their fat reserves during a lactation period of 18 days. The lack of reliable data in other phocids on the percentage of stored fat used by mothers during lactation prevents much comparative analysis of the ecological correlates of weight loss. Northern elephant seal mothers are reported to use about 58% of their stored adipose tissue during an average nursing period of 26.5 days (Costa et al. 1986). How do these values compare with those in the hooded seal? Hooded seal females weigh an average of 179 kg at the beginning of lactation and the sculp makes up 85 kg or 47% of this weight (Table 2). Since hooded and grey seal mothers are about the same size, we have used Fedak and Anderson's (1982) estimate that 10 kg of

TABLE 5. Mass loss in lactating phocid females (sample size given in parentheses)

	Mother's wt. at start of lactation (kg)	Mean wt. loss during lactation		Loss from:		Pup wt. gain (kg)	Pup wt. gain/ mother wt. loss	Mothers feeding
		kg	%	sculp (%)	core (%)			
Grey seal (*Halichoerus grypus*)	170(14)	65	38	—	—	30(14)	0.46[a]	No
	174(15)	56	32	—	—	29(8)	0.52[b]	
	169(1)	43	25	—	—	22(1)	0.51[c]	
Harp seal (*Phoca groenlandica*)	129(78)	29	22	82	18	25(78)	0.86[d]	Some
Hooded seal (*Cystophora cristata*)	179(13)	29	16	83	17	22(21)	0.76[e]	No
Weddell seal (*Leptonychotes weddelli*)	447(9)	205	46	—	—	89(9)	0.43[f]	No
Hawaiian monk seal (*Monachus schauinslandi*)	261(1)	88	34	—	—	45(1)	0.51[g]	No
Northern elephant seal (*Mirounga leonina*)	504(6)	157	42	72	28	86(6)	0.55[h]	No

[a]Fedak and Anderson 1982; regression based on sequential weighing of mothers and pups.
[b]Mansfield 1977; based on sequential weighing of pups, and regression based on cross-sectional sample of mothers.
[c]Amoroso et al. 1951; based on sequential weighing for only 15 days of 18-day lactation period.
[d]Stewart and Lavigne 1984; regression estimate based on statistical sampling of mothers and pups of approximately known age assuming lactation is 9 days.
[e]This study based on mean values from statistical sampling of mothers and regression of known-age pups.
[f]Tedman and Green 1987; based on regressions from sequential weighings of mothers and pups assuming lactation period of 45 days.
[g]Kenyon and Rice 1959; original weights in pounds, values estimated.
[h]Costa et al. 1986; based on sequential weighing of mothers and pups.

TABLE 6. Weight loss in phocid pups during the postweaning fast (sample size given in parentheses)

	Duration of fast (weeks)	Avg. daily wt. loss (kg)	% of initial wt. lost	% wt. loss		Sculp wt./total wt.	
				Core	Sculp	Birth	Weaning
Harp seal[a]	6	0.3(20)	37	56	44	0.28(9)	0.53(20)
Hooded seal[b]	4	0.4	29	49	51	0.37(12)	0.53(6)
Grey seal[c]	4–6	0.53(34)	32[d](5)	—	—	—	0.50(3)
Northern elephant seal[e]	8–10	0.7(5)	33(5)	—	—	—	0.50(5)
Southern elephant seal[f]	1–1.5	2.2	19	—	—	—	0.44(3)
		3.0	23				
Ringed seal[g]	—	—	—	—	—	—	0.46(2)

[a]Worthy and Lavigne 1983*b*; based on a regression given on p. 450, experiment begun with 20 pups; Stewart and Lavigne 1980.
[b]This study; weight loss is average difference between 19 newly weaned pups and 53 fasting pups sampled in late April.
[c]Fedak and Anderson 1982; Mansfield 1977; Øritsland et al. 1985.
[d]Over a 3-week period.
[e]Reiter et al. 1978; Ortiz et al. 1978.
[f]Condy 1980; Bryden and Stokes 1969.
[g]Sterling and McEwan 1975.

the sculp is skin and hair. Worthy (1982) reported that in a single adult harp seal a further 10% of the core weight was fat. Applying these values, we estimate that the average female has about 84 kg of stored fat at the onset of lactation and 56 kg at the end of nursing. This means that females use about 33% of their fat reserves during lactation. Although these calculations are only first approximations and likely underestimate the use of fat, it seems clear that hooded seal mothers invest a smaller portion of their stored fat in their pup than do grey seals and northern elephant seals. This is consistent with the appearance of these mothers at the time of weaning. Both grey and elephant seal females look gaunt while hooded seal females do not.

Although the limited available data suggest that the weight loss by mothers during lactation is roughly proportional to lactation length, no simple relationship emerges. For example, grey seal mothers nurse for 18 days on average and are estimated to use 84% of their stored fat. However, northern elephant seal mothers use only 58% of their stored fat during a nursing period of about 26 days. These comparisons are undoubtedly confounded by the differences in female body size and activity of mothers, and also by differences in the fat content of milk produced throughout lactation.

A comparison of the ratio of pup weight gain to mother weight loss suggests that the transfer of nutrients from mother to pup is more efficient in hooded seals than in other phocids with the possible exception of the harp seal (Table 5). However, as discussed earlier the present values for harp and hooded seals must be considered tentative. Also, of the species listed in Table 5, only harp seal mothers are known to feed during lactation but feeding is limited in most years (Stewart and Murie 1986; W.D. Bowen, unpublished data). Both feeding and the potential biasing effect of cross-sectional sampling could result in an overestimation of the efficiency of nutrient transfer in this species. Available data on hooded seals are consistent with the hypothesis that the abbreviation of lactation allows a reduction in overhead cost and more efficient transfer of nutrients from mother to pup.

An increase in sculp weight (i.e., the blubber layer) accounts for approximately 70% of the weight gained by hooded seal pups during lactation. Similar estimates have been reported in grey seals (Mansfield 1977) and harp seals (Stewart and Lavigne 1980; Kovacs and Lavigne 1985).

Deposition of body fat reserves occurs almost exclusively after birth in most mammals (Adolph and Heggeness 1971; Pond 1977). Hooded seal pups have an average of 1.5 cm of blubber at birth, whereas in most phocids the blubber layer is virtually absent at birth. Shepeleva (1973), working in the Jan Mayen population, reported 2.0 cm of blubber over the sternum of 2 full-term foetues and one 1-day-old pup. In hooded seals, this layer of blubber comprises about 19% of the total body weight at birth, assuming that, as in harp seals (Worthy and Lavigne 1983*a*), the skin represents 17% of total body weight at birth. Southern elephant seals are reported to have about 0.5 to 1.0 cm of blubber at birth (Laws 1953; Bryden and Stokes 1969), but this represents only about 2–9% of the newborn's body weight. In harp seals, born without a measurable sternal blubber layer, only 6 to 7% ($n = 3$) of total body weight at birth is fat (Worthy and Lavigne 1983*a*). Body fat reserves in newborn Weddell seals comprise about 8.5% of total body weight (Tedman and Green 1987).

The high fat content of newborn hooded seals is unusual not only for phocid seals but for mammals in general (Widdowson 1950; Pond 1977). During lactation hooded seal pups store subcutaneous fat at an average rate of 4.6 kg/d. Perhaps this is approaching the physiological limit of the rate of fat deposition. If this is true then prenatal fat storage may be necessary, given a 4-day lactation period, for the pup to achieve a sculp weight equal to 50% of total body weight at weaning, which appears to be typical for phocids (Table 6).

There appears to be a clear energetic advantage to the rapid accumulation of fat by nursing phocid pups, for in all species newly weaned pups fast before nutritional independence (Table 6). Hooded seal pups appear to fast for about 4 weeks and lose an average of 29% of their weaning weight. Similar weight loss, expressed as a percentage of weaning weight, is reported in other phocids. However, direct comparisons between species may be misleading because of the difficulty in determining the precise period of fasting (Table 6). Nevertheless, available data suggest that species must differ in their physiological and behavioural adaptations to the postweaning fast. Hooded seal and northern elephant seal pups both lose about 30% of their weaning weight during the postweaning fast and yet the former fasts for about 4 weeks while the latter fasts for 8–10 weeks.

There is some debate about the relative contribution of protein and fat to the metabolic requirements of the pup during the postweaning fast. This debate involves differences in opinion, but as indicated above may also reflect differences in the biology of species within this family. In this study, mass loss from the core (49%) and blubber layer (51%) contributed about equally to the total mass lost by fasting hooded seal pups. Similar results have been reported in harp seals by Stewart and Lavigne (1980). They argued that although some of this weight loss could be attributed to catabolism of fat found throughout the body core and concentrated around internal organs, these deposits did not appear sufficiently extensive to account for the entire weight loss within the core. Based on their morphometric data and a computer model of energy balance (Øritsland 1977), they suggested that fasting pups, in comparison with other mammals, may derive an unusual amount of energy from the catabolism of protein.

On the other hand, Brodie and Pasche (1982) argued that Stewart and Lavigne's (1980) data on harp seals were anomalous given their observations on grey seals and studies on northern elephant seals which demonstrated an initial priority on fat consumption (Pernia et al. 1979). They suggested that protein would be used as an energy source during starvation only after core lipids and the blubber layer had been utilized to a critical minimum thickness based on the need to preserve the insulating quantities of the blubber layer.

However, the situation in harp seals has been further elaborated by Worthy and Lavigne (1983*b*). They report that core reserves of lipid as well as considerable amounts of core protein supply almost 50% of the metabolic requirements during the initial 2 weeks of the fast. Beyond this point, fat from the blubber layer becomes increasingly important as the source of energy contributing over 90% of requirements between 6 and 8 weeks of fasting. Furthermore, Øritsland et al. (1985) report that weight loss data obtained from the same animals as those used by Brodie and Pasche (1982) suggest a significant catabolism of lean body mass during starvation while considerable blubber deposits are maintained. This is also suggested by our hooded seal data which show that core weights decreased by 32%, while sculp weight decreased by only 26% during the 1st month of the postweaning fast. However, there is a need for chemical studies of the core and sculp to confirm the energy equivalence of this observed loss in mass during fasting. In contrast to the harp and hooded seal data, northern elephant seals use fat almost exclusively to meet their energy requirements during their 10-week land-based fast (Ortiz et al. 1978). Worthy and Lavigne (1983*b*) suggest that this difference may represent a physiological adaptation to the warmer climate inhabited by northern elephant seals.

Our results suggest that efficiency of nutrient transfer in hooded seals during lactation is greater than that reported in most mammals (Brody 1945) and in other phocids for which there are data. Studies on milk consumption by pups, the energy content of pup weight gain, and the energy content of hooded seal milk throughout lactation will undoubtedly provide insights into how this efficiency is achieved.

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