Mass and Energy Transfer during Lactation in a Small Phocid, the Harbor Seal (*Phoca vitulina*)

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Abstract

*In true seals (family Phocidae), the large energetic costs of lactation are supported primarily by mobilization of stored fat. We studied the magnitude of fat and energy depletion in lactating harbor seals (*n = 17*) on Sable Island, and fat and energy storage in their pups, using cross-sectional morphometric and isotopic methods. Initial mass of mothers studied ranged from 87 to 94 kg. Maternal mass declined by 33% over the first 19 d of the 24-d lactation period. Most of this loss (68.8%) was from the sculp (i.e., skin and attached blubber). Estimated maternal body fat, derived from dilution of deuterium oxide, decreased from 24% at parturition to about 7% at 19 d postpartum. Mothers lost 16.3 kg (78.7%) of their stored fat and 3.1 kg (20.0%) of stored protein, representing 713.8 MJ (169 Mcal) or 60.5% of stored energy. Newborn pups contained 93.0 MJ (22.1 Mcal) of energy, divided similarly between fat (46.4%) and protein (53.6%). Pup body mass increased from 10.6 kg to 25.8 kg. Sculp mass accounted for 62.7% of mass gained by the pup. Total body fat of pups increased from 11% at birth to 35% at 19 d. Pups deposited 346.8 MJ (82.2 Mcal) or 48.7% of energy withdrawn by females from body stores. Unlike large phocid species, lactating harbor seals initiate feeding during lactation apparently because energy reserves are insufficient to cover the combined costs of lactation and maternal metabolism.*

Introduction

Within the Phocidae (true seals), lactation is a brief period of 4–45 d characterized by maternal fasting and thus dramatic reduction in stored energy,

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rapid mass gain by the pup, and abrupt weaning when the mother departs to feed at sea (Oftedal, Boness, and Tedman 1986). Although studies have been conducted on species using pack ice, fast ice, and land as a breeding substrate (harp seals, *Phoca groenlandica,* Stewart and Lavigne 1980; Kovacs, Lavigne, and Innes 1991; W. D. Bowen, unpublished data; hooded seals, *Cystophora cristata,* Bowen, Boness, and Oftedal 1987; Weddell seal, *Leptonychotes weddellii,* Tedman and Green 1987; northern elephant seal, *Mirounga angustirostris,* Costa et al. 1986; grey seals, *Halichoerus grypus,* Fedak and Anderson 1982; Anderson and Fedak 1987), most of these studies are with larger species (140–500 kg body mass at parturition). Maternal size and energy stores at parturition are likely to play a critical role in determining the intensity and duration of lactation. Thus, a broad understanding of the evolution of reproductive strategies of phocids requires comparative data on smaller species as well.

The harbor seal (*Phoca vitulina*) is one of the smaller phocid species. Body mass of nonpregnant adult females ranges from 60 to 75 kg (Boulva and McLaren 1979; Markussen, Bjorge, and Øritsland 1989). Harbor seals inhabit coastal waters in many areas of the North Atlantic and the North Pacific and several offshore areas such as Sable Island, Canada, where pups are born on the broad, sandy beaches from mid-May through early June (Boulva and McLaren 1979). Pup production on Sable Island has slowly increased from about 340 pups in the early 1970s (Boulva and McLaren 1979) to almost 600 in 1990 (W. T. Stobo and B. Beck, unpublished data).

Newborn harbor seals are large relative to maternal size and grow slowly compared with most phocids (Bowen, Oftedal, and Boness 1985; Kovacs and Lavigne 1986; Bowen 1991). Also, unlike most phocids, harbor seal neonates follow their mothers into the sea within hours of birth (Lawson and Renouf 1985). During the lactation period, pups spend considerable time actively swimming, either alone or with their mothers. It has been suggested that both the large mass and prenatal molt are adaptations to this aquatic behavior (Oftedal et al. 1991).

The unusually large amount of time spent in the sea and the slow growth rate of harbor seal pups during the lactation period, coupled with the small body size of females, suggest that the energetics of lactation in this species may differ from that of other phocids. However, little is known about the cost of lactation in harbor seals. Mass gain in harbor seal pups over the course of lactation has been studied on Sable Island (Boulva and McLaren 1979) and in Oslo Fjord, Norway (Markussen et al. 1989). On the basis of carcasses collected from the Kattegat-Skagerrak, Harkonen and Heide-Jorgensen (1990) reported estimates of the average mass lost by harbor seal females from the beginning of the pupping period in May to the period after lactation had ended (i.e., July and August). However, changes in mass and body composition of mothers and neonates in relation to pup age, and hence stage of lactation, have not been studied.

A number of different approaches have been used in describing the energetics of lactation in phocids. Fedak and Anderson (1982), Anderson and Fedak (1987), and Kovacs et al. (1991) estimated the cost of lactation in grey seals and harp seals, respectively, from longitudinal measurements of body mass of mothers and pups. A related method, referred to as morphometrics, involves dissecting the body into the principal fat (i.e., blubber) and lean (i.e., the remainder of the body) components and measuring the change in mass of these components over the lactation period (e.g., Stewart and Lavigne 1984; Bowen et al. 1987; Hammill et al. 1991). Isotope methods have been used to estimate milk intake in several species over the lactation period (northern elephant seal, Costa et al. 1986; Weddell seal, Tedman and Green 1987; hooded seal, Oftedal, Bowen, and Boness 1989). Each of these methods has contributed to our growing understanding of the energetics of pinniped lactation.

In this study, we used morphometrics, proximate analysis of blubber, and isotope dilution to estimate mass and energy transfer during lactation in the harbor seal (*P. vitulina concolor*). The use of morphometrics permitted direct comparison of the components of mass transfer in harbor seals, harp seals (Stewart and Lavigne 1984; Kovacs et al. 1991; W. D. Bowen, unpublished data), hooded seals (Bowen et al. 1987), and ringed seals (*Phoca hispida;* Hammill et al. 1991). The concurrent use of isotope dilution to estimate changes in body composition provided information on the energetic equivalents of mass transfer.

Material and Methods

The study was conducted in May and June of 1987 and 1988 on Sable Island, a crescent-shaped vegetated sandbar about 40 km long located 160 km east of Nova Scotia, Canada (43°55′ N; 60°00′ W). A total of 17 mothers and their pups were studied at 0 d ($n = 7$), 5–6 d ($n = 2$), 10–11 d ($n = 3$), 14–15 d ($n = 3$), and 18–19 d ($n = 2$) postpartum. Animals were collected under an experimental permit issued by the Canadian Department of Fisheries and Oceans, Halifax, Nova Scotia.

An individually numbered Roto-tag was placed in the webbing of the hind flipper of pups within 24 h of birth to provide accurate information on pup age and hence lactation stage. At this time, mother-pup pairs were also marked individually using a fast-drying, fluorescent paint (V-285, Lenmar, Baltimore) to permit rapid and reliable identification. To capture mother-pup pairs, we took advantage of the relatively tame nature of the Sable Island population and the tendency of mothers to remain with their pups. Pups were captured by hand or with hoop nets and pulled from the water's edge. Mothers typically followed their pups and could then be captured in a net fastened between two 2-m aluminum poles. The net was hinged at the head end and open at the rear and was closed by bringing the poles together under the animal, once the animal was in the net.

Cross-sectional estimates of mass loss during lactation may be biased if mothers of different size give birth at different times during the pupping season (Anderson and Fedak 1987). Although we do not know if this is the case in harbor seals on Sable Island, we designed our study to minimize the confounding effect of initial body mass by selecting for cross-sectional analysis 13 females whose mass at parturition was within a narrow range (87–94 kg). Four additional females, representing a range of 75–100 kg, were sampled at parturition but not included in the cross-sectional study.

Isotope Dilution Study

The body composition of 16 of the 17 mother-pup pairs was estimated by deuterium oxide (D_2O) dilution prior to the morphometric study. Before administration of the isotope, stomach contents of pups were evacuated by gastric intubation with a 9.5 mm veterinary stomach tube since it has been shown that gastric milk may delay isotope equilibration (Oftedal, Iverson, and Boness 1987). A preweighed quantity of D_2O (99.8% purity, Stable Isotopes Division, ICN Biomedicals, Cambridge, Mass.) was administered by syringe with a number 12 French gastric tube, at a dose of approximately 0.6 g/kg and 1 g/kg body mass in mothers and pups, respectively. Syringe and tube were flushed with two 5-cm^3 quantities of water and about 50 cm^3 of air to ensure complete isotope delivery. After administration, mothers and pups were held in separate but adjacent pens to allow isotope equilibration. Each animal was bled twice from the extradural vein, with about a 30–min interval between bleedings. The time of the first bleeding varied from 2 to 4.5 h after isotope administration.

Blood samples (8 cm^3) were collected without anticoagulants. After centrifugation, sera were transferred to cryovials and stored at −20°C. Total water was recovered from sera by heat distillation and assayed for D_2O concentration with infrared spectrophotometry (Oftedal and Iverson 1987). Body water pool size (*BW*) was then estimated as follows:

$$BW(\text{kg}) = M_\text{d}/(10 \times S_\text{d}),$$

where M_d is the amount (g) of D_2O given and S_d is the percentage of D_2O in the sample. The lean body mass (LBM) of pups was calculated assuming that water constituted 71% of the LBM that has been determined by carcass analysis to be constant over the lactation period in suckling hooded seal pups (Oftedal et al. 1989). In the absence of data on harbor seal females, we estimated LBM by assuming that water constituted 73% of the LBM, the mean value from a number of mammalian species (Blaxter 1989). Percent body fat (*BF*) was calculated by subtraction of LBM from total body mass. We also assumed that protein constituted 22.3% of LBM in harbor seal pups, as was found from carcass analysis in the hooded seal (O. T. Oftedal, W. D. Bowen, and D. J. Boness, unpublished data). Following Blaxter (1989), we assumed that protein comprised 23% of LBM in adult females. An estimate of the energy equivalence of changes in body composition over the course of lactation was calculated assuming protein = 23.6 MJ/g and fat = 39.3 MJ/g (Blaxter 1989).

Morphometric Study

After isotope equilibration, adult females were shot at close range with a high-powered rifle and pups were killed by a sharp blow to the cranium as prescribed by the Canadian Sealing Regulations. Instantaneous death was confirmed by the examination of eye reflexes.

Standard morphometric data were collected from all animals (Bowen et al. 1987). Sculp mass, defined as the mass of skin and attached blubber minus the anterior and posterior flippers, was also measured. Core mass was estimated by subtracting sculp mass from total body mass. After the sculp was removed, mammary glands were dissected from the blubber and weighed. Pups were weighed to the nearest 0.1 kg on a Salter 50-kg scale, whereas mothers were weighed to the nearest 0.5 kg on a Salter 200-kg scale.

Blubber samples (about 1 cm × 2 cm × 2 cm) were taken from the sternal area of the sculp of 12 mothers and 13 pups for proximate composition. Samples were placed in Whirl-pac bags, frozen within 4 h of the animal's death, and stored at −20°C. Total moisture was determined by drying to a constant weight in a forced convection oven at 100°C. Samples were assayed for total nitrogen by a macro-Kjeldahl procedure using a copper catalyst (Horowitz et al. 1975); crude protein was calculated as total nitrogen × 6.25. Total lipid was calculated on dried samples with petroleum ether extraction in Soxhlet extractors (Horowitz et al. 1975).

We normalized percentages using the angular transformation (Sokal and Rohlf 1969) prior to analysis. Regression equations in figures 2, 3, 5, and 6 are given with the transformed parameter estimates. Data are plotted in the original scale with the regression line based on retransformed predictions. The SEM is reported.

Results

Body water pool size could not be calculated for three of the 17 adult females. In one case the female escaped before a postadministration blood sample could be obtained but was subsequently recaptured. In another case D_2O concentration did not reach an equilibration plateau. Time constraints did not permit D_2O administration in a third female. The mean difference in isotope concentration between the first and second bleedings (0.0001% ± 0.0084%, $n = 30$) was not significantly different from zero ($P = 0.934$) indicating that isotope equilibration generally had occurred within 2–4.5 h of administration in the remaining mothers and in all 16 pups.

Postparturient Mothers and Their Newborn Pups

Morphometric and isotope dilution data were obtained from seven harbor seal mothers and their pups within 24 h of birth (table 1). Maternal mass of these females varied from 75.5 to 100.0 kg with an average of 87.5 kg. Sculp and core constituted 42.6% and 57.3% of initial maternal mass, respectively. On the basis of isotope dilution, water constituted 55.2% of maternal mass shortly after parturition. Maternal fat stores accounted for 17%–33% of body mass with an average of 24.3% ± 2.33%. There was no relationship between maternal mass at parturition and the percentage of body fat estimated from isotope dilution ($r = 0.20$; $P = 0.67$). Sculp mass was not significantly correlated with the estimate of total fat from isotope dilution in mothers with newborn pups ($r = .52$; $P = 0.24$).

Newborn pups weighed an average of 10.7 kg, or 12.2% of maternal mass (table 1). Sculp and core constituted 36.4% and 64.5% of birth mass, respectively. Sternal blubber depth measured 1.3 cm in newborn harbor seals. Body water accounted for an average of 62.9% of the mass of newborns. As a percentage of body mass, fat in newborn harbor seal pups varied between 4.2% and 17.2% with a mean of 11.3% ± 1.56% ($n = 7$). Estimated total body fat at birth, derived from D_2O dilution, was not significantly correlated with birth mass ($P = 0.47$) or sculp mass ($P = 0.20$).

TABLE 1
Morphometrics and body composition (mean ± SE) of seven harbor seal mothers and their pups at parturition

	Mother	Pup
Morphometric:		
Body mass (kg)	87.5 ± 3.13	10.7 ± .44
Sculp mass (kg)	37.3 ± 1.61	3.9 ± .13
Core mass (kg)	50.1 ± 1.66	6.9 ± .34
Length (cm)	150.5 ± 2.62	81.5 ± 1.50
Axillary girth (cm)	105.4 ± 1.16	50.1 ± 1.30
Anterior flipper (cm)	21.5 ± .55	16.7 ± .57
Posterior flipper (cm)	28.6 ± .41	20.5 ± .64
Sternal blubber depth (cm)	3.6 ± .10	1.3 ± .08
Isotope dilution:		
Body water (%)	55.2 ± 1.7	62.9 ± 1.1
Pool size (kg)	48.3 ± 2.1	6.8 ± .3
Body fat (kg)	21.4 ± 2.3	1.2 ± .2

Note. Values recorded at <24 h postpartum.

Morphometric and Body Composition Changes in Mothers

Changes in body mass, sculp mass, core mass, and blubber depth of harbor seal mothers over the first 19 d of the 24-d lactation period on Sable Island (Muelbert 1991) are shown in table 2. Over this period, the average mass of mothers declined by 33% at an average rate of 1.6 kg/d. Although most of this decline in mass (1.1 kg/d, or 68.8%) was from the sculp (fig. 1*a*), a 30.9% reduction in core mass was also observed. Other measurements that reflect the quantity of stored fat, such as axillary girth and sternal blubber depth, also decreased significantly during lactation (table 2). Measures of skeletal size such as body length (table 2) and flipper lengths did not change.

The mass of the mammary glands (1.9 ± 0.08 kg, $n = 13$; left and right combined) did not vary significantly over the course of lactation.

Percentage of body water in lactating females increased significantly ($P = 0.015$) over the course of lactation (fig. 2*a*). However, only 54% of the variation in percent body water was explained by pup age. Estimated percentage of body fat decreased significantly ($P = 0.011$) from about 24% at parturition to about 7% at 19 d postpartum (fig. 2*b*).

TABLE 2

Morphometric changes in harbor seal mothers and pups as a function of days postpartum

	Regression Estimates[a]			
	a	*b*	r^2	*P*
Mothers:				
Body mass (kg)	91.2 ± 1.07	−1.6 ± .09	.96	<.0001
Sculp mass (kg)	40.2 ± .70	−1.1 ± .06	.97	<.0001
Core mass (kg)	50.9 ± .80	−.5 ± .07	.82	<.0001
Length (cm)	154.6 ± 1.83	−.3 ± .15	.27	.070
Axillary girth (cm)	108.0 ± 1.70	−1.0 ± .15	.81	<.0001
Sternal blubber depth (cm)	3.8 ± .13	−.1 ± .01	.87	<.0001
Pups:				
Body mass (kg)	10.6 ± 1.06	.8 ± .09	.88	<.0001
Sculp mass (kg)	3.3 ± .69	.5 ± .06	.88	<.0001
Core mass (kg)	7.3 ± .50	.3 ± .04	.81	<.0001
Length (cm)	82.4 ± 1.45	.6 ± .13	.65	.001
Axillary girth (cm)	52.2 ± 1.37	1.5 ± .12	.93	<.0001
Sternal blubber depth (cm)	1.4 ± .09	.1 ± .01	.94	<.0001

Note. $n = 13$.

[a] Based on the linear model $y = a + bx + e$.

Both sculp mass (i.e., skin and attached blubber) and the estimated total body fat of mothers declined over the course of lactation. There was a significant ($P = 0.0003$) relationship between maternal total body fat (TBF, kg) and sculp mass (*SM*, kg):

$$\mathrm{TBF} = -14.2 + 0.92\,SM,$$

$r^2 = 0.68$, SE of the slope of the regression ($\mathrm{SE_b}$) = 0.184.

Morphometric and Body Composition Changes of Suckling Pups

Over the first 19 d of lactation, the average mass of pups increased about 2.5-fold from 10.6 kg to 25.8 kg (fig. 1*b*). Most (62.7%) of the 0.8 kg/d gain in mass was accounted for by an increase in the sculp; however, the core increased by 0.3 kg/d or 37.5% of gain. Axillary girth and sternal blubber depth also increased significantly (table 2). Although harbor seal pups in-

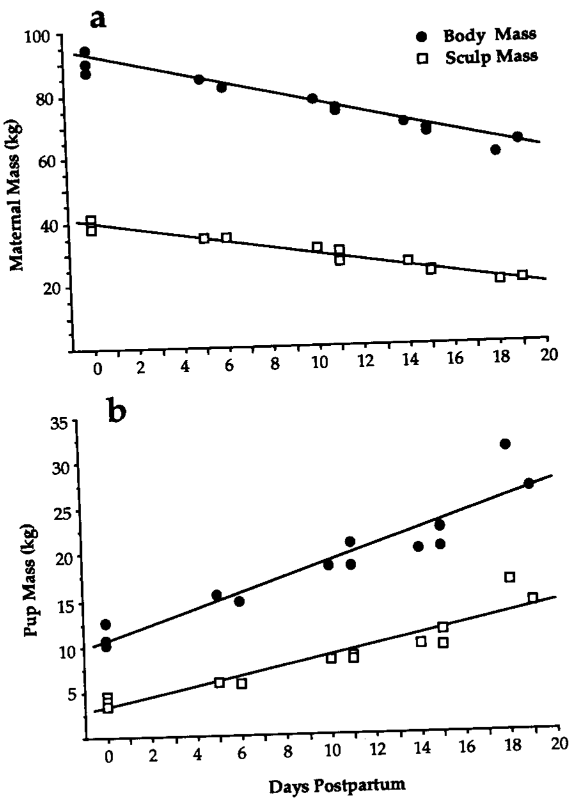

*Fig. 1. Changes in total body mass and sculp mass of 13 harbor seal mothers (*a*) and their pups (*b*) from 0 to 19 d postpartum. Regression eq. given in table 2.*

creased in length at a rate of 0.6 cm/d (table 2), both anterior and posterior flippers did not increase in length over this period of growth ($P = 0.936$ and $P = 0.433$, respectively).

Percentage of body water of pups decreased significantly ($P = 0.0001$) from about 64% of body mass at birth to about 47% in late lactation (fig. 3*a*). Estimated body fat increased significantly ($P = 0.0001$) from about 11% at birth to 35% at 19 d postpartum (fig. 3*b*). There was a significant relationship ($P < 0.0001$; fig. 4) between estimated TBF from isotope dilution and *SM* of suckling pups:

$$\mathrm{TBF} = -1.67 + 0.73\,SM,$$

$r^2 = 0.986$, $\mathrm{SE_b} = 0.023$.

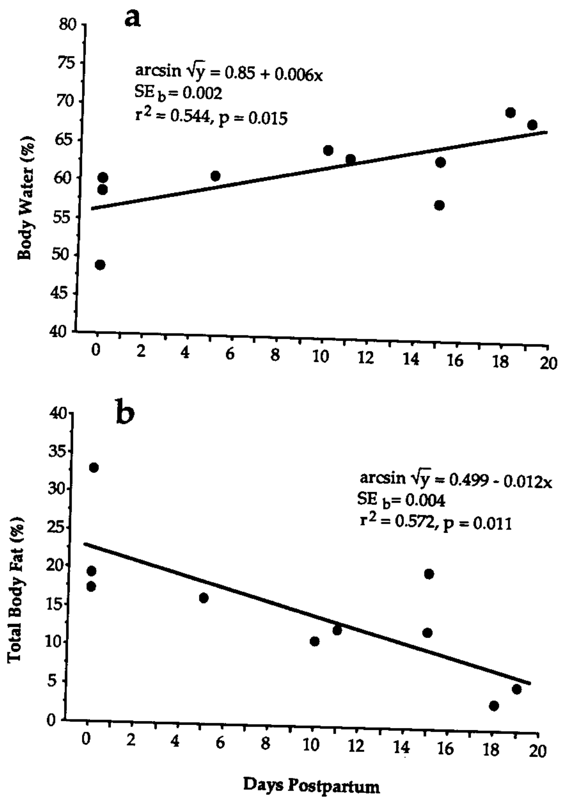

*Fig. 2. Isotope equilibration estimates of percent body water (*a*) and percent body fat (*b*) as a function of days postpartum in 10 lactating harbor seal mothers;* y *= proportion.*

Maternal and Pup Blubber Composition

The proximate composition of sternal blubber of both mothers and pups changed significantly over the course of lactation. The fat concentration of maternal blubber declined linearly from an average of 92.1% at parturition to about 77% at 19 d postpartum (fig. 5*a*). Water concentration rose from about 5% at birth to 15% over the same period (fig. 5*b*). The percentage of protein in maternal blubber increased from 2.2% at birth to about 5% at 19 d postpartum (fig. 5*c*).

The composition of the pup's blubber changed in the opposite direction over the course of lactation; percent fat increased while both percent water and percent protein decreased (fig. 6*a*, *b*, *c*). At birth, fat constituted 75.8% of sternal blubber (fig. 6*a*), whereas, in late lactation, it averaged about 90%; similar to the level in female blubber at the beginning of lactation. The water and protein content of pup blubber decreased from 17% and 5.5% at birth to about 7% and 2.5% near weaning, respectively (fig. 6*b*, *c*).

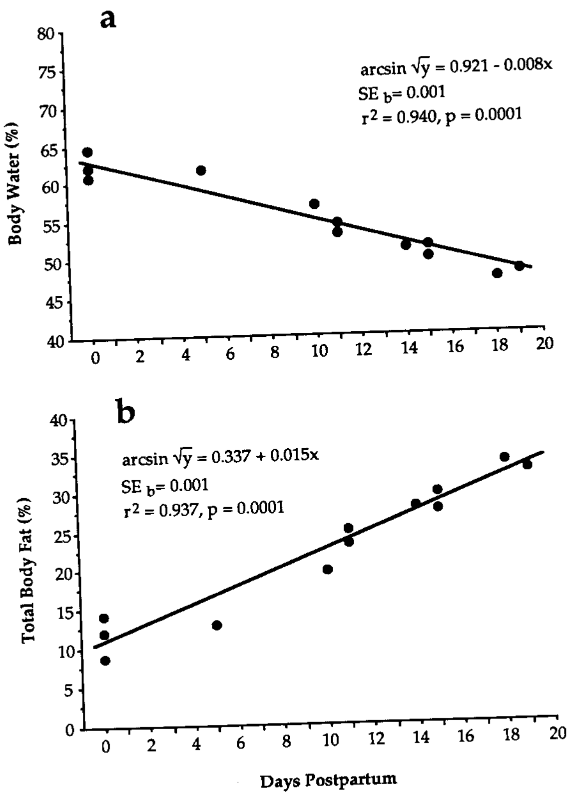

Fig. 3. Isotope equilibration estimates of percent body water (a) *and percent body fat* (b) *as a function of days postpartum in 12 suckling harbor seal pups;* y = *proportion.*

Energy Transfer

The calculated energy content of mothers and their pups changed dramatically over the lactation period (table 3). On the basis of estimates of body composition from isotope dilution (fig. 2), we calculate that females used 16.3 kg or 78.7% of their lipid stores and 3.1 kg or 20.0% of protein stores over the first 19 d of lactation. This represents 713.8 MJ or 60.5% of maternal stored energy at parturition. Of the energy lost by the female, 89.7% was estimated to have come from fat while only 10.3% was from protein.

At birth, harbor seal pups contained 93.0 MJ of energy that was divided relatively evenly between fat (43.2 MJ, 46.4%) and protein (49.8 MJ, 53.6%; table 3). Of the 15.2 kg deposited by pups over the 19-d period, 7.8 kg (51.3%) was fat and 1.7 kg (11.2%) was protein. In terms of energy stored by the pup, fat accounted for 88.4% (306.6 MJ) and protein for 11.6% (40.2

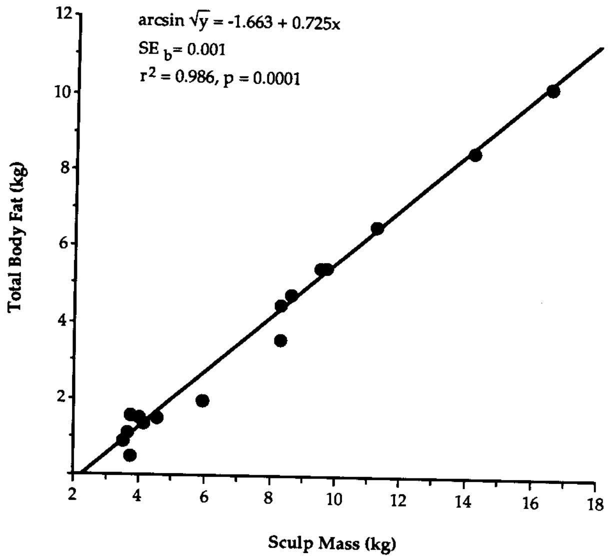

Fig. 4. The relationship between isotope equilibration estimates of total body fat (kg) and sculp mass (kg) in 16 suckling harbor seal pups over the course of lactation.

MJ). Harbor seal pups deposited 18.3 MJ/d or 48.7% of the 37.6 MJ/d lost by females.

Discussion

Body Composition of the Newborn Pup

The newborn harbor seal appears to be highly adapted to aquatic life throughout the lactation period. At birth most pups have shed the lanugo coat that provides effective insulation only when dry (Oftedal et al. 1991). Newborn harbor seals are larger relative to maternal mass at parturition (12.2%) than other phocids (5.7%–11.0%) with the exception of two other precocial species, the hooded seal (12.3%) and the bearded seal (*Erignathus barbatus,* 13.4%; Bowen 1991). Also, harbor seal pups are born with about 1.4 cm of blubber. Thus, the sculp (i.e., blubber and attached skin minus the flippers) of newborn pups accounts for 36% of body mass. Similar values were found in newborn hooded seals, a species that first enters the sea at about 4 d postpartum (Bowen et al. 1987). By contrast, species that do not normally enter the sea until older, such as the grey seal and harp seal, do not have a measurable blubber layer at birth (W. D. Bowen, unpublished data), or in the case of the southern elephant seal, the 0.5–1.0 cm of blubber

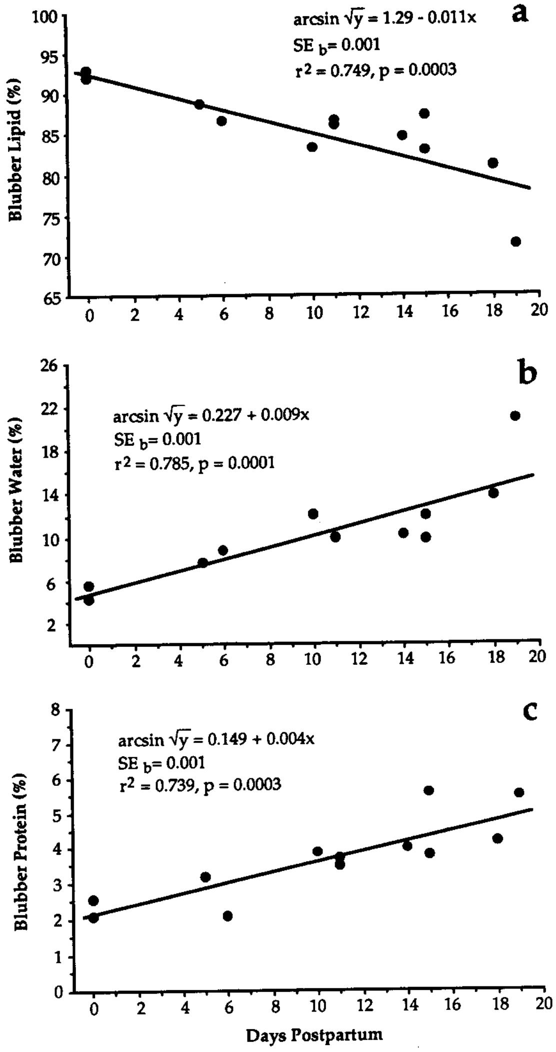

Fig. 5. Changes in (a) *percent lipid,* (b) *percent water, and* (c) *percent protein of sternal blubber in 12 harbor seal mothers from 0 to 19 d postpartum;* y = *proportion.*

at birth represents only 2%–9% of neonatal mass (Laws 1953; Bryden and Stokes 1969).

Both isotope dilution studies and carcass analysis confirm differences in the fatness of newborn harbor seals compared with most other phocid species. Total body fat from isotope dilution constituted 11.3% of body mass in the newborn harbor seal (fig. 2) compared with 8.5% in the Weddell seal (Tedman and Green 1987) and 6%–7% in the harp seal on the basis of carcass analysis (Worthy and Lavigne 1983). The relatively high fat concen-

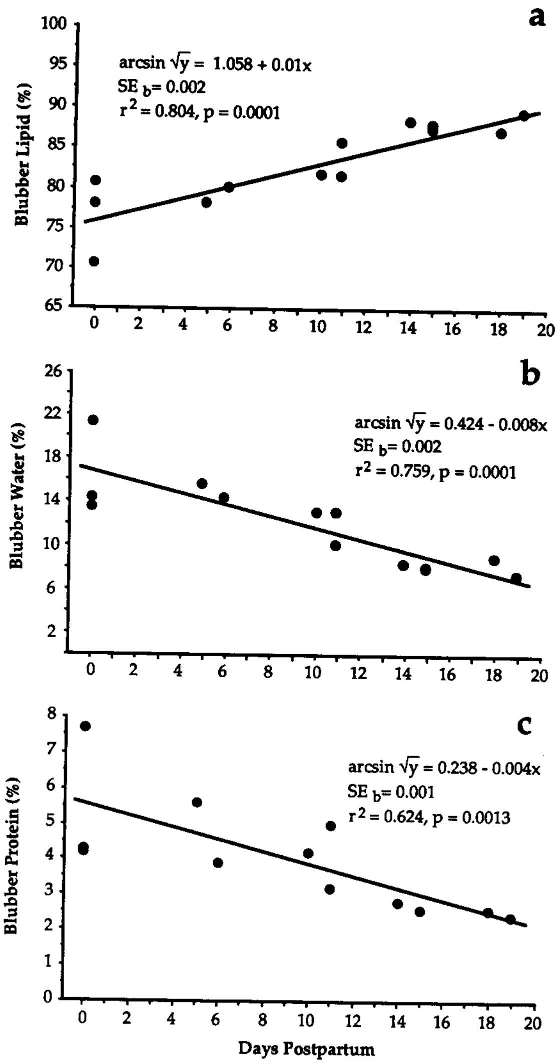

*Fig. 6. Changes in (*a*) percent lipid, (*b*) percent water, and (*c*) percent protein of pup blubber (*n *= 13) over lactation;* y *= proportion.*

tration of the newborn harbor seal and hooded seal (14.0% by carcass analysis; Oftedal et al. 1989) is likely an adaptation to permit entry into the sea within hours or days of birth without thermal stress (Oftedal et al. 1991).

Changes in Pups over Lactation

Previous studies have noted that the rate of mass gain in harbor seal pups is among the lowest reported in phocid seals (Kovacs and Lavigne 1986).

TABLE 3
Estimated changes in mass and energy content of harbor seal mothers and pups over the first 19 d of lactation

	At Birth	19 d Postpartum	Loss
Mother:			
Body mass (kg)	91.2	60.8	−30.4 (33.3)
Pool size (kg)	51.4 (56.4)	41.2 (67.8)	−10.2 (19.8)
Fat (kg)	20.7 (22.7)	4.4 (7.2)	−16.3 (78.7)
Protein (kg)	15.5	12.4	−3.1 (20.0)
Energy (MJ):			
Fat	813.5	172.9	−640.6 (78.7)
Protein	366.5	293.3	−73.2 (20.0)
Total	1,180.0	466.2	−713.8 (60.5)
Loss (mJ/d)			−37.6
	At Birth	19 d Postpartum	Deposition (%)
Pup:			
Body mass (kg)	10.6	25.8	15.2 (143.4)
Pool size (kg)	6.7 (63.4)	12.4 (47.9)	5.7 (85.1)
Fat (kg)	1.1 (10.6)	8.9 (34.5)	7.8 (709.1)
Protein (kg)	2.1	3.8	1.7 (81.0)
Energy (MJ):			
Fat	43.2	349.8	306.6
Protein	49.8	90.0	40.2
Total	93.0	439.8	346.8
Gain (MJ/d)			18.3

Note. Data are from table 2 and figs. 2 and 3. Data in parentheses are percentages of total.

Our estimate of 0.8 kg/d is higher than the 0.6 kg/d given in Boulva and McLaren (1979), which may be related to the large initial mass (92 ± 0.52 kg) of the mothers we studied. The average body mass of all harbor seal mothers weighed at parturition in 1988 was 85.5 ± 1.12 kg ($n = 52$). Large maternal size is associated with rapid pup growth in grey seals (Anderson and Fedak 1987) and southern elephant seals (McCann, Fedak, and Harwood 1989).

Pups both fattened and increased in body length over the course of lactation (table 2). However, harbor seal pups deposit less fat during lactation than do other species. In late lactation, the sculp accounted for 49.6% of body mass compared with 53.3% in the hooded seal (Bowen et al. 1987) and 58% in the harp seal (Stewart and Lavigne 1984). Similarly, harbor seal pups contain an average of only 34% total body fat in late lactation compared to 50% in northern elephant seals (Ortiz, Costa, and Le Boeuf 1978), 46% in harp seals (Worthy and Lavigne 1983), 37% in Weddell seals (Tedman and Green 1987), 45% in hooded seals (Oftedal et al. 1989), and 43% in one grey seal pup near weaning (Reilly and Fedak 1990).

The fat concentration of the blubber of harbor seal pups changed significantly over the lactation period from the 75% at birth to about 90% at 19 d postpartum. Comparable data are available for only one other phocid species. In the harp seal, fat increased from 21% near birth to 88% near weaning (Worthy and Lavigne 1983). Given that female phocids rely on stored energy to support lactation, it is likely that blubber of lactating females contains the greatest concentration of fat at parturition. The fat concentration of the blubber of adult females declined over lactation from 92% at parturition to about 80% at 19 d postpartum (fig. 5*a*). In contrast to our results, Lavigne, Stewart, and Fletcher (1982) found no trend in water content of blubber samples from female harp seals over the course of lactation; fat content was not measured. During the mobilization of blubber stores, fat is depleted from adipocytes resulting in an increased proportion of connective tissue. This was supported by our finding of increasing levels of protein in blubber. These results indicate that attempts to estimate sculp fat content from blubber mass must account for species differences in blubber composition and the effects of lactation stage.

Morphometric versus Isotopic Estimates of Body Composition

Few studies have compared estimates of TBF from isotope dilution or carcass analysis with estimates derived from morphometric data. Our results suggest that estimates of TBF in harbor seal pups can be reasonably predicted from changes in *SM* over the lactation period (fig. 4) but that less precise predictions can be made for lactating females. The lack of a relationship between TBF and *SM* in mothers at parturition is surprising, suggesting that the distribution of body fat may differ among females or, more likely, that our sample of seven females is too small to detect underlying patterns.

Using the measured lipid concentration of blubber along with estimates of skin mass and the fat content of the core, we can attempt to estimate TBF from morphometric data (table 2) and to compare this with the estimate derived from D_2O dilution. By analogy to adult female ringed seals (Hammill et al. 1991), we assumed that the skin of adult female harbor seals weighed

6.8 kg and the core contained 3.1% fat. Adult females were then estimated to have 35% body fat at parturition and 18% at 19 d postpartum. The estimates of TBF derived from isotope dilution were 23% and 7% of *BM*, respectively (fig. 2). Similarly, by analogy to harp seal data (skin weight 17.9% of *BM* at birth and 8.6% near weaning, core 2.5% fat near birth and 12% near weaning; Worthy and Lavigne 1983), we calculated that harbor seal pups had 12% body fat at birth and 43% fat at 19 d postpartum. These compare with 11% at birth and 34% of *BM* at 19 d postpartum from isotope dilution.

The discrepancies between these estimates might have been reduced by using actual skin weights of the study animals, by measuring the lipid content of blubber at more than one site, and by using measured values of the fat content of the core. Furthermore, various studies have reported that D_2O tends to overestimate the size of the water pool by 2–5 percentage points (see Oftedal and Iverson 1987) and thus underestimate TBF by a corresponding percentage.

Mass-Transfer Index

The ratio of pup mass gain to maternal mass loss has been used as a measure of the efficiency of mass transfer during lactation in true seals. This measure is appropriate only if females use stored energy alone to support lactation. However, the common conception that phocid seals typically fast during a relatively brief lactation period appears to apply primarily to large species (table 4). In three of the seven species listed, females are known to feed during the lactation period, while in a fourth, the Weddell seal, feeding is suspected. Unfortunately, in none of these species has food intake during lactation been measured. Thus, the ratio of pup mass gain to maternal mass loss is more aptly viewed as an index of mass transfer rather than as a measure of efficiency.

Our study was conducted over the first 19 d (about 80%) of the 24-d lactation period of harbor seals on Sable Island (Muelbert 1991). Although previous studies generally extrapolate to obtain values for all of lactation, for practical reasons few studies have actually measured mass and/or energy transfer over the entire period. In studies where the age of pups was known, measurements covered an average of 83% ($n = 5$) of the lactation period (table 4). Extrapolation of rates of mass and energy transfer to the end of lactation may be justified in species such as the northern elephant seal and the grey seal in which mothers are known to fast for the duration of lactation. However, evidence from stomach lavage and diving records indicates that harbor seal mothers on Sable Island forage in late lactation (Bowen, Oftedal, and Boness 1989; Boness, Bowen, and Oftedal 1991). Thus, it is likely that

TABLE 4

Breeding habitat, lactation length, mass loss in relation to initial maternal mass and the mass-transfer index in phocids

Species	Hooded	Harp	Grey	Harbor	Southern Elephant	Northern Elephant	Ringed	Weddell
Breeding habitat	Floe ice	Floe ice	Land	Land	Land	Land	Fast ice	Fast ice
Lactation length (d)	4	12	18	24	24	27	39	53
Percentage of lactation studied (*A*)	100[a]	100[a]	83	79	100	78	100[a]	74
Maternal mass at parturition (kg)	179	139	174	91	506	504	81	447
Percentage of maternal mass loss over *A*	16[b]	27[c]	33[c]	33[b]	37[c]	33[c]	31[b]	40[c]
Percentage of maternal mass loss over 80% of lactation	13	22	32	33	30	34	25	43
Mass-transfer index (%)[d]	76	77	45–52	50	46	55	67	43–48
Maternal feeding during lactation	No	Yes	No	Yes	No	No	Yes	Suspected
Maternal cost over 80% lactation ($MJ/kg^{0.75}$)	. . .	25.9	25.2	24.2	. . .	32.6	. . .	. . .
Sources	1	2, 3	4, 5	6	7	8	9	10, 11

Sources. 1, Bowen et al. (1987); 2, Kovacs et al. (1991); 3, Stewart (1986); 4, Fedak and Anderson (1982); 5, Anderson and Fedak (1987); 6, Present study; 7, McCann et al. (1989); 8, Costa et al. (1986); 9, Hammill et al. (1991); 10, Tedman and Green (1987); 11, Testa, Hill, and Siniff (1989).

[a] Age of pups not precisely known, but most of lactation likely covered.

[b] Cross-sectional data.

[c] Longitudinal data.

[d] Pup mass gain/maternal mass loss (kg/d).

mass change and energy transfer in harbor seals may differ between early and late lactation. To avoid potential errors in extrapolation of harbor seal results, we have used 80% of lactation as the basis for comparisons between species.

In harbor seals, only 50% of mass lost by females is stored by the pup. Similar values have been reported in other land-breeding species and the fast-ice breeding Weddell seal (table 4). However, three ice-breeding species have mass-transfer indexes greater than those reported above: the harp seal (77%), hooded seal (76%), and ringed seal (67%) (table 4). The high index in the hooded seal appears to be possible because of the extreme reduction in metabolic overhead during a lactation period of only 4 d. Harp seals also benefit from a short lactation period (12 d), but maternal feeding, which has been reported (Stewart and Murie 1986; W. D. Bowen, unpublished data), may also be a contributing factor. Despite having a relatively long lactation period of about 40 d, the high mass-transfer index in the ringed seal (67%, table 4) may be the result of reduced metabolic costs of pups in protected snow lairs (Smith and Stirling 1975) and maternal feeding (Hammill et al. 1991).

It is also possible that the index of mass transfer is biased in cross-sectional studies such as those in the ringed seal and hooded seal (Anderson and Fedak 1987; Bowen et al. 1987; Hammill et al. 1991). Our estimate of the mass-transfer index in the harbor seal is also based on cross-sectional data. However, in our study pup age and hence the stage of lactation were precisely known. Further, we used only females whose initial mass was within a narrow range, thus reducing the confounding effects of differences in initial female mass on estimates of female mass loss. Therefore, we believe that our estimate should be free of the biases commonly attributed to cross-sectional data.

Cost of Lactation

Lactation is an energetically demanding period for phocid seals, as evidenced by the dramatic loss in body mass observed over the course of the suckling period. Harbor seal mothers lost 33.3% of their initial body mass during the first 80% of lactation. Although this value is similar to that reported in other land-breeding species (table 4), it underestimates the cost to harbor seal females because it does not account for maternal feeding during lactation. Two floe-ice breeding species, the hooded seal and harp seal, lose a smaller percentage of initial maternal mass than do harbor seals and other land-breeding phocids (table 4). Of the two fast-ice species that have been studied, one (ringed seal) loses about 25% of initial mass, whereas the other

(Weddell seal) loses more than 40% of initial maternal mass over the first 80% of lactation (table 4). However, these values likely underestimate the energetic cost to the females because both species are thought to feed during lactation. Perhaps as a consequence of energy obtained via feeding during the lactation period, only 69% of the maternal mass loss was accounted for by a reduction in sculp in harbor seals compared with 79%, 83%, and 83% in the ringed seal, hooded seal, and harp seal, respectively (Stewart and Lavigne 1984; Bowen et al. 1987; Hammill et al. 1991).

The large reduction in sculp mass observed in phocid seals indicates that a significant fraction of the stored fat of females is spent during lactation. On the basis of isotope dilution, we estimate that harbor seal mothers use about 79% of their stored fat during the first 80% of lactation. Estimates of the fraction of stored fat that is used during lactation are also available for several large phocid species that fast for the entire nursing period. Bowen et al. (1987) calculated that hooded seal females use only 33% of stored energy over the 4 d of lactation, although they felt their cross-sectional, morphometric estimate may have underestimated fat mobilization. On the basis of changes in mass and the energy content of mass loss (Fedak and Anderson 1982), female grey seals use about 67% of their fat reserves during the first 80% of an 18-d lactation period. In northern elephant seals, females lose 46% of the mass of their adipose tissue during the same proportion of the 26.5 d of lactation on the basis of isotope dilution (Costa et al. 1986). Isotope dilution studies also show that harbor seals have less stored fat at parturition (24%) than northern elephant seals (39%; Costa et al. 1986). These data are consistent with the hypothesis that lactating females of larger phocid species have greater fat depots and use a smaller fraction of these depots during lactation than do smaller species. However, the various estimates of fat depletion are derived from a number of different methods, each with different assumptions and potential errors. Thus, until comparable methods are used on a number of different species, we must be cautious in reaching conclusions.

Estimates of the depletion of energy reserves during lactation can be calculated for several phocid species (table 4). On the basis of estimates of changes in body composition derived from isotope dilution, harbor seal females used about 24.2 MJ/kg$^{0.75}$ initial mass over the first 80% of lactation. Similar or higher values have been reported in the larger harp seal, grey seal, and northern elephant seal (table 4). Thus, harbor seal females appear to use a larger fraction of stored fat to maintain energy expenditures at a similar magnitude to that reported in larger species.

The harbor seal is one of the smaller phocid species and perhaps the most aquatic member of the family during the lactation period. Unlike other species, pups follow their mothers into the sea within hours of birth and both mothers and pups spend increasing periods at sea as weaning approaches. Our isotope dilution studies indicate that mothers use about 60% of their total energy stores. As noted above, this likely underestimates the actual energy expenditure of females because it does not include energy derived from feeding during the lactation period. Our estimate of depletion of fat reserves (79%) is the highest reported for a phocid species. Yet despite this high level of energy expenditure, pups grow slowly and are leaner at weaning than those of species that do not typically enter the water prior to weaning. We suggest that the small body size of harbor seal mothers coupled with the highly aquatic behavior of their pups during lactation may account for the low rate of energy deposition in pups of this species.

It has been argued that breeding substrate and lactation length have played an important role in the evolution of maternal reproductive strategies (e.g., Stirling 1975). However, the increasing evidence that the females of smaller phocid species feed during lactation suggests that body size may also be an important factor in the evolution of maternal strategies. Until more studies are conducted on these smaller phocids, it will be difficult to come to reliable conclusions about the ecological factors that have shaped the evolution of this mammalian group.

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