Lactation Performance and Nutrient Deposition in Pups of the Harp Seal, *Phoca groenlandica,* on Ice Floes off Southeast Labrador

Olav T. Oftedal[1]
W. Don Bowen[2]
Daryl J. Boness[1]
[1]Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008; [2]Marine Fish Division, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B24-4A2, Canada

Abstract

*Harp seals (*Phoca groenlandica*) give birth on pack ice and nurse their pups for about 13 d. We hypothesized that lactating females would transfer milk and energy to pups at a high rate to compensate for the brevity of lactation. To test this hypothesis, the milk intake of five pups was measured over a 6–8-d period after administration of deuterium oxide; the initial age of pups was estimated to range from 0 to 5 d postpartum. Body water content of 17 pups was also measured by isotope dilution, and body composition of 12 pups was determined by chemical analysis. The proximate composition of harp seal milk (n = 21) was also assayed. Harp seal pups contained little fat (3%) at birth, but 61% of the increase in body mass (average 2.3 kg/d) was fat, with the result that fat accounted for 47% of body mass at weaning. Body water estimated by isotope dilution was not significantly different from that measured directly (n = 9 paired samples); water composed 72% of lean body mass. From birth to weaning, milk lipid increased from 36% to 57%, and milk water declined from 51% to 32%. Pup milk intake averaged 3.7 kg/d. Mass gain of pups was highly correlated with both milk intake and energy intake (r^2 > 0.98 for both). On average, pups consumed about 75 MJ/d, which is equivalent to a maternal energy yield of 1.9 MJ/(kg$^{0.75}$ · d). This rate of energy output is higher than that measured in most other phocids. Daily energy output is inversely related to lactation duration in phocids: a polynomial regression relating energy output to lactation duration explained 99% of the interspecific variation.*

Introduction

Seals that rear their pups on ice floes use an inherently unstable and unpredictable platform that varies greatly in distribution, degree of consoli-

dation, and rate of movement, not only from year to year but also from day to day. This instability has apparently favored a reduction in the period of maternal care (Bonner 1984; Bowen et al. 1985; Oftedal et al. 1987a; Bowen 1991). For example, the ice-breeding hooded seal (*Cystophora cristata*) weans its pups in 4 d (Bowen et al. 1985), and the harp seal (*Phoca groen-landica*) in 12–13 d (Kovacs and Lavigne 1985; Myers and Bowen 1989).

The short lactation period characteristic of phocid seals is associated with a high rate of milk energy output (Costa et al. 1986; Oftedal et al. 1987a; Costa 1991; Iverson et al. 1993). In most species, suckling pups must accumulate sufficient energy reserves, in the form of blubber, to be able to withstand a prolonged postweaning fast (Worthy and Lavigne 1983a, 1987; Stewart and Lavigne 1984; Bowen et al. 1987a; Oftedal et al. 1989). On unstable ice floes, rapid transfer of milk to pups may increase the likelihood that pups attain sufficient energy reserves before storms can cause premature mother and pup separation (e.g., Boness et al. 1992). This may be one explanation for the very high rates of energy transfer in hooded seals (Oftedal et al. 1993b).

Off the southeast coast of Labrador, both harp seals and hooded seals give birth on pack ice in March, although the mean pupping date of the harp seals is somewhat earlier (Bowen and Sergeant 1983; Bowen et al. 1987b). During an expedition in 1984 to study population size and lactation of the hooded seal, we also had the opportunity to collect information on lactation of the harp seal. Published models of harp seal energetics, based on morphometric data and assumed efficiencies of energy deposition in pups, suggested that harp seals produce milk at a high rate (Lavigne et al. 1982a; Stewart and Lavigne 1984). Our intent was to confirm this prediction by direct measurement of milk production using an isotope dilution method.

Material and Methods

This study was conducted in accordance with a research permit issued by the Canadian Department of Fisheries and Oceans, St. Johns, Newfoundland.

A whelping concentration of harp seals was located by fixed-wing aerial survey of ice floes near the southeast coast of Labrador, Canada. Helicopters ferried researchers to study sites from the ship CSS *Baffin*. Newborn pups were identified by the presence of fresh placentas and blood on the ice and the wet, yellowish appearance of the pelage. The age at first capture of older pups was subsequently estimated from body mass, assuming a birth mass of 9.04 kg and mass gain of 2.06 kg/d (Kovacs and Lavigne 1985). Pups were individually tagged in the hind flippers at first capture and were re-

located by use of radio transmitters and fluorescent dye marks placed on the ice and on pups, respectively, as described previously (Bowen et al. 1985; Bowen et al. 1987*a*).

Milk Composition

Milk samples were collected from lactating females that had been chemically immobilized with fentanyl citrate (dose rate 0.5–1.0 mg/kg body mass) and immediately postmortem from lactating females that had been killed with a high-powered rifle for morphometric studies. Immobilized seals were given an intramuscular injection of 20 IU oxytocin about 1 min prior to milking. Milk samples were manually expressed into 30-mL polypropylene bottles. The amount of collected milk averaged 59 ± 14 mL (n = 21). Three sequential samples of about 30 mL each were collected from four animals to determine repeatability of analyses. To evaluate an alternative method of sampling milk that was used by Lavigne et al. (1982*b*) and by Stewart et al. (1983), 17 samples of stomach contents ("gastric milk") were also collected by gastric intubation of the pups of milked mothers. Samples were stored on board the research vessel at −10°C until they could be transferred to −30°C freezers in St. Johns, Newfoundland.

Samples were subsequently thawed, homogenized, and assayed for dry matter by oven drying, for fat by ether extraction (Roese-Gottlieb method), for crude protein (nitrogen × 6.38) by the macro-Kjeldahl method, and for sugar by the phenol-sulfuric acid method with lactose monohydrate as the standard, as described previously (Oftedal et al. 1988). Water percentage was calculated as 100 minus the percentage of dry matter. Milk energy content was calculated from fat, protein, and sugar concentrations, with values of 9.3, 5.86, and 3.95 Mcal/kg, respectively (Oftedal et al. 1993*b*), and converted to megajoules. The energy conversion factor for fat of 9.11 Mcal/kg that we have used previously underestimates the energy in pinniped milk.

Body Composition

Twelve pups that had been collected for morphometric study were chemically analyzed. Carcasses were placed in heavy, sealed plastic bags immediately postmortem to minimize moisture losses and were then frozen until thawed for dissection and analysis in 1986. Of these, five were newborn, two were 1–2 d of age ("yellow-coat" category), and five were near weaning ("grey-coat" category; see Stewart and Lavigne [1980] for description of categories). Collection and dissection methods for these animals have been detailed previously (Oftedal et al. 1989), and the further processing for

chemical analysis followed the procedures described by Oftedal et al. (1993b). The small mass loss that occurred during dissection of the core (95 ± 19 g in newborns and 131 ± 20 g at weaning) was assumed to be water. Partially frozen material was ground in a whole-body grinder (die with 3/8-inch holes) at the Agricultural Research Service of the U.S. Department of Agriculture in Beltsville, Maryland. An average of 7% of the material was lost during grinding, primarily owing to material remaining in the grinder, so no additional correction was made for moisture loss. After further homogenization, samples were assayed in duplicate for dry matter by oven drying, for crude fat by extraction with petroleum ether (Soxhlet procedure), for crude protein (nitrogen × 6.25) by a macro-Kjeldahl procedure, and for ash by incineration, as described by Oftedal et al. (1993b). Energy content was calculated by assuming energy equivalents of 9.3 Mcal/kg fat and 5.65 Mcal/kg protein (Brouwer 1965) and converted to megajoules. Data are expressed in relation to either the whole body or the empty body (whole body − gastrointestinal contents).

Nine pups included in the body composition study were used to validate the use of deuterium oxide dilution to estimate body water content. The isotope administration procedure was the same as in the milk intake study (see below) except that a lower deuterium oxide dose (about 1 g/kg body mass) was used. Isotope was also administered to five pups of intermediate ages ("thin white" and "fat white" categories) to obtain a more even distribution of pup masses for evaluation of the relationship of water pool size to body mass.

Measurement of Milk Intake

The isotope dilution procedures used to measure milk intake in five harp seal pups were the same as have been reported for hooded seals (Oftedal et al. 1993b). Pups were captured by hand; mothers were not captured but appeared to remain in the vicinity in open leads in the pack ice. After gastric milk was removed by intubation, pups were weighed to 0.1 kg and deuterium oxide (ca. 3 g/kg body mass) was administered by gastric intubation. Blood samples were collected from the extradural vein at about 1-h intervals over a period of 2–3 h to determine isotope concentration at equilibration. Pups were released near their birth sites and were recaptured 2–4 times over a period of 6–8 d. They were weighed and bled at each capture.

After clotting, blood serum was removed and frozen in airtight vials. Water was recovered by heat distillation. Deuterium content of water was determined from the infrared absorption at 3.98 μm in a Perkin Elmer ratio recording infrared spectrophotometer (Stansell and Mojica 1968; Oftedal and

Iverson 1987). Daily water intake was calculated from fractional water turnover and estimated change in pool size as described previously (Oftedal et al. 1993b). Pool sizes at intermediate and final bleeds were estimated from linear regression of pool size on body mass for all animals (see Results).

Daily milk intake of each pup was calculated by an equation (Oftedal et al. 1987b) that accounts for metabolic water from the partial catabolism of ingested fat and protein in milk:

$$\text{milk intake} = 100 \cdot \frac{(\text{water intake} + 1.07\ F_D + 0.42\ P_D)}{(\%W_M + 1.07\ \%F_M + 0.42\ \%P_M + 0.58\ \%S_M)},$$
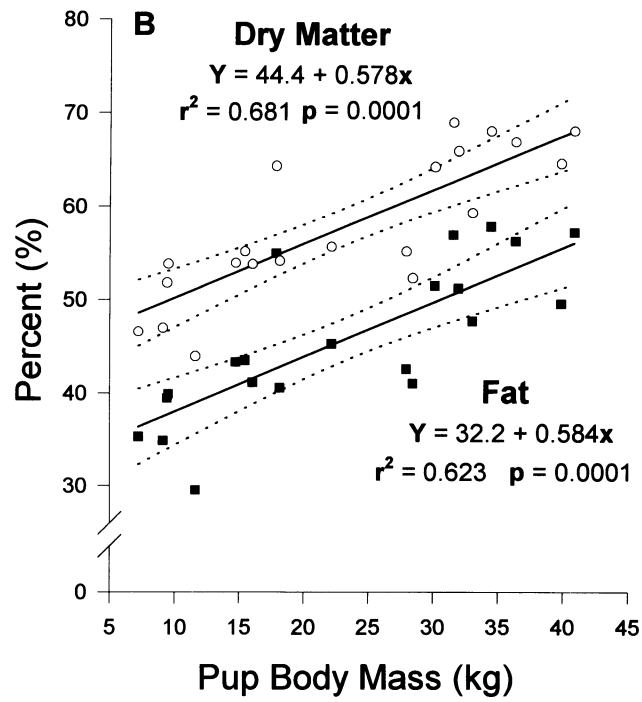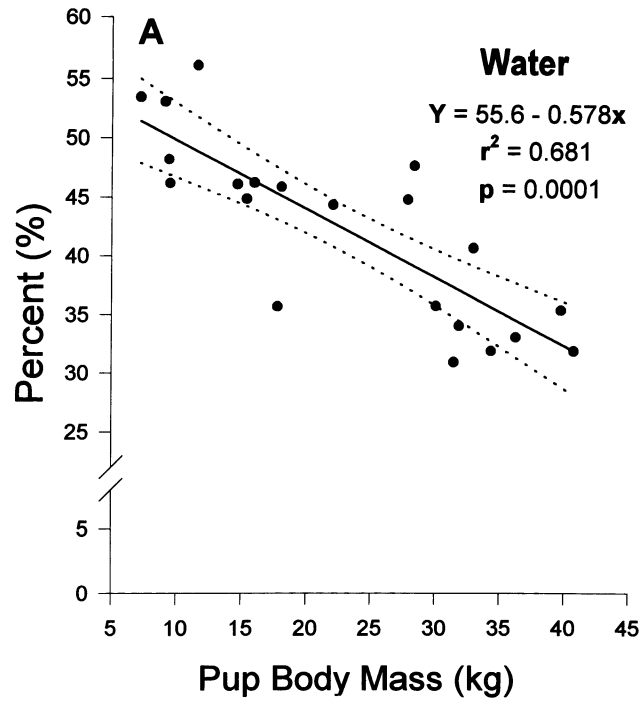
where F_D and P_D represent the amounts of fat and protein deposited per day, and $\%W_M$, $\%F_M$, $\%P_M$, and $\%S_M$ represent the percentages of water, fat, protein, and sugar in milk. The value P_D was calculated for each pup from changes in lean body mass (as estimated from pool size), and the relationship of protein to lean body mass was determined by chemical analysis (see Results). The value F_D was calculated as the difference between body mass gain and lean body mass gain. The composition of ingested milk was estimated separately for each pup by taking its mean body mass from the intake study and inserting that value into predictive equations that related milk nutrient levels to body mass (see Results). Thus, milk intake was calculated individually for each pup. Rates of energy transfer from mother to pup were calculated from milk intake and calculated milk energy content.

Results are expressed as mean ± standard error of the mean (SEM) unless otherwise indicated.

Results

Milk Composition

Milk samples were obtained from 21 harp seals nursing pups that ranged in mass from 7 to 41 kg. Milk composition changed greatly according to lactation stage (Fig. 1). Females with newborn pups ($n = 5$) produced milk containing 51.4% ± 1.83% water, 48.6% ± 1.83% dry matter, 35.8% ± 1.87% fat, 10.4% ± 0.54% protein, 0.79% ± 0.072% sugar, and 3.91 ± 0.016 Mcal/kg (16.4 ± 0.065 MJ/kg) gross energy. By contrast, harp seals with pups in the grey-coat stage near weaning ($n = 3$) produced milk containing 32.4% ± 0.39% water, 67.6% ± 0.39% dry matter, 57.1% ± 0.46% fat, 7.7% ± 0.22% protein, 0.65% ± 0.038% sugar, and 5.68 ± 0.004 Mcal/kg (23.7 ± 0.02 MJ/kg) gross energy. Much of the compositional change was explained by regressions on pup body mass, which is an indicator of pup age.
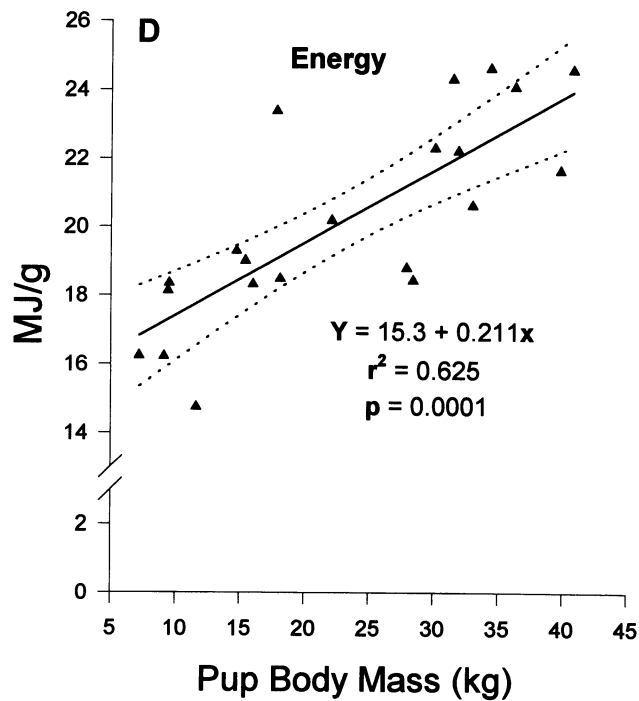
A

Water

$Y = 55.6 - 0.578x$
$r^2 = 0.681$
$p = 0.0001$

Pup Body Mass (kg)

B **Dry Matter**

$Y = 44.4 + 0.578x$
$r^2 = 0.681$ $p = 0.0001$

Fat

$Y = 32.2 + 0.584x$
$r^2 = 0.623$ $p = 0.0001$

Pup Body Mass (kg)

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C

Protein

$Y = 10.2 - 0.072x$
$r^2 = 0.345 \quad p = 0.005$

Sugar

$Y = 0.46 + 0.047x - 0.0011x^2$
$r^2 = 0.445 \quad p = 0.005$

Pup Body Mass (kg)

D

Energy

$Y = 15.3 + 0.211x$
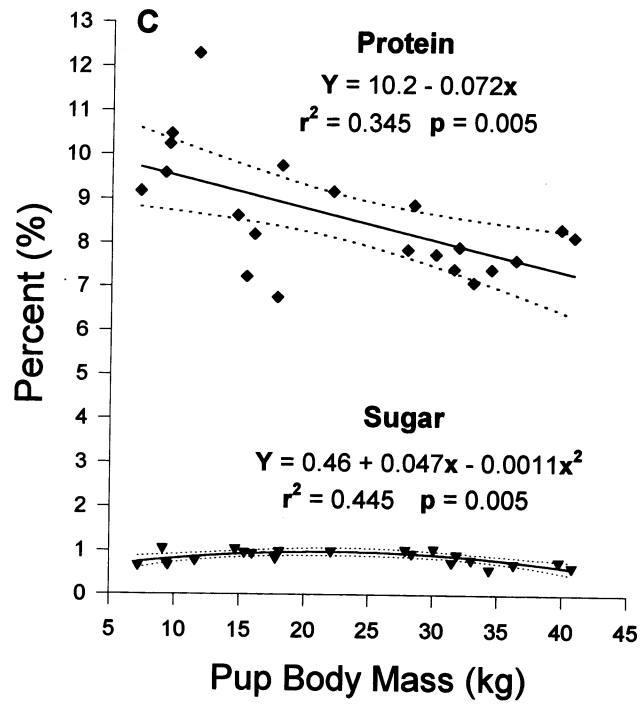$r^2 = 0.625$
$p = 0.0001$

Pup Body Mass (kg)

Fig. 1. The relationship of milk composition to pup body mass: A, water; B, dry matter (open circles) and fat (squares); C, protein (diamonds) and sugar (triangles); D, gross energy. Regressions and their 95% confidence intervals are represented by solid and dotted lines, respectively.

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Water (Fig. 1*A*) and protein (Fig. 1*C*) concentrations decreased with increasing pup body mass, while dry matter (Fig. 1*B*), fat (Fig. 1*B*), and gross energy (Fig. 1*D*) increased. Sugar concentration exhibited a weak but significant curvilinear relationship to pup body mass, with a peak in the middle of lactation (Fig. 1*C*). The regression equations for milk constituents were used to predict the composition of the milk ingested by pups in milk intake studies.

There were no significant differences in water, dry matter, fat, protein, or sugar concentrations among three sequential milk samples taken from the same mammary gland over a period of several minutes ($n = 4$ females with newborn pups; repeated measures ANOVA, $P > 0.05$). For example, milk fat concentration averaged 33.7% ± 1.96%, 35.5% ± 1.80%, and 35.2% ± 2.42% for first, second, and third sequential samples, respectively.

Gastric milk obtained from pups was significantly higher in water and lower in fat and protein than mammary milk obtained from the mothers of these pups ($P < 0.001$ for all three comparisons; paired t-tests) (Fig. 2). Sugar could not be compared, as it was not assayed in the gastric milk samples.
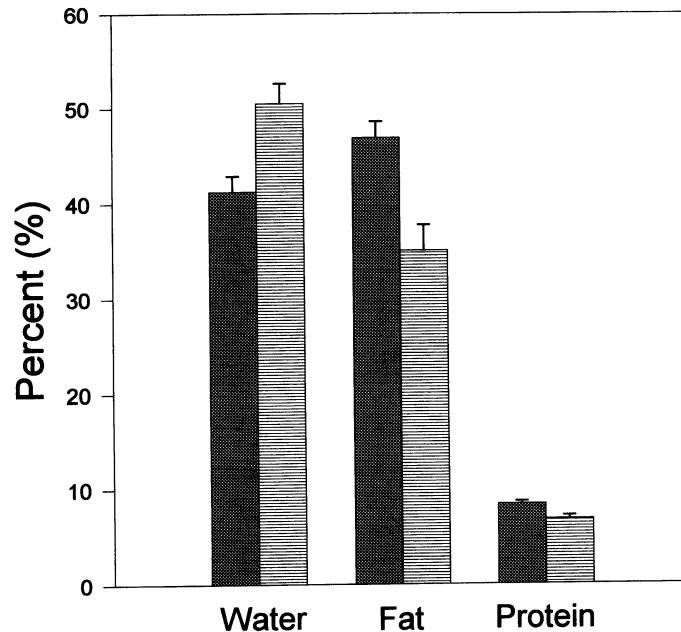

Fig. 2. Comparison of the composition of mammary milk (dark bars) and gastric samples (light bars) collected from the pups of the mothers that were milked. Seventeen pairs of samples were assayed. Data are presented as mean and SEM.

Body Composition of Pups

Body water was measured by isotope dilution in 17 pups ranging in body mass from 8.2 to 44.3 kg. The amount of body water measured by isotope dilution was highly correlated with total body water as determined by direct carcass analysis (Fig. 3). If body water was expressed as a percentage of body mass, the difference between the dilution estimate (pool size) and the estimate obtained by carcass analysis (body water) was not significant (pool size − body water = 1.7% ± 1.21%; n = 9, paired t-test). The regression equation relating pool size to body mass explained 95% of the variance (Fig. 4).

Although newborn pups were low in body fat (about 3%; Table 1), fat concentration increased rapidly to about 7% in yellow-coat pups (1–2 d) and 47% in grey-coat pups (12–13 d). The more than threefold increase in pup energy density from birth to weaning was due almost entirely to fat
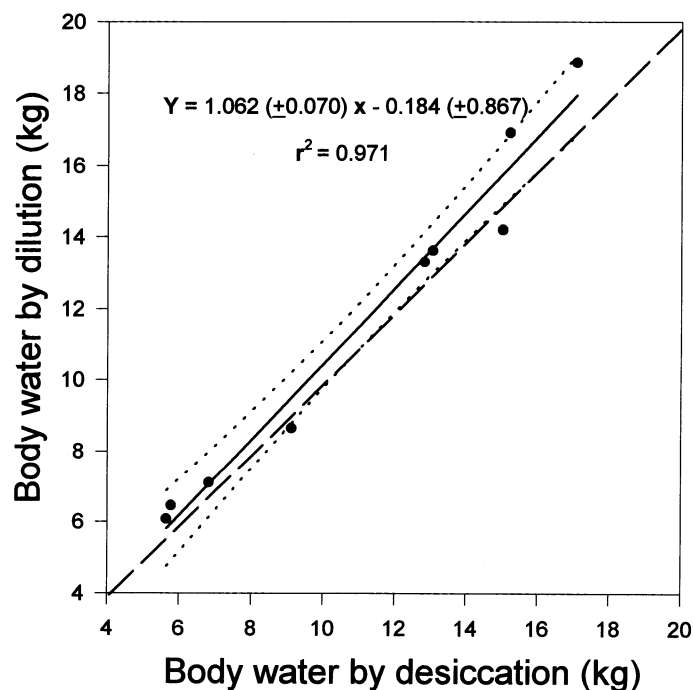

Fig. 3. Comparison of body water pool estimated by isotope dilution to body water measured by desiccation of ground carcasses. Linear regression and the associated 95% confidence interval are represented by solid and dotted lines, respectively. The diagonal dashed line representing equality between dilution and desiccation measures falls within the 95% confidence interval.
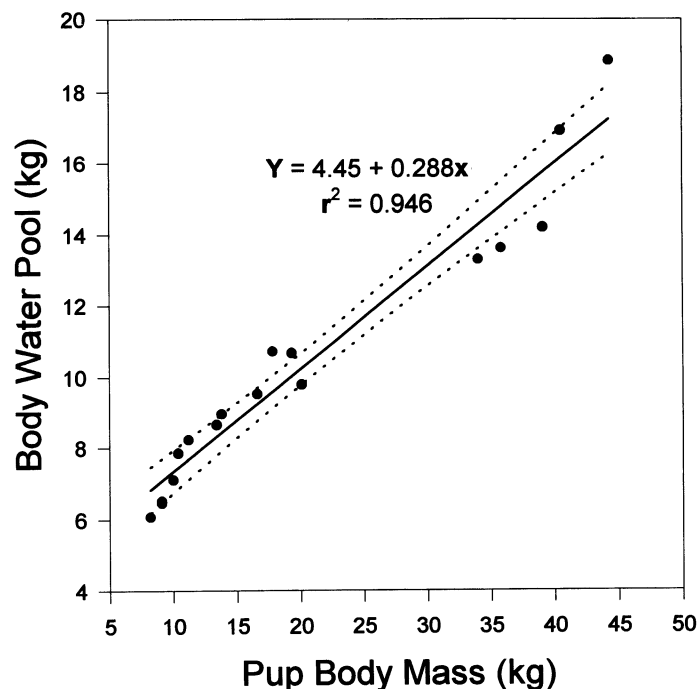
Fig. 4. The relationship of body water pool to body mass in harp seal pups. Linear regression and the associated 95% confidence interval are represented by solid and dotted lines, respectively. The regression equation was used to predict body water pool in recaptured pups.

deposition, because the composition of the lean body mass remained relatively constant (Table 1). The water and protein concentrations of lean body mass were unaffected by pup developmental stage, but ash percentage was lower in the lean body mass of grey-coat pups than in lean body mass at birth ($P < 0.001$, t-test).

Milk Intake and Efficiency of Nutrient Deposition

The progressive decline in milk water concentration (Fig. 1A) suggested that the fractional turnover rate of body water may not be constant. The data for each pup were treated as representing two periods: (I) the first 3–4 d, represented by the initial equilibration and two or three recaptures, and (II) the second 3–4 d, represented by two recaptures (Table 2). The semi-logarithmic decline in isotope concentration was highly linear in the first period (mean $r^2 = 0.995 \pm 0.0066$; $n = 5$). Although fractional turnover rate was lower in Period II than in Period I (paired t-test, $P = 0.013$, $n = 4$),

TABLE 1

Chemical composition of harp seal pups

Stage[a]	Age (d)	Mass (kg)	Water (%)	Crude Fat (%)	Crude Protein (%)	Ash (%)	Gross Energy (MJ/kg)
Empty body mass basis:[b]							
NB (n = 5)	0	9.1 ± .74	69.8 ± .43	3.0 ± .18	21.4 ± .22	3.7 ± .20	6.23 ± .063
Y (n = 2)	1–2	11.0	67.0 ± 2.53	6.9 ± 4.38	20.3 ± 1.58	3.5 ± .49	7.5 ± 1.33
G (n = 5)	12–13	38.4 ± 1.84	37.9 ± .36	47.2 ± .58	11.5 ± .18	1.3 ± .08	21.1 ± .22
Lean mass basis:[c]							
NB (n = 5)	0		72.0 ± .40	...	22.1 ± .21	3.8 ± .21	...
Y (n = 2)	1–2		72.0 ± .67	...	21.8 ± .67	3.7 ± .35	...
G (n = 5)	12–13		71.8 ± .46	...	21.8 ± .38	2.5 ± .13	...

Note. Chemical composition values are means ± SEM.

[a] Developmental stages: NB, newborn; Y, yellow coat; G, grey coat (see Stewart and Lavigne 1980).

[b] Empty body mass is the total body mass minus gastrointestinal contents.

[c] Lean mass is the empty body mass minus body fat.

there was no significant difference in water intake or milk intake between the periods. Milk intake varied from 2.37 to 4.73 kg/d in the first period, and from 2.36 to 4.38 kg/d in the second period (Table 2). About 98% of the variance in milk intake in each period was explained by linear regression on pup body mass gain (Fig. 5*A*).

The energy concentration of ingested milk was estimated separately for each pup and period on the basis of pup body mass. Linear regression on pup body mass gain explained 98%–99% of the variance among pups in gross energy intake (Fig. 5*B*).

The efficiency with which ingested nutrients were deposited in tissues during postnatal growth was estimated by comparing measured intakes to calculated changes in body composition. The body composition of pups in the milk intake study was calculated from body water and the constant relationship of body water to lean body mass (0.72:1) and body protein to lean body mass (0.22:1); body fat was estimated by difference (body mass − lean body mass). Pups were estimated to deposit 91.3% ± 3.28% of ingested fat, 52.1% ± 4.85% of ingested protein, and 85.5% ± 2.44% of ingested energy.

Discussion

The Composition of Harp Seal Milk

The composition of harp seal milk changed over the course of lactation. A decline in water and increase in fat as lactation progressed has also been observed in northern and southern elephant seals (*Mirounga angustirostris* and *Mirounga leonina*), Weddell seals (*Leptonychotes weddellii*), and grey seals (*Halichoerus grypus*) (Peaker and Goode 1978; Riedman and Ortiz 1979; Tedman 1980; Iverson et al. 1993; Lydersen et al. 1995). In most of these species the greatest change in milk composition occurs in the first half of lactation, while relatively little change occurs thereafter. Although our data do not support a curvilinear pattern of change in water and fat concentrations, this may stem from the use of pup body mass, rather than pup age, as the indicator of lactation stage. The very high milk fat level (57%) in females with grey-coat pups is similar to that found in late lactation in grey seals (60%) and hooded seals (61%) (Oftedal et al. 1988; Iverson et al. 1993; Lydersen et al. 1995) and is presumably an adaptation to permit a high rate of fat deposition in pups prior to weaning.

The dry matter, fat, and energy values we measured were considerably higher than those reported for harp seal milk by Lavigne et al. (1982*b*) and Stewart et al. (1983). However, these investigators obtained samples from

TABLE 2
Water and milk intake of suckling harp seal pups

Pup ID (Stage)[a]	Duration of Study (d)	Estimated Age[b] Range (d)	Initial Mass (kg)	Mass Gain (kg/d)	Initial Water Pool[c] (kg)	k[d]	Water Intake (kg/d)	Milk Intake (kg/d)
Period I:								
18106 (NB)	4.1	.0–4.1	11.2	2.2	8.23	.156	1.94	3.83
18107 (TW)	3.9	2.0–5.9	13.2	1.4	8.26	.099	1.29	2.37
18030 (TW)	3.9	3.7–7.6	16.6	2.1	9.53	.134	1.94	3.69
18021 (TW)	2.8	4.3–7.1	17.8	2.8	10.7	.129	1.85	4.56
18062 (FW)	2.7	5.0–7.7	19.3	2.9	10.7	.132	2.11	4.73
Mean			15.6	2.3	9.5	.130	1.83	3.84
SEM			1.49	.28	.55	.0092	.141	.419
Period II:								
18106 (T/FW)	3.8	4.1–7.9	20.1	2.9	10.3	.112	2.16	4.38
18107 (T/FW)	3.0	5.9–8.9	18.5	1.4	9.79	.081	1.25	2.36
18021 (FW)	3.1	7.1–10.2	25.6	2.6	11.8	.078	1.76	3.75
18062 (FW/G)	3.1	7.7–10.8	27.2	2.4	12.3	.086	1.85	3.71
Mean			22.9	2.3	11.0	.089	1.75	3.55
SEM			2.10	.31	.61	.0079	.189	.424

[a] Developmental stages of pups: NB, newborn; TW, thin white; FW, fat white; G, grey coat.
[b] Pup age estimated from mass according to the equation developed by Kovacs and Lavigne (1985).
[c] Initial pool size in Period I calculated from equilibration concentration of deuterium oxide; initial pool size in Period II estimated by regression of pool size on body mass (Fig. 4).
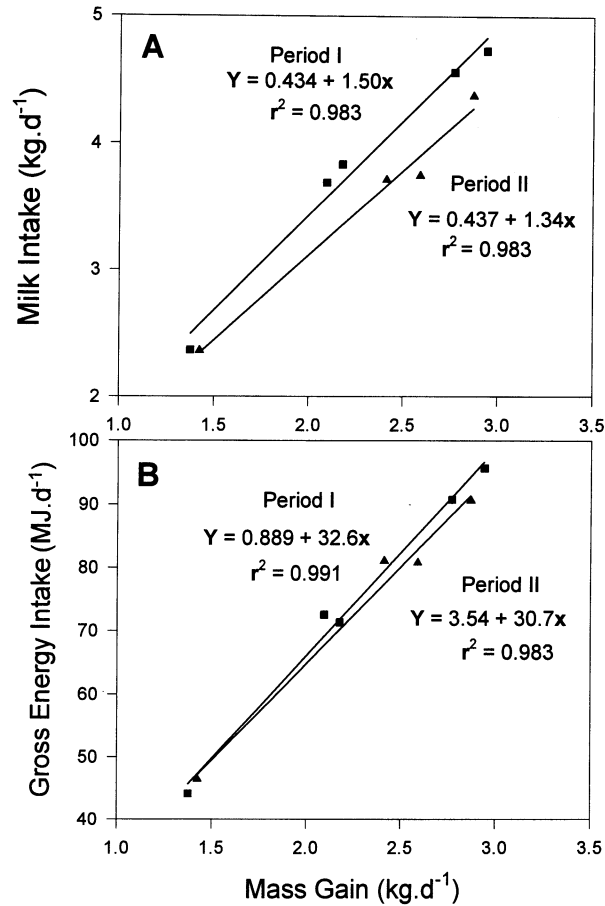[d] Fractional turnover rate per day.

Fig. 5. The relationship of milk intake (A) and gross energy intake (B) to rate of mass gain in harp seal pups. Periods I and II (see text) are represented by squares and triangles, respectively.

pup stomachs rather than by expression from mammary glands, and gastric samples differ substantially in composition from mammary milk (Fig. 2). If we had used gastric samples to estimate milk composition, we would have overestimated water by 24% ± 4.4% and underestimated dry matter, fat, and protein by 16% ± 2.6%, 21% ± 2.7%, and 19% ± 3.4%, respectively. Gastric samples are apparently diluted by salivary and gastric secretions and may undergo partial lipolysis (Iverson et al. 1992). In addition, the Roese-Gottlieb method of fat analysis used by Lavigne et al. (1982*b*) and Stewart et al. (1983) tends to underestimate total lipid levels of hydrolyzed samples due to incomplete recovery of fatty acids (Iverson and Oftedal 1995). Earlier reports on the fat concentration of harp seal milk fall within the range re-

ported herein but were based on few samples of mammary milk and include little information on lactation stage (Sivertsen 1941; Jangaard and Ke 1968; Cook and Baker 1969; Van Horn and Baker 1971).

Stewart et al. (1983) concluded that the sugar concentration of harp seal milk remains constant at about 0.89%, which is similar to our mean value of 0.86%, despite their use of a different analytical method and reliance on gastric samples. However, both the anthrone method used by Stewart et al. (1983) and the phenol-sulfuric acid method used by us may underestimate total carbohydrate if the sugars in seal milks are composed predominantly of hexosamines and galactose, as Messer et al. (1988) reported for the crabeater seal (*Lobodon carcinophagus*). In this species, most carbohydrate is oligosaccharide, with only a trace amount (0.02%) of lactose (Messer et al. 1988).

In many mammals, milk sampling is complicated by compositional changes that occur during the process of milk expression (Oftedal 1984). We could find no evidence that milk composition changes during milk expression in harp seals, which is the same result found in studies of California sea lions (Oftedal et al. 1987*a*), hooded seals (Oftedal et al. 1993*b*), and grey seals (Iverson et al. 1993). It appears that complete mammary evacuation is not necessary to obtain reliable estimates of the proximate composition of pinniped milks.

The Body Composition of Pups at Birth and Weaning

In the newborn harp seal, fat situated in brown adipose tissue plays an important thermogenic role when pups are exposed to cold (Grav et al. 1974; Blix et al. 1975; Grav and Blix 1976). However, the total amount of fat in the body amounts to only 3.0% (Table 1). A low level of body fat may be typical of species born with a special birth coat or lanugo because these species rely primarily on the lanugo, rather than a lipid-rich blubber layer, for insulation in the immediate period after birth (Davydov and Makarova 1965; Ray and Smith 1968; Elsner et al. 1977; Oftedal et al. 1991*b*). For example, in the newborn harp seal the blubber layer represents only 6% of body mass and contains only about 20% lipids (Bailey et al. 1980; Worthy and Lavigne 1983*b*). Other lanugo-clad neonates with low total body fat include ringed seals, *Phoca hispida* (4%–5% fat by carcass analysis; Lydersen et al. 1992), and grey seals (5% fat by isotope dilution; Iverson et al. 1993). Species that have shed the lanugo in utero have more body fat at birth; these species include the hooded seal (14% fat by analysis; Oftedal et al. 1993*b*) and the harbor seal (11% fat by isotope dilution; Bowen et al. 1992).

Isotope dilution and carcass analysis have been demonstrated to pro-
duce comparable estimates of body water in suckling pinnipeds, including
harp seals (this study), ringed seals (Lydersen et al. 1992), hooded seals
(Oftedal et al. 1993*b*), and California sea lions (Oftedal et al. 1987*b*).
The water:lean body mass ratio in neonatal harp seals (0.72:1) is similar
to that of other pinnipeds (0.71:1–0.74:1), but considerably lower than
that of neonatal terrestrial carnivores (0.81:1–0.84:1) that are less de-
veloped at birth (Oftedal et al. 1993*a*). Reilly and Fedak (1990) reported
that the proportionality of water to lean body mass is not fixed in all
life stages and circumstances in grey seals, but in suckling harp seals
body water remains a constant proportion of lean body mass and is
thus an accurate predictor of body composition despite large gains in
fat mass.

Near weaning, body fat of harp seal pups had increased to 47% of body
weight. Muelbert and Bowen (1993) noted that pups of most phocids contain
42%–48% body fat at weaning, and they calculated a body fat concentration
of 47% for harp seals on the basis of data provided by G. A. J. Worthy (Worthy
and Lavigne 1983*b*; G. A. J. Worthy, personal communication). Our data are
consistent with these results. Large fat stores provide both insulation and
an energy reserve for the postweaning fast and the subsequent period in
which feeding skills are acquired (Worthy and Lavigne 1983*a*; Oftedal
et al. 1989). For example, weaned harbor seals continue to lose substan-
tial amounts of body fat even after they begin to feed (Muelbert and
Bowen 1993).

From birth to weaning, harp seal pups increased in body mass from
9.1 to 38.4 kg, a gain of 29.3 kg consisting of 28.0% water, 61.0% fat, 8.4%
protein, 0.6% ash, and 6.14 Mcal/kg (25.7 MJ/kg). The phenomenon that
more than half of the gain was fat is not uncommon in phocids (Costa
1991; Bowen et al. 1992; Iverson et al. 1993; Oftedal et al. 1993*b*), al-
though it is remarkable by comparison to terrestrial mammals, in which
gain during the suckling period is typically about 7%–13% fat (Oftedal
et al. 1987*b*).

Milk and Energy Intakes

Isotope methods have the advantage over other methods of measuring
milk intake that the subjects of study can be left undisturbed for periods
of time. However, a prolonged study period may lead to inaccuracy in
energetic estimates if the composition of the milk changes markedly over
the course of study and rates of milk production are not constant. In such
circumstances an arithmetic average of samples collected at various times

may not accurately represent the proportional contribution of different stages of lactation. We attempted to minimize this error by calculating intakes for short (3–4 d) periods and estimating the composition of milk at that stage from equations relating milk composition to pup body mass. The fact that milk and energy intakes were highly correlated to growth rate ($r^2 > 0.98$) indicates that most of the variability was accounted for (Fig. 5). Using similar methods, Iverson et al. (1993) also found a very high correlation ($r^2 > 0.99$) between milk energy intake and growth rate in grey seals.

Isotope methods will overestimate milk intake if pups consume free water, whether in liquid or frozen form. As our observation time of pups was limited, we cannot rule out this possibility, but it is improbable given the high correlation between estimated milk intake and growth rate and the adverse energetic consequences of using body heat to melt ice. If milk intake had been overestimated, our calculated efficiencies of fat deposition (91%) and energy deposition (86%) would be underestimated. This does not seem likely, as such high efficiencies are rarely encountered in nature, except among rapidly fattening seal pups (Blaxter 1989; Oftedal et al. 1993*b*).

The high correlation between milk energy intake and growth rate indicates that the mean rate of maternal energy transfer can be accurately predicted if mean pup growth rate is known. In the present study, isotope-labeled pups gained 2.3 kg/d body mass, which is identical to the mean obtained by capture-recapture of 20 pups in the Gulf of St. Lawrence (Kovacs et al. 1991). Pups growing at 2.3 kg/d ingest about 18 Mcal/d (75 MJ/d) (Fig. 5). At this growth rate, harp seal pups would reach a weaning body mass of 38 kg in about 13 d and would ingest about 230 Mcal (980 MJ) over the entire lactation period.

Lavigne et al. (1982*a*) modelled milk energy output of harp seals, employing assumed values for pup growth rate (1.6 kg/d), the energy content of gain (5.2 Mcal/kg), the efficiency of energy deposition (80%), and lactation length (18 d). While each of these assumptions involved error, the overall estimate of 240 Mcal is similar to our value of 230 Mcal. In subsequent reports, Lavigne and colleagues modified the input parameters and arrived at somewhat lower estimates of milk energy output, 170 Mcal (710 MJ) to 194 Mcal (810 MJ) (Stewart and Lavigne 1984; Stewart 1986). These lower values derive from an estimated lactation length of 9–10 d, but more recent studies indicate that mean length is 12–13 d (Kovacs and Lavigne 1985; Myers and Bowen 1989; Kovacs et al. 1991).

Maternal Effort and Lactation Length

Across a broad array of mammals, the daily rate of milk energy output tends to vary in proportion to maternal metabolic size, measured as maternal body mass to the 0.75 power (Linzell 1972; Oftedal 1984). We did not capture the mothers of pups used in milk intake studies, but six mothers with new-born pups that were captured at about the same time averaged 135 ± 15.7 kg (range 117–163 kg). Assuming that this mean body mass is representative, the daily rate of milk energy output, corrected for maternal metabolic mass at the start of lactation, was 0.45 Mcal/$kg^{0.75}$ (1.9 MJ/$kg^{0.75}$). This is higher than the rate in phocid species that pup on land, such as grey seals (most populations), harbor seals, and northern elephant seals, and species that pup on stable fast ice, such as ringed and Weddell seals (Fig. 6). However, it is lower than that of the hooded seal, which pups on pack ice but lactates for only 4 d. Interspecific variation in milk energy output appears to be closely related to duration of lactation. A polynomial regression of milk energy output on the logarithm of lactation duration (Fig. 6) accounts for 99% of the variance in milk energy output among species. This may be due in part to the need of phocid females to transfer sufficient energy to their pups to enable them to undergo a prolonged fast after weaning. Species with fewer days of lactation achieve this transfer by higher rates of milk energy output. The tight fit between energy output rate and lactation duration suggests that mean milk energy output of phocids can be predicted from information on lactation length and maternal body mass at parturition. For example, Lydersen et al. (1995) recently found that grey seals that pup on pack ice in the Northumberland Strait, Gulf of St. Lawrence, produce 83 MJ/d during a 15-d lactation. The predicted value for this lactation length (1.5 MJ/[$kg^{0.75}$ · d]) is very similar to the measured value (1.6 MJ/[$kg^{0.75}$ · d]).

In conclusion, the harp seal's reproductive strategy involves relatively intense lactation for a brief period. This brevity may favor pup survival on ice floes prone to break-up during spring storms. Ice instability threatens the pup with immersion in cold water, to which the newborn pup is poorly adapted (Davydov and Makarova 1965; Elsner et al. 1977). In harbor seals, storms result in mother and pup separations (Boness et al. 1992), and the same may be true in harp seals. A short lactation period reduces the exposure to storms and may decrease the likelihood that mothers or pups on the ice are predated by polar bears. By transferring milk energy at a high rate, the harp seal mother can wean her pup at a young age and still provide a large overall energetic investment. The energy output by the lactating harp seal is about 2 MJ/($kg^{0.75}$ · d) over 12–13 d or about 24–26 MJ/$kg^{0.75}$ overall.

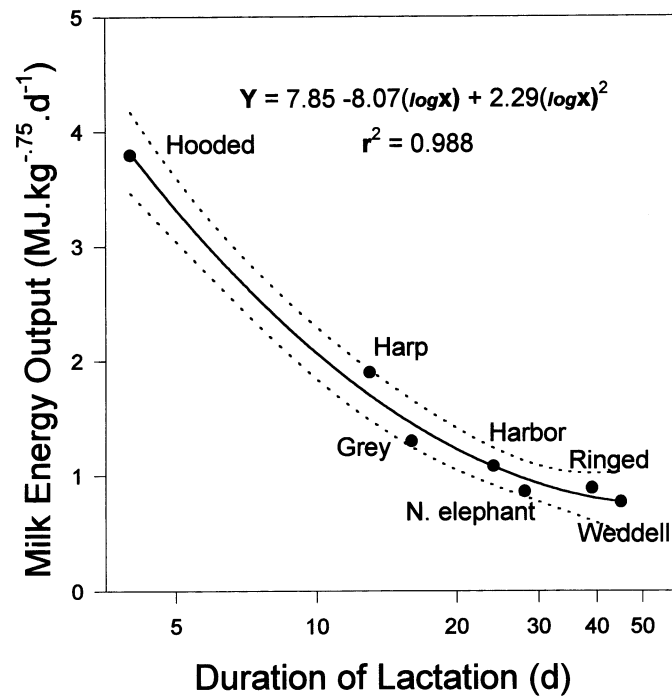*Fig. 6. The inverse relationship between daily milk energy output (expressed per maternal metabolic mass, $kg^{0.75}$) and the duration of lactation in phocid seals. The solid and dotted lines represent the polynomial regression line and its 95% confidence interval, respectively. The species, locales, and references are as follows: hooded seal, Cystophora cristata, near southeastern Labrador (Oftedal et al. 1993b); harp seal, Phoca groenlandica, near southeastern Labrador (this study); grey seal, Halichoerus grypus, on Sable Island, Nova Scotia (Iverson et al. 1993); harbor seal, Phoca vitulina, on Sable Island, Nova Scotia (Oftedal et al. 1991a); northern elephant seal, Mirounga angustirostris, on Año Nuevo Island, California (Ortiz et al. 1984; Costa et al. 1986; Kretzmann et al. 1993); ringed seal, Phoca hispida, at Svalbard, Norway (Lydersen et al. 1992; Lydersen and Hammill 1993); Weddell seal, Leptonychotes weddellii, in McMurdo Sound, Antarctica (Tedman and Green 1987).*

This value is similar to that of other studied phocids (15–21 $MJ/kg^{0.75}$) except ringed and Weddell seals (about 34 $MJ/kg^{0.75}$) (see Fig. 6 for references). The rapid fattening of the pups bears testimony to a high-lipid, high-energy diet: by the time of weaning the harp pup contains 14 times as

much energy as it had contained at birth, and it relies on this store for the period of fasting that follows.

Acknowledgments

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