The composition of hooded seal (*Cystophora cristata*) milk: an adaptation for postnatal fattening

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We obtained milk from 22 hooded seals on pack ice off the southeast coast of Labrador. Milk composition was not affected by degree of mammary evacuation or method of milk collection (drug immobilization vs. postmortem collection). Lactation stage exerted relatively little influence on milk composition over the course of the 4-day lactation period, but colostrum was higher in crude protein content. At mid to late lactation (2–4 days postpartum), hooded seal milk contains the highest dry matter (70%), fat (61%), and gross energy (5.9 kcal/g) contents that have been reported for any mammalian milk. This high fat content may be essential to achievement of the extremely rapid rate of fat deposition (about 4 kg/d) by suckling pups. The relatively low protein content (4.9%) at mid to late lactation is consistent with the small proportion of postnatal weight gain that is lean body mass. The proportion of milk energy contributed by protein is the lowest known for any mammal.

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Nous avons prélevé du lait chez 22 Phoques à capuchon, sur des banquises, au large de la côte sud-est du Labrador. La composition du lait n'est pas affectée par la quantité de lait retirée ou par la méthode de prélèvement (immobilisation provoquée par une drogue vs. prélèvement postmortem). Le stade de lactation a relativement peu d'influence sur la composition du lait au cours de la période de lactation de 4 jours, mais le colostrum a un contenu brut de protéines plus élevé. Du milieu à la fin de la lactation (2–4 jours postpartum), le lait des Phoques à capuchon contient les taux les plus élevés de matières sèches (70%), de graisses (61%) et d'énergie brute (5,9 kcal/g) jamais rencontrés dans le lait d'un mammifère. Ce contenu élevé en matière grasse est probablement essentiel à la production extrémement rapide de la couche de graisse (env. 4 kg/j) des nourrissons. Le contenu relativement faible en protéines (4,9%) du milieu à la fin de la lactation correspond bien au taux relativement faible de gain de masse dû à l'augmentation de la fraction non adipeuse du corps. La proportion d'énergie constituée par les protéines dans le lait ce des phoques est la plus faible jamais rencontrée chez un mammifère.

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Introduction

The high fat and energy contents of pinniped milks are thought to relate to high energy requirements of pups for maintenance and blubber deposition (Jenness and Sloan 1970; Bonner 1984; Oftedal et al. 1987*b*). Species breeding on pack ice tend to have the shortest lactation lengths and highest rates of blubber deposition among pinnipeds (Bowen et al. 1985; Bowen et al. 1987*a*; Kovacs and Lavigne 1986), and hence would be predicted to have particularly fat- and energy-rich milks. The tendency towards abbreviation of lactation reaches an extreme with the hooded seal; pups gain about 7 kg per day during the shortest lactation known for any mammal (4 days) (Bowen et al. 1985).

Relatively little information is available on milk composition of the 10 pinniped species that breed on pack ice (Oftedal et al. 1987*a*). Studies of harp seal (*Phoca groenlandica*) milk indicate that fat levels may range from about 20 to 53% (Sivertsen 1941; Jangaard and Ke 1968; Cook and Baker 1969; Jenness and Sloan 1970; Van Horn and Baker 1971; Lavigne et al. 1982; Stewart et al. 1983). The few samples of hooded seal milk that have been assayed exhibit an even wider range of 23–72% fat (Sivertsen 1941; Beloborodov and Potelov 1966; Jangaard and Ke 1968; Shergin et al. 1969; Shepeleva 1973). Milk fat content is known to increase with lactation stage in some pinnipeds, including harp seals (Lavigne et al. 1982; Stewart et al. 1983; Oftedal et al. 1987*a*), but in many studies lactation stage has not been reported. The use of different sampling and analytical methods may also have influenced the results. For example, in some studies milk has been obtained from pup stomachs (e.g., Lavigne et al. 1982; Stewart et al. 1983). Gastric samples tend to be considerably lower in fat content than maternal milk in the pinnipeds that have been studied (Oftedal et al. 1987*a*).

In 1984 we had the opportunity to collect milk from hooded seals that had given birth on pack ice 180 km off the southeast coast of Labrador. Hooded seals are a migratory, pelagic species inhabiting the deep waters of the North Atlantic near the outer edge of the pack ice. Pups are born over a 2-week period in mid to late March (Bowen et al. 1987*b*). Mothers remain with their pups and fast throughout the 4-day lactation (Bowen et al. 1985; Bowen et al. 1987*a*). We report on changes in milk composition over lactation, and examine the effect of sampling method on milk composition.

Materials and methods

The whelping concentration was initially located by fixed-wing aerial survey on 17 March 1984. For the next week (18–25 March 1984) helicopters were used to ferry researchers from the Canadian

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TABLE 1. The composition of sequential samples obtained during milk collection

	Sample 1	Sample 2	Sample 3	F^a Effect of animal	F^a Effect of sample order
Dry matter, %	66.5±1.9	67.1±1.9	66.6±1.8	152***	1.3 ns
Fat, %	57.8±2.0	57.0±1.7	57.7±2.0	60.5***	1.0 ns
Protein, %	5.53±0.49	5.49±0.46	5.48±0.46	411***	0.4 ns
Sugar, %	0.95±0.06	0.91±0.03	0.99±0.04	1.2 ns	0.9 ns
Gross energy, kcal/g	5.63±0.16	5.55±0.14	5.61±0.17	45.6***	1.0 ns

NOTE: Data based on three 10–15 mL sequential samples obtained from each of seven seals at 0–2 days postpartum. Values are expressed as mean ± SE.
[a]Two-way analysis of variance, with 6, 2, and 12 degrees of freedom for animal, sample order, and error terms, respectively. Interactions could not be tested. ***, significant at $p < 0.001$; ns, not significant ($p > 0.05$).

scientific ship (CSS) *Baffin* to lactating seals on ice pans. Milk was obtained both from live animals that had been chemically immobilized, and from animals shot by high-powered rifle for morphometric studies (Bowen et al. 1987*a*).

Chemical immobilization involved dart administration of fentanyl citrate (30 mg/mL solution) at a dose rate of 0.50–1.17 mg/kg body weight. Darts were fitted with 3.5-in. (89-mm) spinal needles and delivered by blowpipe. Milk was manually expressed into polypropylene bottles following intramuscular injection of 20 IU oxytocin. After about 5 min, naloxone hydrochloride was injected intravenously to reverse immobilization. Because of the relatively short immobilization period, complete mammary evacuation was not possible (mean volume 26 mL ± 12.4 (SD); range 12–44 mL).

Milk expression from shot females began immediately postmortem, and milking was completed by 19 ± 5.9 min after shooting. When possible, an initial series of three sequential milk samples of 24–33 mL was collected in separate 35-mL polypropylene bottles. In cases where manual expression yielded little milk, incision of the teat provided additional milk with no apparent contamination. The amount obtained per female by postmortem expression and nipple incision was variable (mean 120 mL ± 145 (SD); range 8–565 mL). Milk was also collected by deep incision into mammary tissue, but as it was impossible to avoid some blood and (or) lipid contamination, these samples were not included in the present study. Sample volume and pH were measured with graduated cylinder and pH paper (color gradations in 0.5 pH units) before storage. Samples were stored in airtight bottles in a −10°C freezer on board the research vessel. After March 1984, samples were stored at −30°C.

In the fall of 1985, samples were thawed and mixed with a tissue homogenizer. Subsamples were weighed to the nearest 0.1 mg; compositional data are thus expressed as a percentage by weight. Dry matter was determined by drying in a forced-convection oven at 100°C for 5 h. Fat content was measured gravimetrically following repeated extractions with ethanol, diethyl ether, and petroleum ether in the Roese Gottlieb procedure (Association of Official Analytical Chemists 1980). Total nitrogen was assayed by a macro-Kjeldahl method, using copper sulfate as a catalyst (Association of Official Analytical Chemists 1980), and converted to crude protein by multiplying by 6.38, the conversion factor commonly used for milk protein. Sugar content was determined by the phenol – sulfuric acid procedure (Marier and Boulet 1959) using lactose monohydrate for generation of standard curves and calculation of sugar content; the sugar values reported are thus equivalent to the colorimetric response of glucose and galactose in equal proportions. Gross energy (GE) was calculated as follows (Perrin 1958):

$$\text{GE (kcal/g)} = (9.11 \times \%\text{fat} + 5.65 \times \%\text{protein} + 3.95 \times \%\text{sugar})/100$$

Milk samples were analyzed from a total of 22 females. Of these, 15 had pups that were of known age, as the pups had been tagged at birth (see Bowen et al. 1985). The lactation stages of the remaining females were estimated by comparing the body mass and appearance of their pups with those of pups of known age.

Results

Hooded seal milk was highly viscous, with a consistency reminiscent of heavy cream. The color of the milk was somewhat variable, some samples being beige in color, and others having a distinctive peach, rose, or tan tint. Presence or absence of tint was independent of sampling method, and did not appear to be due to contamination. The pH of all samples was between 5.0 and 6.0.

All samples of hooded seal milk ($n = 36$) had high levels of dry matter (57.5–77.4%), fat (47.5–69.0%), and calculated gross energy (4.74–6.62 kcal/g), and low to moderate levels of crude protein (3.65–7.31%) and sugar (0.67–1.21%).

A sequence of three consecutive milk samples was obtained from each of seven seals during the course of manual milk expression. Although there were significant differences among animals in dry matter, fat, protein, and energy content, compositional data did not show any effect of sampling order (Table 1). The differences among animals may stem in part from differences in lactation stage, as three of these animals had newborn pups and four had 2-day-old pups. Among all animals studied ($n = 22$), lactation stage had a significant effect only on protein content (Table 2), although the effects on both fat content ($p = 0.09$) and sugar content ($p = 0.07$) approached the 0.05 probability level. On the day of birth, milk was higher in protein than at subsequent times. There were no compositional differences between milk obtained in mid (2 days) and late (4 days) lactation.

Milk samples represent two different methods of collection, drug immobilization (5 animals) and postmortem expression (17 animals). Comparison of milks obtained by these two methods at mid to late lactation, when composition is stable, did not reveal any significant differences (Table 3).

Discussion

In many mammalian species fat content rises markedly over the course of milk removal (Oftedal 1984), but we found no evidence of such a trend in sequential samples of hooded seal milk. Our data do not represent complete mammary evacuation, however. In other mammals, the greatest differences in milk composition are usually seen between the first and last samples drawn over the course of mammary evacuation.

There were no discernible effects of method of collection (drug immobilization vs. postmortem collection) on the com-

TABLE 2. Effect of lactation stage on milk composition in the hooded seal

	Lactation stage			
	Early (0 days)	Mid (2 days)	Late (4 days)	F^a
No. of animals	7	8	7	
Dry matter, %	66.0±1.7	69.7±0.7	69.8±1.7	2.30 ns
Fat, %	56.3±1.6	61.0±1.1	61.1±2.1	2.81 ns
Protein, %	6.19±0.34	4.74±0.28	5.12±0.20	7.16**
Sugar, %	0.86±0.04	1.05±0.06	0.99±0.07	2.99 ns
Gross energy, kcal/g	5.53±0.14	5.88±0.09	5.90±0.19	2.19 ns

NOTE: Lactation stage of two animals at mid lactation and five animals at late lactation estimated by comparison with known-age pups. Values are expressed as mean ± SE. Where more than one sample per animal was analyzed (e.g., Table 1), the mean values for each animal were used.
[a]By ANOVA. **, significant at $p < 0.01$; ns, not significant ($p > 0.05$).

TABLE 3. Effect of collection method on milk composition at mid to late lactation

	Chemical immobilization (plus oxytocin)	Postmortem expression	t
No. of animals	4	11	
Dry matter, %	69.3±1.7	69.9±1.1	0.30 ns
Fat, %	60.9±2.5	61.1±1.3	0.09 ns
Protein, %	4.72±0.41	4.99±0.20	0.66 ns
Sugar, %	1.03±0.05	1.02±0.06	−0.05 ns
Gross energy, kcal/g	5.86±0.21	5.90±0.11	0.17 ns

NOTE: Values are expressed as mean ± SE. ns, not significant ($p > 0.05$). Where more than one sample per animal was analyzed (e.g., Table 1), the mean values for each animal were used.

position of hooded seal milk. Thus, if any bias was produced as a result of sampling procedure, it was equivalent for the two procedures. Contamination of samples with blood or blubber lipids can occur during mammary incision, but we discarded any samples that were visibly contaminated. Incision of the teat (rather than the gland) proved to be a useful method of collecting uncontaminated samples.

Oxytocin was administered to immobilized seals to facilitate milk removal. In some species, oxytocin has been shown to cause a reduction in milk sugar content when large doses are given repeatedly (Lane et al. 1970; Linzell et al. 1975). The similarity of sugar levels in samples from immobilized and shot animals suggests that the single dose of oxytocin administered to each animal had little, if any, effect. Postmortem changes in milk composition due to loss of physiological function in mammary alveoli would have been minimal because samples were collected immediately from shot animals.

In most pinnipeds, fat content of milk has been shown to increase from early to mid lactation (Oftedal et al. 1987*a*). Our data did not reveal a significant trend in hooded seals, although the calculated probability (p = 0.09) approached the 0.05 level. At the other extreme, a rise from about 10% fat in milk just after birth to about 50% at mid to late lactation has been reported for both northern elephant seals, *Mirounga angustirostris* (Riedman and Ortiz 1979), and southern elephant seals, *Mirounga leonina* (data of Peaker and Goode (1978)), erroneously reported to be from *Arctocephalus tropicalis gazella* (M. Peaker, personal communication; see also Bonner 1984). Hooded seals secrete milk that is as high in fat content (about 56%) on the day of birth as that of other pinnipeds at mid to late lactation (44−55% fat, Oftedal et al. 1987*a*). At 2−4 days postpartum, the mean dry matter (70%), fat (61%), and gross energy (5.9 kcal/g) contents of hooded seal milk are higher than have been reported for any other mammal (Jenness and Sloan 1970; Oftedal 1984; Oftedal et al. 1987*a*).

The fact that fat content was both very high and relatively invariant in this study raises doubts about the validity of the single value of 23% fat reported for hooded seal milk by Jangaard and Ke (1968). Sivertsen (1941) also presented a rather low fat level for hooded seal milk (40.4%). By contrast, the four to six analyses of hooded seal milk reported by Shergin et al. (1969) exhibit ranges of dry matter (64−74%) and fat (54−66%) that are similar to those obtained in the present study. In a brief report, Beloborodov and Potelov (1966) indicate ranges of 65−76% dry matter and 60−72% fat for hooded seal milk, but details on the numbers and origin of samples are not given.

Like other phocid pups, the hooded seal pup achieves a weaning mass equivalent to about one-fourth of maternal mass, but it has only 4 days in which to do so (Bowen et al. 1985). Much of this mass gain (about 70%, or 4.5 kg per day) is blubber and skin (Bowen et al. 1987*a*). The need for rapid acquisition of blubber by the pup has apparently put a premium on production of milk high in fat content throughout lactation. If blubber of hooded seal pups contains about 90% fat, as in fat harp seal pups (Worthy and Lavigne 1983), pups will need to consume about 4 kg of milk fat per day, or about 7 kg milk, simply to cover requirements for blubber deposition. Actual milk intake must be even higher to provide fat for deposition around the viscera, and some fat is undoubtedly catabolized to support metabolic processes.

The elevation in protein content of the initial milk (colostrum) in hooded seals is similar to observed trends in many mammals (Oftedal 1984), although data on other pinniped species are inconsistent in this regard (Oftedal et al. 1987*a*). It may be that hooded seal colostrum contains immunoglobulins to provide systemic or gastrointestinal protection for the neonate, as in other mammals (Brambell 1970), but we did not test this.

At mid to late lactation, hooded seal milk contains a relatively low protein level (about 5%) compared with typical values of 7–12% in other pinniped species (Oftedal et al. 1987*a*). Our analyses may somewhat overestimate the protein content of milk because nonprotein nitrogen was not deducted from total nitrogen before protein content was calculated. The low protein level in hooded seal milk is especially remarkable when compared with gross energy content. Protein accounts for only 4.9% of calculated milk energy in mid to late lactation, compared with calculated values of 9–10% in other phocids (four species) and about 12% in otariids (three species) (calculated from data in Oftedal et al. 1987*a*). Thus the percentage of energy in hooded seal milk supplied by protein is only about one-half of that in the milk of other pinnipeds, and one-quarter to one-seventh of the level typical of most terrestrial mammals (20–35%, Powers 1933; Oftedal 1984). Some primates also produce milk with a low percentage of energy as protein (range 7–17%), a trend which is thought to be related to slow growth rate (Payne and Wheeler 1968; Oftedal 1984). Although hooded seal pups exhibit extremely rapid weight gain, most of this gain is blubber.

The amount of milk required to supply sufficient protein for gain of lean body mass can be estimated from hooded seal growth data. Assuming that the sculp (skin and blubber) and core (carcass including viscera) of hooded seal pups are similar in composition to those of harp seal pups (Worthy and Lavigne 1983), morphometric data on hooded seal pups (Bowen et al. 1987*a*) indicate a lean body mass gain of about 2 kg per day. Because lean body mass of pinniped pups is about 20% protein (Oftedal et al. 1987*b*), hooded seal pups need to consume about 400 g protein daily for lean tissue synthesis. This would be supplied by 8 kg of hooded seal milk (5% protein), an amount similar to that required for blubber deposition. It appears that hooded seals can afford to secrete low-protein milk because only a relatively small part of weight gain by pups is lean tissue. Reduction in milk protein content has the advantage that the drain of lactation on protein reserves of the fasting mother is reduced, and depletion of maternal muscle and other protein-containing tissues is less severe. This may be especially important for female hooded seals, as they undertake a prolonged migration immediately after weaning of their pups (Rasmussen 1960).

Hooded seal milk was found to have a low sugar content, as is typical of pinniped milks (Oftedal et al. 1987*a*). The low carbohydrate content of hooded seal milk may help minimize the osmotic flow of water into milk during synthesis, although the mechanism by which pinnipeds secrete milk of such low water content is not understood (Peaker 1977; Oftedal et al. 1987*a*). The fat content of hooded seal milk is high in part because the water content is so low (about 30%).

The phenol – sulfuric acid method used for sugar analysis is nonspecific and includes protein-bound carbohydrate. Stewart et al. (1983) reported that the phenol – sulfuric acid method yielded somewhat higher values than the picric acid procedure (a reducing sugar method) when applied to samples of harp seal milk obtained from pup stomachs. As the identity and reducing power of the sugar(s) in seal milks are not known, it is more appropriate to use nonspecific methods than to assume that the reducing power of sugar in milk is equivalent to that of a lactose standard. California sea lion milk contains small amounts of sugar (0.3–0.6%) but is devoid of lactose (Pilson and Kelly 1962; Johnson 1975; Oftedal et al. 1987*b*; O. T. Oftedal, D. J. Boness, and S. J. Iverson, unpublished data).

If compositional data are expressed on a fat-free or skim-milk basis, hooded seal milk is somewhat higher in sugar (2.6 g/L skim milk) but lower in protein (125 g/L skim milk) than other pinniped milks that have been studied (0.0–1.7 g sugar and 139–259 g protein per litre skim milk, calculated from data in Oftedal et al. (1987*a*) and O. T. Oftedal, D. J. Boness, and W. D. Bowen (unpublished data). This observation is consistent with the finding of Davies et al. (1983) that protein and lactose (sugar) in mammalian milks are negatively correlated when expressed relative to the skim-milk portion.

In summary, our results suggest that the composition of hooded seal milk has evolved to facilitate rapid blubber deposition by the pup during a short lactation period. High fat and low protein, sugar, and water contents are only appropriate because pup weight gain is primarily fat. One would expect a high efficiency of conversion of milk energy to pup tissue energy because the metabolic costs of fat absorption, mobilization, and deposition should be relatively minor. Studies on milk consumption by hooded seal pups may provide insight into the energetic efficiency of this remarkable growth pattern.

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