

## ORIGINAL PAPER

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**Energetics during nursing and early postweaning fasting in hooded seal (*Cystophora cristata*) pups from the Gulf of St Lawrence, Canada**

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**Abstract** In this study we measured growth and milk intake and calculated energy intake and its allocation into metabolism and stored tissue for hooded seal (*Cystophora cristata*) pups. In addition, we measured mass loss, change in body composition and metabolic rate during the first days of the postweaning fast. The mean body mass of the hooded seal pups ( $n = 5$ ) at the start of the experiments, when they were new-born, was  $24.3 \pm 1.3$  kg (SD). They gained an average of  $5.9 \pm 1.1$  kg · day<sup>-1</sup> of which 19% was water, 76% fat and 5% protein. This corresponds to an average daily energy deposition of  $179.8 \pm 16.0$  MJ. The pups were weaned at an average body mass of  $42.5 \pm 1.0$  kg 3.1 days after the experiment was initiated. During the first days of the postweaning fast the pups lost an average of  $1.3 \pm 0.5$  kg of body mass daily, of which 56% was water, 16% fat and 28% protein. During the nursing period the average daily water influx for the pups was  $124.6 \pm 25.8$  ml · kg<sup>-1</sup>. The average CO<sub>2</sub> production during this period was  $1.10 \pm 0.20$  ml · g<sup>-1</sup> · h<sup>-1</sup>, which corresponds to a field metabolic rate of  $714 \pm 130$  kJ · kg<sup>-1</sup> · day<sup>-1</sup>, or  $5.8 \pm 1.1$  times the predicted basal metabolic rate according to Kleiber (1975). During the postweaning fast the average daily water influx was reduced to  $16.1 \pm 6.6$  ml · kg<sup>-1</sup>. The average CO<sub>2</sub> production in this period was  $0.58 \pm 0.17$  ml · g<sup>-1</sup> · h<sup>-1</sup> which corresponds to a field metabolic rate of  $375 \pm 108$  kJ · kg<sup>-1</sup> · day<sup>-1</sup> or  $3.2 \pm 0.9$  times the predicted basal metabolic rate. Average values for milk composition were 33.5% water, 58.6% fat and 6.2% protein. The pups drank an average

of  $10.4 \pm 1.8$  kg of milk daily, which represents an energy intake of  $248.9 \pm 39.1$  MJ · day<sup>-1</sup>. The pups were able to store  $73.2 \pm 7.7\%$  of this energy as body tissue.

**Key words** Energetics · Lactation · Maternal investment · Doubly labelled water · Hooded seals, *Cystophora cristata*

**Abbreviations** *BM* body mass · *IU* international unit · *BMR* basal metabolic rate · *RQ* respiration quotient · *FMR* field metabolic rate · *TBW* total body water · *HDO* deuteriated water · *VHF* very high frequency · *DLW* doubly labelled water · *T<sub>r</sub>* rectal temperature

**Introduction**

The nursing period in phocid seals is characterised by its short duration, its extreme rate and efficiency of energy transfer and its abrupt termination at weaning. Additionally, it was thought until recently that it was another phocid trait that females derived the energy required to support the cost of lactation from maternal energy deposits without additional feeding. However, the generality of the latter factor has been found to be invalid. Recent investigations have shown that nursing mothers of many phocid species do feed to different degrees during this period [harbour seals, *Phoca vitulina*: Bowen et al. (1992); ringed seals, *Phoca hispida*: Lydersen (1995); grey seals, *Halichoerus grypus*: Lydersen et al. (1994a); bearded seals, *Erignathus barbatus*: Lydersen et al. 1996; harp seals, *Phoca groenlandica*: Lydersen and Kovacs (1996)].

The shortest nursing period within the phocid group, and indeed among mammals, is found in hooded seals (*Cystophora cristata*). In this species the average duration of lactation is only 4 days (Bowen et al. 1985; Kovacs and Lavigne 1992). During this time the pups can grow at rates exceeding  $7$  kg · day<sup>-1</sup> increasing their BM

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from about 23 kg at birth to about 45 kg at weaning (Bowen et al. 1985, 1987a; Kovacs and Lavigne 1992). This extreme rate of growth is accomplished through the intake of the most energy-rich milk produced by any mammal: 60–70% fat (Ofstedal et al. 1988), by low activity levels in nursing pups, and through the very efficient transfer of milk energy into stored tissues by the pups (Ofstedal et al. 1993). Hooded seal mothers spend the whole nursing period on the ice attending their pup without entering the water (Bowen et al. 1987a). Thus, in this species all the typical phocid nursing characteristics are fulfilled, including female fasting.

Hooded seal pups molt in utero and are born with a subcutaneous blubber layer. This is considered to be an adaptation to tolerate early entrance to the water (Ofstedal et al. 1991). Two other phocid species, the harbour and bearded seals, are also born with thin subcutaneous blubber layers and molt in utero, and these pups normally swim with their mothers from the day they are born (Lawson and Renouf 1985; Kovacs et al. 1996). Hooded seal pups do not normally enter the water during the nursing period. However, they are born and nursed in unstable drifting ice areas and if rough weather should wash them into the cold ocean, their congenital subcutaneous blubber layer would give them enough thermal protection to survive such an event. Another reason for the prenatal blubber deposition in hooded seals may be that weaned pups need sufficient energy stores to ensure normal development and survival, and in order to accomplish this during a nursing period of only 4 days, prenatal deposition of energy is crucial (Ofstedal et al. 1993). Hooded seal pups are large at birth; they are 12% of maternal BM versus the phocid norm of 6–9%. The high fat content of new-borns (14%) gives them the highest energy density of any new-born seal pup [ $10.1 \text{ MJ} \cdot \text{kg}^{-1}$ ; Ofstedal et al. (1993)]. Because of these differences at birth, hooded seal pups are weaned with body compositions similar to other weaned phocid pups despite the brevity of the nursing period. This is accomplished through extreme rates of energy intake and deposition during the short dependence period, and also by the mother's ability to replace some of the usual phocid postnatal energy transfer with prenatal energy deposition (Ofstedal et al. 1993).

Hooded seals give birth in four geographical distinct breeding areas, the "west-ice" around Jan Mayen, in the Davis Strait, off the coasts of Labrador and Newfoundland, and in the Gulf of St Lawrence (Kovacs and Lavigne 1986). Pup production in the two latter areas are about 60 000 and 3000, respectively (Bowen et al. 1987b; Hammill et al. 1996). Growth rates for pups in these two areas, based on longitudinal data for individual animals, vary between  $4.2$  and  $7.1 \text{ kg} \cdot \text{day}^{-1}$  (Bowen et al. 1985, 1987a; Kovacs and Lavigne 1992; Ofstedal et al. 1993). In a nursing study of hooded seals off Newfoundland pups were growing at rates from  $4.2$ – $6.6 \text{ kg} \cdot \text{day}^{-1}$ . This involved a daily intake of  $7.5 \text{ kg}$  of milk which corresponds to  $187 \text{ MJ}$  of energy consumed (Ofstedal et al. 1993). These pups were depositing

$84\%$  of the received energy as body tissue. During the course of lactation the fat content of these pups increased from  $14\%$  of BM in new-borns to  $45\%$  of BM at the time of weaning. The hooded seal pups in the Gulf population grow at rates similar to those off Newfoundland. The maternal BM and BM at birth and weaning for the Gulf population is, however, significantly higher than for animals off Newfoundland (Kovacs and Lavigne 1992).

In the present study we measure growth, milk and energy intake and its allocation into metabolism and stored tissue for hooded seal pups from the Gulf of St Lawrence. This is accomplished using longitudinal growth and milk samples and the DLW technique. In addition, we measure mass loss and change in body composition and metabolic rate during the first days of the postweaning fast for these hooded seal pups.

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## Materials and methods

This study was conducted on the drifting pack-ice in the Gulf of St Lawrence, Canada, in March 1993 and 1995. The hooded seal whelping patches were initially located using fixed-wing aircraft. Subsequently, the study site was visited by helicopter. To facilitate daily relocation the site was marked with a VHF-transmitter and fluorescent dye powder was put on the ice for increased visibility.

In March 1993 five hooded seal mother-pup pairs were used in a DLW study. Pairs were captured when the pups were new-born, as revealed by size and colouration or by still being wet from the amniotic fluids. Three of the five pairs were recaptured just prior to weaning, while only the newly weaned pups were found for the remaining pairs. These newly weaned pups had milk remains in their stomachs and an abundance of milk fat in their blood plasma. Finally, about three days postweaning, all five pups were again recaptured for termination of the experiments. Adult females in this experiment were captured using a sling net to facilitate safe handling of the pups. Pups were hand captured. Prior to weighing and injection of isotopes, a veterinary lavage tube was used to evacuate the stomach of the hooded seal pups. They were then weighed using a Salter spring scale ( $50 \pm 0.5 \text{ kg}$ ). A blood sample ( $10 \text{ ml}$ ) was taken from the epidural vein to measure background levels of deuterium and  $^{18}\text{O}$ , then  $5 \text{ ml}$  HDO (99.5%, ICN Biochemicals, Cleveland, Ohio USA) was injected intravenously into each pup. In addition  $2 \text{ ml}$  per  $\text{kg}$  of pup of  $^{18}\text{O}$  (ca.  $10\%$ , Iso-Yeda Co. Ltd, Rehovot 76100, Israel) was injected into the same vein. NaCl had been added to both water isotope solutions to reach a concentration of  $0.9\%$  (physiological saline solution). A VHF transmitter was glued to the back of each pup to facilitate recapture. Upon recapture the pups stomachs were again evacuated and the pups were reweighed. A blood sample was taken and  $5 \text{ ml}$  HDO was again injected into the epidural vein. Two hours post-injection another blood sample was taken to estimate the new body water dilution space and to give new background levels for the isotopes. Since the whole experiment lasted less than 1 week, no re-injections of  $^{18}\text{O}$  were performed. The same procedure was conducted at the third and final capture, in addition to removal of the VHF transmitters before the pups were released. At each capture of hooded seal mothers, a milk sample (ca.  $50 \text{ ml}$ ) was collected about  $10 \text{ min}$  after an intramuscular injection of  $20 \text{ IU}$  oxytocin. All blood and milk samples were stored in frozen at  $-20^\circ\text{C}$  until analyses.

For analyses of isotopes, whole blood samples ( $5 \text{ ml}$ ) were initially vacuum distilled. The total amount of free water was distilled from each blood sample to avoid fractionation. For the deuterium analyses  $5 \mu\text{l}$  of the distilled water was transferred to a glass ampoule, frozen and the air was pumped out until vacuum was es-

established. Through a cryogenic distillation the sample was transferred into a quartz ampoule filled with ca. 0.25 g Zn. Vacuum was again established before this ampoule was sealed by melting using a H<sub>2</sub>O<sub>2</sub> flame. The quartz ampoule was then placed in an oven for 10 min at 900 °C during which time hydrogen gas and ZnO was formed. This sample was then transferred to a Finnigan MAT Delta E gas mass-spectrometer for determination of deuterium. The accuracy of these measurements is ± 1.0%. In order to calculate the daily water influx in the hooded seal pups we used Eq. 6 from Nagy and Costa (1980) for body water volumes changing exponentially with time. This value was then used to calculate the water influx through the animal for the whole measurement period as described in Lydersen et al. (1992). The body compositions of the hooded seal pups were calculated based on measurements of BM and TBW using Reilly and Fedak's (1990) equations for grey seals. To measure <sup>18</sup>O concentrations 1 ml of the distilled water was transferred to a 10-ml vacutainer. Vacuum was re-established and the vacutainer was filled with CO<sub>2</sub> gas to a pressure of 1 bar. The vacutainer was then stored for 16 h in a thermostat-controlled water bath in order to reach equilibrium between the gas and the liquid. The CO<sub>2</sub> gas was dried through a P<sub>2</sub>O<sub>5</sub> cartridge and then transferred to a Finnigan MAT 251 mass spectrometer to determine the ratios of <sup>18</sup>O/<sup>16</sup>O. The accuracy of these measurements is ± 0.1%. CO<sub>2</sub> production was calculated using Eq. 3 in Nagy (1980) for body water changing exponentially with time. A conversion factor of 26.98 kJ per litre of CO<sub>2</sub> produced was used; this is equivalent to a RQ of 0.74. The amount of protein (x) and fat (y) catabolized by the pups was calculated by solving for two unknowns in the following equations:

$$17.99x + 39.33y = E_{\text{total}}$$

$$0.782x + 1.433y = \text{CO}_2 \text{ total}$$

where 17.99 and 39.33 are energy content (kJ) per g protein and fat catabolized (Costa 1987);  $E_{\text{total}}$  is total energy consumption for the period; 0.783 and 1.433 are litres CO<sub>2</sub> produced per g of protein and fat catabolized (Costa 1987) and CO<sub>2 total</sub> is the CO<sub>2</sub> production for the whole period. The metabolic water fraction was then calculated using 0.396 g of water produced per gram protein and

1.071 g of water produced per gram of fat catabolized (Schmidt-Nielsen 1986).

For analyses of milk composition thawed milk samples were homogenised and total dry matter was determined by drying a subsample in an air oven at 100 °C for 3 h. Fat content in the milk was determined using the acid hydrolyses method (AOAC 1990), and total nitrogen was determined by the Kjeldahl method. The latter value was converted to crude protein by multiplying the nitrogen content by 6.38 (AOAC 1990). The energy content of the milk was calculated using information on protein and fat content and multiply this by 17.99 kJ per gram of protein and 39.33 kJ per gram of fat (Schmidt-Nielsen 1986). The contribution of milk water to the total water influx in the pups was calculated as the difference between total water influx and metabolic water production.

In March 1995 we measured  $T_r$  in both nursing and weaned hooded seal pups. This was done because calculations of FMR based on the experiment in 1993 showed relatively high values for the very sedentary nursing hooded seal pups compared with the FMR values for the much more active weaners [and also compared with FMR values in relatively sedentary nursing pups of other ice-breeding species (Lydersen et al. 1995; Lydersen and Kovacs 1996)]. To explore whether this difference in FMR could be detected as a difference in body temperature,  $T_r$  was measured in 19 nursing and 32 weaned hooded seal pups using a copper-constantan thermocoupler Model BAT-12 (Physitemp Instruments Inc, Clifton, USA; range -100 °C to +200 °C, 0.1° resolution). The rectal temperatures are henceforth referred to as "body temperature".

## Results

The mean BM of the hooded seal pups at the start of the experiments, when they were new-born, was  $24.3 \pm 1.3$  kg (SD) (Table 1). They gained an average of  $5.9 \pm 1.1$  kg · day<sup>-1</sup> of which 19% was water, 76% fat and 5% protein (Tables 1, 2). This corresponds to an

**Table 1** Mass gain, water flux and metabolic rates of nursing hooded seal pups from the Gulf of St Lawrence, Canada

Pup no	Duration of experiment (days)	Initial body mass (kg)	Daily mass gain (kg)	Daily water influx (ml · kg <sup>-1</sup> )	CO <sub>2</sub> production (ml · g <sup>-1</sup> · h <sup>-1</sup> )	Metabolic rate (kJ · kg <sup>-1</sup> · day <sup>-1</sup> )	Multiples of BMR
2214	3.0	24.0	6.3	105.9	1.09	707	5.8
2220	2.9	26.0	5.5	126.8	0.97	629	5.2
2227	3.8	25.0	4.3	101.7	1.03	666	5.4
2232	3.0	22.5	7.2	121.9	1.45	939	7.7
2236	3.0	24.0	6.0	166.8	0.97	629	5.1
Mean	3.1	24.3	5.9	124.6	1.10	714	5.8
± SD	0.4	1.3	1.1	25.8	0.20	130	1.1

**Table 2** Composition of mass gain and efficiency of storage of energy for nursing hooded seal pups from the Gulf of St Lawrence, Canada

Pup no	Daily mass gain (kg)	Daily fat gain (kg)	Daily water gain (kg)	Daily protein gain (kg)	Daily energy gain (MJ)	Ingested energy stored as tissue (%)
2214	6.3	4.5	1.5	0.3	182.4	67.2
2220	5.5	5.0	0.6	< 0.1	196.7	74.5
2227	4.3	3.9	0.4	< 0.1	153.4	83.4
2232	7.2	4.5	2.1	0.5	186.0	76.8
2236	6.0	4.5	1.1	0.2	180.6	64.0
Mean	5.9	4.5	1.1	0.3	179.8	73.2
± SD	1.1	0.4	0.7	0.2	16.0	7.7

**Table 3** Mass loss, water flux and metabolic rates of hooded seal pups during the first days of their postweaning fast

Pup no	Duration of experiment (days)	Initial body mass (kg)	Daily mass loss (kg)	Daily water influx (ml · kg <sup>-1</sup> )	CO <sub>2</sub> production (ml · g <sup>-1</sup> · h <sup>-1</sup> )	Metabolic rate (kJ · kg <sup>-1</sup> · day <sup>-1</sup> )	Multiples of BMR
2214	3.1	43.0	0.8	10.9	0.38	246	2.1
2220	3.2	42.0	1.0	20.8	0.53	343	2.9
2227	2.1	41.5	1.1	24.1	0.69	448	3.8
2232	2.1	44.0	1.8	8.3	0.49	318	2.8
2236	2.0	42.0	1.8	16.2	0.80	518	4.4
Mean	2.5	42.5	1.3	16.1	0.58	375	3.2
± SD	0.6	1.0	0.5	6.6	0.17	108	0.9

average daily energy deposition of  $179.8 \pm 16.0$  MJ (Table 2). The pups were weaned at an average BM of  $42.5 \pm 1.0$  kg, 3.1 days after the experiment was initiated (Table 3). During the first days of the postweaning fast the pups lost an average of  $1.3 \pm 0.5$  kg daily, of which 56% was water, 16% fat and 28% protein.

During the nursing period the average daily water influx for the pups was  $124.6 \pm 25.8$  ml kg<sup>-1</sup> (Table 1). The average CO<sub>2</sub> production during this period was  $1.10 \pm 0.20$  ml · g<sup>-1</sup> · h<sup>-1</sup>, which corresponds to a FMR of  $714 \pm 130$  kJ · kg<sup>-1</sup> · day<sup>-1</sup>, or  $5.8 \pm 1.1 \times$  BMR (Table 1). During the postweaning fast the average daily water influx was reduced to  $16.1 \pm 6.6$  ml · kg<sup>-1</sup> (Table 3). The average CO<sub>2</sub> production during this period was  $0.58 \pm 0.17$  ml · g<sup>-1</sup> · h<sup>-1</sup>, corresponding to a FMR of  $375 \pm 108$  kJ · kg<sup>-1</sup> · day<sup>-1</sup>, or  $3.2 \pm 0.9 \times$  BMR (Table 3). The FMR during the postweaning fast was significantly lower than the FMR during the nursing period (Wilcoxon signed-rank test,  $P = 0.04$ ). The body temperature of nursing hooded seal pups ( $T_r = 37.40 \pm 0.20$  °C,  $n = 19$ ) was significantly higher than for pups during the postweaning fast ( $T_r = 37.10 \pm 0.34$  °C,  $n = 32$ ; Mann-Whitney U-test,  $P = 0.0003$ ).

The composition of the milk varied considerably among mothers (Table 4). Average values for the composition of the milk were 33.5% water, 58.6% fat and 6.2% protein. The three longitudinal samples showed no consistency in change in composition. One showed an increase in water content, another a decrease, while the

**Table 4** Composition of milk from lactating hooded seal mothers

Mother of pup no	Fat content (%)	Water content (%)	Protein content (%)	Ash (%)
2214 <sup>a</sup>	61.7	31.6	6.9	0.36
2214 <sup>b</sup>	68.1	25.4	5.2	0.35
2220 <sup>a</sup>	58.5	34.0	5.6	0.42
2227 <sup>a</sup>	56.8	35.1	5.3	0.44
2232 <sup>a</sup>	58.5	33.1	7.2	0.43
2232 <sup>b</sup>	59.7	32.0	6.3	0.43
2236 <sup>a</sup>	56.9	34.0	6.3	0.43
2236 <sup>b</sup>	48.3	42.7	7.0	0.59

<sup>a</sup>first capture when pup was newborn

<sup>b</sup>second capture just before weaning

third showed almost no difference (Table 4). In order to calculate milk intake, the average value for milk composition for each mother was used in the three cases where longitudinal samples were available. For the two remaining pups, milk composition at the start of the experiment, for each respective mother, was used. The pups drank an average of  $10.4 \pm 1.8$  kg of milk daily. This corresponds to an energy intake of  $248.9 \pm 39.1$  MJ · day<sup>-1</sup> (Table 5). The pups were able to store  $73.2 \pm 7.7\%$  of this energy as body tissue.

## Discussion

The average nursing period for pups in the present study was 3.1 days, which is in the lower end of the range of previously reported values (Bowen et al. 1985; Kovacs and Lavigne 1992). This may have been due to our interference. Two of the pups in this study were naturally abandoned by their mothers after 3.8 and 2.9 days, respectively. In order to get longitudinal milk samples the three remaining pairs were recaptured 3.0 days into the nursing period. Immediately after these recaptures the females left with their respective attending males and the pups were thus weaned. We have reasons to believe that weaning was imminent even without our presence. If we consider the energy intake through milk in the present study, the 248.9 MJ received daily (Table 5) extrapolates to 772 MJ for a 3.1-day period. In another milk intake study of hooded seals, pups were found to receive 746 MJ of energy during an average 4-day nursing period (Oftedal et al. 1993). Even if our disturbance late in lactation resulted in premature weaning, the energy received by the pups indicates that this occurred at a point very close to when they would have been naturally abandoned.

The FMR measured for nursing hooded seal pups in the present study is within the interval of values measured for other nursing phocid seal pups [grey seal pups:  $3.7$  and  $4.5 \times$  BMR (Reilly 1989; Lydersen et al. 1995); ringed seal pups:  $3.8 \times$  BMR (Lydersen and Hammill 1993); harp seal pups:  $3.9 \times$  BMR (Lydersen and Kovacs 1996); northern elephant seal pups (*Mirounga angustirostris*):  $4.3 \times$  BMR (Kretzmann et al. 1993); bearded seal pups:  $6.0 \times$  BMR (Lydersen et al. 1996)]. It

**Table 5** Milk and energy intake of nursing hooded seal pups from the Gulf of St Lawrence, Canada

Pup no	Total water influx (ml · day <sup>-1</sup> )	Metabolic water production (ml · day <sup>-1</sup> )	Milk water flux (ml · day <sup>-1</sup> )	Daily milk intake (kg)	Daily energy intake (MJ)
2214	3543	638	2905	10.2	271.6
2220	4318	573	3745	11.0	264.2
2227	3381	591	2790	7.9	184.0
2232	4059	827	3232	9.9	242.2
2236	5504	556	4948	12.9	282.4
Mean	4161	637	3524	10.4	248.9
± SD	841	111	878	1.8	39.1

is somewhat surprising that our values lay towards the upper end of the range, because nursing hooded seal pups are extremely inactive. Potential errors during isotope turnover studies such as intake of water from other sources than the milk and sequestration of labelled H-atoms into stored body tissues can be rejected with respect to this study. Pups spend all of their nursing period on the ice and do not have access to water except through eating snow. During all of our fieldwork, which has included extensive observation periods for behaviour studies (K.M. Kovacs et al. unpublished data), nursing hooded seal pups were never observed eating snow. Incorporation of labelled isotopes into body tissue has been shown to create great errors in calculations of water and CO<sub>2</sub> fluxes in growing pigs, especially during fat deposition (Haggarty et al. 1991); however, this is a problem that is valid only during lipogenesis. In cases where the excess dietary energy is in the form of fat, direct storage of this fat results in no labelled H-sequestration (Haggarty et al. 1991). This would be the case for hooded seal pups, since milk fatty acids are deposited directly into blubber tissue with no significant modifications (Iverson et al. 1995). Some concern may be raised on the accuracy of measuring CO<sub>2</sub>-production using DLW over such a small measurement interval (about 3 days). In general the precision of such measurements are best between one-half and three biological half-lives of the hydrogen isotope (Schoeller 1983). The reduction in specific activity of the deuterium isotope in the five hooded seal pups during the short nursing period was  $50.5 \pm 5.1\%$ . This corresponds to one biological half-life of this isotope, and consequently the precision in the measurements of the CO<sub>2</sub> production should be satisfactory.

The most conspicuous difference between nursing hooded seal pups and pups of other phocids is their extremely high growth rate. In the present study, the average daily mass gain was 5.9 kg of which 76% or about 4.5 kg was deposited as fat. If we consider the process of creating such tissue, about 7% of the energy of the fat itself is lost (mostly as heat) during the transfer from dietary fat into blubber tissue (Flatt 1978). Storage of 4.5 kg of fat would thus require 12.4 MJ of energy. The average BM of the nursing hooded seal pups during this study was 33.3 kg. For animals of this BM,

$1 \times \text{BMR}$  is 4.1 MJ. Thus, the energy involved in depositing fat at the rate measured in this study, corresponds to an elevation of FMR of about  $3 \times \text{BMR}$ . If we perform the same calculations for ringed and harp seal pups, the deposition of fat would account for an increase in FMR of 0.3 and  $1.1 \times \text{BMR}$ , respectively [calculated from Lydersen and Hammill (1993) and Lydersen and Kovacs (1996)]. A lot of assumptions are made when conducting such calculations, and the 7% cost of fat deposition could be less in hooded seals due to the very similar fatty acid composition in milk and blubber (Iverson et al. 1995). However, cost of protein deposition would increase the value further, so the relative values when doing these interspecific comparisons would probably be within an order of magnitude as shown here. The calculations show that significant amounts of energy (although less than 5% of ingested energy, see Table 5) are involved in growing when the process is done at the extreme rates displayed by the nursing hooded seals. If we subtract the calculated costs of deposition of blubber from calculated FMRs for harp and hooded seals, which are both very sedentary during the nursing period, both species have a FMR of  $2.8 \times \text{BMR}$ . The relatively high FMR of the hooded seal pups thus seems to be an effect of their extremely high growth rates. This process involves substantial energy being lost as heat. This is consistent with the elevated body temperatures we recorded in nursing animals compared to weaned hooded seal pups. Prior to weaning pups are very sedentary, but shortly after they are weaned they start travelling around on the ice. Activity generally increases the body temperature in mammals (Shellock and Rubin 1984), so all other things being equal a higher body temperature would be expected in weaned compared to nursing hooded seal pups. All temperatures were recorded around midday for all individuals, so variation in body temperature due to normal circadian cycles (Powell et al. 1980) will not bias our samples.

If we consider the fraction of received milk energy that has to be allocated to cover the energy involved in connection with the FMR of hooded seal pups, this represents a very low value compared to other seal species. Hooded seal pups have been shown to ingest 248.9 MJ of energy daily (Table 5). Based on an average BM of

33.3 kg, over the period of study, a daily FMR of  $5.8 \times \text{BMR}$  corresponds to 23.6 MJ. In other words, only 9.5% of the received milk energy is allocated to the pup's own metabolism. Corresponding calculations for other phocid seals show that between 14.6 and 41.4% of the received milk energy is allocated to the FMR [ringed seals 41.4%; grey seals 29.9%; harp seals 14.6%; bearded seals 28.6%; based on calculations from Lydersen (1995), Lydersen et al. (1995), Lydersen and Kovacs (1996), and Lydersen et al. (1996)]. Hooded seal pups thus have a high FMR during the nursing period, but use a very small fraction of the received milk energy to cover this expense, since the intake is so tremendously high. A large fraction of the received energy is therefore available for storage. However, this process, when it occurs at the rate it does in hooded seals, has associated costs which are seen in the elevated FMR values.

In another study on nursing energetics of hooded seals the pups were found to store 84% of the ingested energy as body tissues (Oftedal et al. 1993). The corresponding figure in the present study was 74.7%. The difference between these two studies could be due to different methodologies used to calculate energy values. A similar difference was revealed using these two methods on nursing harp seals [85.5% of received energy stored (Oftedal et al. 1996) versus 66% stored (Lydersen and Kovacs 1996)]. However, in energetic studies of grey seal pups the two methods produced similar results [72% stored (Iverson et al. 1993) versus 74.7% stored (Lydersen et al. 1995)]. A more likely reason for these apparent differences is simply sampling artefacts due to small sample sizes. This is reflected in the range of this parameter in the present study from 64.0 to 83.4% (see Table 2). Regardless of whether 74 or 84% efficiency is more accurate, it is clear that hooded seals have an extreme capacity for transforming received milk energy into stored body tissues. This capacity is not so very remarkable when compared with the efficiency of other seal species, but if we consider the quantities of energy that are received and stored relative to BM and in absolute terms, hooded seals are by far the most extreme seal and thus probably the most extreme mammal with respect to this characteristic.

The normal pattern of change in composition of milk in phocid seals is that water is replaced by fat as lactation progresses (Oftedal et al. 1987). The reason for this general pattern among phocids is that the mothers substitute milk fat for water probably in order to maintain their water balance during the energy draining nursing period (Kooyman and Drabek 1968; Reidman and Ortiz 1979). However, this is not the case for hooded seals (Oftedal et al. 1993; this study). Hooded seal mothers appear to have no problems with their water balance during their short lactation periods and thus produce a constant fat-rich milk throughout lactation. Such a short nursing period dramatically reduces the "metabolic overhead" (Fedak and Adnersson 1982) related to lactation. Hooded seal maternal investment, measured as milk energy output, is the lowest among

phocid seals both in relation to the size of females and even in raw, total energy value when comparing hooded seals with much smaller species [hooded seals 746 MJ and 772 MJ (Oftedal et al. 1993, present study); ringed seals 930 MJ (Lydersen 1995); harp seals 954 MJ (Lydersen and Kovacs 1996); grey seals 1239 MJ (Lydersen et al. 1995); bearded seals more than 2500 MJ (Lydersen et al. 1996)].

So why have not all the other phocid species evolved towards a shorter and more intense nursing period if this is energetically profitable? In the discussion above only postnatal investment has been considered. Hooded seals give birth to a large, molted pup that has subcutaneous blubber layer. Based on the low body water concentration on lean body mass basis, hooded seal pups must be considered to be, physiologically speaking, among the most precocial of all phocid pups at birth (Oftedal et al. 1993). The energy density in new-born hooded seal pups is the highest of any neonatal mammal [ $10.1 \text{ MJ} \cdot \text{kg}^{-1}$ ; Oftedal et al. (1993)]. Prenatal investment is very high in hooded seals. However, when interspecific comparison of total maternal investments are made among phocids relative to maternal metabolic size hooded, grey and harbour seals are remarkably similar (Oftedal et al. 1993). Probably as a consequence of whelping in an extremely unstable drift-ice habitat, hooded seals have, through evolutionary time, replaced postnatal investment with prenatal deposition (Oftedal et al. 1993).

The bearded seal also gives birth and nurses its young in unstable drift-ice. In this species, the pups are also born with a subcutaneous blubber layer indicating significant prenatal maternal investment. However, the nursing strategy in this species is very different from that of hooded seals. Bearded seal pups are active swimmers and divers from the day they are born (Lydersen et al. 1994b). This is probably an adaptation to high levels of predation from polar bears (*Ursus maritimus*). The duration of the nursing period of bearded seals is thought to be 12–18 days (Burns 1967) but there are indications that it might be even longer (Lydersen et al. 1996). The bearded seal nursing strategy is consequently much more energetically demanding. Not surprisingly, bearded seal mothers feed during this period (Lydersen et al. 1996), while this is not the case for hooded seal mothers (Bowen et al. 1987a). There are developmental advantages of the extended period of care. Bearded seal pups are weaned as skilled divers that are capable of independent feeding and of avoiding predators, while hooded seal pups at weaning normally have not entered the water. This is thus an example of two species that have developed remarkably different nursing strategies although they breed in a similar unstable habitat and give birth to pups at similar developmental stages. These differences are probably a consequence of differences in environmental factors such as predation and food availability.

The measurements in the present study of hooded seal pups during the three first days of their post-weaning fast showed an average daily mass loss of 1.3 kg,

of which 16% was fat, 28% protein and the rest water. In another study where hooded seal pup mass loss during the post-weaning fast was monitored over a 4-week period, an average daily mass loss of only 0.4 kg was recorded (Bowen et al. 1987a). However, in that study, the mass loss at the start of the fasting period was much higher than the overall average. From day 4 to day 5 post-weaning the pups were losing an average of 1.2 kg, which is in close agreement with our findings. Fasting in mammals can generally be divided into three periods. Initially, there is a relatively short period of high but decreasing mass loss (phase I), followed by a longer mid period of steady but low mass loss (phase II) and finally a third period of increasing mass loss (phase III) (Groscolas 1988). The high mass loss during phase I is mainly caused by water loss in connection with catabolism of proteins. This is a so-called adaptation period for phase II (Le Maho 1983). This phase is also characterised by a reduction in mass loss and nitrogen excretion throughout the period while mobilisation of fat as fuel increases. Phase II is called a period of economy (Le Maho 1983) where mass loss is low. Most of the energy fueling metabolism during this phase is derived from burning lipids and metabolic rates are normally depressed. Phase III is called the critical period (Le Maho 1983). In this phase the lipid stores are normally depleted and the animals start to catabolise proteins again. The measurements in our study clearly describe phase I of the fasting period of hooded seal pups. Since this is a phase where the metabolic rates gradually are lowered to the depressed rates experienced in phase II, it is reasonable to assume that FMR measured in the present study ( $3.8 \times \text{BMR}$ ) will be further reduced in the hooded seal pups as starvation proceeds.

In the present study we have measured energy intake in hooded seal pups and demonstrated how this energy is allocated into metabolism and stored tissues. We have also measured metabolism during phase I of the post-weaning fasting period and shown which tissues are used for maintaining metabolism during this period. The hooded seal pups were shown to grow at extreme rates in relation to BM, and to be very efficient in transferring received milk energy into stored tissues mainly as blubber. The energy transfer efficiency, expressed as percentage, is high but is not exceptionally so among seals, since other phocids are capable of transferring energy at similar efficiencies. The extreme feature in hooded seals lays in their capacity to receive and store energy at exceptionally high rates in relation to their BM. A physiological consequence is that nursing hooded seal pups experience a high FMR even though their activity levels are very low.

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