

CHANGES IN ENERGY STORES DURING POSTNATAL DEVELOPMENT OF THE HARP SEAL, *PHOCA GROENLANDICA*

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ABSTRACT.—Postnatal harp seals, collected during the 1979 and 1980 whelping seasons in the Gulf of St. Lawrence, were examined with respect to proximate composition and energy content of psoas muscle, blubber, viscera, and carcass (eviscerated lean body mass). During nursing, blubber stores of pups increased qualitatively as well as quantitatively, with caloric density increasing from 3.7 kcal/g to 8.9 kcal/g by age 9 days. Over the same time period, caloric density of carcass doubled to 2.5 kcal/g, with neutral lipid stores accounting for 12.5% of carcass wet weight. Neutral lipid levels in viscera approached 9% at weaning. These lipid stores in the carcass and viscera represent important energy sources during the subsequent postweaning fast.

Pinnipeds are characterized by rapid postnatal growth during a relatively short lactation period (Laws, 1959). Such growth is usually described by measuring changes in total body weight (Reiter et al., 1978; Condy, 1980) or weight increases of various body components, such as blubber or lean body mass (Sivertsen, 1941; Bryden, 1968; Stewart and Lavigne, 1980). Measurement of weight changes alone can be misleading, however, if the relative proportions of fat, protein, and water incorporated in body tissues vary throughout the period of growth. A few studies have circumvented this limitation by measuring the proximate composition of whole carcasses to describe growth in energetic terms (e.g. Nelson and Barnett, 1970; Stirling and McEwan, 1975; Fedak and Anderson, in press).

To date, the prodigious growth of pups of the harp seal, *Phoca groenlandica*, has been described only in terms of morphometric changes (Stewart and Lavigne, 1980). The present study expands on this work and reports changes in the amount of energy involved in growth of various body components from birth to early stages of the postweaning fast.

MATERIALS AND METHODS

Harp seals ($n = 11$), from newborn (Stewart et al., 1981) to recently weaned animals, were obtained during the 1979 and 1980 whelping seasons in the Gulf of St. Lawrence and were classified into the qualitative age categories described by Stewart and Lavigne (1980). In addition, one nearly full term fetus was obtained on 16 February 1980 from Les Escoumins, Quebec. Stillborn ($n = 2$) and starveling greycoat ($n = 3$) pups (terminology from Stewart and Lavigne, 1980) were also collected from the Gulf of St. Lawrence during March 1980. All animals were frozen and transported to Guelph, Ontario, for analyses.

After thawing, animals were divided into sculp (skin with blubber attached) and lean body mass. Blubber was subsequently separated from the skin and each was sampled separately. The remaining lean body mass was eviscerated and the skeleton, musculature, and brain were homogenized in a large animal grinder (model 801B, Autio Co., Astoria, OR). Subsamples of psoas muscle, blubber, skin, and ground homogenized carcass were freeze-dried (The Virtis Co., model 50 SRC, Gardiner, NY). Viscera were initially freeze-dried and then ground and sub-sampled. Freeze-dried subsamples of carcass and viscera were subsequently re-ground in a Thomas-Wiley laboratory mill (model 4, Thomas-Wiley Co., Philadelphia, PA).

Analyses of proximate composition was not performed on skin samples; these were analyzed only for caloric density (kcal/g), using an adiabatic bomb calorimeter (model 1241, Parr Instrument Co., Moline, IL). For the other samples, water content was calculated as the difference between wet weight and freeze-dried weight. Neutral and total lipids were extracted over a 4-h period on a Goldfish apparatus (Lab Con Co., Kansas City, MO) using petroleum ether or chloroform-methanol (2:1, v:v), respectively, as the solvent. Samples were subsequently oven-dried at 72°C for either 12 h (petroleum ether) or 48 h (chloroform-methanol) and weight of lipid was estimated as the difference between the pre- and post-extraction sample weights. Polar lipid content was calculated as the difference between total and neutral lipids. Ash content was determined by burning samples in a muffle furnace for 24 h at 550°C. Protein content was estimated by subtraction of neutral and polar lipids, ash, and water content from 100%.

TABLE 1.—Total weights and weights of the four body components for sampled harp seals.

Age group	I.D. no.	Skin weight (kg)	Blubber weight (kg)	Carcass weight (kg)	Viscera weight (kg)	Total weight (kg)
Fetus	F1	1.7	0.5	2.4	0.8	4.6
Stillborn	SB1	0.8	0.3	2.0	0.9	3.9
	SB2	1.2	0.3	3.5	1.1	6.0
Newborn	NB2	1.0	0.4	4.0	1.4	6.8
	NB3	1.2	0.4	3.5	1.1	6.1
	NB4	1.5	0.5	5.0	1.8	8.9
Yellowcoat	Y1	1.7	1.1	4.7	1.7	9.2
	Y2	1.8	1.2	5.0	1.4	9.2
Thin White	TW2	2.3	5.0	5.0	2.3	14.6
Fat White	FW1	3.2	10.6	10.0	3.3	27.3
Greycoat	G1	2.8	15.6	13.7	2.8	35.0
	G2	2.5	17.6	13.4	2.5	36.0
Greycoat starveling	GS1	1.7	0.0	5.2	1.4	8.4
	GS2	1.4	0.0	3.4	1.4	6.3
	GS3	2.1	0.4	1.6	1.1	5.2
Beater	B1	2.3	14.1	11.6	2.0	30.0
	B2	2.7	18.3	17.1	2.9	41.0

Caloric density was estimated indirectly for all samples from the proximate compositions, using caloric equivalents of 9.4 kcal/g for lipid and 5.65 kcal/g for protein (Pike and Brown, 1975). In addition, caloric density was also estimated directly for some samples of blubber, carcass, and viscera, using an adiabatic bomb calorimeter.

RESULTS

Growth of body components.—Weights of all four body components increased during the nursing period (Table 1). Largest increases were in blubber, increasing from 0.42 ± 0.01 kg at birth ($n = 3$) to 16.1 ± 1.0 kg at weaning age of ≈ 9 days (greycoat stage) ($n = 2$) (Table 1). Carcass mass increased slowly from 4.2 ± 0.06 kg at birth ($n = 3$) to 5.0 kg at 3 days ($n = 1$), but increased rapidly thereafter to 13.6 ± 0.15 kg at age 9 days ($n = 2$) (Table 1). Skin and viscera both increased from between 1.2 and 1.4 kg, respectively, at birth to approximately 2.6 kg at weaning (Table 1). Three starveling greycoat animals had depleted blubber stores, with two animals having no dissectible blubber. Carcass, viscera, and skin weights were less than those of newborns (Table 1).

Proximate composition and caloric density.—A linear regression of indirect versus direct caloric densities yielded an equation of equality with a multiple R^2 of 99.43%. For the present purposes, indirect estimates, based on proximate compositions of all samples, are used.

Subcutaneous tissue of newborns had a high water content and a low caloric density. During nursing, blubber stores increased both quantitatively and qualitatively, with the caloric density increasing from 3.7 kcal/g ($n = 3$) at birth to approximately 8.9 kcal/g at age 9 days ($n = 2$). Similarly, neutral lipid in blubber increased from approximately 21% at birth to 88.8% at age 9 days (Fig. 1). Caloric density and percentage neutral lipid in blubber increased slightly between age 9 and 18 days (Fig. 1).

Caloric density of the carcass almost doubled from its initial value of 1.4 kcal/g at birth to 2.5 kcal/g in 9 days. Neutral lipid content of the carcass increased from newborn levels of 2.3% to 12.5% at weaning (Fig. 2). Similarly, neutral lipid content of viscera increased from 3.7% to 8.8% over the same time (Fig. 3). Between 9 and 18 days, carcass composition remained unchanged; however, there was a slight decrease in visceral neutral lipids from 8.8% to 7.5% (Fig. 3).

Analyses of muscle samples showed that neutral lipid stores decreased from 3.8% in a near

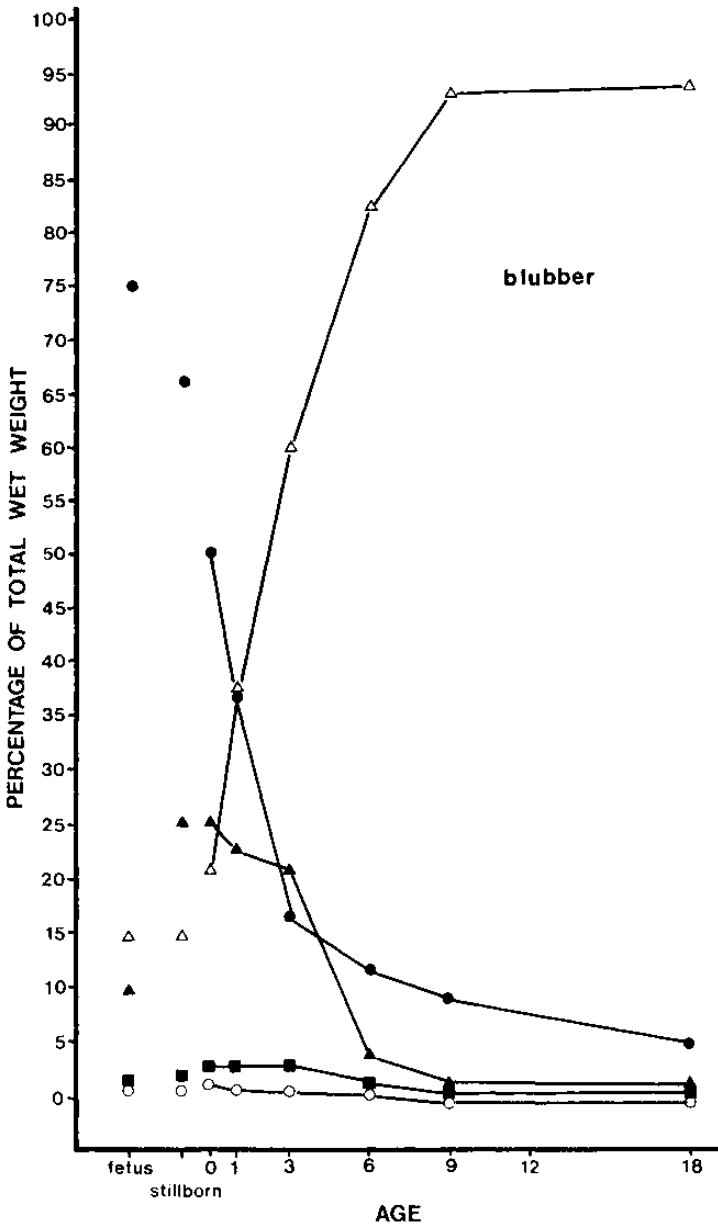


FIG. 1.—Changes in proximate composition of blubber of postnatal harp seals with respect to neutral lipids (Δ), polar lipids (■), protein (▲), ash (○), and water (●). All components are expressed as a percentage of total wet weight, and age is in days.

full term fetus to $1.6 \pm 0.3\%$ at birth ($n = 3$), then increased to 7.1% at age 9 days (Table 2). Water declined in relation to increases in neutral lipid, while percentage protein was 18.9% at birth and 21.1% at age 9 days (Table 2). Caloric density of muscle increased during the same time period from $1,420.7 \pm 44$ cal/g ($n = 3$) to $2,010.0$ cal/g ($n = 1$) (Table 2). After weaning, neutral lipid declined to 2.6% by 18 days of age and caloric density decreased to $1,664.5$ cal/g ($n = 1$) (Table 2).

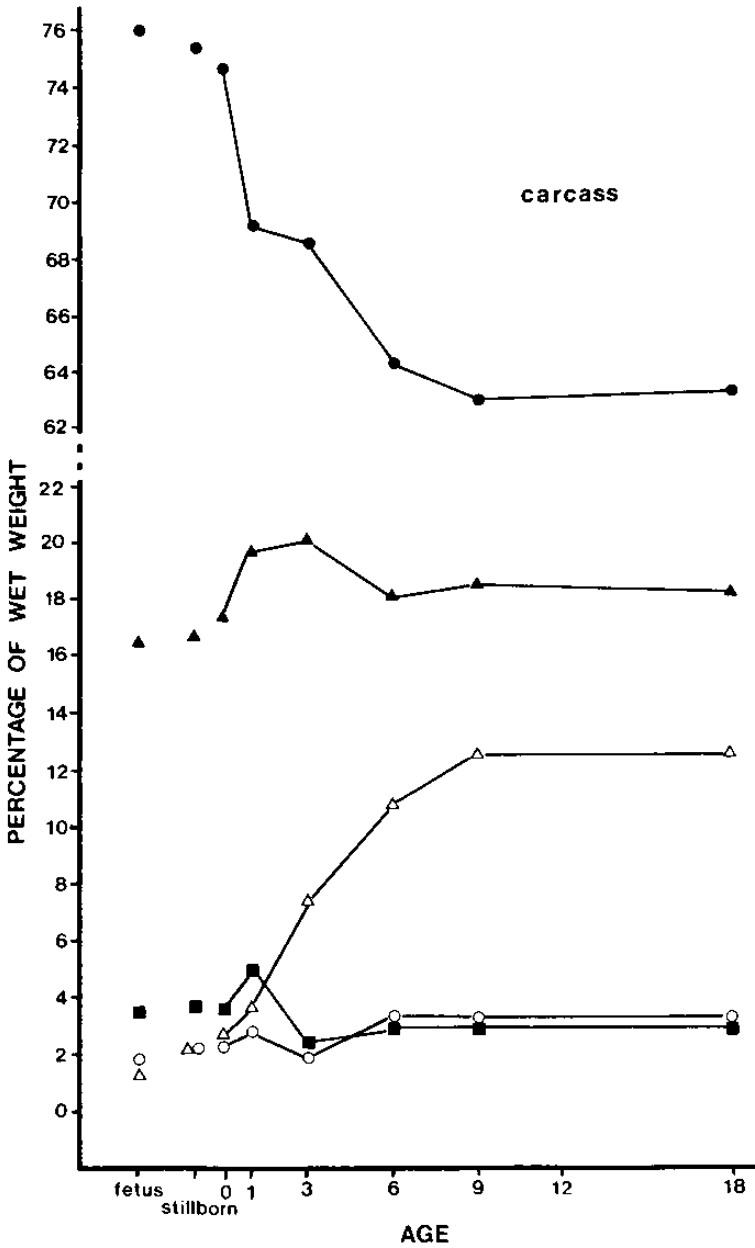


FIG. 2.—Changes in proximate composition of carcass of postnatal harp seals. Symbols and axes as in Fig. 1.

Two stillborn pups differed greatly from each other in size (Table 1) and caloric content (Table 3). Three starveling greycoats sampled had virtually no blubber layer and exhibited low caloric densities of both carcass and viscera. Muscle samples from these animals were also very low in neutral lipid and had caloric densities similar to newborns (Table 2).

After birth, total caloric content of all body components of healthy pups increased with age (Table 3). Caloric content of an average newborn was $12,511 \pm 2,296$ kcal (Table 3), with a

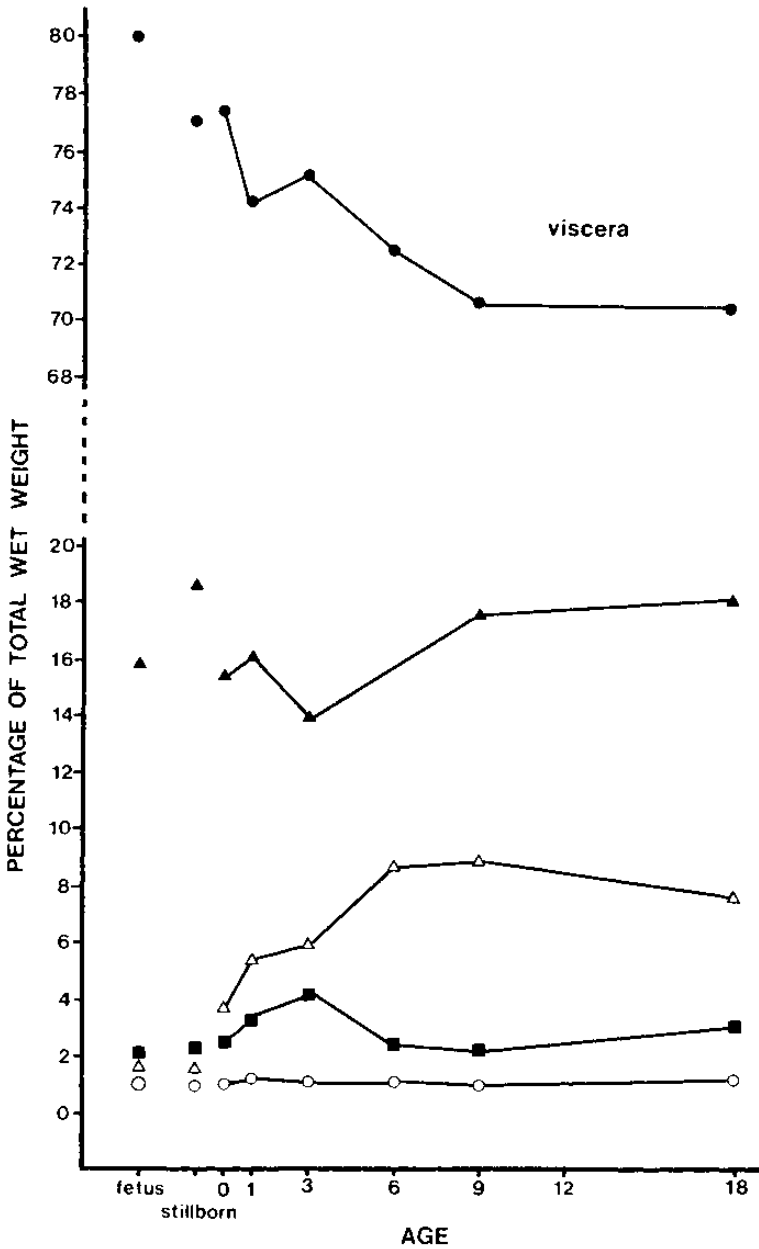


FIG. 3.—Changes in proximate composition of viscera of postnatal harp seals. Symbols and axes as in Fig. 1.

caloric density of 1.73 ± 0.05 kcal/g. Greycoat pups, aged 9 days had a mean caloric content of $186,865 \pm 7,423$ kcal, an increase of approximately 174,000 kcal from birth (Table 3). Average caloric density of newly weaned pups was 5.3 ± 0.19 kcal/g ($n = 2$) (wet weight).

DISCUSSION

Although the three newborn pups in the present study were lighter than those sampled between 1976 and 1979 [7.3 ± 2.2 ($n = 3$) vs 10.8 ± 0.65 (95% C.I.) Stewart and Lavigne,

TABLE 2.—Proximate composition changes in muscle samples obtained from harp seals.

ID no.	Water (%)	Neutral lipids (%)	Polar lipids (%)	Protein (%)	Ash (%)	Caloric density (cal/g)
F1	75.6	3.8	1.4	18.2	1.1	1,517.1
SB1	76.0	3.2	1.4	18.4	1.0	1,472.0
SB2	77.4	0.7	1.9	18.9	1.2	1,312.3
NB2	76.2	2.0	2.9	17.8	1.1	1,466.3
NB3	77.2	1.3	2.3	18.1	1.2	1,361.1
NB4	75.3	1.4	1.3	20.9	1.1	1,434.7
Y1	71.0	3.2	0.9	23.3	1.6	1,701.9
Y2	72.1	2.1	2.1	22.6	1.1	1,617.7
TW2	70.4	6.7	0.7	20.9	1.3	1,876.5
FW1	69.3	6.7	1.5	21.2	1.3	1,968.6
G1	69.0	7.1	1.6	21.1	1.2	2,010.0
GS1	77.3	0.8	1.5	18.0	2.4	1,233.2
GS2	76.3	0.8	1.5	20.1	1.3	1,351.9
GS3	75.5	0.3	1.3	21.8	1.1	1,382.1
B1	72.5	2.6	2.0	21.8	1.1	1,664.1

1980], growth rates were similar, and it is assumed that changes in proximate composition reported herein are generally representative of postnatal harp seals.

In estimating proximate composition, the assumption that 'protein' is the sole remaining constituent when one has accounted for lipid, ash, and water is not entirely correct; however, due to the low levels of carbohydrate usually found in most tissues, it is a reasonable assumption. The high correlation between indirect and direct estimates of caloric density supports this conclusion.

Lavigne and Stewart (1979) estimated that an 11 kg newborn harp seal pup would contain 24,000 kcal. Lacking data for harp seals, they used an average caloric density of 2.16 kcal/g obtained for ringed seals, *Phoca hispida*, less than one month old (Stirling and McEwan, 1975). Average caloric density of newborn harp seals in the present study, 1.73 kcal/g ($n = 3$), was not significantly different from Stirling and McEwan's (1975) values ($\alpha = 0.05$, Students t test). However, if the present figure is used to refine estimates of production energy realized by a female harp seal at whelping (Lavigne and Stewart, 1979), an 11-kg newborn harp seal pup would represent only 19,000 kcal. The placenta contributes an additional 1,400 kcal (Lavigne and Stewart, 1979), bringing total production energy at whelping to 20,400 kcal. Assuming net energy represents 68 to 75% of gross energy (Lavigne and Stewart, 1979), a female harp seal would require an intake of 27,000 to 30,000 kcal, or approximately 20% less energy than was originally calculated, to account for the energy contained in a pup and its placenta.

Newborn harp seals and the fetus sampled in the present study had virtually no blubber stores. At this time, subcutaneous tissue had a high water, low fat content and a correspondingly low caloric density. Soon after birth, the pup begins nursing on milk containing $\approx 25\%$ lipid (Lavigne et al., 1982). Over the course of the 9-day lactation period (Stewart and Lavigne, 1980), lipid content of the milk increases to $\approx 40\%$ (Lavigne et al., 1982), and during this time blubber increases in depth and fat content.

Bailey et al. (1980) noted that between the newborn and thin-white age categories there was a 2.5 fold increase in the triacylglycerol content of a unit amount of blubber. This mirrors the increase in percentage neutral lipid of blubber observed in the present study. These authors also found, however, that the triacylglycerol content of the liver remained fairly constant throughout the first month of postnatal development. The results of the present study indicate that even though no dissectible fat is readily apparent, large amounts of lipid are deposited in the carcass and viscera, although perhaps not in the liver. Neutral lipid levels in the psoas muscle of pups

TABLE 3.—Caloric content (kcal) of postnatal harp seals.

Age group	I.D. no.	Skin	Carcass	Viscera	Blubber	Total
Fetus	F1	4,427	2,828	1,029	1,058	9,342
Stillborn	SB1	2,021	2,688	1,302	1,107	7,118
	SB2	3,070	4,724	1,330	496	9,621
Newborn	NB2	2,559	5,534	2,063	1,409	11,566
	NB3	2,943	4,578	1,486	1,285	10,292
	NB4	3,710	7,464	2,543	1,958	15,675
Yellowcoat	Y1	4,466	8,430	2,950	6,270	22,116
	Y2	4,606	8,038	2,525	5,223	20,392
Thin white	TW2	5,885	7,695	3,926	35,091	52,598
Fat white	FW1	8,188	24,176	6,312	84,831	123,507
Greycoat	G1	7,164	34,281	5,637	132,359	179,442
	G2	6,397	33,530	5,033	149,328	194,288
Starveling greycoat	GS1	4,431	7,137	2,010	0	13,578
	GS2	3,660	5,647	1,448	0	10,755
	GS3	5,281	2,132	1,607	1,509	10,529
Beater	B1	5,885	28,830	4,008	125,384	164,107
	B2	6,909	42,499	5,812	162,733	217,952

were over three times that reported for adult harp seals (George et al., 1971; Worthy, 1982) and carcass and visceral neutral lipids were twice those of adults (Worthy, 1982).

Concomitant with the increase in lipid content of the core, there was a decrease in water content as well as a small change in the protein content (Figs. 2, 3). The change in water content is due to replacement of water in cells with fat. Lack of a relative change in protein should not, however, be misinterpreted as no change; because the core is increasing in size, there are increases in the absolute amount of protein present.

Every year some pups are either deserted or become separated from their mother soon after birth. Three such starveling greycoats sampled in 1980 had virtually no blubber layer present and showed very low caloric density of both carcass and viscera. Assuming a metabolic rate of 76 kcal kg⁻¹ d⁻¹ (Worthy, unpubl. data), an extrapolation can be made backwards to the time of desertion by the female. These particular pups were deserted either at birth or very soon thereafter, and were possibly never suckled. Such desertion may be mediated by a variety of factors; in some cases low energy stores in postpartum females may be involved (Stewart and Lavigne, 1981).

Some of the energy stored during nursing is soon utilized by young seals during the period of fasting, which is commonly associated with the post-weaning period in many pinnipeds, including harp seals (Condy, 1980; Reiter et al., 1978; Stewart and Lavigne, 1980; Worthy et al., in press). Stewart and Lavigne (1980) noted that during the initial few weeks of the post-weaning fast, harp seal beaters initially lost weight from the core. This observation led to speculation that newly-weaned fasting animals obtain a large portion of their energy requirements from protein. The results of the present study, however, indicate that extensive, albeit diffuse, stores of lipid are deposited throughout the carcass and viscera during nursing. The energy available from these lipid stores subsequently sustains the young seal during the post-weaning fast (Worthy, 1982) which may last 6 weeks or longer (Worthy et al., in press); however, during the initial few weeks of the fast, protein contributes =16% of total energy requirements (Worthy, 1982).

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LITERATURE CITED

- BAILEY, B. A., R. G. H. DOWNER, AND D. M. LAVIGNE. 1980. Neonatal changes in tissue levels of carbohydrate and lipid in the harp seal, *Pagophilus groenlandicus*. *Comp. Biochem. Physiol.*, 67B:179-182.
- BRYDEN, M. M. 1968. Lactation and suckling in relation to early growth of the southern elephant seal, *Mirounga leonina* (L.). *Australian J. Zool.*, 16:739-748.
- CONDY, P. R. 1980. Postnatal development and growth in southern elephant seals (*Mirounga leonina*) at Marion Island. *South African J. Wildl. Res.*, 10:118-122.
- FEDAK, M. A., AND S. S. ANDERSON. In press. The energetics of grey seal lactation. *J. Zool.*
- GEORGE, J. C., N. V. VALLYATHAN, AND K. RONALD. 1971. The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). VII. A histophysiological study of certain skeletal muscles. *Canadian J. Zool.*, 49: 25-30.
- LAVIGNE, D. M., AND R. E. A. STEWART. 1979. Energy content of harp seal placentas. *J. Mamm.*, 60: 854-855.
- LAVIGNE, D. M., R. E. A. STEWART, AND F. FLETCHER. 1982. Changes in composition and energy content of harp seal milk during lactation. *Physiol. Zool.*, 55:1-9.
- LAWS, R. M. 1959. Accelerated growth in seals with special reference to the Phocidae. *Norsk Hvalfangst-Tidende*, 9:425-452.
- NELSON, R. W., AND H. J. BARNETT. 1970. Preliminary study of the proximate composition of meat of fur seal, *Callorhinus ursinus*. *Fish. Industrial Res.*, 6:89-92.
- PIKE, R. L., AND M. L. BROWN. 1975. Nutrition: an integrated approach. John Wiley and Sons, Inc., New York, London, Sydney, and Toronto, 1082 pp.
- REITER, J., N. L. STINSON, AND B. J. LE BOEUF. 1978. Northern elephant seal development: the transition from weaning to nutritional independence. *Behav. Ecol. Sociobiol.*, 3:337-367.
- SIVERTSEN, E. 1941. On the biology of the harp seal, *Phoca groenlandica* Erxl. Investigation carried out in the White Sea, 1925-1937. *Hvalradets Skrifter*, 26:1-166.
- STEWART, R. E. A., AND D. M. LAVIGNE. 1980. Neonatal growth in Northwest Atlantic harp seals (*Pagophilus groenlandicus*) *J. Mamm.*, 61:670-680.
- . 1981. Energetics of nursing in the harp seal, *Phoca groenlandica*: energy transfer and female condition. *Northwest. Atl. Fish. Organ. SCR Doc.* 81/XI/160, 30 pp.
- STEWART, R. E. A., N. LIGHTFOOT, AND S. INNES. 1981. Parturition in harp seals. *J. Mamm.*, 62: 845-850.
- STIRLING, I., AND E. H. McEWAN. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behaviour. *Canadian J. Zool.*, 53:1021-1027.
- WORTHY, G. A. J. 1982. Energy sources of harp seals, *Phoca groenlandica*, during the post weaning fast. Unpubl. M.S. thesis, Univ. Guelph, Guelph, Ontario, Canada, 100 pp.
- WORTHY, G. A. J., D. M. LAVIGNE, AND W. D. BOWEN. In press. Post-weaning growth. In *Perspectives in vertebrate science. The harp seal* (D. M. Lavigne, K. Ronald, and R. E. A. Stewart, eds.). Dr. W. Junk bv Publishers, The Hague, The Netherlands.

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