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Effects of Suckling and the Postsuckling Fast on Weights of the Body and Internal Organs of Harp and Hooded Seal Pups

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Abstract. The weights of harp seal pups quadruple during 13 days of suckling while hooded seal pups double in weight in a lactation period of just 4 days. Pups of both species then fast for a month or longer. As a first measure of tissue responses to this 'feast and famine' pattern, we weighed the body, sculp (blubber and attached skin), core (carcass including viscera) and major internal organs of seal pups at birth, at the end of suckling, and at the end of the fast. When expressed as a percentage of body weight, the weights of the internal organs of newborn harp and hooded seals were within the range reported for newborn land mammals. During suckling, harp and hooded seals gained 2.3 and 6.5 kg/day body weight, respectively, but a large part (64–73%) of this gain was blubber and skin rather than core. Even though pups were ingesting great quantities of fat, their digestive organs (stomach, small and large intestines, pancreas) were neither particularly large at birth nor did these organs gain in weight or length unusually rapidly. Most organs increased in weight in proportion to the increase in core weight, but the liver and spleen increased proportionately more than the core, and the stomach, heart and kidneys increased proportionately less. At the end of suckling, sculp accounted for more than half of the body weight in both species. The subsequent 4-week fast resulted in weight loss from both the sculp and core, and the liver and spleen decreased in weight by about 70%. The net effect of sequential suckling and fasting was particularly striking in the hooded seal pup, which had a lighter core, heart, liver and spleen at 1 month postpartum than at birth. These data illustrate a remarkable cycle of nutrient deposition and depletion which is undoubtedly central to the survival of young seals in the harsh pack-ice environment.

Introduction

At birth, the developing mammal is confronted with profound changes in both the immediate environment and the mode of nutrient transfer from the mother. The ingestion of milk results in rapid growth of the intestines in the first 1–3 days after birth in pigs, rabbits, rats and dogs [1–4]. It appears that the amount and composition of milk or formula and the frequency of intake may have effects on growth of the intestines and other organs in the young of these species [3–7]. As mammals exhibit widely different lactation patterns, including differences in milk composition, milk yield and suckling frequency [8, 9], we expected that there might be substantial differences among species, not only in growth rate of the body as a whole, but also in the relative growth patterns of individual organs during the suckling period. This paper describes a comparison of the patterns of weight change of the body and internal organs of the young of two marine mammals, the harp seal *(Phoca groenlandica)* and the hooded seal *(Cystophora cristata)*. The changes in organ weights of young seals are also compared with the patterns of organ growth that have been reported for land mammals.

Although seals (order Pinnipedia, family Phocidae) are adapted to life in the sea, they haul out of the water onto land or ice to bear and rear their young. In the north Atlantic, harp and hooded seals deliver their single young on floating pack-ice in March (fig. 1a). Spring storms and fluctuating temperatures can rapidly break up the ice. In this unstable habitat seals have evolved very short lactation periods during which the pups gain weight rapidly. For example, harp seal pups suckle for only 12–15 days while gaining about 2 kg (20% of birth weight) per day [10]. Hooded seals are even more remarkable, having the shortest lactation known for any mammal (4 days) and a rate of weight gain of 7 kg (32% of birth weight) per day [11]. At the end of lactation both harp and hooded seal mothers return to the sea to feed, while the pups remain on the disintegrating ice (fig. 1b), drifting with wind and currents, and do not begin to feed for 4–6 weeks [12]. The pups then leave the ice, and begin a northward migration to summer feeding grounds. Hence, in both species pup development represents a considerable departure from typical patterns of land mammals.

In seals, as in other mammals, weight gain of the body as a whole is a result of complex changes within the body. Much of the postnatal gain of both harp and hooded seal pups consists of thick deposits of subcutaneous fat or blubber [12, 13]. Blubber provides a store of energy as well as insulation in an environment in which ambient temperature may be as low as −20 °C [14]. High rates of blubber deposition are achieved by consumption, digestion and absorption of large amounts of milk lipids. The milks of harp and hooded seals contain 52 and 61% fat on a fresh weight basis, respectively [15, 16]. Isotope dilution methods indicate that the daily milk intake of harp seal pups is equivalent to 30% of birth weight, while that of hooded seal pups is about 48% of birth weight [15]. Thus the digestive organs of newborn harp and hooded seals must be able to deal with an amount of fat equivalent to 16 and 29% of birth weight per day, respectively.

In the course of field studies on harp and hooded seals in 1984 we obtained pups of both species at the beginning and end of lactation and at the end of the postsuckling fast.

a

b

Fig. 1. **a** Lactating hooded seal with newborn pup on pack-ice off the southeast coast of Labrador, Canada. **b** Hooded seal pup at the end of suckling. This pup had been tagged in the rear flippers at birth and was therefore known to be 4 days of age. Photographs by W.D.B.

As a first indicator of the tissue responses of young seals to this 'feast and famine' pattern we weighed and measured the bodies of pups and their major internal organs. These dissections also served to prepare the bodies for chemical analysis, the results of which will be described in a subsequent paper.

Methods

Collection of Material

Whelping herds of harp and hooded seals were located in early March 1984 by fixed-wing aerial survey of ice floes at the 'Front', an area off the southeast coast of Labrador, Canada. Three of us (W.D.B., O.T.O., and D.J.B.) and two assistants were ferried daily to seal herds by helicopters based on the Canadian scientific ship (CSS) Baffin, an ice-strengthened vessel 87 m long. LORAN-C navigational equipment and long-range radiotransmitters placed on the ice permitted relocation of the study area despite unpredictable movements of pack-ice and reduced visibility during bad weather. Animals were collected under an experimental permit issued to the Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans, Government of Canada.

Newborn pups of both species could be identified by the presence of fresh placentas and blood, thin body condition and wet appearance of the pelage. Six harp seals and 4 hooded seals were collected on the day of birth. Although all were considered to be newborn, two of the harp seals had some milk in their stomachs as did all of the hooded seals. An additional 5 hooded seal pups were flipper-tagged shortly after birth and released. These pups were relocated and weighed at approximately daily intervals until they were collected at 4–5 days postpartum. Due to inclement weather and logistical constraints, it was not possible to recapture known-age, tagged harp seal pups, but an age estimate for suckled harp seal pups could be made by comparison of pelage, weight and appearance to known-age pups studied by Kovacs and Lavigne [10] and Myers and Bowen [17]. The change in coat appearance from white to 'gray' that occurs with the onset of shedding of the natal coat is a useful indicator of the end of the suckling period in harp seals [10, 18]. Five harp seal pups obtained in the graycoat stage were estimated to be about 13 days of age and would have been left by their mothers shortly.

Pups were weighed to the nearest 0.2 kg at the field site on the ice. Gastric contents were removed by intubation. As prescribed by Canadian Sealing Regulations, pups were killed instantaneously by a hard blow to the head, and were immediately placed in thick plastic bags to prevent fluid losses. They were stored in a chest freezer on the ship but, toward the end of the work, freezer space was insufficient to accommodate all carcasses so the larger carcasses were alternated between the freezer and the ship's deck where ambient temperature ranged from −13 to +3 °C. At the end of March, all specimens were removed from the ship and transferred to a walk-in freezer at −25 to −30 °C.

In the terminology of sealing, the blubber and attached skin (excluding skin on the flippers) are defined as the 'sculp' and the remainder of the body as the 'core'. We have adopted this terminology since it has been used by previous investigators, and it provides a crude means of distinguishing between gain (or loss) in blubber and in the rest of the body. In late May 1984 each pup was partially thawed at room temperature for about 24 h in a large tray. Standard length, as defined by the American Society of Mammalogists [19], was measured from nose to tip of tail. Foreflippers were detached. The combined blubber and skin layers were separated from the rest of the body with a sharp knife and weighed. The entire body and all recovered fluids were placed in the original bags and immediately re-frozen. The live weights and body measurements of the hooded seal pups have been included in previously published data sets [11, 12] but are reported here for comparative purposes.

Dissection of the Bodies

In April 1986 the bodies were thawed in their plastic bags in a cool room (10 °C) for 2–3 days. Core and sculp were reweighed on a digital balance of 1 g sensitivity to improve precision and to estimate moisture losses. Fluids that had collected in the bags were transferred into bottles and weighed. These fluids were considered to originate from the core for purposes of calculation. The sums of the weights of the sculp, core, gastric contents and fluids agreed closely with the live weights measured in the field (mean difference = 0.065 kg, n = 20) indicating that moisture losses during collection and storage were insignificant. The core was opened by mid-line incision. All organs except the brain were in a good state of preservation. The gastrointestinal tract was tied off at the esophagus and rectum and the entire tract removed and weighed. It was divided into stomach and small and large intestine. Small and large intestines were separated from the omentum and connective tissue, laid out without stretching and their lengths measured. All 3 parts were emptied, and tissue and contents separately weighed. The sum of the empty weights of the 3 parts are termed the 'total GI tract'. 'Empty body weight' is defined as live weight minus gastrointestinal contents. Kidneys, adrenals, pancreas, spleen and thymus were removed and weighed. After extraction of blood clots, the liver, heart and lungs were also weighed.

An additional expedition to the 'Front' was organized in April 1984 by one of us (W.D.B.) to obtain morphometric data on harp and hooded seal pups that had been fasting for about 4 weeks. On 18–20 April, 34 harp and 36 hooded seal pups were collected. Only a few had begun to feed, based on examination of gastric contents [12; W.D. Bowen, unpubl. data]. In the field, weights of the body, sculp, core, liver, spleen and heart were obtained from freshly killed animals by the methods described above. While incomplete, these data are included herein for comparative purposes.

Statistical Analysis of Results

Data on suckling animals were analyzed using a two-way analysis of variance model [20] in which the effects of species (harp vs. hooded) and of suckling (newborn vs. end of suckling) were tested, along with the interaction of these two effects. Mean values for the two species were compared at birth, at the end of suckling, and at the end of the postsuckling fast by independent t tests. Results are expressed as means ± SEM.

Table 1. Body measurements (means ± SEM) of seal pups at birth and at the end of suckling

	Harp seal		Hooded seal		ANOVA[1]		
	newborn	end	newborn	end	species effect	suckling effect	INT
n	6	5	4	5			
Live weight, kg	9.30±0.62	38.6±1.45	24.1±0.91*	43.6±1.78 NS	0.001	0.001	NS
Empty body, kg	9.07±0.61	38.5±1.86	23.2±0.67*	42.8±1.44 NS	0.001	0.001	NS
Body length, cm	82.3±1.76	101±4.1	103±6.4*	113±2.9 NS	0.001	0.001	NS
Body weight/length, g/cm	110±5.5	382±24.5	228±9.5*	381±14.9 NS	0.001	0.001	NS
Empty core, kg	6.43±0.41	17.0±1.09	14.4±0.62*	19.6±0.45 NS	0.001	0.001	NS
Sculp, kg	2.64±0.22	21.4±0.94	8.78±0.26*	23.1±1.58 NS	0.001	0.001	NS
Sculp/body, %	29.0±0.86	55.8±1.11	37.9±1.20*	53.8±2.03 NS	0.001	0.001	0.05

End = end of suckling.

* Significant difference ($p < 0.05$, t test) between the hooded seal and harp seal at the stage indicated by column heading.

[1] Values in columns indicate probability levels at which significance is observed; INT = interaction (species × suckling).

Results

Comparison of the Seals during the Suckling Period

Body, Sculp and Core. The newborn harp seal was smaller than the newborn hooded seal in both weight and length; if weight (g) is expressed relative to length (cm), the hooded seal was twice as heavy (table 1). The sculp comprised a smaller proportion of empty body weight in the newborn harp seal than in the newborn hooded seal, reflecting the virtual absence of blubber in newborn harp seals as compared to blubber about 1.5 cm in depth in newborn hooded seals [12].

The harp seals more than quadrupled their birth weight in 13 days while the hooded seals doubled theirs in less than 4 days. The harp seal pups collected at 13 days all had milk in their stomachs and were still suckling. Since the hooded seal pups had been captured repeatedly during the suckling period, we determined that 2 had ceased suckling at 3.0 and 3.9 days (fig. 2), but the other 3 were gaining weight and had milk in their stomachs when collected at 3.7 days. Thus, the hooded seal pups suckled for 3.6 ± 0.15 days, and during this time gained 6.5 ± 0.61 kg/day (fig. 2). By comparison the harp seals had gained 2.3 kg/day, assuming a birth weight of 9.3 kg (table 1).

Statistical analysis showed that both species and suckling effects were highly significant for all body measurements, with a similar pattern of change in both species (table 1). Although rates of weight gain were greater in hooded seals than in harp seals, the longer suckling period of the harp seals resulted in greater total weight gains in this species. By the end of suckling the weights of the empty body, core and sculp of the two species were not significantly different (ta-

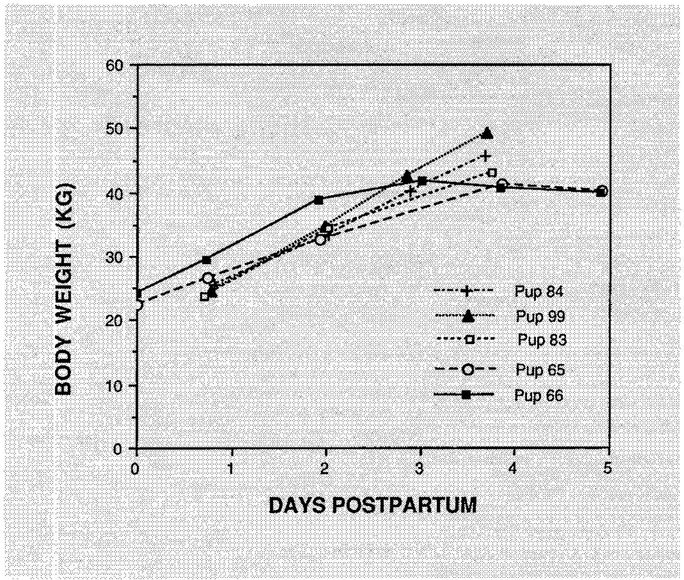

Fig. 2. Growth of hooded seal pups from birth until they were collected for this study. All 5 pups were tagged shortly after birth but 3 were not weighed initially. Note that 2 pups had ceased to suckle and had begun to lose weight before they were collected.

ble 1). In both species a large proportion of the gain in empty body weight was accounted for by gain in sculp weight. Gain in core weight constituted only 36 and 27% of the total gain in empty weight of suckling harp and hooded seals, respectively.

Gastrointestinal Tract. The intestinal tract of suckling harp and hooded seals is characterized by a simple stomach, a long small intestine, a short large intestine and a single suspension from a continuous mesentery, as is typical of seals [21]. In table 2 the weights of these organs are presented both as absolute values and as percentages of core weight. Organ weights are expressed in relation to core weight rather than body weight so that changing amounts of blubber in the sculp do not produce a confounding effect on relative organ weights.

The relative weight of the small intestine of the newborn harp seal (2.86% of core) was significantly less than that of the newborn hooded seal (4.84% of core) (table 2). It was also shorter and the weight/length ratio of the small intestine of the harp seal was about one third of that of the hooded seal. The weight/length ratio of the large intestine was also less for the newborn harp seal than for the newborn hooded seal (table 2). The lengths of the small and large intestines were about 14 and 0.3 times the body length, respectively, regardless of species or age (table 2).

The total GI tract increased in weight in both species during suckling, but the proportional increase was no greater than that of the core. In relation to core weight, the stomach weighed less at the end of suckling than at birth. The small intestine increased in weight more rapidly than the core in the harp but not in the hooded seal (table 2). The ratio of weight/length of the small intestine increased greatly in the harp seal, but did not change in the hooded seal. The large intes-

Table 2. Measurements (means ± SEM) of the gastrointestinal tract of seal pups at birth and at the end of suckling[1]

	Harp seal		Hooded seal		ANOVA		
	newborn	end	newborn	end	species effect	suckling effect	INT
Organ weight, g							
Total GI tract	249 ± 19.9	737 ± 50.6	817 ± 54.3*	885 ± 59.4 NS	0.001	0.001	0.01
Stomach	49.7 ± 4.10	98.7 ± 3.32	84.1 ± 4.19*	95.9 ± 3.36 NS	0.001	0.001	0.01
Small intestine	183 ± 15.4	609 ± 46.9	698 ± 55.3*	744 ± 58.8 NS	0.001	0.001	0.01
Large intestine	16.5 ± 2.23	29.7 ± 2.64	35.3 ± 3.71*	44.8 ± 4.09*	0.001	0.001	NS
Organ weight as percent of core, %							
Total GI tract	3.89 ± 0.260	4.36 ± 0.227	5.67 ± 0.347*	4.51 ± 0.315 NS	0.01	NS	0.05
Stomach	0.78 ± 0.054	0.59 ± 0.025	0.59 ± 0.041*	0.49 ± 0.026*	0.01	0.01	NS
Small intestine	2.86 ± 0.211	3.59 ± 0.211	4.84 ± 0.348*	3.79 ± 0.300 NS	0.001	NS	0.01
Large intestine	0.25 ± 0.030	0.18 ± 0.015	0.25 ± 0.030 NS	0.23 ± 0.026 NS	NS	NS	NS
Length, cm							
Small intestine	1,005 ± 45	1,403 ± 81	1,534 ± 125*	1,630 ± 107 NS	0.001	0.01	NS
Large intestine	25.7 ± 2.72	36.1 ± 1.09	32.1 ± 3.19 NS	36.0 ± 3.62 NS	NS	0.05	NS
Weight/length, g/cm							
Small intestine	0.187 ± 0.017	0.414 ± 0.039	0.460 ± 0.038*	0.459 ± 0.029 NS	0.001	0.001	0.01
Large intestine	0.64 ± 0.053	0.83 ± 0.085	1.11 ± 0.057*	1.27 ± 0.117*	0.001	0.05	NS
Length/body length, cm/cm							
Small intestine	12.0 ± 0.34	14.3 ± 1.30	15.0 ± 1.30 NS	14.4 ± 0.60 NS	NS	NS	NS
Large intestine	0.31 ± 0.033	0.36 ± 0.015	0.31 ± 0.027 NS	0.32 ± 0.032 NS	NS	NS	NS

[1] Statistical results presented as in table 1.

tine increased in weight per unit length in both species (suckling effect, $p < 0.05$). At the end of suckling the weights and lengths of most parts of the digestive tract were similar in the two species, although the stomach of the harp seal was a larger proportion of core weight (table 2).

Weights of Organs. At birth the weights of all measured organs except the spleen and thymus were greater in hooded seals than in harp seals (table 3), as would be expected from the larger body size of newborn hooded seals. As a percentage of core weight, the liver was heavier in the newborn hooded seal than in the harp seal, whereas the lungs were heavier in the harp seal. There were no significant differences in other organs at birth (table 3); the adrenals of harp seals were significantly heavier than those of hooded seals if both stages (newborn and end of suckling) are considered (species effect, $p < 0.05$).

Although all organs increased significantly in absolute weight during the suckling period (table 3), the pattern of growth rela-

Table 3. Organ weights (means ± SEM) of seal pups at birth and at the end of suckling[1]

	Harp seal		Hooded seal		ANOVA		
	newborn	end	newborn	end	species effect	suckling effect	INT
Organ weight, g							
Liver	277±24.2	1,062±115	1,077±161*	1,683±171*	0.001	0.001	NS
Spleen	32.2±4.73	263±22.1	124±36.2 NS	208±27.8 NS	NS	0.001	0.01
Pancreas	14.1±1.50	34.7±5.03	25.4±2.71*	39.7±2.87 NS	NS	0.001	NS
Heart	90.1±7.31	173±14.0	190±11.8*	209±19.5 NS	0.001	0.001	NS
Lungs	232±26.5	561±48.2	398±35.9*	707±46.6 NS	0.001	0.001	NS
Kidneys	85.0±3.47	189±24.4	192±25.2*	229±25.9 NS	0.01	0.001	NS
Adrenals	1.00±0.08	2.60±0.35	1.65±0.28*	2.37±0.24 NS	NS	0.001	NS
Thymus	4.30±1.07	7.44±1.21	4.07±0.38 NS	10.97±0.67 NS	NS	0.01	NS
Organ weight as percent of core, %							
Liver	4.30±0.24	6.20±0.38	7.38±0.87*	8.55±0.81*	0.001	0.01	NS
Spleen	0.51±0.078	1.54±0.070	0.85±0.234 NS	1.06±0.142*	NS	0.001	0.01
Pancreas	0.22±0.026	0.20±0.018	0.18±0.016 NS	0.20±0.017 NS	NS	NS	NS
Heart	1.40±0.082	1.02±0.067	1.31±0.037 NS	1.06±0.102 NS	NS	0.001	NS
Lungs	3.57±0.209	3.29±0.102	2.77±0.271*	3.59±0.188 NS	NS	NS	0.05
Kidneys	1.34±0.057	1.10±0.075	1.32±0.139 NS	1.16±0.104 NS	NS	0.05	NS
Adrenals	0.016±0.0014	0.015±0.0014	0.011±0.0013 NS	0.012±0.0009 NS	0.05	NS	NS
Thymus	0.068±0.016	0.043±0.0041	0.028±0.0028 NS	0.054±0.0024 NS	NS	NS	NS

[1] Statistical results presented as in table 1.

tive to core weight differed among organs. As a percentage of core weight, the liver and spleen increased in weight while the heart and kidneys decreased. Growth of the other organs (pancreas, lungs, adrenals, thymus) paralleled that of the core and there were no significant trends when expressed in relation to core weight. The increase in weight of the spleen was significantly greater in the harp seal than in the hooded seal (interaction, $p < 0.01$).

The liver of the harp seal nearly quadrupled in weight while that of the hooded seal less than doubled, but at the end of suckling the liver was still lighter in the harp than in the hooded seal, both on an absolute basis and as a percentage of core weight. By contrast the spleen was relatively heavier in the harp seal (table 3). Other organs were similar in size between the two species at the end of suckling.

The values given in tables 2 and 3 for the weight of internal organs as a percent of the weight of the core indicate that the internal organs accounted for only a small part of the whole core. All the viscera together contributed less than 20% to the weight of the core. Skeletal muscle and bone were undoubtedly the largest components of the core at both ages.

Table 4. Body measurements (means ± SEM) and selected organ weights of seal pups after 1 month of the postsuckling fast

	Harp seal	Hooded seal	t test[1]
Animals, n	34	36	
Body measurements			
Empty body[2], kg	24.4±0.66	31.4±0.98	***
Body length, cm	100±1.0	105±1.1	**
Sculp, kg	13.8±0.43	18.1±0.55	***
Empty core[3], kg	10.6±0.27	13.3±0.57	***
Percentage of empty body, %			
Sculp	56.4±0.53	57.8±0.75	NS
Empty core	43.7±0.56	42.2±0.75	NS
Body weight/ length, g/cm	243±5.2	297±6.9	***
Organ weight, g			
Liver	339±11.8	500±17.8	***
Spleen	66.5±6.99	73.8±5.18	NS
Heart	138.8±2.99	174.4±4.62	***
Organ weight as percent of core, %			
Liver	3.19±0.072	3.82±0.095	***
Spleen	0.62±0.065	0.56±0.027	NS
Heart	1.33±0.031	1.35±0.033	NS

1 Significance levels indicated by asterisks: ** = p < 0.01; *** = p < 0.001.
2 As animals had fasted for about 1 month, live weight measured in the field was assumed to be equal to empty weight.
3 Core weight was calculated by difference, and was assumed to be equal to empty core weight.

Comparison of Weight Losses during the Postsuckling Fast

At the end of the suckling period both harp and hooded seal pups undergo a fast of about 4 weeks before beginning to feed. At the end of this period harp and hooded seal pups had lost about 14 and 11 kg body weight, respectively (table 4). Approximately half of this loss was from the sculp in both harp (54%) and hooded seals (44%). In both species the core was reduced to about two thirds of its weight at the end of suckling (harp seals, 62%; hooded seals, 68%). The most dramatic weight change among the organs measured was that of the liver, which, by the end of the 4-week fast, had lost 68 and 70% in harp and hooded seals, respectively. The liver of the fasted hooded seal pup weighed only half as much as it had at birth. However, it was still a larger proportion of core weight than that of the fasted harp seal pup. In both species the spleen was also greatly reduced in weight, whereas the heart lost relatively little weight and was in fact a larger percentage (1.3%) of core weight at the end of the fast than at the beginning (1.0–1.1%). Although harp seals were somewhat lighter at the end of the fast, the proportions of sculp and core were not different from those of hooded seals, nor were the percentages of core weight represented by spleen or heart (table 4).

Discussion

Comparison of Newborn Seals with Newborn Terrestrial Mammals

The newborn of these two species of ice-breeding seals are adapted to a cold environment, and their organs to a high fat diet. Whether expressed relative to weight of the empty body (table 5) or of the core (tables 2, 3), the organs of the two species were relatively similar in weight at birth. The small intestine and liver were somewhat larger in the hooded seal, and the stomach and lungs somewhat larger in the harp seal. These data may be compared to reported weights for the major internal organs of the newborn of man and some terrestrial ani-

Table 5. Comparison of organ weights, as a percentage of body weight, among newborn mammals[1]

<table>
<tr><th></th><th>Rat</th><th>Rabbit</th><th>Dog</th><th>Pig</th><th>Human</th><th>Sheep</th><th>Harp seal</th><th>Hooded seal</th></tr>
<tr><td>Body weight, kg</td><td>0.006</td><td>0.053</td><td>0.25</td><td>1.2</td><td>3.4</td><td>9.0</td><td>9.1</td><td>23.2</td></tr>
<tr><td>Stomach, %</td><td>0.65</td><td>1.51</td><td>0.47</td><td>0.38</td><td>0.23</td><td>1.40</td><td>0.55</td><td>0.36</td></tr>
<tr><td>Small intestine, %</td><td rowspan="2">2.52</td><td>2.28</td><td>3.10</td><td>2.20</td><td>1.16</td><td>2.00</td><td>2.03</td><td>3.00</td></tr>
<tr><td>Large intestine, %</td><td>0.65</td><td>0.23</td><td>0.48</td><td>0.50</td><td>0.70</td><td>0.18</td><td>0.15</td></tr>
<tr><td>Liver, %</td><td>4.31</td><td>5.21</td><td>5.75</td><td>2.99</td><td>3.65</td><td>2.39</td><td>3.05</td><td>4.61</td></tr>
<tr><td>Spleen, %</td><td>–</td><td>0.02</td><td>0.50</td><td>0.08</td><td>0.20</td><td>0.18</td><td>0.37</td><td>0.53</td></tr>
<tr><td>Pancreas, %</td><td>–</td><td>–</td><td>0.31</td><td>0.10</td><td>0.08</td><td>0.11</td><td>0.15</td><td>0.11</td></tr>
<tr><td>Heart, %</td><td>0.58</td><td>0.61</td><td>0.93</td><td>0.66</td><td>0.56</td><td>1.09</td><td>0.99</td><td>0.89</td></tr>
<tr><td>Lungs, %</td><td>2.34</td><td>1.38</td><td>2.31</td><td>1.52</td><td>1.52</td><td>3.31</td><td>2.54</td><td>1.72</td></tr>
<tr><td>Kidneys, %</td><td>0.99</td><td>1.17</td><td>1.35</td><td>0.57</td><td>0.71</td><td>0.61</td><td>0.95</td><td>0.82</td></tr>
</table>

[1] Data were obtained from the following sources: rat [6], rabbit [2], dog [4, 22, O.T.O. and E.M.W. unpubl. data], pig [1, 23], man [Widdowson, Southgate, and Hey, unpubl. data], sheep [24], harp and hooded seals [present study].

mals (table 5). These species all ingest milk of lower fat concentration (1–15%) than do the seals [8].

Given the large amounts of fat that newborn seals process shortly after birth, we had expected that their digestive tracts might be unusually large. A comparison of the seals to terrestrial species does not bear this out, however (table 5). There was nothing remarkable about the weights of the stomach, small or large intestine of the newborn harp or hooded seal. The proportional lengths of the small intestine (12–15 × body length) and large intestine (0.3 × body length) of the newborn seals were quite similar to adult seals [25–27].

Although the seal digestive tracts do not stand apart from those of other mammals, the data in table 5 indicate other interesting differences among species. Both the newborn rabbit and sheep have relatively large stomachs (1.4–1.5% body weight). The newborn rabbit suckles only once per day for 3–5 minutes and undoubtedly requires a large stomach to accommodate the great amount of milk (25% body weight) consumed in this short time [2, 28]. The newborn lamb has a multi-chambered stomach, and even though only the abomasum participates in milk digestion, the other compartments develop rapidly after birth in response to solid food intake [29]. It is not clear why the small intestine of the human baby is so disproportionately light (1.16% of body weights vs. 2.0–3.1% for all other species) or whether this is of functional significance. The large intestines of the newborn dog and seals are a very small percentage of body weight, as is typical of carnivorous species [30].

Although the range in body weights of the species in table 5 varies nearly 4,000-fold (from 6 g to 23 kg), the digestive tract remains a similar proportion of neonatal body weight from the smallest to the largest species. By analogy to adult mammals, Blaxter [31, 32] predicted that the weight of the digestive tract of suckling animals would be directly proportional to body weight rather than to metabolic body size (body weight to the power 0.75). The data in table 5 are consistent with this hypothesis.

The size of some organs, such as the liver, may scale more closely to metabolic size than to body weight [33, 34] with the result that organ weight as a percentage of body weight changes with body size. For example, in the smallest adult mammals (shrews) liver represents 7.6% of body weight, while in the largest (baleen whales) it is only 0.9% [34]. Among newborn mammals the smaller species (rat, rabbit, dog) also tend to have larger livers than do the bigger species (table 5), but there is considerable interspecies variation.

Kovacs and Lavigne [10] reported that the liver of the newborn harp seal was 2.6% of body weight, which they regarded as 'extremely large'. Even if comparison is restricted to the larger species in table 5 (pig, human and sheep), this does not appear to be true. On the other hand, the liver of the hooded seal is a rather high percentage (4.6%) of body weight for a large mammal; in the similarly sized foal (30 kg body weight) liver comprises only 3.0% of body weight [35]. The near-term bearded seal fetus *(Erignathus barbatus)* also has a relatively large liver (4.1%), but the suckling elephant seal *(Mirounga leonina)* does not (2.8%) [30, 36]. The notion that the livers of marine mammals are generally very large [26, 37] has recently been challenged [34].

While the spleen of the adult animal serves as a reservoir of blood, the newborn spleen may also be responsible for the synthesis of erythrocytes and granulocytes [38]. The spleen of newly born harp and hooded seals formed a larger percentage of body weight than in the terrestrial mammals except the dog. Neonatal harbor seals *(Phoca vitulina)* and bearded seal fetuses also have relatively large spleens (0.44–0.48% body weight) [36, 39]. Bryden [26, 30] speculated that a large spleen in adult seals might play a role in blood storage during deep diving.

The relative weights of the pancreas, heart, lungs and kidneys of the newborn seals were within the range for the land mammals shown in table 5. Although relative organ weights varied 2- to 3-fold among species, we did not discern any consistent patterns that would explain this variation.

Body Weight Gains of Seals and of Terrestrial Mammals

Pups of ice-breeding seals gain weight very rapidly during suckling, as is evident in estimated growth rates of 2.0–2.5 kg/day for harp seals [10, 18] and 6.5–7.1 kg/day for hooded seals [11, 12]. Our estimated rates of weight gain fell within these ranges. Such high rates of gain are quite different from those of most large terrestrial mammals. For example, the newborn of large herbivores such as horses, rhinoceroses and elephants gain only 1–1.5 kg/day during the suckling period, or about 1–2% of their birth weight per day [40–42].

Species that are small at birth generally multiply their birth weights more rapidly than those that are larger when they are born. This is illustrated in table 6, where gains in weight per day during suckling are expressed as percentages of birth weight. The harp and hooded seals clearly do not fit within the series of terrestrial mammals, for they increase their weight faster than the rat which weighs only 5 g at birth.

Comparisons of gains in weight of the whole body can be misleading since the com-

Table 6. Comparison of rates of growth of some suckling animals[1]

Species	Weight (kg) at birth	Weight gain (g) per 100 g birth weight per day
Rat	0.005	20
Dog	0.3	14
Pig	1.2	18
Sheep	9	10
Horse	30	2
Ox	35	2
Harp seal	9	25
Hooded seal	23	28

[1] Data were obtained from the following sources: rat, pig and ox [43], horse and sheep [31], harp and hooded seals [present study].

position of the tissue gained, especially the relative proportions of lean and fat, may differ greatly between species. In most species studied, including the human infant, triglycerides are deposited in subcutaneous adipose tissue during the suckling period [44]. The pig is often regarded as a species that gains fat particularly rapidly: 18% of the gain in weight during early suckling in the pig is fat, and 82% lean tissue [45]. Although chemical analyses of the bodies of the harp and hooded seals are yet to be completed, it is evident from the increase in the amount of blubber that fat deposition is far more rapid than in land mammals so far investigated. Increase in weight of sculp accounted for 64% of the gain in weight of harp seals and 73% of the gain of hooded seals. Blubber accumulation must be important for survival in the harsh environment of the pack-ice, both for insulation and as an energy store in preparation for the long post-suckling fast [46].

Growth of the Organs of Seals Compared with Those of the Pig

Comparisons of the growth rates of the organs of different species are complicated by differences in initial (birth) weight, in relative rates of body weight gain, and in the proportion of gain that is fat. Moreover, there are relatively few studies that present data on changes in organ weights during the suckling period. We compared the growth of the organs of harp and hooded seals to those of the pig (fig. 3). The pig was chosen for comparison because: (1) the newborn pig is moderately large (> 1 kg); (2) it grows quite rapidly (18% of birth weight per day); (3) it deposits substantial amounts of fat during suckling, and (4) the organ weight data [1, 23] were collected in a similar way to that used for the two species of seals. For this comparison the daily increase in organ weight or length was expressed as a percentage of the weight (or length) of the organ at birth. The data for the seals cover the entire suckling period (3.7 and 13 days for hooded and harp seals, respectively) while the pig data are restricted to the first 10 days postpartum.

Most of the organs of the pig increase in weight relatively more rapidly than do those of the seals even though the body of the pig gains weight less rapidly. The most striking difference between the pig and the seals was in the growth of the organs concerned with digestion: the stomach, small and large intestines, and pancreas. The slow growth of these organs in the seals was in contrast to our expectation of rapid growth to deal with the large amounts of milk, and particularly of fat, that have to be processed each day. None of these organs grew more rapidly than the core in either species of seal.

It is not clear why the digestive tract of the pig grows so rapidly. Rapid postnatal

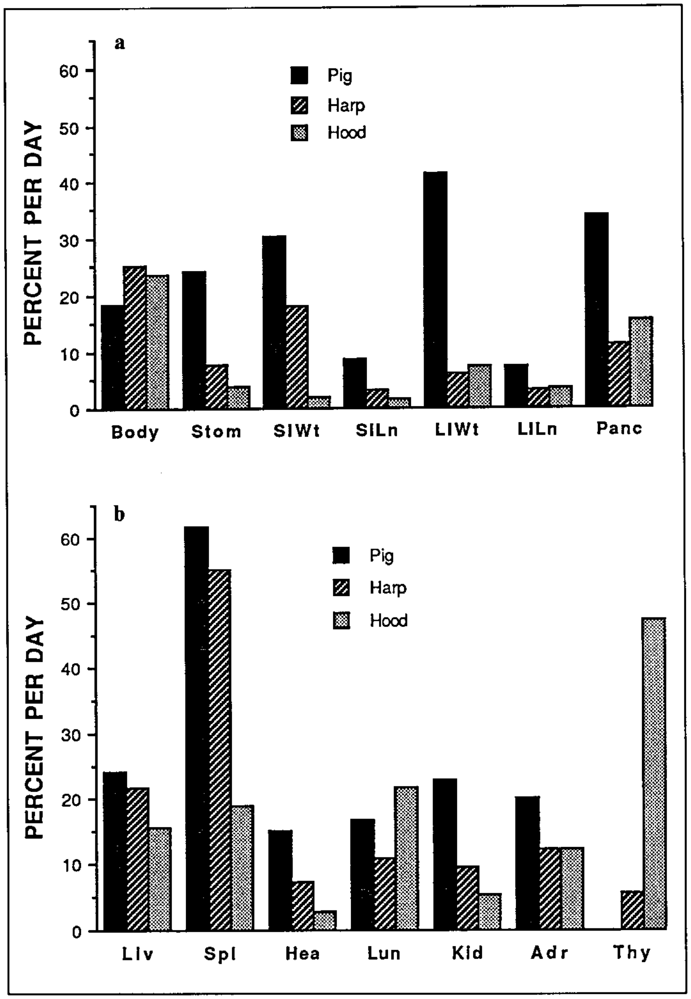

Fig. 3. Comparison of the rates of increase of the body, digestive tract and pancreas (**a**) and of other organs (**b**) among the pig, harp seal and hooded seal. Daily gains in weight or length are expressed as a percentage of the weight or length of that organ at birth. Organ measurements are abbreviated as follows: Body = body weight, Stom = stomach weight, SIWt = small intestine weight, SILn = small intestine length, LIWt = large intestine weight, LILn = large intestine length, Panc = pancreas, Liv = liver, Spl = spleen, Hea = heart, Lun = lungs, Kid = kidneys, Adr = adrenals, Thy = thymus. Data cover the entire suckling period for harp and hooded seals, but only the first 10 days postpartum for the pig. Pig data are from Widdowson and Crabb [23] and Widdowson et al. [1].

growth of the intestines has also been reported for rabbits, rats and dogs [2–4]. In the newborn pig most of the gain in intestinal weight and length takes place in the first 24 h after birth [1]. Some of the weight gain may be associated with the rapid postnatal absorption of large quantities of immunoglobulins [47], producing a quadrupling of plasma globulin concentration and a 30% increase in plasma volume in the first 24 h after birth; the gut closes to macromolecules thereafter [48]. Although there have been no studies of immunoglobulin transfer in harp or hooded seals, studies of northern fur seals *(Callorhinus ursinus)* indicate little or no absorption of colostral proteins from the gut and a fall in serum protein concentration during the first week after birth [49]. Thus the relatively slower growth of the intestines of seals may reflect an absence of immunoglobulin absorption.

Growth of the small intestine of the pig involves both muscle and mucosal tissue and results in an increase in the ratio of weight to length from 0.077 g/cm at birth to 0.174 g/cm at 10 days [1]. The small intestine of the harp seal showed a similar increase, though it was relatively heavier at birth (0.187 g/cm) and at 13 days (0.414 g/cm). The pattern in the hooded seal was quite different in that the small intestine was heavy in relation to length both at birth and at the end of suckling (table 2). In the absence of data on the relative proportions of muscle and mucosa in the intestines of the seals, the functional significance of the differences in weight per unit length is not clear.

It appears that the absorption of large amounts of fat is not associated with a specific enlargement of the digestive tract or the pancreas of the seals. It is difficult to imagine how the seals absorb such quantities of triglyceride (8.1 and 10.0 g lipid/g small intestine/day for harp and hooded seals, respectively). Gastric hydrolysis has been demonstrated in pups of both species, and may play an important role in the degradation of milk lipid globules [50]. The milk of these species also contains high activity of bile salt-stimulated lipase [51]. Pancreatic and other lipases probably contribute to lipolysis in the small intestine. It is also possible that some triglyceride is absorbed intact, as has been suggested for the rat [52, 53], but this needs further investigation.

In both the pig and the seals the liver increased in weight during suckling at about the same rate as the whole body. Bryden [30] suggested that the increase in liver weight of suckling southern elephant seals might represent, in part, accumulation of fat. Our preliminary analyses indicate that hooded seal livers were indeed high in fat (up to 30%) at the end of suckling, but the livers of harp seals were not (about 3% fat; unpubl. data).

The spleen grew very rapidly during suckling in the harp seal (54% of weight at birth per day) as it does in the pig (fig. 3), dog [38] and elephant seal [30]. The lean tissues of the body of these species grow rapidly after birth and presumably so does blood volume; the rapid growth of the spleen may be associated with this. In contrast, the spleen of the hooded seal gained less than 20% of weight at birth per day (fig. 3), which is consistent with the slower growth of the core and therefore of the volume of blood within it.

The heart, kidneys and adrenals gained proportionately less weight per day in the seals than in the pig (fig. 3). There was no consistent difference between the seals and the pig in relative weight gain of the lungs. The particularly large weight gain of the thymus in the hooded seal was striking.

In conclusion, when daily weight gains of individual organs are expressed relative to organ weights at birth, the organs of the seals do not grow any faster than those of the newborn pig, and in fact most of them grow more slowly. This is consistent with the fact that much of the rapid gain in body weight of suckling harp and hooded seals is due to fat deposition. It is the rate of fattening, not the growth rate of the lean body, that makes seals unique.

The Significance of the Postsuckling Fast

Most mammalian young are weaned from milk onto solid foods while still with their mothers, but phocid (true seal) mothers usually abandon their pups long before the pups begin to feed for themselves [12, 15]. Seal mothers must provide sufficient energy and nutrients to their pups to provide nutrient reserves that will cover the metabolic

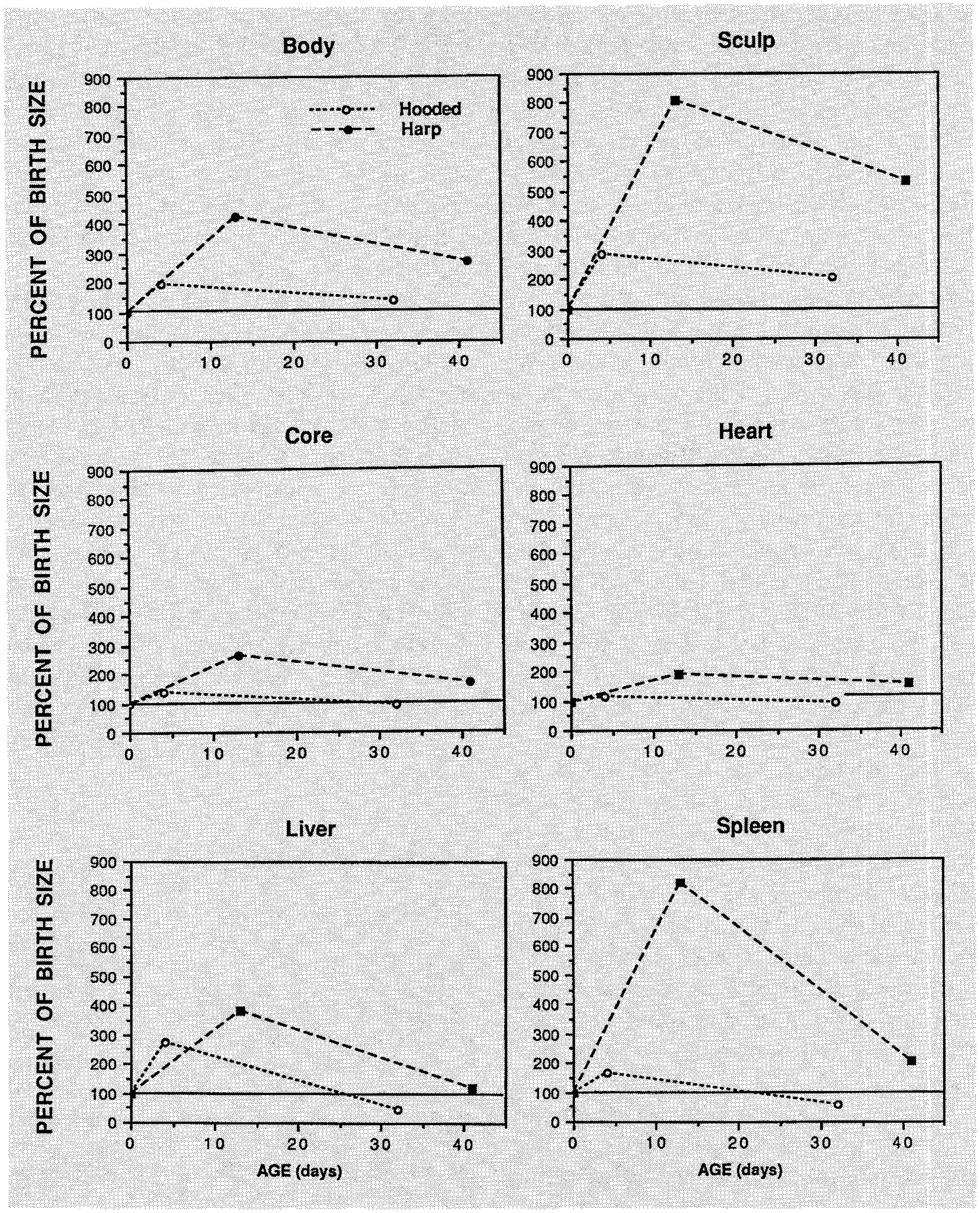

Fig. 4. Relative size of the empty body and its components, and of selected organs, of harp and hooded seals at the beginning and end of suckling and after 4 weeks of fasting. Size is expressed as a percentage of the weight of each component or organ at birth. The horizontal line in each graph represents size at birth (100%).

costs of fasting. Although harp and hooded seal pups started out very different in size and blubber content, by the end of suckling they had become remarkably similar in both absolute body size and in the proportional weights of sculp, core and organs (tables 1–3). The similarity in size and body composition of seal pups at the end of suckling has been noted before [11, 12, 54] and presumably reflects preparedness for fasting.

During fasting harp and hooded seals apparently mobilized nutrients from both blubber and tissues of the core. Since blubber stores were so massive at the end of suckling, substantial amounts remained even after 4 weeks without food. At this point the sculp still comprised 56–58% of empty body weight in both species, which is more than the percentage in adult harp and hooded females (40–50%) [12, 55]. Previous studies have indicated that fasting pups of ice-breeding species conserve blubber to a greater extent than do pups of land-breeding species [46].

The substantial loss of core weight observed in both species is not equally shared by all organs. As previously reported by Kovacs and Lavigne [10], the heart lost comparatively little weight. One would expect heart muscle to be spared during starvation, as compared with skeletal muscle. On the other hand, some organs show a great reduction in size. The liver and spleen lost about 70% of their weight over the 4 weeks of starvation.

The consequences of the fast are demonstrated by a comparison of weight gains during suckling to weight losses during fasting (fig. 4). In harp seals weight gains of body components and organs were so great during suckling that all components and organs were still heavier after 4 weeks of fasting than they had been at birth. This was not true for hooded seals. After fasting the core and heart of the hooded seal pup weighed only 92% of their weights at birth, and the liver and spleen had lost even more, weighing only 46 and 60% of their respective weights at birth (fig. 4). Only the sculp was still substantially heavier at the end of the fast than it had been at birth.

It is not clear why harp and, especially, hooded seals have evolved this remarkable pattern of pup development. Fattening of the pup is certainly a necessary preparation for the prolonged postsuckling fast, but what is the function of this fast? It is possible that the seals are constrained to give birth in March because the ice subsequently deteriorates, but that adequate food resources are not available to the pups for a month or more thereafter. On the other hand it may be that the pup requires time to develop behavioral, motor or physiological mechanisms that are necessary for efficient foraging. Further research is required to resolve these issues.

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