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Energetics of nursing in the harp seal, *Phoca groenlandica*, energy transfer and female condition

by

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Abstract

Lactating female harp seals and nursing females with their pups were collected on the "whelping" ice in the Gulf of St. Lawrence in 1976 and from 1978 to 1980 respectively. During lactation females lost weight at a rate of 3.4 $kg.d^{-1}$, for a total energy loss of about 261,630 kcal. Pups grew at a rate of 2.7 $kg.d^{-1}$ for a total energy gain of 191,200 kcal. Since 1976 there has been a decline in condition (stored energy) of adult females. Coincidentally there has been a decline in newborn lengths and girths. There is a statistically non-significant trend in these years suggesting nursing harp seals adjusted their total energy transfer by adjusting the rate of transfer. It remains possible however, that females may abort or abandon the young pup more readily when in poor condition and that a successfully weaned pup may be socially disadvantaged after puberty if size is important in harp seal mating systems.

1. Introduction

Female harp seals (*Phoca groenlandica* Erxleben 1777) fast or ingest only minute quantities of food during lactation (Sergeant 1973, Lavigne et al. Appendix 1). At this time, they produce a fat-rich milk of high caloric density (calorific value) (Lavigne et al. Appendix 1) permitting prodigious growth of their pups during a nursing period of less than two weeks (Stewart and Lavigne 1980). In addition to supplying the pup with energy, the female's energy reserves must meet associated costs of milk production (heat increment of lactation, Brody 1945) and her own maintenance requirements. Lactation is therefore a period of negative energy balance for females (Lavigne et al. 1976) during which mothers show definite declines in blubber stores. Thus it is possible to investigate aspects of energy balance by monitoring changes in morphometric parameters associated with fatness or "condition" of females and their pups (McLaren 1958, Usher and Church 1969, Innes et al. 1981).

Since females depend on energy garnered from earlier feeding, their condition at parturition is a reflection of prior prey abundance and foraging success, i.e. food availability. Fluctuations in condition related to changes in food availability may then be relayed to the pups. Here we examine the decline in female condition throughout lactation in relation to growth of the pup as well as between-year variation in female condition, to consider the effects of changes in food availability on maternal investment in harp seals.

2. Materials and methods

From 1976 to 1980, nursing female harp seals were sampled on whelping "patches" (Sergeant 1976) in the Gulf of St. Lawrence in March. Too few samples of mothers were obtained in 1977 to be included in the present analysis. From 1978, pups were sampled with their mothers (Table 1) and aged according to Stewart and Lavigne (1980) to estimate stage of lactation.

Adults were aged by dentinal annuli (Fisher and Mackenzie 1954) following the procedure outlined by Stewart and Lavigne (1979). Thin cross-sections of canine teeth, cut just below the gum line, were examined using transmitted light and a variable power dissecting microscope. Three to 5 independent counts were made for each section. If 3 of the readings were identical this value was recorded as the final age estimate. If fewer than 3 readings were the same, the mean and 95% confidence interval were calculated for all 5 counts. Outliers beyond the 95% confidence intervals were deleted (Snedecor and Cochran 1967) and the median of remaining values taken as the final age estimate. All readings were made by one observer (REAS) to avoid problems associated with between observer variation (Stewart and Lavigne 1979). Ages are given as integers to the last birthday, arbitrarily assigned 1 March.

Standard morphometric data were taken (American Society of Mammalogists 1967) as well as sculp weight (weight of skin and attached blubber, Stewart and Lavigne 1980, Innes et al. 1981) and sampling date. Blubber thickness and axillary girth were standardized for body size by dividing by standard length (McLaren 1958, Usher and Church 1969, Sergeant 1973). Lean body mass ("core" weight) was estimated by subtracting sculp weight from total weight (Stewart and Lavigne 1980, Innes et al. 1981).

For each parameter, differences between means were tested using Games and Howel's modified Tukey's test (Keselman and Rogan 1978). Between-year differences in the age distribution of sampled females were examined using a chi-square test with four age groups (ages 4-8, 9-13, 14-18, and 19+) to create cells of adequate sample size (Snedecor and Cochran 1967). Regression analysis was used to examine each parameter in relation to stage of lactation or sampling date. Pup age was deemed the most precise indicator of stage of lactation and used as the independent variable in analysing 1978, 1979, and 1980 data. As pup ages were not available for 1976, sampling date was the independent variable in comparisons of data from all four years. Differences between regressions were tested by analysis of covariance. Overall significance in this analysis was substantiated by paired comparisons of variance (F-test), slopes, and intercepts (Student's t-test; Snedecor and Cochran 1967).

3. Results

3.1 Annual means

Table 1 lists samples taken in the 4 seasons. Tables 2 and 3 present mean values for each parameter in each year for mothers and pups respectively. For females, all measurements pertaining to stored fat (sculp weight, girth, and blubber thickness) were significantly greater in 1976 than in subsequent years ($p < 0.05$). In contrast, there were no significant differences in mean core weight, in mean age of females sampled, or in the distribution of the 5-year age groups ($X^2 = 16.53$, 12 df, $p = 0.18$). Mean standard lengths of females sampled in 1979 and 1980 were significantly shorter than those of 1976 and 1978 females. Average sampling dates in 1976 and 1980 were not significantly different from each other but were earlier than in 1978 and 1979 which were not significantly different from each other. As animals were sampled in pairs, this last relationship pertains to pups as well as adults with the exclusion of 1976 when only a small number of pups (5) were sampled. For pups, only standard length showed significant yearly variation; pups sampled in 1978 were significantly longer than those in 1979 and 1980.

The sex ratios of pups did not differ from 1:1 (X^2, $p > 0.05$) in any year (Table 4).

3.2 Biomass transfer during lactation

Condition parameters of both mothers and pups changed throughout lactation. Regressions of female fat-related measurements as functions of pup age (stage of lactation) were significant in all years (Table 5) and indicated a decline in stored energy as nursing progressed. Regressions of maternal core weight and standard length on pup age were not statistically significant ($p > 0.05$). For pups, regressions of all condition and growth parameters in relation to pup age were statistically significant and had positive slopes (Table 6). Correlations between condition parameters of females and their pups were highly significant (Table 7).

3.31 Annual variation in female condition: 1978-1980

For parameters showing no significant differences in regression lines among years, all data were pooled and a common regression fitted (Tables 5 and 6).

Female sculp weight index (sculp weight$\cdot$length^{-1}) (Fig. 1) as a function of pup age showed a significant difference in variance between 1978 and 1979. Bearing this in mind, lines for these two years showed no differences in slope but the 1978 intercept was significantly smaller than that of 1979 ($p < 0.025$). Female girth index (girth$\cdot$length^{-1}) was significantly smaller at the onset of nursing in 1978 than in 1980 ($p < 0.025$). Pups showed significant differences in length, girth, blubber thickness, blubber index and girth index (Table 8).

3.32 Annual variation in female condition: 1976, 1978-80.

To allow comparisons of 1976 females with those from later years, morphometric parameters were examined with respect to sampling date (Tables 9 and 10). In 1978, 1979 and 1980, pup age and sampling date were highly correlated ($r = 0.75$, $p < 0.0001$; $r = 0.90$, $p < 0.0001$; and $r = 0.88$, $p < 0.0001$ respectively). All regressions related to fatness were significant ($p \leq 0.05$) for 1978-1980 data but for 1976, only sculp weight produced a statistically significant line. Comparisons among years were therefore restricted to this measurement (Fig. 2).

The difference in rate of sculp weight loss between years was not statistically significant but the 1976 intercept was significantly greater than those of subsequent years ($p < 0.005$) and that of 1979 was greater than those of 1978 and 1980 ($p < 0.001$). Although not included in the statistical analysis, other measurements of female condition were greatest in 1976.

4. Discussion

4.1 Annual means

Mean values for all measurements concerning the fatness of females were greater in 1976 than in subsequent years sampled. Fatness may be related to female age, stage of lactation and absolute body size. The mean ages of females sampled and their age distribution however did not vary significantly over these 4 years. The date of sampling, hence approximate stage of lactation appears to have been earlier in 1976 and 1980 (Table 2). However mean pup age was not less in 1980 than in 1978 and 1979 suggesting this conclusion is erroneous, probably due to the imprecise correlation between pup age and sampling date. Pup age is a more accurate indicator of stage of lactation as pupping may continue over a week. This may result for example in the presence of newborns and 7 day-old animals a week after the first newborn was collected.

Absolute body size of females is approximated by both lean body mass, which showed no significant differences among years, and standard length. Females sampled in 1979 and 1980 were significantly shorter than those sampled in 1976 and 1978. Since mean age was about the same in all years

($\pm$ 13.6 y) females sampled in the last half of the study were born 2 years after those from the first half, i.e. in 1966-67 compared to 1963, 1965. In 1965 females were for the first time, protected from hunters on the whelping patches (Lavigne 1978). Between 1960 and 1964, an average of 15,000 1^+ harps were taken in the Gulf (Sergeant 1966).

Since females feed in southern waters after weaning their pups (Sergeant 1973) one hypothesis is that this management change resulted in an abrupt increase in competition for food between pups and females. This in turn could suppress pup growth and result in smaller adults (Innes et al. 1981). In this respect it is also worth noting that in the present study, shorter mothers produced shorter pups (Tables 2 and 3). Further monitoring is required to ascertain the relationships involved in the decline in standard length of Gulf breeding females.

4.2 Energy transfer during lactation

Total body weight can be partitioned into sculp weight plus core weight, and weight losses from these compartments provide an estimate of total metabolic requirements during the fast of lactation for female harp seals.

Rates of decline in female core weights were small and the regressions non-significant (Tables 4 and 8). The average loss based on the overall equation (Table 4), assuming a 9 day nursing period (Stewart and Lavigne 1980) was 6.24 kg or 9.43% of initial core weight. This weight loss may be the result of catabolism of body fat or muscle but the metabolic pathways are as yet unclear (Lavigne et al. Appendix 1). By far the largest weight loss is from the sculp, averaging 22.86 kg or 37.51% of initial sculp weight (Table 4, overall equation).

For the present discussion we assumed that the entire female weight loss in total weight was fat, with a caloric density of 8.55 $kcal.g^{-1}$ (Worthy et al. in prep.). From the overall equation for total weight (Table 4) weight loss was 3.40 $kg.d^{-1}$ or 261,630 kcal over 9 days. Some of this energy loss is attributable to maintenance costs. Assuming harp seal basal metabolic rate is not significantly different from Klieber's (1975) equation for mammals (Gallivan and Ronald 1979, Gallivan in press):

$$M = 70W^{0.75} \qquad (1)$$

where M is metabolic rate in $kcal \cdot d^{-1}$ and W is weight in kg, then average daily metabolic rate, including BMR and energy costs associated with locomotion etc. is in the order of

$$ADMR = 2(70W^{0.75}) \qquad (2)$$

(Lavigne et al. 1976). Average weights of females at parturition was about 132 kg (Table 4) and energy costs of maintenance by such a female would be around 49,068 kcal over 9 days (Eq. 2). The implications of this calculation and those following are not significantly altered by using female weights of 120 to 150 kg at parturition, weights which span the range of our observations since 1976. Subtracting this estimated energy cost from the total energy loss during lactation yields a total energy cost of lactation of 261,630 - 49,068 = 212,562 kcal.

Pups in the present study grew at 2.73 $kg \cdot d^{-1}$ (Table 5) of which 1.91 $kg.d^{-1}$ was added to the sculp and 0.82 $kg \cdot d^{-1}$ to core weight. This growth is supported solely by assimilation of maternal milk (Stewart and Lavigne 1980) making it possible to estimate milk production required to meet the pup's energy requirements during lactation. Lavigne et al. (1976) made this calculation using Moen's (1973) equation for daily milk production (MP in kcal):

$$MP = \frac{A + GI + 2(70W^{0.75})}{E} \qquad (3)$$

where A ($kcal \cdot d^{-1}$) is an estimate of the net cost of locomotion, considered negligible in sedentary young harp seals; GI is the daily growth increment in energy ($kcal \cdot d^{-1}$); $70W^{0.75}$ estimates BMR (Eq. 1); the factor 2 accounts for the higher BMR of young mammals (Denckla 1970, Nordan et al. 1970) and E is the net energy coefficient for milk, representing the proportion of milk energy available to the pup as net energy. We follow Moen and Lavigne et al. in using E = 0.80.

Total milk production (MP_T) over 9 days of nursing is therefore:

$$MP_T = \sum_{i=1}^{n} \frac{A + GI_i + 2(70W_i^{0.75})}{E} \qquad (4)$$

where n is the length of lactation (days); W_i is the weight of the pup on day i such that W_1 = birth weight, $W_2 = W_1 + GI_1$ etc. From Table 10 and Eq. 4, energy content of milk available to the average pup was about 191,000 kcal. This is somewhat lower than was estimated by Lavigne et al. (1976) as it incorporates better data for pup weight and duration of nursing.

Thus calculated, the amount of milk required to meet the pup's demands for growth and metabolism does not represent the total cost to the female to produce that milk. Subtracting the pup's energy consumption from the total energy cost of lactation for the female (212,562-191,165) we estimated this cost of milk production (heat increment of lactation; Brody 1945) to be 21,397 kcal over 9 days. This represents an upper limit; if the female's ADMR is greater than $2(70W^{0.75})$ kcal.d^{-1} this cost of milk production will be an overestimate. However, as calculated, the total cost of milk production would be 212,562 ÷ 191,165 or about 1.11 times the amount of energy realized in the milk, less than the 1.6 factor derived for dairy cattle (Compton and Harris 1969). However fatty acid composition of harp seal milk and blubber are virtually identical in terms of component proportions (Jangaard and Ke 1968) and mobilization of fats from the blubber of lactating females may be accomplished with a minimum of biosynthesis. Also, the assimilative efficiency of the pup in converting milk back to blubber may be greater than 0.80. This would have the effect of reducing MP_T, thereby raising the estimated milk production factor above 1.11.

4.3 Between year variation in female condition

There are year to year differences in the amount of stored energy mothers have at the onset of lactation. Since 1976, lactating female harp seals in the Gulf of St. Lawrence have been in poorer condition, as determined by the weight of their blubber. The difference in sculp weight at parturition between 1976 and 1978, the extreme years in our data, was 21.8 kg, a difference of 186,305 kcal net energy, very nearly the total energy requirement for growth, fattening and maintenance of a pup during lactation. Alternatively, if a 132 kg female requires about 5450 kcal$\cdot d^{-1}$ net energy (Eq. 2), it equates with approximately 34 days of fasting.

Sergeant (1973) examined harp seal condition for this same Northwest Atlantic population. He used (girth$\cdot$100)$\cdot$length^{-1} and fat thickness as measures of condition, and although he did not provide details as to how these measurements were taken, we have assumed they were essentially comparable to our own measures. His figures 1 and 2 (pp. 22 and 23) plotted changes in condition over a year. Data from these figures have been reproduced in Fig. 3 with the corresponding regressions for 1976 and 1978. It is apparent that the decline between 1976 and 1978 is but a continuation of a trend since Sergeant's sample from the late 1960's and 1971.

We approximated sculp weight from Sergeant's figures in the following way. We assumed the average length of his seals was the same as our 1976 and 1978 samples, about 169 cm (Table 2) and applied a predictive equation for sculp weight (Innes et al. 1981):

$$SWT = 0.00191\ L^{0.269} \cdot Ga^{2.31} \qquad (5)$$

where SWT is sculp weight (kg), L is standard length (cm) and G_a is axillary girth (cm). Values for Sergeant's seals were back calculated from his figures as 139 and 134 for G_a at parturition and weaning. Initial and weaning values for our samples for G_a were derived from the regressions (Table 8) and used to calculate sculp weight from Eq. 5. A 9 day nursing period was used for both data sets (Stewart and Lavigne 1980). As illustrated in Fig. 4, this calculation underestimated condition for 1976. It remains however that the 1978 sample was distinctly lean and that in 1976 females may also have been thinner than 5 to 10 years previously.

The decline in net energy in females from 1976 to 1978 must reflect either changes in ecological efficiency or decreased <u>per capita</u> consumption. There is no evidence either way for a change in harp seals' digestive or assimilative powers. Thus we conclude energy availability has changed either through a decline in prey availability or an increase in harp seal numbers. It is currently unclear if the Northwest Atlantic population is decreasing, stable or increasing (Lett and Benjaminsen 1977, Lavigne 1978, 1979, Winters 1978, Beddington and Williams 1979). There has however been a marked decline in capelin (<u>Mallotus villosa</u>) abundance in exploited offshore stocks (Fisheries and Environment Canada 1978, Beddington and Williams 1979, Carscadden and Misra 1980). Although not specifically analysed, capelin in the Gulf of St. Lawrence are thought to follow the same patterns of abundance as those in areas examined (J.

Carscadden, pers. comm.). Since capelin are considered an important prey species for harp seals, especially in the Gulf of St. Lawrence in January-April (Sergeant 1973, 1976) the hypothesis of reduced prey abundance thus appears plausible.

Fluctuations in prey species have been also implicated in population shifts in other marine mammal consumer species. For example, this same decline in capelin has also been correlated with altered spatial distribution of baleen whales off Newfoundland (Lien and Merdsoy 1979, Lien and Gray 1980, Lien and McLeod 1980). Similarly, Bonner et al. (1978) found decreases in growth rates of Australian fur seal pups (Arctocephalus gazella) when krill (Euphausia superba) failed to swarm. The decline in condition may be expected to affect seal productivity through reduced female reproductive success. The effects of lowered nutritional plane on reproductive performance have been well documented for terrestrial wildlife and domestic animals and the consequences may include reduced ovulation rates, delayed estrous (Woodside et al. 1980), reduced pregnancy rates (Verme 1969, Grainger and Wilhelm 1979), increased foetus resorption (Woodside et al. 1980), reduced biomass of offspring per reproduction (Frobisher 1970, Newton et al. 1980), reduced milk and milk-fat production (Grainger and Wilhelm 1979) and lower growth rates (Woodside et al. 1980) resulting in turn in smaller adults (Allden 1979). In wild animals it may also lead to increased abandonment of neonates and female mortality. In species with sexual selection based at least in part on adult size, where smaller adults are socially disadvantaged, poorer condition of mothers of one generation may not result in lowered reproductive success until expressed through her offsprings' reduced ability to reproduce (Trivers and Willard 1972). In such a social system, their may also be a shift to a female biased sex ratio of pups (Trivers and Willard 1972).

The theory of parental investment (Trivers 1972) suggested that a female, acting physiologically as if she were able to evaluate her probability of successfully weaning a pup, should abort or abandon the pup if this probability is small and the effort would lower her future reproductive potential. It further stipulated that the determining criterion would be future investment required to ensure success rather than past investment committed to this offspring (Dawkins and Carlisle 1976).

The costs of gestation are generally small compared to those of lactation (Young 1976) and include costs of maintaining the pregnant uterus, foetal growth, increased maternal work and endocrine influences on maternal metabolism (Brody 1945). Brody (1945) derived an equation for the heat increment of gestation (Q, kcal) in mammals:

$$Q = 4400\ M^{1.2} \qquad (6)$$

where M is birth weight in kg. The heat increment of gestation associated with the production of a 10.3 kg pup is thus estimated as 72,253 kcal. This cost is slightly lower than the only previous estimate (Lavigne et al. 1976) due to their lower estimate of newborn weight, and differences between equation 6 and Moen's (1973) equation which they employed. Upon re-examination, it now appears that Moen's equation has little interspecific validity.

Total maternal investment at parturition is thus equal to the energy content of the pup and placenta at birth (1.73 kcal g^{-1} x 10.3 kg + 1400 kcal; Lavigne and Stewart 1979, Section 5.5, this report) plus the heat increment of gestation (72,253 kcal) or about 91,000 kcal. Spread over a gestation period of approximately 11 months, this cost is small in comparison to the 261,630 kcal invested over 9 days of nursing.

Based on the relative total cost of gestation, the proximity of a major food source in the Gulf immediately prior to whelping and the theory of parental investment, we hypothesize that under conditions of moderately limited energy availability, pregnant harp seals would act as if they delayed the decision to produce and nourish a pup through the relatively inexpensive gestation period and evaluate their chances of successful weaning after the pre-whelping feeding season. We therefore predict that in times of moderately reduced energy consumption there would be no obvious condition related changes in ovulation or fertility rates but a higher proportion of pups might be abandoned at birth or shortly thereafter (Fig. 5). Changes in ovulation and fertility rates would be expected if energy stores continued to decline (Fig. 5). Females continuing to nurse should strive to produce as large a pup as possible. Existing data do not refute this hypothesis. Ovulation frequency of Gulf females has remained constant from 1966 to 1979 (Bowen et al. 1981).

Bowen et al. (1981) also examined fertility based on January-February samples of southbound migrants on the north shore of the Gulf of

St. Lawrence between 1951 and 1979 and found an increase. Scattered and missing data do not permit analysis of fertility rates over the shorter time span when population fluctuations were smaller and perhaps positive (Winters 1978). Unfortunately these winter samples may overestimate fertility if pregnant and non-pregnant animals have different migration regemes.

Summer samples are required to relate implantation rates to female condition and abortion rates prior to the southward migration.

Data are however absent on an important segment of the population; those females which have terminated their pregnancy prematurely or abandoned their pups at birth. Our own sample sustains at least one serious bias with respect to determining abandonment rates; it includes only females with nursing pups. Females seen without pups have not necessarily abandoned or aborted one. Conversely, females that have terminated prematurely are not available on the whelping ice for sampling.

Abandonment rates may be reflected however in the apparent increase in 1980 in the incidence of starvlings and pups which had died in the first few days of life. Unfortunately this was our subjective estimate. No quantitative determination of neonatal mortality has been attempted for Northwest Atlantic harp seals.

Foetal and neonatal growth may be influenced by female condition. Over the 3 years under consideration there has been a consistent though statistically non-significant trend towards smaller pups (shorter, lighter cores) with less fat at birth. These smaller pups were however weaned at about the same weight. This compensatory growth may be made possible through increased milk production and consumption. Changes in milk fat between 1980 and 1981 are currently being analysed (Webb et al. in prep.) but preliminary findings suggest no significant differences. Milk production based on rates of female weight loss and pup weight gain (Tables 4, 5, 8 and 9) appear however to be inversely related to female condition, and may contribute to compensatory growth when a female commits herself to nursing a pup.

Differences in pup standard length however persist at weaning. In discussing population changes between 1950 and the late 1970's, Innes et al. (1981) presented data suggesting length differences at age 0 persist-ed through adult life. Although the mating system of harp seals remains obscure, it appears both epigamic and intrasexual selection base on male body size may occur (Nazarenko 1975, Merdsoy et al. 1978). Reproductive success of females in poor condition may therefore be latent, not expressed until her male offspring suffer reduced reproductive opportunities through sexual selection. If size is more important for the reproductive success of a male offspring than for a female, there may be a bias towards female pups (Trivers and Willard 1972). Empirical determination of such a shift in pup sex ratio however requires a large sample size (Trivers 1972). There is not yet such a sample that includes morphometric data for pups and mothers. Stewart and Lavigne (1980) however reported a sample of 1174 pups examined in 1976, 77, 78, 79 and which included the pups mentioned here. The sex ratio (51% males:49% females) was not significantly different from 1:1.

In light of the aforementioned theoretical framework, it appears as predicted, female harp seals conceive and carry a low cost foetus and "evaluate" the investment risk at or about parturition. If she possesses adequate reserves, the pup is weaned at a "normal" weight. The hypothesized reduction in reproductive success of the sons of mothers in poor condition remains untested.

Continued monitoring of breeding harp seals is essential to track trends reported here and to establish ecosystem correlations. Assuming Front breeding harp seals consume offshore capelin before whelping, we would predict that they would show similar trends. This comparison awaits suitable data from this region.

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Table 1. Samples of female harp seals and their pups.

Year	No. of Females	No. of Pups
1976	26	5
1978	25	25
1979	23	23
1980	30	30

Table 2. Statistics on morphometric parameters for all adult female harp seals sampled.

Parameter	Year	n	$\bar{X}$	1 SD	Significance*
Total Wt (kg)	1976	26	140.5	17.8	76 78 79 80
	1978	25	113.9	17.0	
	1979	23	118.4	24.9	
	1980	30	110.5	18.0	
Sculp Wt (kg)	1976	26	74.5	9.5	76 78 79 80
	1978	20	45.7	8.4	
	1979	22	53.0	14.9	
	1980	30	47.0	13.0	
Core Wt (kg)	1976	26	66.0	12.3	76 78 79 80
	1978	20	65.6	11.2	
	1979	22	66.4	14.4	
	1980	30	63.5	7.5	
Standard Length (cm)	1976	26	168.8	7.0	76 78 79 80
	1978	25	169.8	7.2	
	1979	23	162.6	8.6	
	1980	29	160.9	7.9	
Axillary Girth (cm)	1976	26	133.4	7.1	76 78 79 80
	1978	25	119.2	8.1	
	1979	23	120.0	9.0	
	1980	30	119.3	8.1	
Blubber Thickness (mm)	1976	25	60.0	7.4	76 78 79 80
	1978	25	44.2	9.5	
	1979	22	46.5	10.1	
	1980	30	43.3	9.1	
Blubber Thickness (mm) / Standard Length (cm)	1976	25	0.355	0.045	76 78 79 80
	1978	25	0.260	0.055	
	1979	22	0.286	0.070	
	1980	29	0.266	0.055	
Axillary Girth (cm) / Standard Length (cm)	1976	26	0.790	0.039	76 78 79 80
	1978	25	0.703	0.041	
	1979	23	0.738	0.062	
	1980	29	0.740	0.046	
Sculp Wt (kg) / Standard Length (cm)	1976	26	0.440	0.046	76 78 79 80
	1978	20	0.269	0.046	
	1979	22	0.326	0.088	
	1980	29	0.288	0.075	
Age (yrs)	1976	25	13.7	4.8	76 78 79 80
	1978	25	14.4	6.3	
	1979	22	11.0	5.7	
	1980	26	14.9	6.7	
Date	1976	26	7.2	3.1	78 79 80 76
	1978	25	9.6	4.3	
	1979	23	12.1	6.4	
	1980	30	7.3	4.1	

* Q = 0.05. Underlining denotes non-significant differences in means. (modified Tukey's test - Keselman & Rogan 1979)

Table 3. Statistics on morphometric parameters for all harp seal pups sampled.

Parameter	Year	n	$\bar{X}$	1 SD	Significance*
Total Wt (kg)	1976	5	16.6	3.4	78 79 80
	1978	25	27.1	11.7	
	1979	23	24.4	10.5	
	1980	30	22.3	12.7	
Scult Wt (kg)	1976	5	6.6	3.6	78 79 80
	1978	25	14.1	7.3	
	1979	23	12.5	7.9	
	1980	30	10.6	8.5	
Core Wt (kg)	1976	5	10.0	1.6	78 79 80
	1978	25	12.9	4.9	
	1979	23	11.9	3.4	
	1980	30	11.7	4.6	
Standard Length (cm)	1976	4	88.8	3.1	78 79 80
	1978	25	99.0	7.6	
	1979	23	92.4	7.2	
	1980	30	93.0	8.1	
Axillary Girth (cm)	1976	4	55.8	6.1	78 79 80
	1978	25	75.9	13.7	
	1979	23	68.3	15.1	
	1980	30	69.5	17.3	
Blubber Thickness (mm)	1976	4	16.3	4.8	78 79 80
	1978	25	30.9	12.2	
	1979	21	25.8	12.5	
	1980	30	22.6	15.8	
Blubber Thickness (mm) / Standard Length (mm)	1976	4	0.183	0.054	78 79 80
	1978	25	0.307	0.113	
	1979	21	0.269	0.123	
	1980	30	0.233	0.152	
Axillary Girth (cm) / Standard Length (cm)	1976	4	0.629	0.077	78 79 80
	1978	25	0.763	0.102	
	1979	23	0.731	0.127	
	1980	30	0.732	0.126	
Sculp Wt (kg) / Standard Length (cm)	1976	4	0.062	0.034	78 79 80
	1978	25	0.139	0.067	
	1979	23	0.130	0.077	
	1980	30	0.109	0.080	
Age (days)	1976	3	2.7	2.9	78 79 80
	1978	25	5.5	3.5	
	1979	23	5.2	3.9	
	1980	30	4.9	3.2	
Date	1976	5	5.2	1.8	78 79 80
	1978	25	9.6	4.3	
	1979	23	12.1	6.4	
	1980	30	7.3	4.1	

*α = 0.05. Underlining denotes non-significant differences in means. (modified Tukey's test, Keselman & Rogan 1979).

Table 4. Sex ratios of harp seal pups sampled in 1976, 1978-1980.

Year	Number of Males	Number of Females	Ratio ♂: ♀
1976	1	3	1:3
1978	18	6	1:0.33
1979	17	23	1:1.35
1980	12	11	1:0.92
overall	48	43	1:0.90

None of the ratios is significantly different from 1:1 (χ^2, 1 d.f., $p > 0.05$).

Table 5. Regression analysis of adult female harp seal parameters as a function of the estimated age of their pups.

Variable	Year	n	Slope	Intercept	R^2	p[1]
Weight (kg)	1978	25	-2.84	129.68	35.14	**
	1979	23	-3.84	138.42	35.60	**
	1980	30	-3.71	128.36	44.42	**
	overall	78	-3.40	131.50	35.47	**
Sculp Wt (kg)	1978	20	-1.82	57.28	52.24	**
	1979	22	-2.75	66.91	50.73	**
	1980	30	-2.91	60.95	52.24	**
	overall	72	-2.54	62.01	48.13	**
Core Wt (kg)	1978	20	-0.41	67.98	1.60	NS
	1979	22	-0.98	71.35	6.90	NS
	1980	30	-0.81	67.40	12.30	NS
	overall	72	-0.72	68.72	5.32	NS
Standard Length (cm)	1978	25	-0.19	170.71	0.81	NS
	1979	23	-0.01	162.83	0.00	NS
	1980	29	0.01	160.85	0.00	NS
	overall	77	0.026	164.19	0.01	NS
Axillary Girth (cm)	1978	25	-1.47	127.36	41.93	**
	1979	23	-1.62	128.42	48.64	**
	1980	30	-1.64	127.13	43.20	**
	overall	78	-1.57	127.53	44.12	**
Blubber Thickness (mm)	1978	25	-1.84	54.38	46.70	**
	1979	22	-1.89	56.74	49.65	**
	1980	30	-2.13	53.52	57.66	**
	overall	77	-1.91	54.46	48.58	**
Blubber Thickness (mm) / Standard Length (cm)	1978	25	-0.011	0.319	45.71	**
	1979	22	-0.012	0.349	46.87	**
	1980	29	-0.013	0.327	56.83	**
	overall	76	-0.011	0.330	47.26	**
Axillary Girth (cm) / Standard Length (cm)	1978	25	-0.008	0.746	46.73	**
	1979	23	-0.010	0.788	35.75	**
	1980	29	-0.010	0.788	49.18	**
Sculp Wt (kg) / Standard Length (cm)	1978	20	-0.0104	0.3351	58.57	**
	1979	22	-0.0165	0.4092	52.78	**
	1980	29	-0.0177	0.3745	60.81	**

[1] F test [NS] $p > 0.05$, * $p < 0.05$, ** $p < 0.01$.

Table 6. Regression analysis of harp seal pup parameters as a function of their estimated age.

Variable	Year	n	Slope	Intercept	R^2	p[1]
Weight (kg)	1978	25	2.37	13.61	56.23	**
	1979	23	2.60	10.82	91.95	**
	1980	30	3.15	7.29	64.79	**
	overall	78	2.73	10.29	68.02	**
Sculp Wt (kg)	1978	25	1.66	4.98	64.31	**
	1979	23	1.96	2.27	91.25	**
	1980	30	2.06	0.76	61.00	**
	overall	78	1.68	3.88	58.16	**
Core Wt (kg)	1978	25	0.71	8.63	23.74	*
	1979	23	0.64	8.55	52.88	**
	1980	30	1.09	6.52	58.04	**
	overall	78	0.82	7.87	40.56	**
Standard Length (cm)	1978	25	1.39	91.28	42.53	**
	1979	23	1.54	84.64	68.41	**
	1980	30	1.25	83.98	40.70	**
Axillary Girth (cm)	1978	25	2.95	59.51	58.30	**
	1979	23	3.77	48.57	93.54	**
	1980	30	4.58	46.90	79.48	**
Blubber Thickness (mm)	1978	25	2.57	16.63	56.10	**
	1979	21	3.19	7.52	87.32	**
	1980	30	4.32	1.84	79.01	**
Blubber Thickness (mm) / Standard Length (cm)	1978	25	0.023	0.180	51.69	**
	1979	21	0.032	0.091	81.08	**
	1980	30	0.042	0.051	79.88	**
Axillary Girth (cm) / Standard Length (cm)	1978	25	0.020	0.652	47.76	**
	1979	23	0.029	0.578	79.80	**
	1980	30	0.035	0.564	80.26	**
	overall	78	0.028	0.596	69.14	**
Sculp Wt (kg) / Standard Length (cm)	1978	25	0.015	0.055	64.51	**
	1979	23	0.019	0.030	91.43	**
	1980	30	0.020	0.014	63.65	**
	overall	78	0.018	0.030	71.38	**

[1] F test NS > 0.05, * $p < 0.05$, ** $p < 0.01$

Table 7. Correlation coefficients for pooled 1978-1980 data for changes in female harp seal and pup condition (paired data).

Measure of Condition	n	r	P
Sculp Wt	72	-0.65	< 0.00001
Sculp Wt / Standard Length	71	-0.68	< 0.00001
Blubber Thickness	76	-0.69	< 0.00001
Blubber Thickness / Standard Length	75	-0.67	< 0.00001
Girth	78	-0.58	< 0.00001
Girth / Standard Length	77	-0.54	< 0.00001

Table 8. Points of significant differences for harp seal pup regressions as functions of pup age for 1978, 1979 and 1980 samples.

Parameter	Slope (P = 0.05)	Intercept (P = 0.05)
Standard Length	NS	78 > 79 + 80
Girth	78 < 80	78 > 79 + 80
Blubber Thickness	78 + 79 < 80	78 > 79 + 80
Blubber Thickness / Standard Length	78 < 80	78 > 79 + 80
Girth / Standard Length	78 < 80	78 > 79 + 80

Table 9. Regression analysis of adult female harp seal parameters as a function of sampling date in March.

Variable	Year	n	Slope	Intercept	R^2	p^1
Weight (kg)	1976	26	-0.94	147.27	2.68	NS
	1978	25	-2.51	138.00	39.29	**
	1979	23	-2.02	142.85	27.43	**
	1980	30	-2.90	131.62	43.90	**
Sculp Wt (kg)	1976	26	-1.24	83.43	16.64	**
	1978	20	-1.51	61.64	35.94	**
	1979	22	-1.57	71.60	47.19	**
	1980	30	-2.39	64.37	57.03	**
Core Wt (kg)	1976	26	0.30	63.84	0.60	NS
	1978	20	-0.21	67.57	0.42	NS
	1979	22	-0.37	70.81	2.79	NS
	1980	30	-0.57	67.25	7.97	NS
Standard Length (cm)	1976	26	-1.26	177.94	31.31	**
	1978	25	-0.15	171.08	0.71	NS
	1979	23	-0.10	164.04	0.56	NS
	1980	29	-0.23	162.59	1.49	NS
Axillary Girth (cm)	1976	26	-0.50	136.97	4.71	NS
	1978	25	-1.23	131.01	42.06	**
	1979	23	-0.83	129.99	35.23	**
	1980	30	-1.23	128.21	39.31	**
Blubber Thickness (mm)	1976	25	-0.17	61.19	0.47	NS
	1978	25	-1.64	59.91	53.23	**
	1979	22	-0.92	57.95	32.46	*
	1980	30	-1.62	55.07	53.77	**
Blubber Thickness (mm) / Standard Length (cm)	1976	25	0.0019	0.342	1.56	NS
	1978	25	-0.0094	0.351	52.37	**
	1979	22	-0.0055	0.355	29.21	*
	1980	29	-0.0092	0.334	48.00	**
Axillary Girth (cm) / Standard Length (cm)	1976	26	-0.003	0.769	5.83	NS
	1978	25	-0.007	0.765	46.17	**
	1979	23	-0.005	0.793	22.67	*
	1980	29	-0.006	0.786	32.06	**
	overall	77	-0.005	0.773	23.98	23.66*
Sculp Wt (kg) / Standard Length (cm)	1976	26	-0.0043	0.4710	8.37	NS
	1978	20	-0.0089	0.3623	42.30	**
	1979	22	-0.0093	0.4359	46.81	**
	1980	29	-0.0140	0.3913	61.30	**
Age (years)	1976	25	0.08	12.98	0.21	NS
	1978	25	-0.05	14.83	0.11	NS
	1979	22	0.09	10.13	0.77	NS
	1980	26	-0.03	15.08	0.03	NS

[1] F test ^{NS} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$

Table 10. Regression analyses of harp seal pup parameters as a function of sampling date in March.

Variable	Year	n	Slope	Intercept	R^2	p[1]
Weight (kg)	1978	25	1.68	10.60	40.99	**
	1979	23	1.44	6.99	78.18	**
	1980	30	2.44	4.70	62.58	**
Sculp Wt (kg)	1978	25	1.11	3.59	41.21	**
	1979	23	1.07	-0.49	76.11	**
	1980	30	1.58	-0.84	58.08	**
Core Wt (kg)	1978	25	0.57	7.07	22.08	*
	1979	23	0.37	7.47	47.61	**
	1980	30	0.86	5.55	57.58	**
Standard Length (cm)	1978	25	0.79	91.46	19.42	NS
	1979	23	0.81	82.92	52.16	**
	1980	30	1.25	83.98	40.70	**
Axillary Girth (cm)	1978	25	1.98	56.86	37.68	**
	1979	23	2.09	42.99	79.65	**
	1980	30	3.23	45.36	64.05	**
Blubber Thickness (mm)	1978	25	2.01	11.57	49.30	**
	1979	21	1.68	3.98	65.81	**
	1980	30	3.06	0.35	63.87	**
Blubber Thickness (mm) / Standard Length (cm)	1978	25	0.019	0.123	51.61	**
	1979	21	0.017	0.057	60.13	**
	1980	30	0.029	0.020	62.07	**
Axillary Girth (cm) / Standard Length (cm)	1978	25	0.015	0.622	37.45	**
	1979	23	0.017	0.531	70.43	**
	1980	30	0.024	0.554	63.45	**
	overall	78	0.016	0.593	48.59	**
Sculp Wt (kg) / Standard Length (cm)	1978	25	0.011	0.038	44.99	**
	1979	23	0.011	0.002	77.28	**
	1980	30	0.015	-0.001	59.46	**

[1] F test NS > 0.05, * < 0.05, ** < 0.01

Table 11. Calculation of gross energy requirements of nursing harp seal pups.

Time (days)	Age Category[1] t	Estimated Age (days)[1]	Pup Weight (kg)	$2(70W^{0.75})$ kcal·d^{-1}	Sculp Wt kg	G I[2] kcal·d^{-1}	Core Wt kg	G I[2] kcal·d^{-1}	Total Daily Energy requirement kcal (Σcol 5,7,9)	Milk 3 Caloric Density kcal g^{-1}	Grams of mil Required To Meet Pups Needs
0	NB	0	10.29	804	2.42	0	7.87	0	804	2.99	269
1	y	1	13.02	960	4.33	10,601	8.69	1,142	12,703	3.16	4,323
2	TW	2	15.75	1107	6.24	13,084	9.51	1,164	15,355	3.33	4,611
3	TW	3	18.48	1248	8.15	13,084	10.33	1,164	15,496	3.50	4,427
4	TW	4	21.21	1384	10.06	13,084	11.15	1,164	15,632	3.67	4,259
5	FW	5	23.94	1515	11.97	14,994	11.97	1,714	18,223	3.84	4,746
6	FW	6	26.67	1643	13.88	14,994	12.79	1,714	18,357	4.00	4,589
7	FW	7	29.40	1768	15.79	14,994	13.61	1,714	18,476	4.17	4,431
8	G	8	32.13	1889	17.70	15,070	14.43	1,927	18,886	4.34	4,352
9	G	9	34.86	2009	19.61	15,070	15.25	1,927	19,006		
				14,327		124,975		13,630	152,932		36,011

$$Eq = MP_T = \frac{0 + (124,975 + 13,630) + 14,327}{0.80}$$

$$= 191,165 \text{ kcal}$$

1 Stewart and Lavigne 1980

2 G.A.J. Worthy, unpublished data for caloric densities of sculp and core:

Age Category	Caloric Density of Blubber	Caloric Density of Core
NB	5.56	1.29
Y	5.55	1.35*
TW	6.85	1.42
FW	7.85*	2.09
G	7.89	2.35*

3 Lavigne et al. 1981, caloric density of harp seal milk (kcal g^{-1}) = 2.99 + 0.169 pup age (d).

Table 12. Changes in sculp weight and compensatory fattening in harp seal pups (data from Table 6).

Year	Sculp Weight at Birth (kg)	Rate of Sculp Weight Gain (kg·d^{-1})	Sculp Weight at Weaning (day 9, kg)
1978	4.98	1.66	19.92
1979	2.27	1.96	19.91
1980	0.76	2.06	19.30

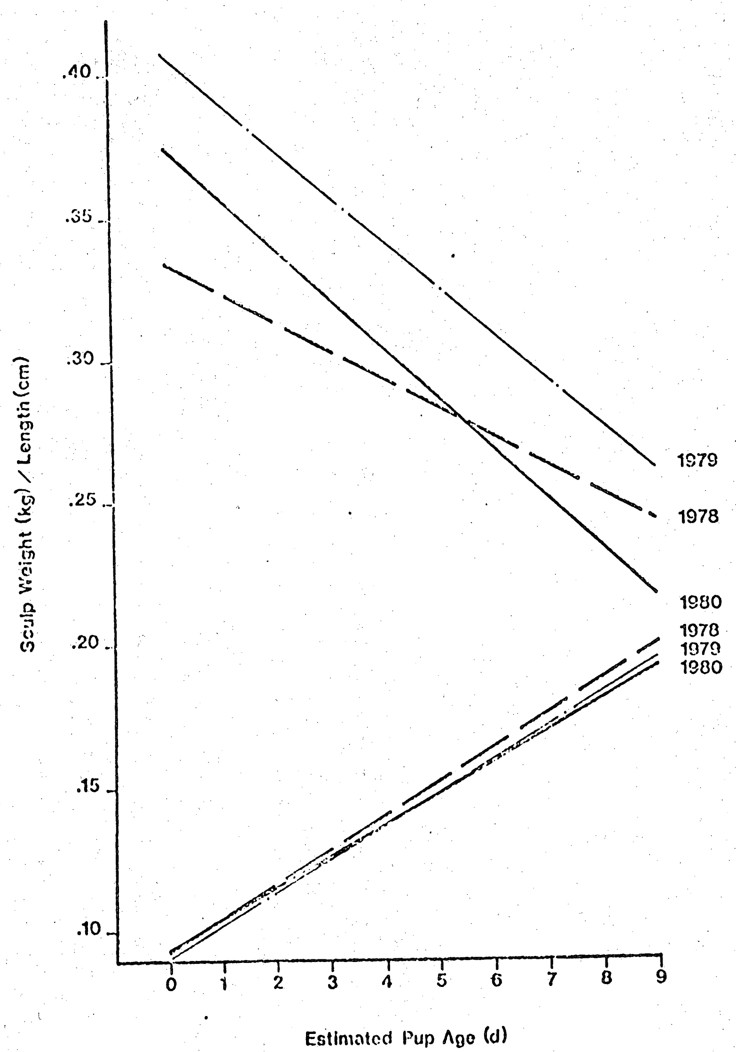

Fig. 1. Harp seal sculp weight index (sculp weight ÷ length) as a function of pup age (stage of lactation). Upper lines are females, lower lines are their pups. Numbers on the lines are years of collection.

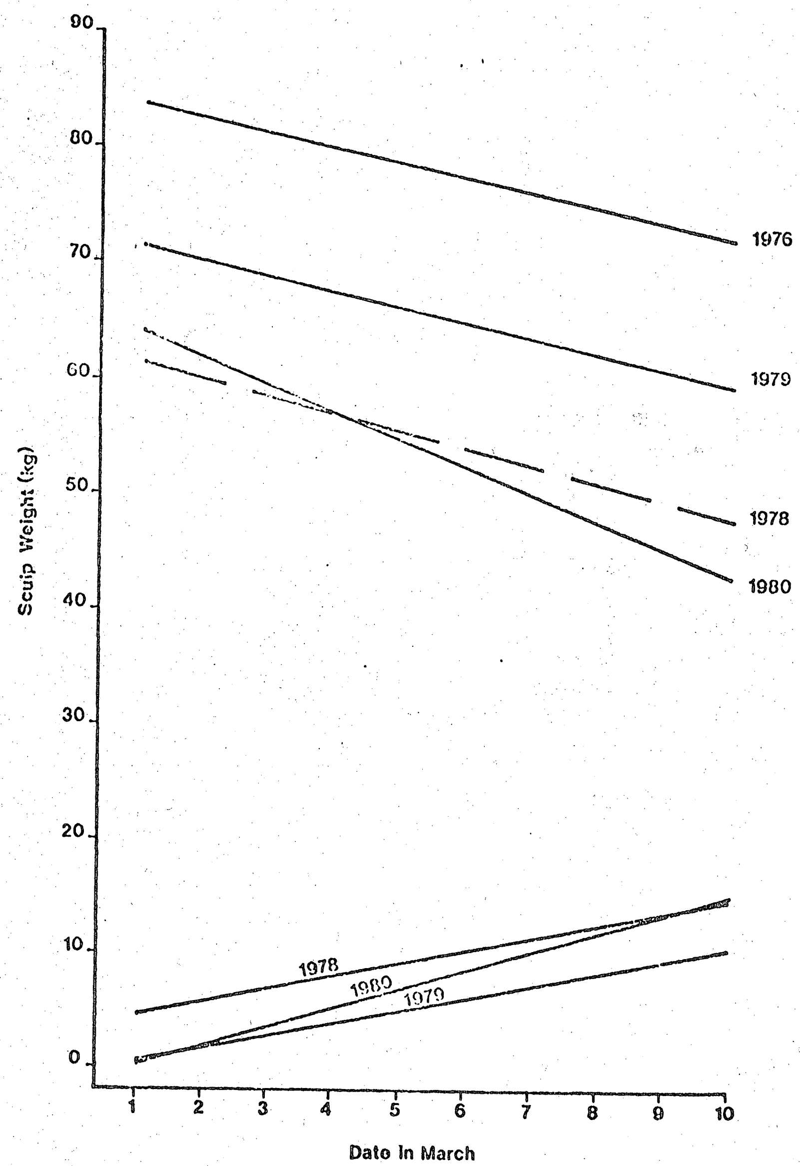

Fig. 2. Harp seal sculp weight as a function of sampling date in March. Upper lines are females, lower lines are their pups. Numbers indicate the years of collection.

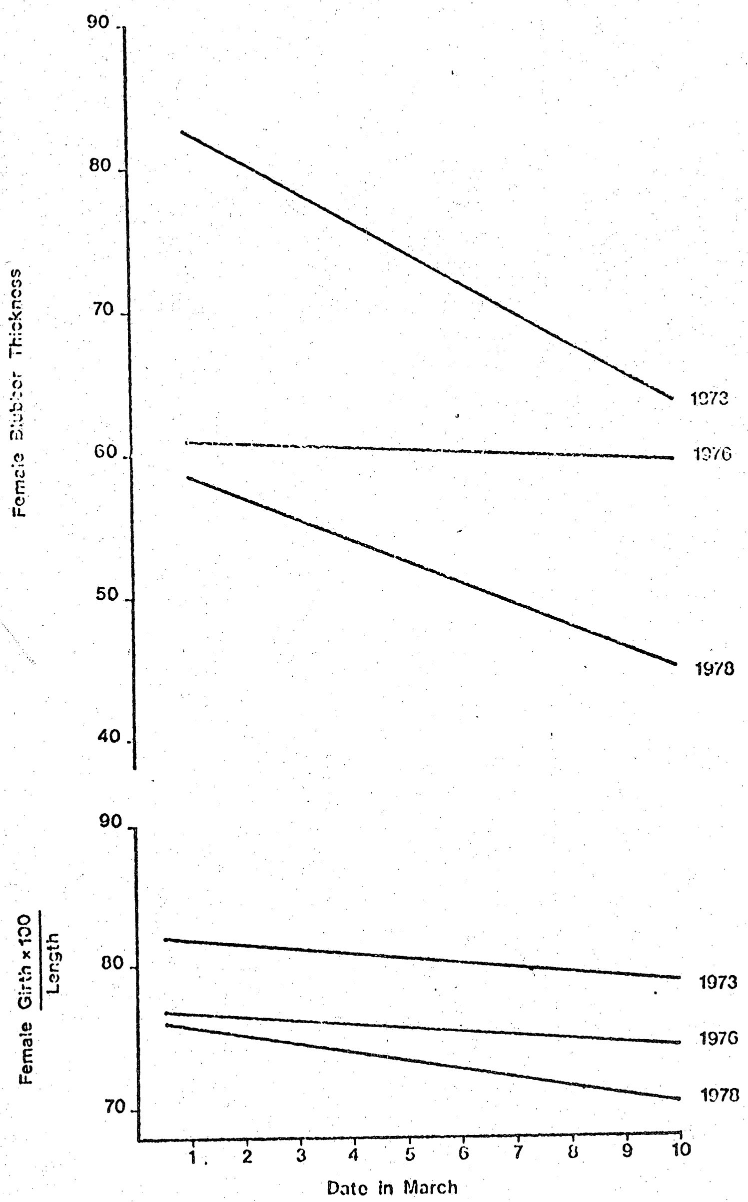

Fig. 3. A comparison of published data for the condition of female harp seals in the late 1960's early 1970's (Sergeant 1973), 1976 and 1978. (a) blubber thickness, (b) (girth.100).length^{-1} as functions of date in March.

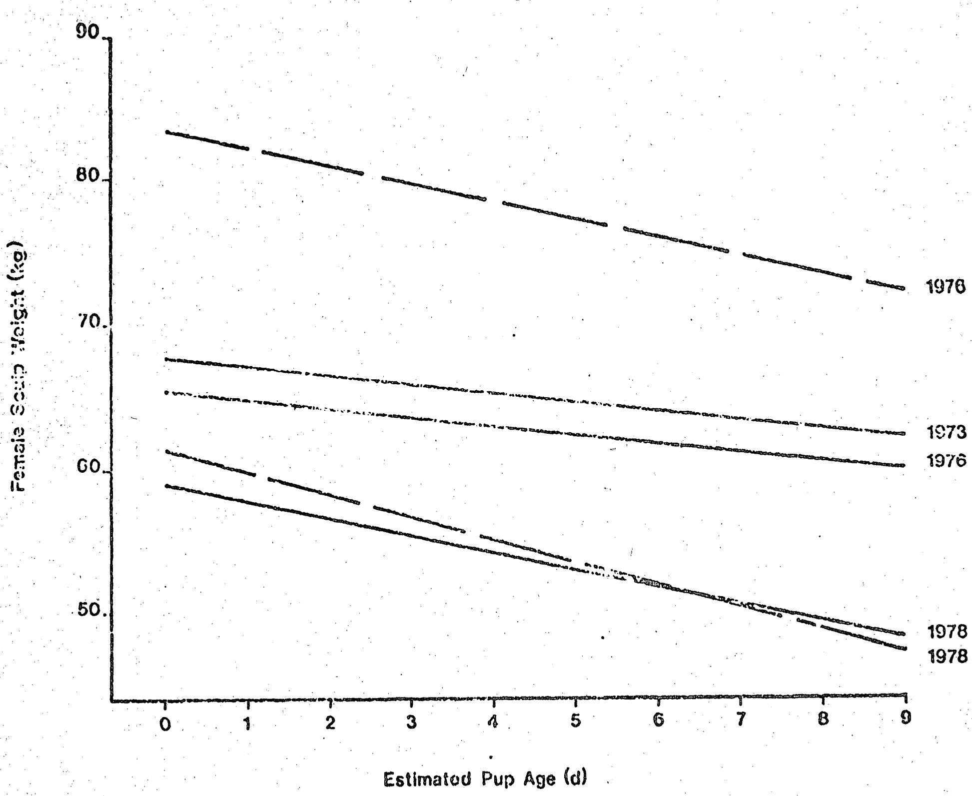

Fig. 4. Female harp seal sculp weight from Sergeant (1973) 1976 and 1978 determined by the equation SWT = $0.00191\ L^{0.269} \cdot Ga^{2.31}$ (see text for details).

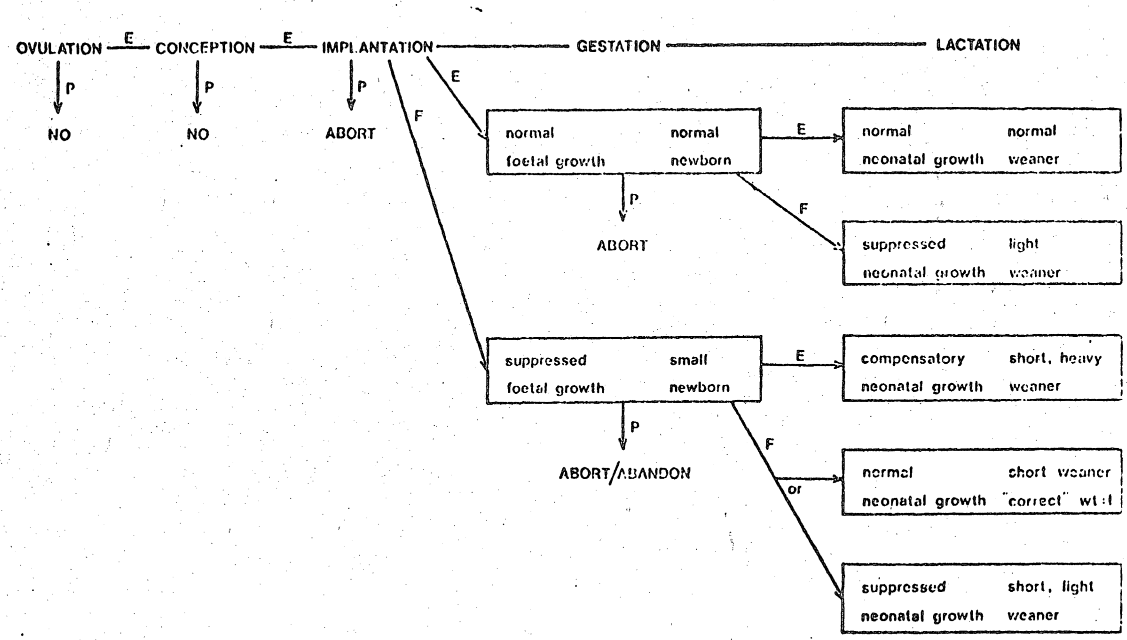

Fig. 5. Diagramatic representation of possible "choice" pathways for females depending on condition. E = excellent condition, F = fair, P = poor. These condition classifications are continuous and qualitative.