Fetal growth and the condition of pregnant northern fur seals off western North America from 1958 to 1972

ANDREW W. TRITES[1]
Resource Ecology and Department of Zoology, University of British Columbia, 2204 Main Mall, Vancouver, B.C., Canada V6T 1Z4

Received October 1, 1991
Accepted May 29, 1992

TRITES, A. W. 1992. Fetal growth and the condition of pregnant northern fur seals off western North America from 1958 to 1972. Can. J. Zool. **70**: 2125–2131.

Annual estimates of the condition of pregnant northern fur seals (*Callorhinus ursinus*) and the size of their fetuses were determined from over 2600 samples collected in the North Pacific from 1958 to 1972. A condition index related the observed mass of pregnant females (adjusted for fetal mass) to their predicted mass (calculated from body length). It showed that females carrying male fetuses were in poorer condition than those carrying female fetuses. It also showed that the mean condition of pregnant females improved from 1958 to 1964, but dropped sharply in 1965. Body condition remained poor until 1972, when it plunged again. Fetal mass declined throughout the 1960s, unlike body length, which changed very little. It is suggested that fetal growth, particularly mass, is a sensitive indicator of feeding conditions during the last trimester of pregnancy while pregnant females are in the Gulf of Alaska and Bering Sea. It is further speculated that the condition index for adults reflects overall feeding conditions experienced throughout the annual migration.

TRITES, A. W. 1992. Fetal growth and the condition of pregnant northern fur seals off western North America from 1958 to 1972. Can. J. Zool. **70** : 2125–2131.

La condition physique de femelles encientes de l'Otarie à fourrure (*Callorhinus ursinus*) et la taille de leurs fétus ont été estimées à l'examen de plus de 2600 animaux échantillonnés dans le nord du Pacifique entre 1958 et 1972. Un indice reliant la masse observée des femelles enceintes (ajustée en fonction de la masse du fétus) à leur masse théorique (calculée en fonction de leur longueur totale) a permis d'évaluer leur condition physique. Les résultats ont démontré que les femelles qui portaient des fétus mâles étaient en moins bonne condition que celles qui portaient des fétus femelles; de plus la condition moyenne des femelles enceintes s'est améliorée entre 1958 et 1964, puis a décliné abruptement en 1965. Cette mauvaise condition physique s'est maintenue jusqu'en 1972, après quoi elle a empiré davantage. La masse des fétus a diminué durant toute la décennie des années 1960, contrairement à la longueur totale qui a très peu changé. Il est possible que la croissance fétale, particulièrement la croissance en masse, constitue un indicateur assez sensible des conditions alimentaires durant le dernier trimestre de la grossesse, au moment où les femelles sont dans le golfe d'Alaska et dans la mer de Bering. Il est également probable que l'indice qui définit la condition physique des adultes reflète les conditions alimentaires générales rencontrées au cours de la migration annuelle.

[Traduit par la rédaction]

Introduction

Fetal growth and development are the outcome of many factors. Studies of humans and domestic animals have shown that fetal growth is influenced by 'intrinsic' factors such as the size, age, and parity of the mother (e.g., Walton and Hammond 1938; Dickinson *et al.* 1962; Miller and Merrit 1979; Price and White 1985). They have also shown that the size of the fetus is 'externally' affected by the quality and quantity of food available to the mother (e.g., Wallace 1948; Hight 1966; Payne and Wheeler 1967; Thorne *et al.* 1976; Mellor 1983; Holst *et al.* 1986).

In the current study the neonatal size of northern fur seals (*Callorhinus ursinus*) born on the Pribilof Islands, Alaska, was estimated from a regression analysis of over 2600 fetuses collected at sea from 1958 to 1972. The goal was to determine whether changes in fetal growth could be detected among years and related to the buildup of commercial fishing that began in the Gulf of Alaska and Bering Sea during the early 1960s. A second goal was to determine the average 'condition' of pregnant females for each year from 1958 to 1972.

Condition indices describe the relationship between body mass and length, and have been used to compare the effects of biotic and abiotic factors on the well-being of individuals and populations. Individuals with more mass at a given length are assumed to be in better condition. This technique has been extensively applied to fish populations (see Gershanovich *et al.* 1985; Bolger and Connolly 1989; Cone 1989), but rarely to pinnipeds and other species (e.g., Boyd and McCann 1989; Ryg *et al.* 1990; Trites and Bigg 1992).

Materials and methods

Pregnant females were collected from 1958 to 1974 by investigators from Canada and the United States under the auspices of the North Pacific Fur Seal Commission (Lander 1980). The biases inherent in the data set and the procedures used to measure and age the fetuses and adults are discussed in Lander (1980) and Trites (1991). Fetal growth curves and condition indices were only calculated for multiparous females between the ages of 8 and 13 years to minimize biases attributable to maternal age, size, and parity (Trites 1991). The analyses were further limited to data collected during the months of February through June to reduce the effect of incomplete mixing of seals of different ages and reproductive status during migration. Although data were collected until 1974, sample size was insufficient to estimate female condition and average fetal size in 1973 and 1974 (see Table 1 in Trites 1991).

Female condition index

The physical condition of a single pregnant female was quantified with a condition index (CI) defined as the ratio between the observed mass of the mother (M_m) and her expected mass ($\hat{M}_m$) adjusted for fetal mass. Thus

$$[1] \quad CI = \frac{M_m}{\hat{M}_m}$$

[1]Present address: Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, B.C., Canada V9R 5K6.

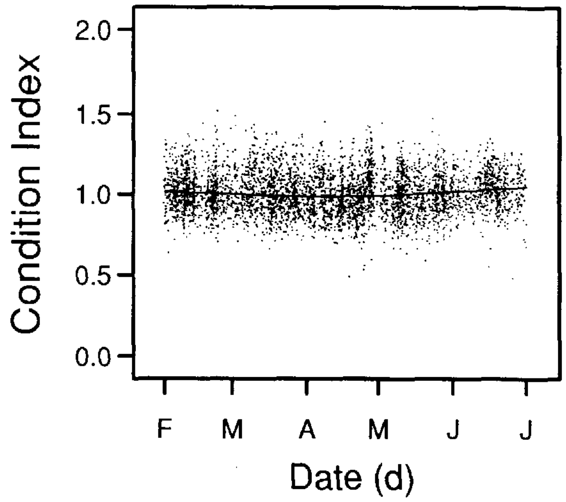

FIG. 1. Female condition versus sampling date (February 1 – June 30) for $\alpha = 1.75$. The data were jittered (by adding a small amount of random variation to each data point) to reduce overlap associated with roundoff error. All females, collected from 1958 to 1972, were multiparous and between the ages of 8–13 years. The condition indices were fit with nonparametric regressions, *lowess* (Cleveland 1979), and show little change as the fetus develops over time.

and

$$[2] \quad M_{\mathrm{m}} = M'_{\mathrm{m}} - \alpha M_{\mathrm{f}}$$

where M'_{m} is the mass of the mother (including fetus) and M_{f} is the mass of the fetus. The coefficient α corrects for additional mass associated with growth of the placenta, uterus, increased blood volume, etc. The expected mass of the mother, $\hat{M}_{\mathrm{m}}$, was estimated from the allometric relationship between length and mass. It was derived by regressing the mother's adjusted mass (eq. 2) against her measured body length, using all 2623 multiparous females, aged 8–13 years, collected from February to June, 1958–1972. Thus, expected mass was predicted from body length.

If α is chosen correctly, the mean condition of all females (from all years) will remain stable (i.e., CI = 1.0) throughout the period of fetal growth. Different values of α were tried systematically. For a given α, a condition index was calculated for each of the 2623 females and plotted against the date each female was sampled. If a linear regression fit to the data did not have an intercept of one and a slope of zero, the α was rejected and another value tested.

An annual estimate of female condition is the mean of the condition indices for all individuals collected in any given year. Thus, on an annual basis, the estimated mean index of condition will fall about the grand mean, depending upon whether conditions in any given year were 'good' (CI > 1.0) or 'bad' (CI < 1.0). The terms good and bad are relative, not absolute. For example, the entire population could experience poor conditions from 1958 to 1974, but conditions in some years may be worse than in others.

Annual fetal growth

The relationships between length and gestational age, and between mass and gestational age, were linearized. Linear models were fit to samples of male and female fetuses to determine the average growth rate by sex for each year from 1958 to 1972.

The gestational age of the fetus was assigned according to the date when the fetus was collected at sea. The date of implantation is believed to occur in early to mid November and is thought to vary little among years and individuals (Craig 1964). Thus, the fetuses were assigned a gestation age of 0 on November 10 (i.e., t = 0 d). Growth curves were therefore constructed for the period t = 82 (February 1) to t = 231 (June 30). The sizes (mass and length) of pups at birth (i.e., on June 30th) were estimated from these growth equations.

TABLE 1. Changes in the mean mass (in kilograms) of mothers and pups weighed at term (from Costa and Gentry 1986; males: n = 8, females: n = 11)

Sex of pup carried	Mother's mass: Pregnant (M'_{m})	Mother's mass: Postpartum (M_{m})	Pup mass (M_{f})	α
Male	52.5	42.3	6.23	1.64
Female	49.7	40.4	5.10	1.82

NOTE: Mothers were weighed pre- and post-partum and pups were weighed at birth. The coefficient α was calculated by rearranging the terms of eq. 2 such that $\alpha = (M'_{\mathrm{m}} - M_{\mathrm{m}})/M_{\mathrm{f}}$.

There appears to be very little annual variability in the return of adult females to the Pribilof Islands and in the timing of birth (Gentry and Francis 1981; Trites 1992). Pupping begins on about June 20 and finishes about 40 days later (Bartholomew and Hoel 1953; Peterson 1965). Over 50% of the pups are born during the first 2 weeks of July (Trites 1992).

Results

Approximately 3000 multiparous pregnant females aged 8–13 years were shot between February and June, 1958–1972. Of the total, 2623 adults were both weighed and measured; 2864 fetuses were weighed and 2869 fetuses measured.

Female condition index

Various α levels were tested before selecting $\alpha = 1.75$. This value gave a mean condition index of 1.0 when the data from all years were combined (Fig. 1) and was very close to the α value estimated from changes in the mean mass of pregnant females and pups weighed at term (Table 1). The predicted mass of adult females (in kilograms and adjusted for the mass of the fetus) was estimated from the mother's length, L_{m} (in centimetres), according to the linear relation $M'_{\mathrm{m}} = -45.150 + 0.643\, L_{\mathrm{m}}$.

There was a general improvement in the condition of females sampled from 1958 to 1964 (Fig. 2*a*). In 1965, the condition index dropped below 1.0 and remained relatively constant until 1972, when another sharp drop occurred. Overall, mothers carrying male fetuses were in poorer condition than those with female fetuses (Fig. 2*b*).

Annual fetal growth

Various transformations were tried to linearize the fetal length–time and mass–time relationships before selecting the linear models $L_t = a + bt^{0.5}$ and $M_t^{1/2.75} = a + bt^{0.5}$ (Fig. 3). The reciprocal power (2.75) was drawn from the relationship between length and mass of northern fur seal fetuses (Trites 1991). Sex-specific growth curves are shown in Fig. 4.

Annual estimates of fetal size at term (June 30) were derived from linear regressions and are contained in Fig. 5 and Tables 2 and 3. Estimates were rejected in 2 of the 15 years examined. In one case, 1963, the few data represented about 2 days of sampling and gave a poor fit (Tables 2 and 3). In the other case, 1967, sample sizes were also insufficient. Sex-specific regressions for male and female fetuses were compared with regressions for the sexes combined. In all years except 1967, estimates of the mass and length of fetuses at term from the pooled samples fell between those of the males and females estimated independently. But in 1967, the average

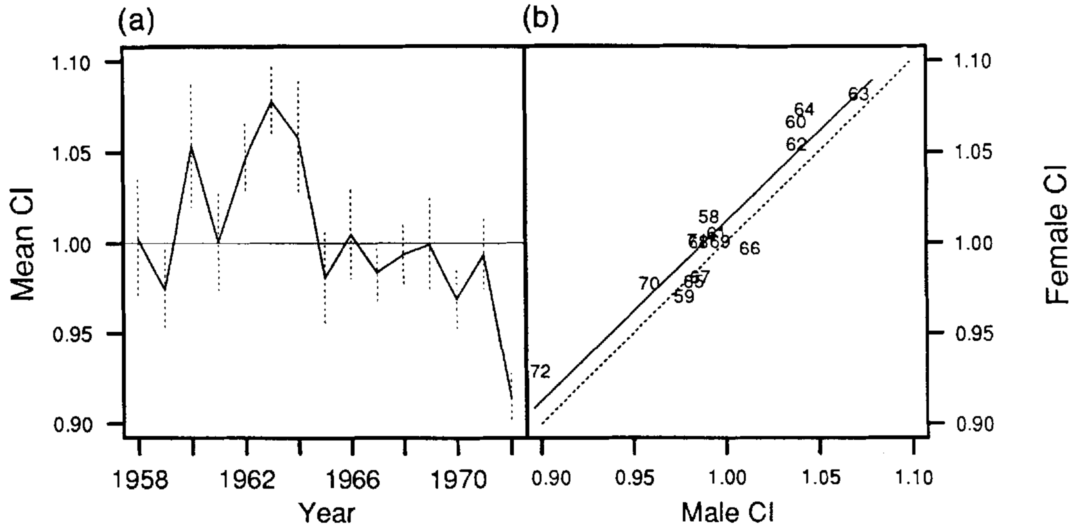

FIG. 2. (*a*) Mean condition of multiparous females, aged 8–13 years, carrying male and female fetuses. The vertical bars mark 95% confidence limits and the horizontal reference line shows CI = 1.0. (*b*) Condition index of mothers carrying female fetuses (female CI) versus those carrying male fetuses (male CI). Data are identified by year and were fit with a linear regression (solid line). The broken line represents female CI = male CI.

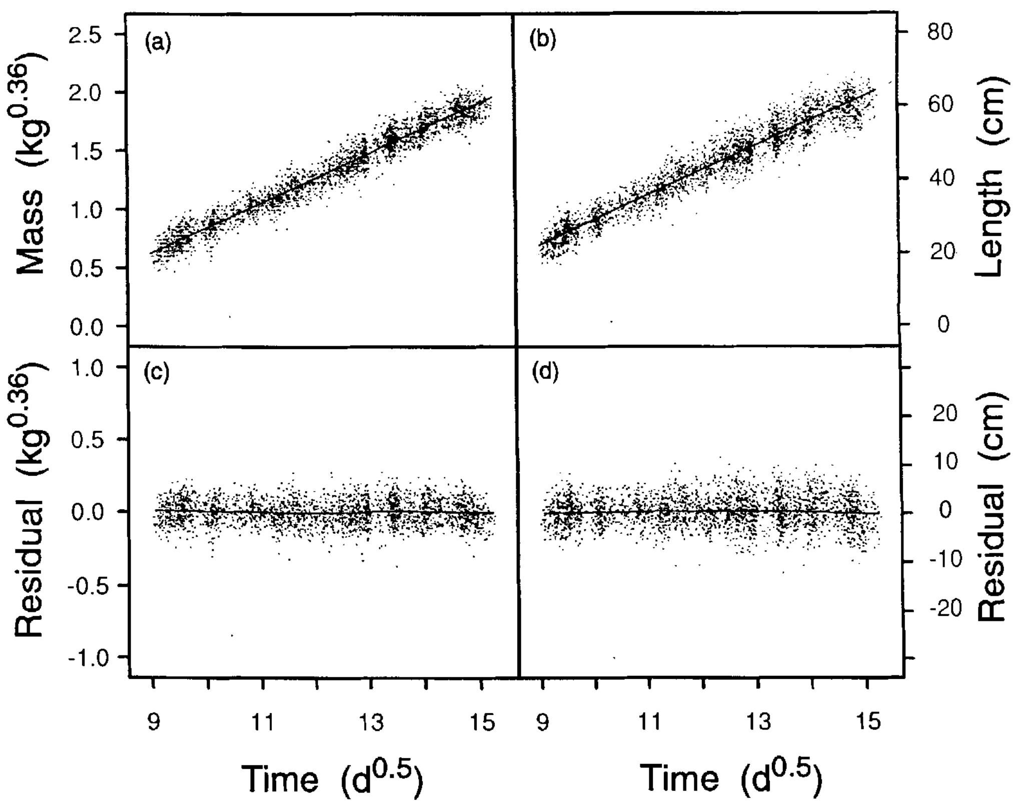

FIG. 3. Linear regression of fetal length and mass over time. (*a* and *b*) Jitter plots of 2869 lengths (in cm) and 2864 masses (in $kg^{0.36}$) versus the Julian date when collected (with units $d^{0.5}$). A least-squares regression line is superimposed on each data set. No systematic structure appears in the residual plots that were smoothed with *lowess* (*c* and *d*). Fetuses were from 2869 multiparous females aged 8–13 years, sampled over the period February 1 – June 30, 1958–1972.

size of all fetuses combined exceeded the estimated mass of males and females derived separately from sex-specific regressions, thereby putting the reliability of the 1967 data into doubt.

There was considerable variability in the estimated average size of fetuses at term (Fig. 5). The general trend from 1958 to 1972 was a relatively stable fetal length (weighted linear regression $F_{[1,11]} = 2.13$, $p = 0.17$), but a decrease in mass ($F_{[1,11]} = 5.68$, $p = 0.03$). Annual estimates of length and mass of fur seal fetuses at birth compared favorably with those predicted from the empirical mass–length relationship (Fig. 5*c*). The exceptions were 1958 and 1960, when fetuses were much heavier than expected, and 1970, 1971, and 1972, when

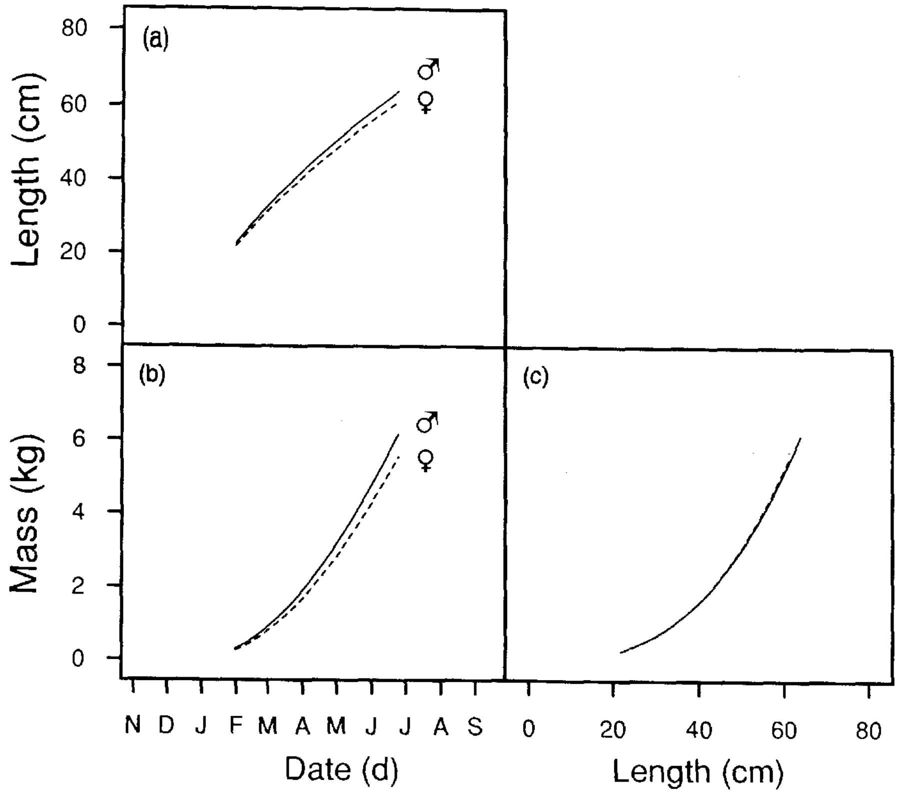

FIG. 4. Growth curves for male (solid line) and female (broken line) fetuses taken from multiparous females aged 8–13 years. The growth curves for each sex were derived from least-squares regressions of the data contained in Fig. 3.

TABLE 2. Regressions of fetal length (L_t) in centimetres as a function of time (t) in days such that $L_t = a + bt^{0.5}$ and $82 \leq t \leq 231$ (February 1 – June 30)

Year	Intercept (a)	Slope (b)	L_{231}	Sample size	r^2	F
1958	−38.144	6.739	64.29	564	0.925	6952.1
1959	−41.111	6.931	64.22	452	0.909	4496.5
1960	−28.181	5.910	61.64	577	0.811	2463.6
1961	−38.092	6.664	63.20	319	0.886	2461.2
1962	−33.244	6.380	63.72	189	0.894	1569.3
1963	27.773	2.239	61.80	67	0.045	3.0
1964	−42.486	7.101	65.44	74	0.592	104.6
1965	−32.479	6.332	63.76	68	0.690	146.6
1966	−37.708	6.630	63.05	93	0.856	540.6
1967	−45.142	7.394	67.23	18	0.971	533.9
1968	−34.041	6.483	64.49	157	0.955	3314.2
1969	−30.227	6.054	61.79	101	0.888	784.3
1970	−37.932	6.761	64.82	62	0.921	700.4
1971	−43.775	7.244	66.33	68	0.858	399.7
1972	−40.100	7.019	66.59	57	0.862	343.3
1958–1972	−38.203	6.717	63.88	2869	0.934	40711.1

NOTE: The fetuses were from multiparous mothers aged 8–13 years. All regressions (except 1963) were highly significant ($p < 0.0001$).

fetuses were considerably lighter than expected. These good and bad years might reflect general feeding conditions in the Gulf of Alaska and Bering Sea.

There appears to be no relationship between the physical condition of the mother and the mass ($F_{[1,11]} = 0.29$, $p = 0.60$) and length ($F_{[1,11]} = 3.02$, $p = 0.11$) of the fetus at term.

Discussion

The proposed condition index is similar to the relative weight procedure of Wege and Anderson (1978), which relates observed mass to a hypothetical ideal mass based on length. Cone (1989) points out that the relative weight procedure depends upon determining an assumed ideal relationship and is doubtful that such a relationship exists for all populations of a species. However, he notes that this approach may be suitable for comparisons made within a given size class.

The fur seal condition index was calculated for multiparous females (ages 8–13 years) sampled between February and June. As such, it can be argued that the comparisons were restricted to a given size class. Furthermore, by pooling all of

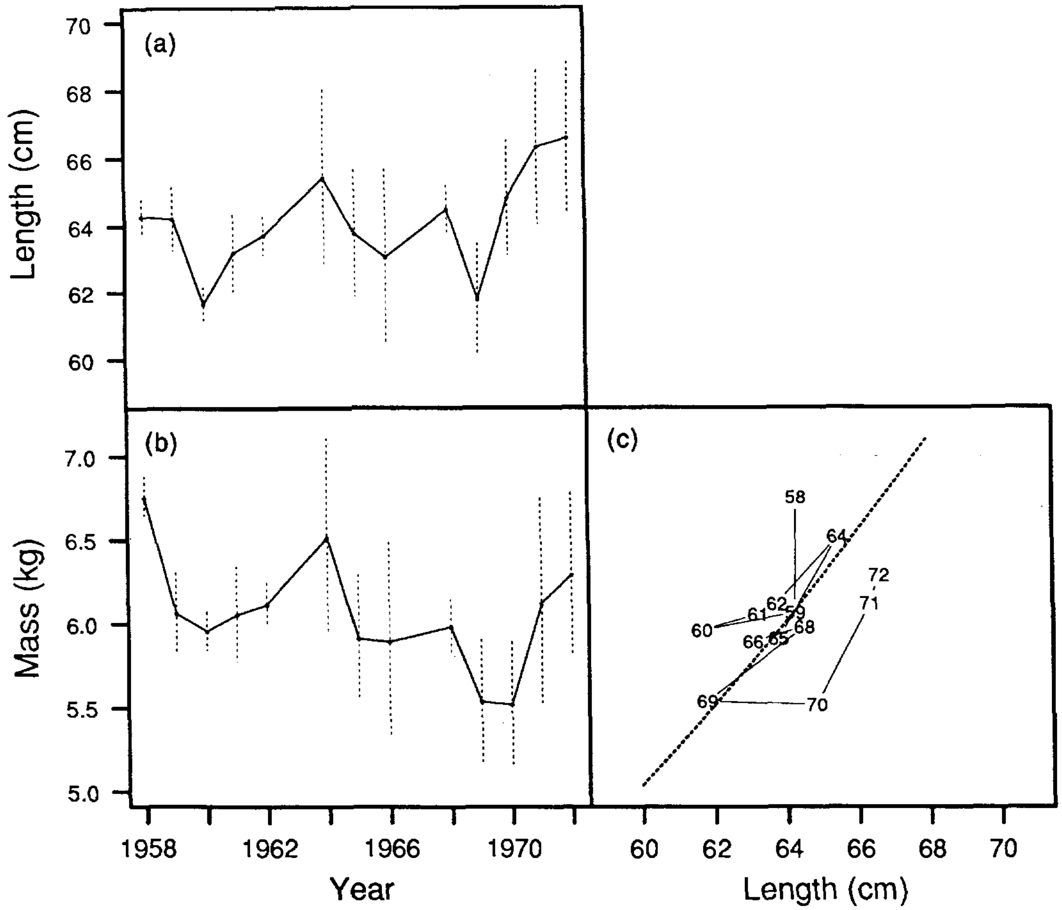

FIG. 5. (*a*, *b*) Mean mass and length of fetuses at term (June 30) from 1958 to 1972. Estimates were derived from the linear regressions contained in Tables 2 and 3 and are shown with 95% confidence limits (vertical bars). No estimates are shown for 1963 and 1967. (*c*) The estimated mass at birth versus length at birth. Each point is identified by year. Superimposed is the predicted relationship between fetal mass and length (from Trites 1991).

TABLE 3. Regressions of fetal mass (W_t) in kilograms as a function of time (t) in days such that $W_t^{1/2.75} = a + bt^{0.5}$ and $82 \leq t \leq 231$ (February 1 – June 30)

Year	Intercept (a)	Slope (b)	W_{231}	Sample size	r^2	F
1958	−1.4698	0.228	6.754	563	0.949	10501.5
1959	−1.2897	0.212	6.069	452	0.918	5065.2
1960	−1.1339	0.200	5.963	578	0.884	4387.3
1961	−1.2123	0.206	6.060	320	0.902	2921.3
1962	−1.1784	0.205	6.120	182	0.927	2283.0
1963	−0.2183	0.139	5.829	69	0.216	18.4
1964	−1.6765	0.240	6.518	73	0.741	203.1
1965	−1.1364	0.200	5.914	68	0.806	273.5
1966	−1.2050	0.205	5.896	93	0.895	777.7
1967	−1.4624	0.232	7.284	18	0.964	428.0
1968	−1.1033	0.199	5.985	157	0.965	4306.2
1969	−0.9606	0.186	5.540	101	0.915	1064.4
1970	−0.9984	0.188	5.520	62	0.928	767.9
1971	−1.3125	0.213	6.124	68	0.846	361.7
1972	−1.3379	0.216	6.291	57	0.909	550.1
1958–1972	−1.2713	0.211	6.190	2864	0.952	56315.8

NOTE: The fetuses were from multiparous mothers aged 8–13 years. All regressions (except 1963) were highly significant ($p < 0.0001$).

the data to determine the average relationship between length and mass, each hypothetical mass estimated for any given individual represents a deviation from the total. Thus, the use of the condition index is sound because it reflects the condition of an individual fur seal relative to the condition of all others sampled.

The morphometric data suggest that it costs a fur seal mother more to produce a male fetus than a female fetus given that females carrying male fetuses were in poorer condition than those with female fetuses (Fig. 2*b*). Such deductions are consistent with other pinniped studies that have shown females (grey seals, sea lions, and fur seals) investing more in male than in female offspring (Costa and Gentry 1986; Kovacs and Lavigne 1986*a*; Trillmich 1986; Anderson and Fedak 1987). Differential investment strategies may be related to the size of the mother, given that some pinniped species (e.g., harp seals and southern elephant seals) do not appear to withhold resources from female fetuses (Kovacs and Lavigne 1986*b*; Campagna *et al.* 1992).

It is not known whether the extra cost of producing a male pup, in terms of overall metabolic cost to the mother, is significant. Boyd and McCann (1989) estimated that the average metabolic cost of fetal growth incurred by Antarctic fur seals was under 2% of normal metabolic costs, although fetal growth may represent 5–15% of the mother's energy budget in the final months of gestation. The difference between male and female Antarctic fur seal fetuses was about 0.3% of the mother's total metabolic cost. Set in this context, the differential costs of producing a male or female offspring (as shown in Fig. 2) may be overstated. Perhaps some of the observed differences are related to the selection of α (eq. 2).

Many studies of domestic animals have shown that the size of the fetus is affected by the quality and quantity of food available to the mother (e.g., Wallace 1948; Hight 1966; Payne and Wheeler 1967; Thorne *et al.* 1976; Mellor 1983; Holst *et al.* 1986). In particular, the fetal growth rate is extremely sensitive to underfeeding rather than overfeeding because there is a physiological upper limit on growth. Furthermore, undernourishment causes larger reductions in the mass of fetuses than in their length (Mellor 1983). Food restrictions are felt more during the later part of pregnancy than during early development. During early pregnancy, females can draw on their own body reserves to meet the requirements of their growing fetus. But during the last trimester of pregnancy, the females must rely on an external supply of good-quality food to nourish their fetuses (Mellor and Murray 1982; Mellor 1983; Holst *et al.* 1986).

It is not known how female fur seals use their body resources over the course of a pregnancy. However, there is no reason to suppose that fur seals are unlike domesticated mammals. Increases in fur seal fetal length and mass occur primarily during early and late pregnancy, respectively (Trites 1991). Fetal growth curves indiate that 32% of body length and 4% of body mass at term are attained in the first trimester of pregnancy, and that a further 28% of length and 63% of mass are attained in the last trimester (Trites 1991). Signs of malnourishment or improved nutrition are most likely to be noted in fetal mass in the last trimester of pregnancy, when females are unable to rely on their body reserves alone to nourish their fetuses.

The annual fur seal migration extends 5000 km from the Bering Sea to California (Kajimura 1980; Bigg 1990). Pregnant females begin leaving the Pribilof Islands in the fall. By early February, most have arrived off the coast of southern California and are ready to return north. Most of the population passes through the coastal waters of Washington in April, and British Columbia waters in early May, arriving on the Pribilofs in late June or early July.

The North Pacific can be divided into two main coastal fish-producing domains, the coastal downwelling domain (northern British Columbia and Alaska) and the coastal upwelling domain (southern British Columbia to Baja California) (Ware and McFarlane 1989). The downwelling domain is dominated by walleye pollock, Pacific herring, sand lance, and capelin, all of which figure prominently in the fur seal diet (Perez and Bigg 1981, 1986; Kajimura 1985). Dominant species in the upwelling domain include northern anchovy, Pacific hake, and jack mackerel.

Fur seals of all ages experience rapid growth and weight gains while migrating northward through the coastal waters of northern British Columbia and Alaska, the downwelling domain (Trites 1990). Body mass is maintained or lost during the remainder of the year.

During the last trimester of pregnancy, while in the downwelling domain, the average fur seal fetus gains over 63% of its final body mass. But over 72% of the body length at term is achieved while the mothers are off the coasts of California, Oregon, and Washington, in the upwelling domain. Thus, it could be inferred from the estimates of length (Fig. 5) that females experienced satisfactory feeding conditions from 1958 to 1972. The significant declining trend in mass at birth suggests reduced food availability in the Gulf of Alaska and Bering Sea through the 1960s and into the 1970s.

The condition index for pregnant females suggests that their physical condition improved from 1958 to 1974, and was poor, relative to other years, from 1965 to 1972 (Fig. 2). But it is not clear how readily the condition index reflects changes in food availability. Given that female northern fur seals have a low innate capacity to store fat reserves and do not have a great deal of body fat relative to phocids, it may not be possible to statistically detect annual changes in body mass with small sample sizes. The condition index applied to female fur seals may not be very sensitive to short-term changes in food, but instead may be an integration of the growth conditions experienced over several years. Should this be true, the estimated condition of fur seals between 1958 and 1972 may reflect general feeding conditions over many years and areas, but may not be useful in identifying significant years of malnourishment and depleted geographic feeding areas.

The relationship between condition index and fetal size was not statistically significant, although the correlation between CI and fetal length ($r^2 = 0.22$, $n = 13$, $p = 0.11$) was much higher than the correlation between CI and fetal mass ($r^2 = 0.02$, $n = 13$, $p = 0.60$). In all likelihood, females draw on their own body resources during the initial development of the fetus when most of fetal body length is established. But during the last trimester, the mother relies much more on external energy sources. Thus, fetal mass is probably a good indicator of feeding conditions encountered in the Gulf of Alaska and Bering Sea.

Fur seal prey abundance can be influenced by commercial fisheries and natural environmental fluctuations (Trites and Bigg 1992). These factors can potentially alter the quantity and quality of prey available to pregnant fur seals and hence could affect fetal growth. Unfortunately, only inferences can be made from fetal size and adult condition because little is known about the size of fish stocks during the time that fur seals were sampled at sea (1958–1972). As such, the fetal measurements and condition of pregnant females suggest that pregnant females encountered better feeding conditions in the North Pacific in the early 1960s than in the latter part of the decade.

Acknowledgements

I am grateful to the Department of Fisheries and Oceans, Canada, and to the National Marine Fisheries Service, U.S.A., for allowing me access to the pelagic fur seal data base. The data set represents thousands of hours of collection and preparation, and has involved the efforts of many individuals. Mike Perez and Michael Bigg helped to verify questionable data with the original field records. I also extend my appreciation to Michael Bigg, Monique Bournot, Ian Boyd, Dean Fisher, Harry Joe, Don Ludwig, Carl Walters, Peter Watts, and an anonymous reviewer for their constructive comments and suggestions on earlier drafts of the manuscript.

Anderson, S. S., and Fedak, M. A. 1987. Grey seal, *Halichoerus grypus*, energetics: females invest more in male offspring. J. Zool. (Lond.), **211**: 667–679.

Bartholomew, G. A., and Hoel, P. G. 1953. Reproductive behaviour of the Alaska fur seal *Callorhinus ursinus*. J. Mammal. **34**: 417–436.

Bigg, M. A. 1990. Migration of northern fur seals (*Callorhinus ursinus*) off western North America. Can. Tech. Rep. Fish. Aquat. Sci. No. 1764.

Bolger, T., and Connolly, P. L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. **34**: 171–182.

Boyd, I. L., and McCann, T. S. 1989. Pre-natal investment in reproduction by female Antarctic fur seals. Behav. Ecol. Sociobiol. **24**: 377–385.

Campagna, C., Le Boeuf, B. J., Lewis, M., and Bisioli, C. 1992. Equal investment in male and female offspring in southern elephant seals. J. Zool. (Lond.), **226**: 551–562.

Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. **74**: 829–836.

Cone, R. S. 1989. The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. **118**: 510–514.

Costa, D. P., and Gentry, R. L. 1986. Free-ranging energetics of the northern fur seals. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R. L. Gentry and G. L. Kooyman. Princeton University Press, Princeton, N.J. pp. 79–101.

Craig, A. M. 1964. Histology of reproduction and the estrus cycle in the female fur seal, *Callorhinus ursinus*. J. Fish. Res. Board Can. **21**: 773–821.

Dickinson, A. G., Hancock, J. L., Hovell, G. J. R., Taylor, St. C. S., and Wiener, G. 1962. The size of lambs at birth—a study involving egg transfer. Anim. Prod. **4**: 64–79.

Gentry, R. L., and Francis, J. M. 1981. Part 2. Behaviour and biology, Pribilof Islands. *In* Fur seal investigations, 1980. *Edited by* P. Kozloff. U.S. Department of Commerce, National Marine Fisheries Service, Northwest Atlantic Fisheries Commission Proceedings Rep. 81-2. pp. 23–30.

Gershanovich, N. M., Markevich, N. M., and Dergaleva, Zh. T. 1985. Using the condition factor in ichthyological research. J. Ichthyol. (Engl. Transl. Vopr. Ikhtiol.), **24**: 78–90.

Hight, G. K. 1966. The effects of undernutrition during late pregnancy on beef cattle production. N.Z. J. Agric. Res. **9**: 479–490.

Holst, P. J., Killeen, I. D., and Cullis, B. R. 1986. Nutrition of the pregnant ewe and its effect on gestation length, lamb birth weight and lamb survival. Aust. J. Agric. Res. **37**: 647–655.

Kajimura, H. 1980. Distribution and migration of northern fur seals (*Callorhinus ursinus*) in the eastern Pacific. *In* Preliminary analysis of pelagic fur seal data collected by the United States and Canada during 1958–74. *Edited by* H. Kajimura, R. H. Lander, M. A. Perez, A. E. York, and M. A. Bigg. Available from National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way N.E., Seattle, Wash. pp. 9–49.

Kajimura, H. 1985. Opportunistic feeding by the northern fur seal, (*Callorhinus ursinus*). *In* Marine mammals and fisheries. *Edited by* J. R. Beddington, R. H. J. Beverton and D. M. Lavigne. George Allen and Unwin, London. pp. 300–318.

Kovacs, K. M., and Lavigne, D. M. 1986*a*. Growth of grey seal (*Halichoerus grypus*) neonates: differential maternal investment in the sexes. Can. J. Zool. **64**: 1937–1943.

Kovacs, K. M., and Lavigne, D. M. 1986*b*. Maternal investment and neonatal growth in phocid seals. J. Anim. Ecol. **55**: 1035–1051.

Lander, R. H. (*Editor*). 1980. Summary of northern fur seal data and collection procedures. Vol. 2. Eastern Pacific pelagic data of the United States and Canada (excluding fur seal sighted). NOAA Tech. Mem. No. NMFS F/NWC-4.

Mellor, D. J. 1983. Nutritional and placental determinants of foetal growth rate in sheep and consequences for the newborn lamb. Br. Vet. J. **139**: 307–324.

Mellor, D. J., and Murray, L. 1982. Effects of long term undernutrition of the ewe on the growth rates of individual fetuses during late pregnancy. Res. Vet. Sci. **32**: 177–180.

Miller, H. C., and Merrit, T. A. 1979. Fetal growth in humans. Year Book Medical Publishers, Chicago.

Payne, P. R., and Wheeler, E. F. 1967. Comparative nutrition in pregnancy. Nature (London), **215**: 1134–1136.

Perez, M. A., and Bigg, M. A. 1981. An assessment of the feeding habits of the northern fur seal in the eastern Pacific Ocean and eastern Bering Sea. Available from National Marine Mammal Laboratory, National Marine Fisheries Service, 7600 Sand Point Way N.E., Seattle, Wash.

Perez, M. A., and Bigg, M. A. 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fish. Bull. **84**: 957–971.

Peterson, R. S. 1965. Behavior of the northern fur seal. Ph.D. thesis, School of Hygiene and Public Health, The John Hopkins University, Baltimore, Md.

Price, M. A., and White, R. G. 1985. Growth and development. *In* Bioenergetics of wild herbivores. *Edited by* R. J. Hudson and R. G. White. CRC Press, Bocan Raton, Fla. pp. 183–236.

Ryg, M., Smith, T. G., and Oritsland, N. A. 1990. Seasonal changes in body mass and body composition of ringed seals (*Phoca hispida*) on Svalbard. Can. J. Zool. **68**: 470–475.

Thorne, W. T., Dean, R. W., and Hepworth, W. G. 1976. Nutrition during gestation in relation to successful reproduction in elk. J. Wildl. Manage. **40**: 330–335.

Trillmich, F. 1986. Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. Behav. Ecol. Sociobiol. **19**: 157–164.

Trites, A. W. 1990. The northern fur seal: biological relationships, ecological patterns and population management. Ph.D. thesis, Department of Zoology, University of British Columbia, Vancouver.

Trites, A. W. 1991. Fetal growth of northern fur seals: life history strategy and sources of variation. Can. J. Zool. **69**: 2608–2617.

Trites, A. W. 1992. Reproductive synchrony and the estimation of mean date of birth from daily counts of northern fur seal pups. Mar. Mammal Sci. **8**: 44–56.

Trites, A. W., and Bigg, M. A. 1992. Changes in body growth of northern fur seals from 1958 to 1972: density effects or changes in the ecosystem? Fish. Oceanogr. **1**: 127–136.

Wallace, L. R. 1948. The growth of lambs before and after birth in relation to the level of nutrition. J. Agric. Sci. **38**: 93–153.

Walton, A., and Hammond, J. 1938. The maternal effects on growth and conformation in Shire horses – Shetland pony crosses. Proc. R. Soc. London B, **125**: 311–335.

Ware, D. M., and McFarlane, G. A. 1989. Fisheries production domains in the northeast Pacific Ocean. *In* Effect of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. *Edited by* R. J. Beamish and G. A. McFarlane. Can. Spec. Publ. Fish. Aquat. Sci. **108**: 359–379.

Wege, G. J., and Anderson, R. O. 1978. Relative weight (W_r): a new index of condition for largemouth bass. *In* New approaches to the management of small impoundments. *Edited by* G. D. Novinger and J. G. Dillard. Am. Fish. Soc. Spec. Publ. No. 5. pp. 79–91.