

# Fetal growth of northern fur seals: life-history strategy and sources of variation

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Sex-specific growth curves are described for northern fur seal fetuses, *Callorhinus ursinus*. The relationships between body length, body mass, and gestational age are derived by regression analysis based on 7000 fetuses collected during 1958–1974 as part of a joint Canadian–American pelagic research effort. Male fetuses grow faster and larger than female fetuses. Length approaches an asymptote with time, but the increase in fetal mass appears exponential until parturition. The size of the fetus is influenced by the age, size, and reproductive history of the mother. Primiparous females produce smaller pups than multiparous females. This difference in fetal size is presumably due to physiological changes associated with having been previously pregnant and is not explained merely by differences in the size and age of the different parities. Older and larger females produce progressively larger fetuses until reaching their reproductive prime at about the age of 10–11 years. Adult females continue to grow beyond this age, but there is a senescent decline in the length and mass of the young they carry. There is no indication that the sex ratio differs from unity either between months, across years, or between mothers of different ages and parities.

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On trouvera ici la description des courbes de croissance spécifiques au sexe chez l'otarie à fourrure *Callorhinus ursinus*. Les relations entre la longueur du corps, la masse du corps et l'âge du fœtus ont été obtenues par une analyse de régression de données recueillies chez 7000 fœtus récoltés entre 1958 et 1974 au cours d'un programme conjoint Canada – États-Unis de recherche sur la zone pélagique. Les fœtus mâles croissent plus vite et deviennent plus gros que les fœtus femelles. La longueur des fœtus suit une courbe asymptotique, mais l'augmentation de la masse fœtale semble exponentielle jusqu'à la parturition. La taille du fœtus est fonction de l'âge, de la taille et de l'expérience reproductrice de la mère. Les femelles primipares produisent des rejetons plus petits que les femelles multipares. La différence dans la taille des fœtus semble due surtout à des changements physiologiques associés à des grossesses antérieures et ne peut pas s'expliquer seulement par des différences dans la taille et l'âge au moment des parturitions. Les femelles plus vieilles et plus grosses produisent des fœtus progressivement plus gros jusqu'à l'âge optimal de la reproduction, soit 10–11 ans. Les femelles continuent de croître après cet âge, mais il se produit une diminution, reliée à la sénescence, de la longueur et de la masse des rejetons qu'elles portent. Le rapport mâles:femelles ne semble pas différer significativement de 1:1 d'un mois à l'autre, d'une année à l'autre ou chez les mères d'âges différents ou d'expériences reproductrices différentes.

[Traduit par la rédaction]

## Introduction

Quantitative descriptions of fetal growth are useful for exploring the evolution of various life-history strategies (e.g., Huggett and Widdas 1951; Stephenson 1962; Evans and Sacks 1973; Frazer and Huggett 1974; Frazer 1977; Case 1978; Calder 1982; Peters 1983). They are also potentially useful when applied on a population level to assess environmental stresses, or used to interpret the impact of maternal age, size, and parity on the developing fetus. This is particularly relevant to studies that make inferences about population status from the size of individuals measured at birth.

There are few studies of fetal growth in pinnipeds (see Hewer and Backhouse 1968; Stewart *et al.* 1989). This is due to the large number of samples required to accurately quantify growth and the difficulty of obtaining them. Early studies of northern fur seals (*Callorhinus ursinus*) provided anatomical descriptions of the developing fetus and discussed the timing of implantation (Enders *et al.* 1946; Pearson and Enders 1951; Baker 1957; Scheffer 1960, 1962; Craig 1964, 1966), but were insufficient for quantifying the fetal growth process because of limited sample sizes. In 1958, a pelagic research program was started by Canada and the United States as members of the North Pacific Fur Seal Commission (Lander 1980a). By 1974, over 7000 fetuses had been collected. Preliminary analyses of this data set indicated that males fetuses were larger than female fetuses (Fiscus *et al.* 1964; Lander 1979a; York 1987). It was also suggested that the

size of fetuses increased with the age of the mother (Lander 1979a).

In the current study, I present an in-depth analysis of the fetal data collected from 1958 to 1974. I begin by briefly reviewing the reproductive biology of northern fur seals and proceed with an analysis and discussion of the biases contained within the data set. My aim is to test for differences between the sizes of male and female fetuses and to describe growth curves for the length and mass of each sex. I also test whether there is any difference between the sizes of fetuses taken from primiparous and multiparous females and whether the age and size of the mother has an effect on fetal growth.

## Biology of fur seal reproduction

Pregnant northern fur seals return to land, in order of decreasing age, to give birth to a single pup (M. A. Bigg, personal communication). The earliest births on the Pribilof Islands occur shortly after the first females arrive ashore on about June 20 (Batholomew and Hoel 1953; Peterson 1968). Few pups are born after July 20. Over 50% of the females arrive to give birth during the first 2 weeks of July (Trites 1992). This pattern of birth appears to occur at the same time each year (Gentry and Francis 1981; Bigg 1986; Trites 1992).

Direct observations indicate that mating occurs 3–7 days after parturition (Batholomew and Hoel 1953; Dorofeev 1961; Gentry and Goebel 1982), and ovulation follows coitus (Craig 1966). For 3.5–4 months after fertilization, the blastocyst is free in the uterus, bathed in uterine secretions. The blastocyst moves to one of two uterine horns in early to mid November (Craig 1966;

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Yoshida *et al.* 1978). From there, it passes through the epithelial layer of the endometrium and begins to form tissues and organs. The period of delayed implantation from mid-July to mid-November coincides with the lactation period (Craig 1966; Daniel 1981). A mean photoperiod of  $12.5 \text{ h d}^{-1}$  occurring 62 days after the mean date of parturition (or 65 days before implantation) may act as a cue for the initiation of implantation (Temte 1985).

### Materials and methods

Canadian and American biologists collected reproductive tracts and morphometric measurements from female fur seals along the coasts of Canada (British Columbia) and the United States (California, Oregon, Washington, and Alaska) from 1958 to 1974 (Lander 1980a). They sectioned the ovaries and recorded the condition and diameter of follicles, the formation or presence of a corpus luteum, and the presence of corpora albicantia. On the basis of these examinations each female was classified as nulliparous (female had never been impregnated), primiparous (first time impregnated, regardless of whether the pregnancy is carried to term), or multiparous (previously pregnant and either pregnant or nonpregnant at the time of collection). The dead fetus was sexed, weighed, and measured (crown-rump length) if normal, and otherwise noted as aborted or reabsorbed.

Adult females were weighed (with their fetus), measured (tip of nose to tip of tail, belly up, on a measuring board), and aged (by counting dentinal annuli in canine teeth). Birthdays had been assigned to January 1 (Lander 1980a) rather than July 1 when they were born. The age data were therefore adjusted to reflect the true biological age of the samples, as discussed by Trites and Larkin (1989). The timing of collection during leap years and nonleap years was standardized by assigning Julian dates.

Exploratory data analysis was conducted with S (Becker and Chambers 1984), and statistical analyses were completed using BMDP software (BMDP 1988).

#### Verification and detection of biases in data collection

Data were plotted and examined for outliers. These were verified by comparison with the original field notes.

Possible biases in the sexing of fetuses and in the over- or under-sampling of primiparous females by month were tested by contingency analysis. The proportion of male fetuses and the proportion of primiparous females captured were determined by month, and confidence limits for the proportions were calculated (Zar 1984).

Similarity in the maternal age distributions of the samples between months and years was visually inspected using box plots and statistically tested by analysis of variance. Post hoc pairwise comparisons identified which group differences accounted for significant overall *F* values. The equality of group variability was tested with Levene's test, and Box-Cox diagnostic plots (log of standard deviations versus log of the group means) assisted in selecting transformations to achieve greater homogeneity of variance. Welch (1938) and Brown-Forsythe (1974) procedures were used when the homogeneity of variance assumption was not met.

#### Average fetal growth

Changes in the body length of male and female fetuses were described by four sigmoid growth curve models for the purpose of comparison: the Richards (Richards 1959), von Bertalanffy (von Bertalanffy 1938, 1957, 1960), Gompertz (Gompertz 1825), and logistic (Verhulst 1838) models were fitted using a nonlinear least-squares procedure. Nonlinear methods have been shown to have some superior structural properties that produce more accurate and precise parameter estimates than linear methods (Vaughan and Kanciruk 1982).

Growth of body mass (*M*) was linearized and estimated as a function of gestational age (*t*). In theory, mass varies with the cube of length ( $L^3$ ) and of time ( $t^3$ ), assuming geometric similarity (Gunther 1975). The actual relationship between fetal length and mass was estimated by linearizing the relationship  $M = aL^b$ , so that  $\log(M) = \log(a) + b \log(L)$ , where *b* is the slope and  $\log(a)$  is the intercept.

It has been suggested that the geometric mean of the regression of mass on length and the inverse of the regression of length on mass should be used to give the appropriate linear regression for mass-length comparisons because length is not truly independent of mass (Ricker 1973, 1975, 1979). However, others have indicated that ordinary least-squares regression is appropriate and easier to interpret than geometric mean regression (Sprent and Dolby 1980; Cone 1989), therefore I conducted ordinary least-squares regressions.

Separate growth curves were determined for 3239 male and 3377 female fetuses. Data from parous females collected from November to June were combined, but samples collected in July were excluded because they were not considered random.

#### Differences between primiparous and multiparous females

Differences between the sizes of fetuses carried by primiparous and multiparous females were tested by analysis of covariance (ANCOVA), correcting for the gestational age (i.e., Julian date when sampled) and the age and size of the mother. Possible biases in data collection were reduced by restricting the analysis to females aged 4–7 years that were sampled from February to June, a period of time when fetal growth can be linearized. Mass to the power of 0.36 and the square root of gestational age (measured in Julian days) were the only transformations required to linearize the relationship between the dependent variable and the covariates (Trites 1990a). A parallelism test indicated whether the slope between the dependent variable and the covariate was parallel for all groups (BMDP 1988).

Differences between the size (length and mass) of primiparous and multiparous females were also tested by ANCOVA after adjusting for the effects of age and annual growth. The mass of the mother was set equal to her total mass minus that of her fetus. The logarithm of the resulting mass and the square root of gestational age (Julian day) linearized the relationship between these variables.

#### Effect of maternal age on fetal size

Much of the variability in the sizes of adults and fetuses collected over a year is due to differing stages of growth and development when the animals were sampled. As in the previous analysis, this can be removed by using the day of capture as a covariate. In this way, an analysis of covariance tested whether the fetal size of multiparous mothers was dependent upon the mother's age. The dependence of fetal size (length and mass) on maternal age was further described using a quadratic regression. If the quadratic term is negative and contributes significantly to the regression, it can be concluded that older females have smaller fetuses. A *t* value equal to the ratio of the coefficient to its standard error was used as a two-tailed test of significance for this quadratic coefficient. The analysis was restricted to multiparous females collected from February to June, because of possible biases in fetal size related to parity.

### Results and discussion

#### Verification of data

Screening the length and mass data for outliers and distributional consistency revealed over 300 possible errors in measurement or data entry. Consistency in the length-mass relationship confirmed the reliability of about half of these suspect observations. A further 20 were key-punching errors and were corrected. The remaining suspect data were rejected. In one case the lengths of 78 fetuses collected during June 1959 exceeded expected lengths when they were compared with the known mass-length relationship and with the lengths expected on the basis of other June samples as well as of those collected earlier in the year. It appears in this case that the observer may have measured curvilinear length rather than crown-rump length. In other cases the measurements may have been incorrectly written on the data card. Inspection of the original data cards further suggests that some of the errors might have arisen when several animals were on the ship deck at one time, and the measures were inadvertently recorded on the wrong card. Despite these shortcomings,

TABLE 1. Numbers of fetuses collected at sea, by month, from 1958 to 1974

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Nov.	Dec.	Jan.-Dec.
1958	0	154	337	143	391	95	0	0	0	0	1120
1959	95	576	202	324	34	0	0	0	0	0	1231
1960	0	1	165	290	364	150	38	0	0	2	1010
1961	311	284	100	204	26	1	0	0	0	0	926
1962	0	32	3	14	20	329	65	1	0	0	464
1963	0	0	0	0	12	112	67	0	0	0	191
1964	0	0	0	58	108	6	22	0	0	0	194
1965	0	0	0	86	61	35	0	0	0	0	182
1966	30	105	126	21	3	0	0	0	0	0	285
1967	41	26	0	16	5	0	0	0	3	63	154
1968	55	93	6	51	75	137	21	0	0	0	438
1969	0	51	87	40	32	0	0	0	0	0	210
1970	32	18	66	18	54	2	0	0	0	0	190
1971	26	2	87	48	28	0	0	0	0	11	202
1972	19	2	38	23	47	0	0	0	0	2	131
1973	22	8	0	0	0	0	2	0	0	3	35
1974	25	0	0	0	0	0	15	0	0	0	40
1958-1974	656	1352	1217	1336	1260	867	230	1	3	81	7003

NOTE: No fetuses were sampled in September and October. Of the 7003 fetuses collected, 98 were not sexed and 156 were either not measured or not weighed.

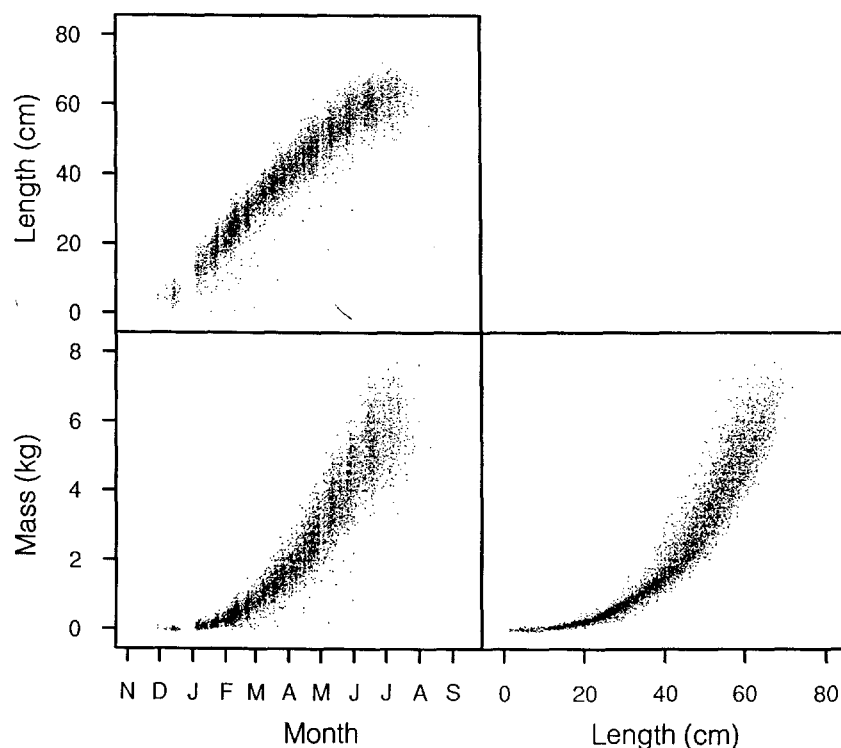


FIG. 1. Length and mass of 7003 fetuses, by sampling date. A small amount of random noise was added to each variable to reduce the overlap caused by measurement roundoff. The letters on the x-axis denote the beginning of each month.

the suspect measurements rejected are few (202) and the number of observations remaining is considerable (7003).

Over 60% of the fetuses measured were collected during the first 4 years of pelagic surveys, 1958-1961 (Table 1). During this period, approximately 1100 fetuses were collected annually from a population of approximately 350 000 pregnant females (Lander 1980b; Trites 1989). From 1962 to 1972 the number of fetuses measured was reduced to an average of 240, then to under 40 in 1973-1974.

Pooled fetal samples (1958-1974) cover the entire development period from implantation to birth (Fig. 1). The only gap in data collection was during a 2-week period at the end of December and beginning of January, when the biologists and ship's crew were ashore on holiday.

There is a distinct seasonality in fetal growth, considering that few fetuses failed to conform to the general growth pattern (Fig. 1). None of the fetuses collected was exceptionally large compared with the others, but some (<50) were unusually small

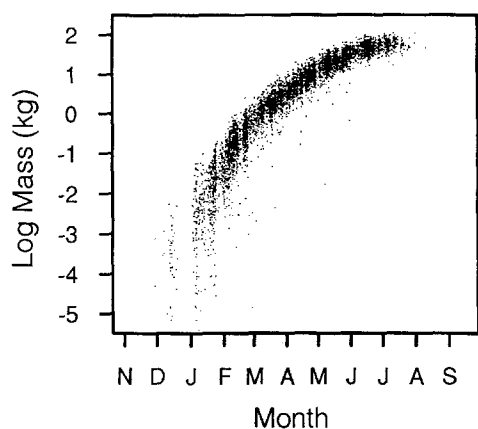


FIG. 2. Natural logarithm of fetal mass, by sampling date. A small amount of random noise was added to each of the 7003 data points to reduce the overlap caused by measurement roundoff. The letters on the x-axis denote the beginning of each month.

(see Fig. 1). These small fetuses (<0.7% of all fetuses sampled) were proportionally the correct size (based on the length-mass relationship) but had probably implanted much later than the rest of the population and (or) had grown more slowly.

With the exception of very small fetuses, the distribution of fetal lengths and masses does not indicate any substantial problems with measurement error (Fig. 1). However, Fig. 2 suggests that the mass of small fetuses may not be overly reliable. Perhaps this is due to the difficulty of separating the tiny fetus from uterine tissues and fluids. The large variation in fetal mass at this stage of development may also be related to the difficulties of weighing aboard ship.

#### Age and parity biases

The age distribution of the pregnant mothers was positively skewed (Fig. 3). Most females began reproducing at the age of 4 or 5 years, although a few were as young as 3 years old and one was only 2 years old. The oldest primiparous female was 15 years old, but this and other observations of old primiparous females are highly suspect. Pregnant females were classified as primiparous if a corpus albicans was not present. A corpus albicans was presumed to indicate a previous pregnancy, although in actual fact it results from ovulation regardless of whether pregnancy ensues. Furthermore the absence of a corpus albicans does not necessarily mean the seal is primiparous because corpora albicantia degenerate over time and may not be present 2–4 years following a pregnancy (Craig 1966). Thus, many of the older females recorded as primiparous (>8 years?) may have been misclassified. Retaining these data, however, should not significantly alter subsequent analyses, given that old primiparous females are few.

The relative frequencies of primiparous and multiparous females collected from December to July differed by month (Pearson  $\chi^2_7 = 35.48$ ,  $p < 0.001$ ). Proportionally more primiparous females were sampled during December and July than at any other time of the year (Fig. 4A). But no significant difference could be detected in the relative frequencies of primiparous and multiparous females taken from January to June (Pearson  $\chi^2_5 = 5.73$ ,  $p < 0.334$ ).

The age distribution of pregnant females collected was similar in all months but three: December, April, and July (Fig. 4B). The seals sampled during these 3 months were, on average, younger than at other times of the year. The significance of differences in mean age of seals captured each month was assessed by analysis

of variance using the logarithm of age to reduce the skewness. But the transformation failed to significantly equalize variances (Levene's  $F_{[7,6905]} = 4.01$ ,  $p < 0.001$ ), therefore the Welch ( $W_{[7,1019]} = 7.20$ ,  $p < 0.001$ ) and Brown-Forsythe ( $F^*_{[7,1938]} = 7.55$ ,  $p < 0.001$ ) tests were used. They confirm the bias in ages of animals sampled from December to July.

The underrepresentation of older animals in April was not expected and cannot be readily explained. However, the oversampling of young and primiparous fur seals in December and July probably reflects the timing of migration to and from the breeding islands. Females appear to return to the Pribilof Islands in order of decreasing age and give birth within a few hours or days of arriving on land (Bartholomew and Hoel 1953; Peterson 1965, 1968; Bigg 1984, 1986). Pupping begins about June 20 and finishes July 20 (Bartholomew and Hoel 1953; Peterson 1968; Trites 1992). Therefore many of the older, multiparous females have already given birth by the end of June, and are not available for sampling in July.

The females suckle their pups until October – early November, whereupon they leave the Pribilofs and begin their southward migration (Peterson 1968). Those seals impregnated for the first time are not encumbered with a pup and presumably leave the islands earlier. Thus, the samples collected in December in the north Pacific are probably not well mixed with respect to age, and reflect the segregated fur seal departure.

The Welch ( $W_{[16,891]} = 11.60$ ,  $p < 0.001$ ) and Brown-Forsythe tests ( $F^*_{[16,2274]} = 10.41$ ,  $p < 0.001$ ) indicate a highly significant difference in the mean age of seals sampled each year during 1958–1974. This result is not surprising. Age biases could have arisen because the migrating seals were not well mixed and the months sampled differed among years (Table 1). The bias might also reflect differences in year-class strength caused by high variability in annual mortality rates of young animals (Chapman 1964; Lander 1979b; Smith and Polacheck 1984; Trites 1989). Similarly, the annual age structure was undoubtedly altered by the harvesting of 315 000 adult females that occurred from 1956 to 1968 (Lander 1980b).

#### Sex ratio biases

The relative frequencies of male and female fetuses (i.e., the sex ratios) collected each month were the same from February to July (Pearson  $\chi^2_6 = 4.67$ ,  $p = 0.587$ ), but differed with the inclusion of the December and January samples (Pearson  $\chi^2_6 = 14.87$ ,  $p = 0.038$ ; see Fig. 4C). Significantly more female than male fetuses were collected in December and January than in any other month. The most likely explanation for this is human error in sexing the small, developing fetus. If fetuses were sexed by the presence or absence of a penis, there is a higher probability of misclassifying a fetus as female because the penis is not always clearly distinguishable. It also takes some time for the fetus to develop to the point at which gender can be identified. This probably means that all the identified males were true males, but some of the recorded females were in fact males.

It has been suggested that the sex ratio of the fetuses might be biased by the physical condition of the mother (Trivers and Willard 1973). If so, young mothers might produce more females than older mothers because the smaller female fetuses would require less maternal resources (e.g., Thomas *et al.* 1989). However, there is no indication of such a phenomenon occurring in northern fur seals. The frequencies of male and female fetuses carried by mothers of different ages (grouped as in Fig. 5) from February to July did not differ from unity (Pearson  $\chi^2_6 = 5.08$ ,  $p = 0.53$ ). Similarly, there was no difference in the sex ratio

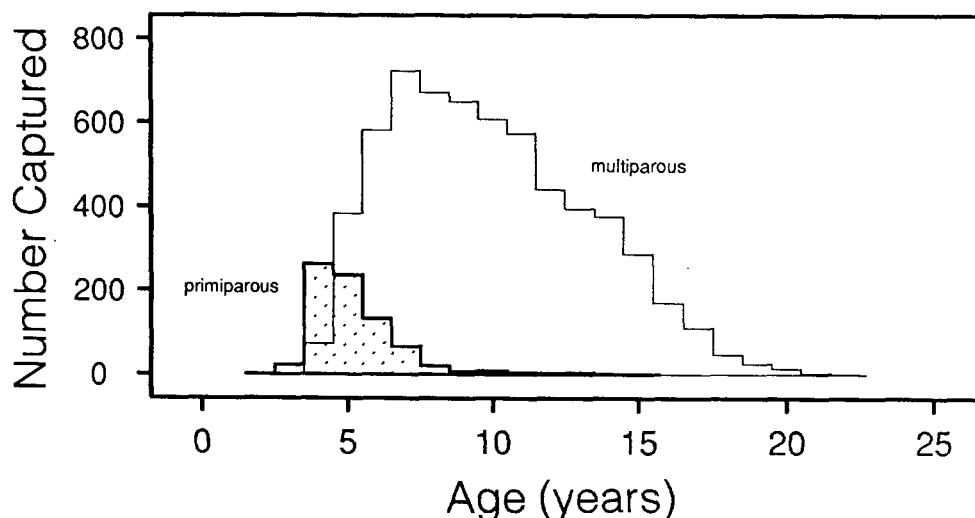


FIG. 3. Numbers of primiparous and multiparous females captured, by age, from 1958 to 1974.

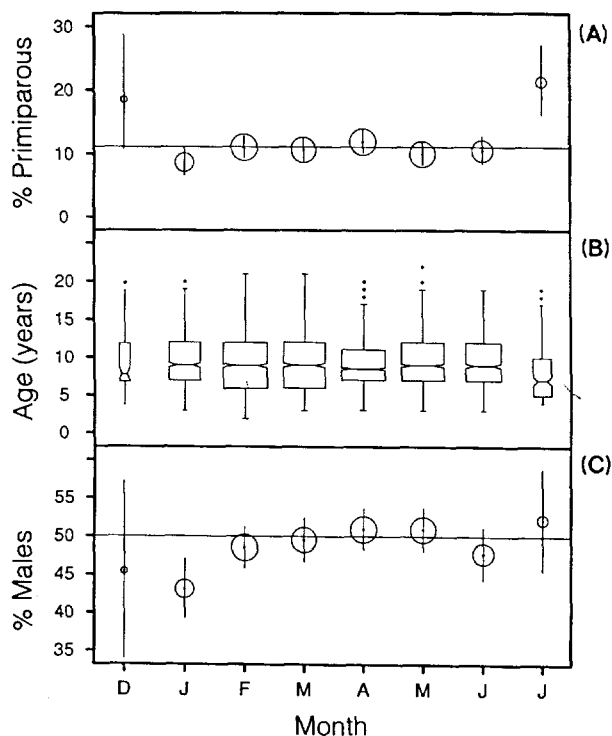


FIG. 4. Biases in monthly samples. (A) Percentage of pregnant females that were primiparous. The size of the circles surrounding each estimate is proportional to the sample size, and the bars show 95% confidence intervals. The solid line is the mean estimate for all months combined. (B) Age distributions of the pregnant females collected. The line in the middle of each box shows the median. The central 50% of the data is shown by the length of the rectangle, and the vertical lines show how stretched the tails of the distribution are (25% of the data in each tail). The width of each box is proportional to the sample size, and outliers are indicated by dots. Notches in the box plots provide an approximate 95% test of the null hypothesis that the true medians are equal. If the two notches overlap, then the null hypothesis is not rejected with (approximately) 95% confidence. (C) The sex ratio of the fetuses collected. The solid line indicates the expected 50:50 ratio. Again, the size of the circle surrounding each estimate is proportional to the size of the sample, and the bars show 95% confidence intervals. The total sample size was 6905 seals.

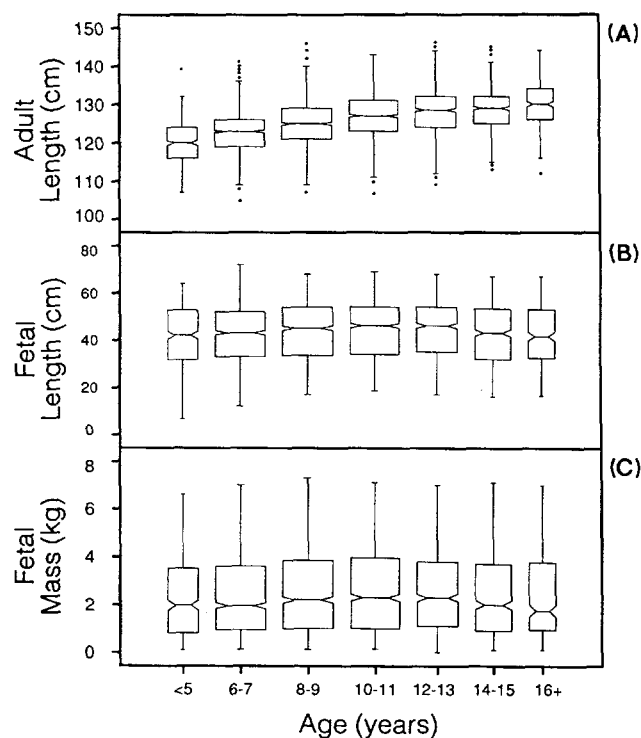


FIG. 5. Maternal size and the effect of maternal age on fetal size in multiparous females. (A) Distribution of maternal lengths of multiparous females, by age. (B and C) Effect of maternal age on fetal length and mass in multiparous females. In all, the distributions include 5276 fetuses collected during the entire sampling season, from early implantation in December to full term at the end of June. The notches on the box plots provide an approximate 95% test of the null hypothesis that the true medians are equal. The width of each box is proportional to the size of the sample.

of fetuses carried by primiparous ( $\chi^2_2 = 1.40$ ,  $p = 0.50$ ) or multiparous mothers ( $\chi^2_6 = 5.71$ ,  $p = 0.46$ ). Furthermore, there was no difference in the sex ratio of fetuses collected from one year to the next from 1958 to 1972 ( $\chi^2_{14} = 14.18$ ,  $p = 0.44$ ). In all, 3067 male and 3097 female fetuses were collected from February to July.

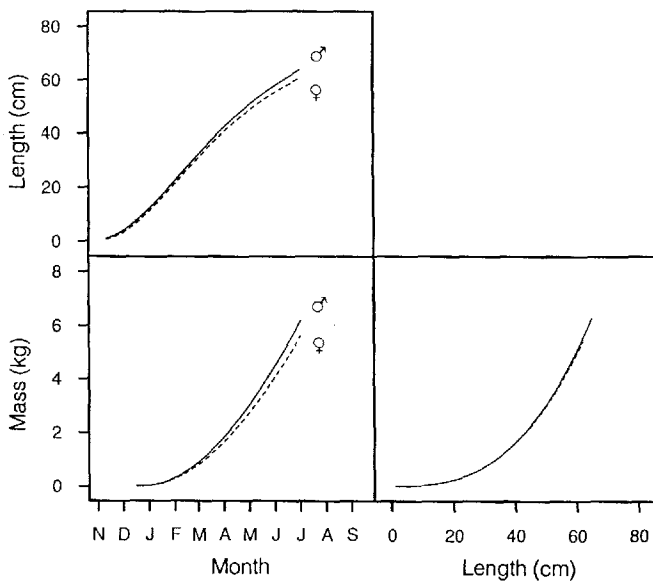


FIG. 6. Growth curves for male (solid lines) and female fetuses (broken lines). Length is described by the von Bertalanffy equation (see Table 2). Equations describing changes in body mass and the length-mass relationship are contained in the text. Confidence limits (95%) were calculated but are indistinguishable at the scale shown. The letters on the x-axis denote the start of each month.

#### Average fetal growth

Male fetuses are bigger than female fetuses (Fig. 6). Coefficients of linear regressions of male and female lengths according to age ( $F_{[2,6906]} = 273.73, p < 0.001$ ) and male and female masses according to age ( $F_{[2,6884]} = 413.71, p < 0.001$ ) are both significantly different. The growth differential between the sexes begins shortly after implantation and increases through to birth.

Sigmoid growth curves were reasonable models for describing changes in body length. The von Bertalanffy model proved to be marginally better than the Gompertz and logistic models (Table 2). But parameter estimates for the Richards equation failed to converge. This might be explained by the number of data points fitted or by the efficiency of the computer algorithm used (Fitzhugh 1976). Some authors have further reported difficulty in fitting the Richards equation because of the high correlation between two of the four parameters,  $K$  and  $n$  (Rutledge *et al.* 1972; Brown *et al.* 1976; Davies and Ku 1977).

Several authors have encouraged the use of the Richards equation because it is the general form of the other growth equations and permits comparisons with growth curves constructed for other species (see White and Brisbin 1980; Brisbin *et al.* 1987). However, the Richards model is effectively at three-parameter model because two of the four parameters are highly correlated (Zach 1988). Furthermore, the Richards model usually fails to explain a larger portion of the variation in the data than the simpler three-parameter models (Zach *et al.* 1984). Given these limitations and the performance of the Richards model when fitted to the fetal data, its value is questionable.

Unlike length, fetal mass does not approach a distinct asymptote. Instead, body mass appears to increase exponentially, never reaching an inflection point (or perhaps reaching it at parturition). Human fetal studies further support the observation that the initial increment of body mass is slow, followed by rapid exponential growth to a peak value near term (Vorheer 1975). Growth (mass) of human fetuses slows markedly after the

normal gestation time of 38 weeks, and stops after 40 weeks. A similar phenomenon may well occur in the growth of fur seal fetuses.

Changes in male and female mass ( $M$ , kg) with gestational age ( $t$ , days), can be described for  $t \geq 35$  days by the equations  $M = (-1.214 + 0.207\sqrt{t})^{2.75}$  and  $M = (-1.183 + 0.201\sqrt{t})^{2.75}$ , respectively, where  $t = 0$  represents November 10 and  $t = 50$  represents January 1 (Fig. 6). November 10 is approximately the time that the blastocyst moves from the uterus to one of two uterine horns (Craig 1966). The models provide good representations of increases in tissue mass from February to June but do not adequately describe the initial 2-month stage. A plot of the residuals against fitted values shows that the model underestimates mass during December and January. This result is in keeping with fetal studies of other species which suggest that there is an initial lag phase in development, during which the placenta becomes established (Payne and Wheeler 1967a).

The relationship between fetal length (cm) and mass (kg) for both sexes combined was  $M = 10^{-4.20} L^{2.75}$ . Note that the exponent is significantly less than the predicted value of 3.0 ( $t_{6823} = 47.16, p < 0.001$ ). Individually, the mass-length relationship was  $M = 10^{-4.23} L^{2.77}$  for male fetuses and  $M = 10^{-4.18} L^{2.74}$  for females. Although this difference between the exponents of the male and female mass equations is small, it is nevertheless statistically significant ( $F_{2,6821} = 86.33, p < 0.001$ ). It means that a male fetus that is the same length as a female fetus will weigh marginally more.

Males weigh more than females because their skeleton (i.e., length) grows faster than the female's. Greater mass can presumably be accumulated on the larger male frame. The most rapid increase in fetal length occurs during the first half of pregnancy, but body mass does not increase rapidly until the latter part of pregnancy.

The possible bias detected earlier in sexing the fetuses during December and January does not affect the growth patterns described for males, but may slightly increase the pooled mean size of females during the first 2 months because a few of the males were incorrectly sexed as females. However, the number of individuals is small, as is their size, and would not significantly alter the results. The July data were excluded from the analysis because young and primiparous females were over-represented in this month. If young and primiparous females have smaller fetuses than other females, including the July data would have underestimated fetal growth.

#### Differences between primiparous and multiparous females

There was a significant difference between the adjusted mean size of primiparous and multiparous females after the effect of the mother's age and the sampling date had been removed. Primiparous females were found to be lighter ( $F_{[1,2054]} = 15.59, p < 0.001$ ) and shorter ( $F_{[1,2064]} = 13.36, p < 0.001$ ) than multiparous females. Similarly, primiparous females carried smaller fetuses than multiparous females. Differences in fetal length ( $F_{[1,2052]} = 54.80, p < 0.001$ ) and mass ( $F_{[1,2052]} = 74.72, p < 0.001$ ) are attributable to the parity of the mother. However, the fact that multiparous females have bigger fetuses cannot be entirely attributed to greater maternal size. It appears instead that females are somehow physiologically altered by their first pregnancy. For example, perhaps increases in the numbers of uterine blood vessels associated with the growth of an earlier fetus lead to the provision of better nutrition to developing fetuses in successive pregnancies.

All the assumptions of the ANCOVA were met. In all cases

TABLE 2. Three growth models representing the length of fetuses ( $L_t$ ), in centimetres, over time,  $t$ , recorded in days (where  $t = 0$  represents November 10)

Model	Equation	Parameter			Residual mean square	Sex
		A	c	K		
Von Bertalanffy	$L_t = A(1 - ce^{-Kt})^3$	84.55	0.76	0.009	10.45	m
		77.91	0.79	0.010	10.38	f
Gompertz	$L_t = Ae^{-ce^{-Kt}}$	78.16	3.34	0.012	10.53	m
		72.54	3.49	0.013	10.47	f
Logistic	$L_t = A/(1 + ce^{-Kt})$	69.30	10.69	0.020	10.92	m
		65.00	11.38	0.021	10.95	f

NOTE: The data, for 3239 male and 3377 female fetuses, were pooled from November to June for the years 1958–1974. Parameters A, c, and K are the asymptote, constant of integration, and growth rate constant, respectively, as defined by Zach *et al.* (1984).

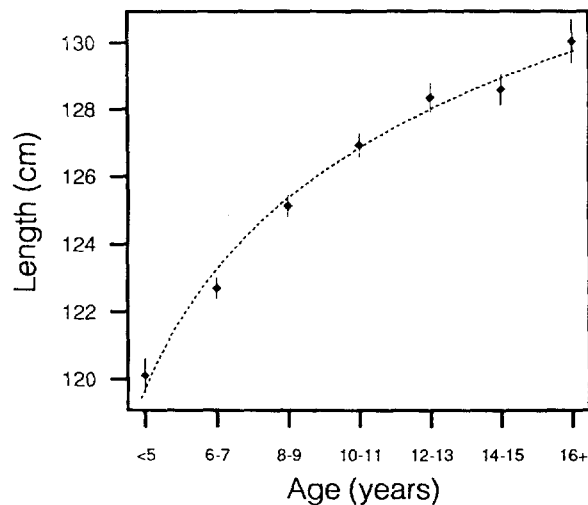


FIG. 7. Mean lengths of multiparous females collected from December to June (see Fig. 5A). The vertical bars show 95% confidence limits on the mean. The growth curve was fitted by linear regression.

there was a linear relationship between the dependent variables and the covariates in each group. Furthermore, the  $p$  values for the test of equality of slopes were all nonsignificant.

#### Effect of maternal age on fetal size

Fetal size is dependent upon the age of the multiparous mother. There were significant differences among the mean sizes of fetuses carried by multiparous females of different ages after the effect of gestational age (Julian date) was removed (length:  $F_{[4,4368]} = 39.64$ ,  $p < 0.001$ ; mass:  $F_{[4,4355]} = 48.26$ ,  $p < 0.001$ ). Older females had increasingly bigger fetuses until their apparent reproductive prime was reached, at the age of 10–11 years, based on fetal size (Fig. 5). As females continued to age, their fetuses became increasingly smaller. This 'senility' effect is presumed to be real, based on the significance of the quadratic coefficient of the polynomial regression (length:  $t_{6081} = -3.26$ ,  $p = 0.002$ ; mass:  $t_{6063} = -3.02$ ,  $p = 0.005$ ).

Old females may produce small fetuses, but they themselves are in fact very large (Fig. 5A). Although the annual growth increment of adult females decreases with time, they nevertheless grow continuously and may never reach an asymptote before dying (Fig. 7). This result is surprising, but is consistent with the fact that annual growth increments are regularly noted on hard body parts such as teeth. It is also consistent with the observation

that many species of fish, amphibians, and reptiles that live in the supporting medium of water continue to grow beyond the self-retarding plateau phase (Batt 1980).

#### Overview

Most pinnipeds are sexually dimorphic, with males being larger than females (Alexander *et al.* 1979; King 1983). Data from grey seals, *Halichoerus grypus* (Kovacs and Lavigne 1986; Anderson and Fedak 1987), northern elephant seals, *Mirounga angustirostris* (Le Boeuf *et al.* 1989), and southern elephant seals, *Mirounga leonina* (McCann *et al.* 1989), show that the mass of males exceeds that of females at birth. Among otariids such as the Antarctic fur seal, *Arctocephalus gazella* (Doidge *et al.* 1984a), northern fur seal (Costa and Gentry 1986), Galapagos fur seal, *Arctocephalus galapagoensis* (Trillmich 1986), and California sea lion, *Zalophus californianus* (Oftedal *et al.* 1987), it has been shown that male pups are bigger at birth and grow faster than female pups.

#### Observed and predicted neonatal size

Based on the fetal growth curves (Fig. 6), male northern fur seals are 10% heavier and 5% longer than females at birth. On June 30, the average male pup is predicted to be 63.6 cm long and to weigh 6.1 kg. Females should be 60.5 cm long and weigh 5.6 kg. Measurements of newborn pups taken on the rookeries indicate a mean mass of 5.7 kg for males and 5.1 kg for females (Scheffer and Wilke 1953; Lander 1979a; Fowler 1990). The average length for both sexes was about 62 cm. Comparing these field estimates with the predictions of the fetal growth curves suggests that newborn pups maintain their length but lose about 8% of their body mass after birth.

The discrepancy between observed and predicted body mass at birth may be real or may be an artifact of sampling biases. For example, in a study of southern elephant seals, McCann *et al.* (1989) weighed neonates and noted that growth (measured as mass) was slow or negative for the first 2–3 days for the majority of pups. There is also evidence that human infants usually lose some mass in the first 2–5 days after parturition, possibly as much as 10% of the infant's birth mass (Reeder *et al.* 1983). The mass loss at birth may be related to the hormone estrogen, which increases water retention and blood volume and is likely produced at high levels by the female fur seal during pregnancy; the pup would be born with high levels of the mother's estrogen. But after birth, the pup's ability to retain water is reduced because the source of estrogen is removed, and the pup loses body mass for a few days.

Another possible explanation for the discrepancy in neonatal



mass of northern fur seals is related to the timings of birth and fieldwork. If fieldwork is conducted in mid-July, most of the newborns will have young primiparous mothers and will be smaller than pups born earlier in the season. This has been shown to be the case for Antarctic fur seals. Boyd and McCann (1989) found that smaller adult females returned over the 40-day breeding season, and that they produced progressively smaller pups. Newborn male and female Antarctic fur seal pups (which are about the same size as northern fur seal pups) were about 0.5 and 0.4 kg lighter, respectively, at the end of the breeding season than at the beginning.

#### Length of gestation

Little is known about the gestation time of primiparous and multiparous females. Since primiparous females pup later in the breeding season than multiparous females, it is possible that they also implant later in the season. However, it has been suggested that photoperiod, through an effect on pineal gland secretion, is an exogenous cue to initiate implantation and later synchronization of the timing of parturition (Keyes *et al.* 1971; Elden *et al.* 1971; Temte 1985). Thus, all females should implant at about the same time, although even an exogenous cue to implantation will leave some variation in implantation dates.

Younger and primiparous females would have longer gestation times if implantation is synchronous because they give birth after the older multiparous females. Extending the gestation period gives the fetus more time to grow and the pup would presumably be larger than normal at birth. Since lipids are deposited in fetal tissue late in gestation, a slight delay in parturition could mean a boost in fetal energy stores with only a slight increase in mass. However, studies on humans reveal that prolonged pregnancies result in degeneration and calcification of the placenta which causes fetuses to lose mass and increases their postnatal mortality rates (Vorherr 1975; Knuppel and Drukker 1986). There is also evidence of higher fetal perinatal mortality for primiparous than multiparous human females, particularly when the pregnancy proceeds beyond term (Vorherr 1975). A further disadvantage in prolonging the birth of northern fur seals is that the neonatal pup will have less time to suckle while on the rookery before the breeding season ends. This may have a bearing on the observation that neonatal mortality among Antarctic fur seals increases as the breeding season progresses and increasing numbers of primiparous females give birth (Doidge *et al.* 1984b).

#### Maternal resources

Boyd and McCann (1989) suggest that growth of the male Antarctic fur seal fetus is limited by maternal size and resources, but that female fetuses do not fully exploit their mother's resources. This could be the case for northern fur seals as well. However, another study on Antarctic fur seals (Costa *et al.* 1989) and one on southern elephant seals (McCann *et al.* 1989) found that the size of female pups was more closely related to maternal size than that of males. Unfortunately, this observation may be inconclusive, owing to a sampling bias that was common to both of these studies (Boyd and McCann 1989).

An estimate of the condition of pregnant northern fur seals showed that females carrying male fetuses were in poorer condition than those with female fetuses (Trites 1990a). Male fetuses grow faster and demand more resources than female fetuses. Even when fetal length is standardized for both sexes, males are marginally heavier. Thus, males would seem to be the 'greedy' sex. It is curious that female fetuses do not fully use the maternal resources, given that a greater birth size would probably imply a higher survival rate during the first few months of

life (Calambokidis and Gentry 1985; Trites 1990b). Of course, fetal growth is probably not independent of the mother. If the cost of producing a successful daughter is less than the resources the mother has, she may withhold some to improve her chances of reproducing the following year. It is also possible that growth rates of female fetuses are heritable and sex-linked if there is selection for adult females to be the size they are.

#### Conclusions

Male northern fur seal fetuses grow faster and larger than female fetuses. Moreover, fetal size is influenced by the size, age, and parity of the mother. Mothers that were pregnant in previous years produce bigger offspring than females carrying their first pup. Also, older females tend to carry progressively bigger fetuses until the age of 10–11 years. As females continue to grow beyond age 11 years, there is a senescent decline in the mass and length of their pups at birth. These observations are unlikely to be restricted to northern fur seals alone, but can undoubtedly be applied to other species of fur seals and perhaps to other pinnipeds as well.

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