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GROWTH IN BODY SIZE OF THE STELLER SEA LION (*EUMETOPIAS JUBATUS*)

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Growth models (mass and length) were constructed for male (≥1 year old), female (≥1 year old), and pregnant female Steller sea lions (*Eumetopias jubatus*) shot on rookeries or haulouts, or in coastal waters of southeastern Alaska, the Gulf of Alaska, or the Bering Sea ice edge between 1976 and 1989. The Richards model best described growth in body length and mass. Females with fetuses were 3 cm longer and 28 kg heavier on average than females of the same age without fetuses. Males grew in length over a longer period than did females and exhibited a growth spurt in mass that coincided with sexual maturity between 5 and 7 years of age. Average predicted standard lengths of males and females ≥12 years of age were 3.04 and 2.32 m, respectively, and average predicted masses were 681 and 273 kg, respectively. Maximum recorded mass was 910 kg for an adult male. Males achieved 90% of their asymptotic length and mass by 8 and 9 years of age, respectively, compared with 4 and 13 years, respectively, for females. Residuals of the size-at-age models indicated seasonal changes in growth rates. Young animals (<6 years old) and adult males grew little during the breeding season (May–July), and adult males did not resume growth until sometime after November.

Key words: *Eumetopias jubatus,* length, mass, seasonality, sexual size difference, Steller sea lion

Growth of pinnipeds is often described by models applied to cross-sectional, or less frequently, longitudinal data on body length or mass (Boyd et al. 1994; Garlich-Miller and Stewart 1998; Hammill et al. 1995; Innes et al. 1981; Lima and Páez 1995; McLaren 1993; Murie and Lavigne 1992; Olesiuk 1993; Rosas et al. 1993; Trites 1991). Such models have several advantages. First, they describe the complex physical growth process using only a few parameters, which allows comparisons between sexes, populations, and species (McLaren 1993). Second, residual variances in models of growth can be used to assess variability of size within populations and species, including seasonal size fluctuations (McLaren 1993). Third, growth models are important components of bioenergetic models, which are often used to assess food requirements (Boyd et al. 1994; Markussen et al. 1992; Olesiuk 1993).

The primary goal of our study was to mathematically describe growth of Steller sea lions (*Eumetopias jubatus*) from lengths and weights of animals of known age shot between 1976 and 1989. Our secondary goal was to explore questions concerning the relationship between pinniped growth and energetics, life histories, behavior, and environmental conditions (Bryden 1972;

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Innes et al. 1981; Lavigne et al. 1982; Laws 1956; McLaren 1993).

Information on growth of the Steller sea lion has been reported in previous studies (Brandon et al. 1996; Calkins and Pitcher 1982; D. G. Calkins and E. Goodwin, in litt.; Fiscus 1961; Isono 1998; Loughlin and Nelson 1986; Merrick et al. 1995; Nitto et al. 1998; P. F. Olesiuk and M. A. Bigg, in litt.; Scheffer 1945; Spalding 1964; Thorsteinson and Lensink 1962). However, models have been used by only McLaren (1993) and Calkins et al. (1998) to describe growth. McLaren (1993) analyzed data on body length for 3 localities. Calkins et al. (1998) described growth in body length and mass for females <14 years old in the Gulf of Alaska. Thus, no study has modeled growth in mass of females >14 years of age, or of males of any age. In addition, only 2 studies have assessed seasonal fluctuations in size (mass) of males (Nitto et al. 1998; P. F. Olesiuk and M. A. Bigg, in litt.).

We compared the relative merits of 5 models to describe the growth of male and female Steller sea lions and evaluated 8 potential sources of bias that are common to cross-sectional growth data. We used those growth equations to estimate the relative size difference between male and female Steller sea lions and to determine if greater size of males is related to a longer period or higher rate of growth. We also tested Laws' (1956) postulate that female pinnipeds attained puberty when they obtain 87% of the asymptotic length, and we estimated the relative lengths and masses of males and females at sexual maturity. Finally, we contrasted relative growth of males and females in terms of life-history strategies and determined if Steller sea lions grew monotonically throughout the entire year or only during winter and spring, as has been shown for other species of pinnipeds (e.g., northern fur seals [*Callorhinus ursinus*]—Trites and Bigg 1996).

MATERIALS AND METHODS

We used data on Steller sea lions that were shot from 1976 to 1989 on rookeries or haulouts or in coastal waters of southeastern Alaska, the Gulf of Alaska, or along the Bering Sea ice edge during earlier research studies (Calkins and Pitcher 1982; D. G. Calkins and E. Goodwin, in litt.; Castellini and Calkins 1993); data are available through the Alaska Department of Fish and Game, Anchorage. Animals were brought aboard a vessel, weighed to the nearest kilogram, and measured for standard length or dorsal standard length to the nearest 0.5 cm. Standard length was the straight-line length from nose to tail while an animal was on its back, and dorsal standard length was the same measurement while the animal was on its stomach (McLaren 1993). Age in years was estimated by counting annuli in the cementum of P2 and using a reference collection of known-age teeth (Calkins and Pitcher 1982). All teeth were aged by D. G. Calkins. Age in days was estimated assuming 15 June as the mean date of birth (Calkins et al. 1998; Pitcher and Calkins 1981). Ovaries and uteri were collected from females and examined to determine reproductive status (D. G. Calkins and E. Goodwin, in litt.; Calkins and Pitcher 1982). Females were classified originally as pregnant, not pregnant, or unknown (Calkins and Pitcher 1982; D. G. Calkins and E. Goodwin, in litt.). In our study, females were reclassified as either pregnant with fetus or other (not pregnant or pregnant with no fetus). The Steller sea lion exhibits delayed implantation of the blastula and little fetal growth before February, so only pregnant females collected after 1 February were reclassified as pregnant with fetus (i.e., assuming implantation was 15 October, we defined a fetus as >108 days of age). Females <3 years of age were assumed to be not pregnant because sexual maturity before that age was rare (Harrison 1969; Pitcher and Calkins 1981).

A total of 235 males, 201 females without fetus, and 81 females with fetus of all ages were measured. When only dorsal standard length was measured, we estimated standard length with an equation developed for specimens on which both dorsal standard length (DSL) and standard length (SL) were measured: $SL = 0.98734DSL + 5.758$ ($r^2 = 0.97$, $P < 0.0001$), where standard length and dorsal standard length were in centimeters (K. Pitcher, pers. comm.). All analyses of length were done using standard length, hereafter referred to as ''length.''

Data were examined for biases in age and collection date. More juveniles aged 1–3 years were

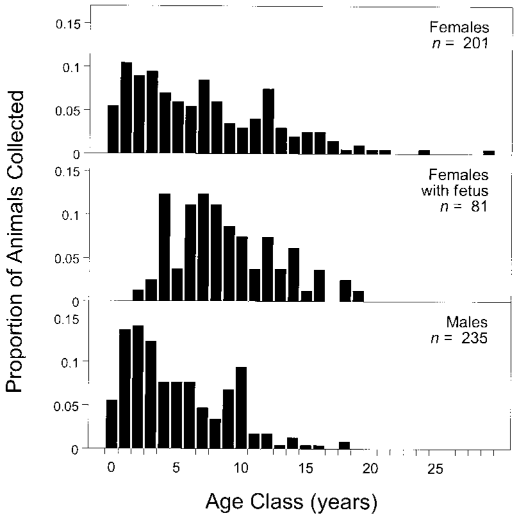

FIG. 1.—Age-frequency distributions of specimens used in this study (collected in Alaska, 1976–1989).

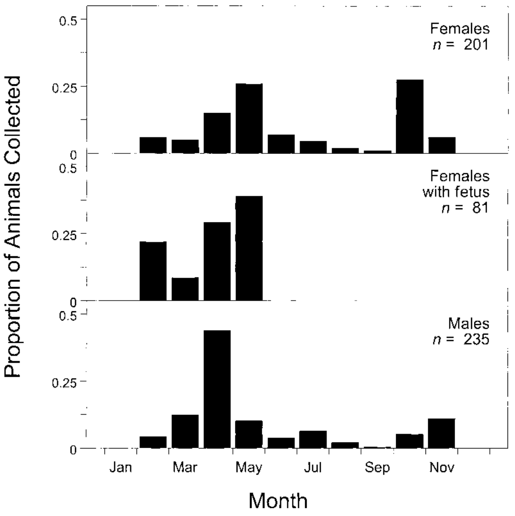

FIG. 2.—Month-frequency distributions of specimens used in this study (collected in Alaska, 1976–1989) showing seasonal trends in collection date.

collected than any other age group (Fig. 1). Only 17% of males collected were >10 years of age and only 10% of females without a fetus were >15 years. Most (87%) females with a fetus were 4–14 years of age. With respect to time of year, most animals (89%) were collected in February–May and October–November (Fig. 2). A small number of animals were collected in June–September, but no animals were collected in January or December.

Data also were examined for outliers. One male (10 months of age) was unusually large in length and mass, suggesting age was recorded incorrectly; that specimen was not used for size-at-age analyses. Data for 3 males, 9 females without fetus, and 1 female with fetus were outliers in respect to length-at-age and length per unit mass, but not mass-at-age, which suggested that length was recorded incorrectly so only data on mass for those animals were used. Finally, 1 old female (29 years) with unusually small length and mass was excluded from analyses.

Growth in length and growth in mass were described with several mathematical models of growth (Table 1). Only data for animals >0.75 years of age were used because growth of fetuses and pups differed from that of older animals and no single equation adequately described growth of pinnipeds over the entire life span (McLaren 1993). Including data for fetuses and pups, or "anchoring" models at the beginning of growth or parturition, introduced biases when fitting models that only described growth of older animals. For females, an extra parameter (b) was added to models to control for presence or absence of a fetus (Table 1). Depending on the model, that parameter produced either an additive size effect (additive female model) or a multiplicative size effect (proportional female model) due to presence of a fetus. Growth models were fitted using nonlinear least-squares regression (Nonlin, SYSTAT, Inc. 1992). Goodness-of-fit was evaluated using the coefficient of determination (r^2) and by comparing the fitted models to robust locally weighted regressions of the data (Cleveland and Devlin 1988; Statistical Sciences, Inc. 1995). The statistical significance of the extra parameter (b) in the female models was tested using Student's t-test (SYSTAT, Inc. 1992; Zar 1996). The age at which sexual size differences became statistically significant was determined by comparing mean size (length and mass) for each year class using Student's t-test (SYSTAT, Inc. 1992). The result of Student's t-test was considered significant when $P < 0.05$.

The allometric relationship of length (L) to mass (M) was examined by fitting a linearized power relationship ($\log_{10} M = \log_{10} a + b \log_{10} L$, where $\log_{10} a$ is the Y intercept and b is the linear regression coefficient) to $\log_{10}$-trans-

TABLE 1.—Growth models fit to size (S) at age (t) data. A is asymptotic size, S_0 is size at $t = 0$, t_0 (time parameter) and k (a parameter indicative of growth rate) are fitted parameters that do not necessarily represent the same property in different growth models, T is the growth period indicative of growth rate, m is the Richards shape parameter, ''base model'' refers to 1 of the first 5 models, b is the size difference (additive model) or proportional size difference (proportional model) between females with and without a fetus, and F is a fetus presence–absence dummy variable (1 = present, 0 = not present).

Model	Equation	References
Pütter or von Bertalanffy	$S_t = A(1 - e^{-k(t-t_0)})$	Ricker (1979); von Bertalanffy (1938)
von Bertalanffy	$S_t = A(1 - e^{-k(t-t_0)})^3$	Ricker (1979); von Bertalanffy (1938)
Logistic	$S_t = \frac{A}{1 + e^{-k(t-t_0)}}$	Ricker (1979)
Gompertz	$S_t = Ae^{-e^{-k(t-t_0)}}$	Ricker (1979)
Richards	$S_t = [A^{1-m} - (A^{1-m} - S_0{}^{1-m})e^{[-2t(1+m)]/T}]^{1/(1-m)}$	Leberg (1989); Richards (1959)
Additive female	Base model + bF	
Proportional female	Base model (1 + bF)	

formed data using linear least-squares regression.

Proportional residuals of the fitted size-at-age models ([observed size − predicted size]/predicted size) were smoothed using locally weighted regression (Statistical Sciences, Inc. 1995) to investigate seasonal patterns of growth. Proportional residuals were used because regression of absolute residuals would have been influenced by interactions between collection date and ages of individuals collected. Length and mass of males and females were plotted by day of the year and smoothed (Statistical Sciences, Inc. 1995) to further examine seasonal fluctuations in size. For the latter analysis, data were grouped into 2 age groups (1–5 years and ≥6 years) to increase samples.

RESULTS

Length-at-age models.—All growth models described the data well, and their r^2 values were very similar (Appendix I). However, the Richards model was chosen as the best-fitting model because it had the highest r^2 and most closely approximated the locally weighted regressions (Table 2). With the Richards models for females, we were unable to obtain standard errors of the parameter estimates because of correlation among parameters. Growth in body length was asymptotic for males and females (Fig. 3; Table 3). Growth rate of females declined with age, with length reaching 90% of asymptotic length by 4 years of age. The extra parameter (b) was significant in the additive and proportional female models ($P < 0.05$), indicating that females with a fetus were longer than other females of the same age. The additive model was chosen over the proportional model because r^2 was greater, but the difference was marginal (Appendix I). Presence of a fetus was associated with a 0.03-m increase in body length (Fig. 3; Table 3). The growth rate in length of males was greatest at about 4 years of age, after which it decreased with age. The maximal growth rate (m/day) was 6% greater than the growth rate at 2 years of age. Body length of males did not reach 90% of asymptotic length until about 7.5 years of age.

TABLE 2.—Parameter estimates (±*SE*) for Richards models describing the growth of Steller sea lions (standard length and mass at age in years). The female model is the additive model with the Richards model as the base model (Table 1). Data used were from animals ≥0.75 years old.[a]

Model	A	m	S_0	T	b	r^2	*n*
Length (m)							
Male	3.061 ± 0.054	7.121 ± 3.163	1.635 ± 0.048	31.990 ± 2.465		0.883	203
Female (additive)	2.324	−3.218	0	−17.107	0.032	0.787	222
Mass (kg)							
Male	681.112 ± 16.254	8.041 ± 3.392	101.148 ± 9.087	12.365 ± 0.890		0.850	217
Female (additive)	287.829 ± 9.979	−0.690 ± 0.187	1.2E-04 ± 2.6E-19	4.225 ± 1.821	27.554 ± 4.201	0.795	250

[a] A = asymptotic size; m = Richards shape parameter; S_0 = size at time 0; T = growth period indicative of growth rate; b = size difference.

A significant sexual difference in length first appeared in year-class 3 (males = 2.20 m ± 0.138 *SD*, females = 2.02 ± 0.106 m; $P < 0.001$).

Length-at-age models for males and females failed to accurately predict birth length (Fig. 3). The female length-at-age model underestimated birth length and, thus, overestimated the average growth rate during the 1st year of life. The male model overestimated birth length, and, thus, underestimated the average growth rate of animals < 1 year old. Those results led to an apparent convergence in body length from ages 0.75 to 2 years and a divergence thereafter, although at 2 years of age, predicted male length was still greater than predicted female length (Fig. 3).

Mass-at-age models.—All growth models described data on mass well, and their r^2 values were very similar (Appendix I). The Richards model was again chosen over the other growth equations based on its highest value of r^2 and its similarity to the locally weighted regressions (Table 2). We were unable to obtain standard errors for the parameter estimates of the Richards model for females without the extra parameter (b). Growth in mass was asymptotic for males and females (Fig. 4; Table 3). The growth rate in mass of females declined with age, with body mass reaching 90% of asymptotic mass by 13 years of age. As for length, the extra parameter (b) was significant in additive and proportional models for females ($P < 0.05$). The additive model was chosen for its high r^2 value, although the r^2 was similar to the proportional model (Appendix I). Females with a fetus averaged 28 kg heavier than other females of the same age (Fig. 4; Table 3). The growth rate of mass in males increased with age to a maximum during the 7th year of life, after which it decreased with age. The growth rate (kg/day) at 7.5 years of age was about 3 times that at 2 years of age. Body mass of males was 90% of asymptotic mass at about 9 years of age. Analysis of the data revealed a significant difference between

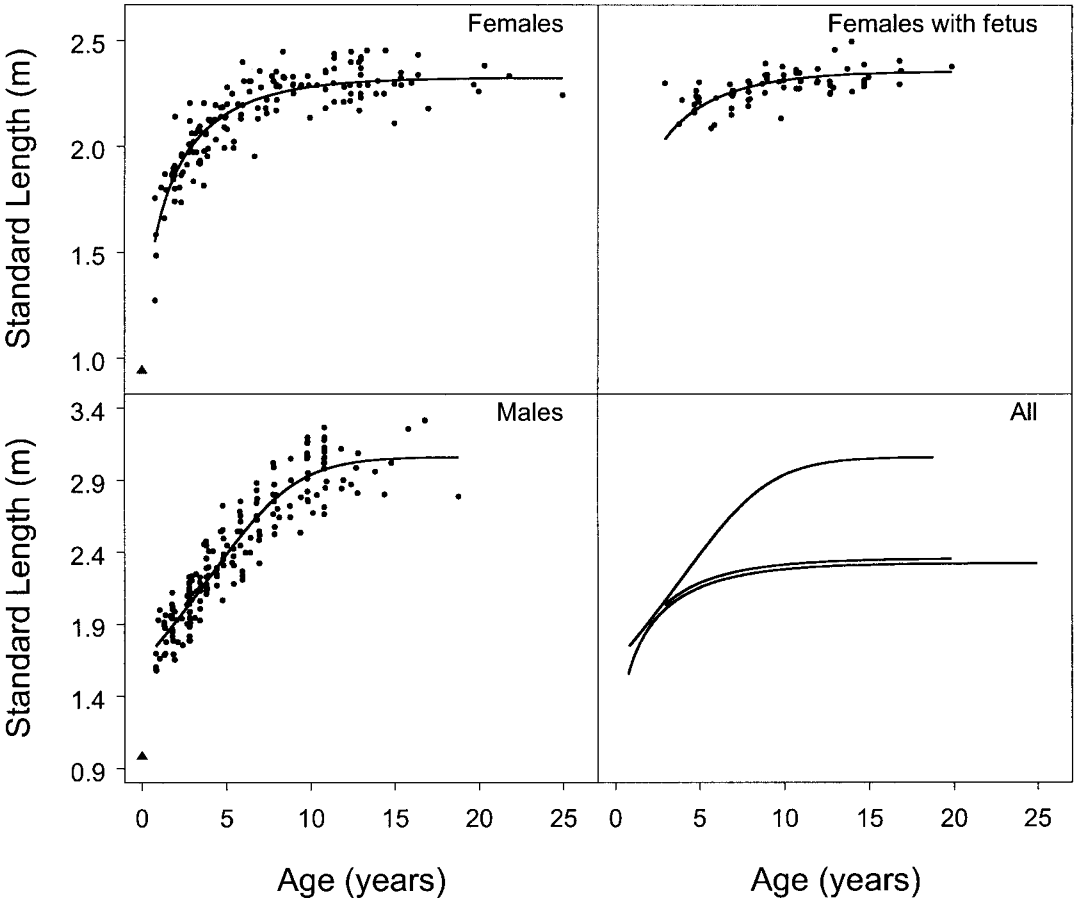

FIG. 3.—Growth in length of Steller sea lion males (≥0.75 year old), females (≥0.75 years old), and females with a fetus. The fitted curves are from Richards models (Table 2). Triangles show mean lengths of newborn pups (0–5 days old) from Brandon et al. (1996).

the size of males and females at age 2 (males = 174 kg ± 36.0 *SD,* females = 144 ± 34.8 kg; $P < 0.01$).

As with length (Fig. 3), mass-at-age models failed to accurately predict birth mass for both sexes (Fig. 4). Those results led to an apparent convergence in body mass from ages 0.75 to 2 years and a divergence thereafter, although at 2 years of age, predicted male mass was still greater than predicted female mass (Fig. 4). Our size-at-age models cannot be used to estimate length or mass of Alaskan Steller sea lions <1 year old.

Allometric relationship of length to mass.—The allometric relationship between body length and mass of females was described well by a power function (Table 4; Fig. 5). However, the model tended to overestimate mass of females at smaller lengths and underestimate mass at greater lengths. For males, a change occurred in the length–mass relationship around 2.6 m (Fig. 5) such that we divided data into 2 groups (≤2.6 m and >2.6 m) and fit 2 separate power functions. Both described their respective data well (Table 4; Fig. 5). Males >2.6 m long were heavier per unit length than shorter males. Males (≤2.6 m long) and females were similar in mass for a given length, whereas females with a fetus were slightly heavier per unit length.

TABLE 3.—Predicted standard length and mass of Steller sea lions ≥1 year old. Sizes at age 0 (birth) are observed mean sizes of newborn (0–5 days old) Steller sea lions from various locations in Alaska (Brandon et al. 1996). All other sizes were calculated from fitted Richards growth models (Table 2).

	Standard length (m)			Mass (kg)		
Age (years)	Male	Female	Female with fetus	Male	Female	Female with fetus
0	0.98	0.94		22	20	
1	1.77	1.64		125	89	
2	1.92	1.88	1.91	153	128	156
3	2.07	2.01	2.04	189	156	184
4	2.23	2.09	2.13	232	178	206
5	2.39	2.15	2.19	286	195	223
6	2.54	2.20	2.23	351	210	237
7	2.67	2.23	2.26	430	221	249
8	2.78	2.25	2.28	521	231	259
9	2.87	2.27	2.30	605	240	267
10	2.94	2.28	2.31	656	247	274
11	2.98	2.29	2.32	675	252	280
12	3.01	2.30	2.33	680	257	285
13	3.03	2.30	2.34	681	262	290
14	3.04	2.31	2.34	681	265	293
15	3.05	2.31	2.34	681	269	296
16	3.05	2.32	2.35	681	271	299
17	3.06	2.32	2.35	681	274	301
18	3.06	2.32	2.35	681	276	303
19		2.32	2.35		277	305
20		2.32			279	
21		2.32			280	
22		2.32			281	
23		2.32			282	
24		2.32			283	

Seasonal patterns of growth.—Determining seasonal patterns of growth was complicated by a lack of animals collected in December and January and small samples in June–September. Despite those shortcomings, residuals of the fitted growth models indicated seasonal variability in growth rate, especially for males (Fig. 6). The regression on residuals of the length model for females without fetuses deviated little from 0 (±1%), suggesting low seasonal variability in growth of length. The regression on residuals of the mass model for females without fetuses was within ±5% throughout the year, with observed mass higher than predicted mass in October–November and lower than predicted in April–May. Regressions on residuals of length and mass models for males exhibited a distinct seasonal pattern. Observed length and mass of males were higher than predicted in February–March and lower than predicted in the breeding season (May–July) and in October–November. That indicated that the average growth rate of males was higher than predicted by models between November and February and lower than predicted during May and June. The regression on the residuals of the length model for males was within ±3%, whereas the regression on the residuals of the mass model was within ±10% throughout the year.

Patterns exhibited by the regressions on the residuals were supported when size was regressed on day of the year (Fig. 7). By grouping the data into 2 age classes, bias

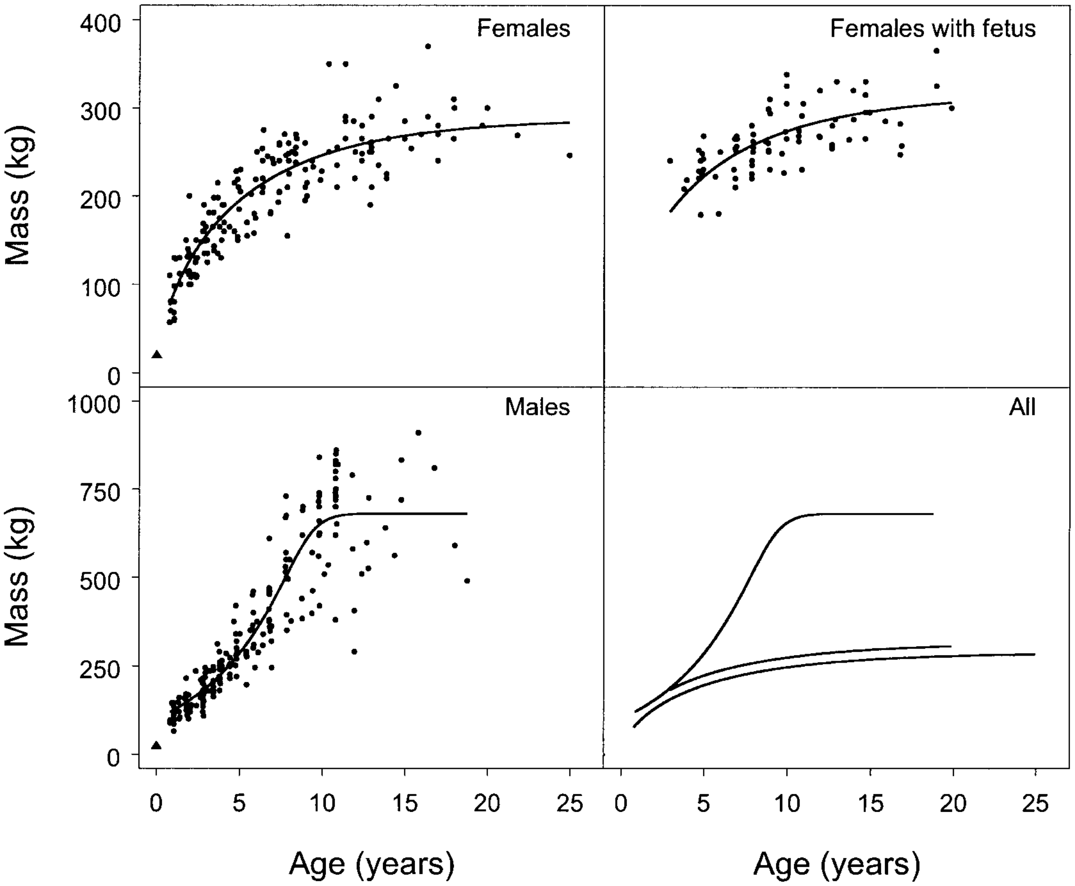

FIG. 4.—Growth in mass of Steller sea lion males (≥0.75 years old), females (≥0.75 years old), and females with a fetus. The fitted curves are from Richards models (Table 2). Triangles show mean masses of newborn pups (0–5 days old) from Brandon et al. (1996).

TABLE 4.—Results of allometric regression of body mass (M in kg) on standard length (L in m) for Steller sea lions ≥0.75 years old ($\log_{10}$ M = $\log_{10}$ a + b $\log_{10}$ L).[a]

	Parameter (±*SE*)			
Sex/size class	$\log_{10}$ a	b	*n*	r^2
Male ≤ 2.6 m	1.34 ± 0.026	2.94 ± 0.079	118	0.92
Male > 2.6 m	1.20 ± 0.120	3.40 ± 0.257	75	0.71
Female	1.34 ± 0.036	2.89 ± 0.110	129	0.84
Female with fetus	1.42 ± 0.111	2.79 ± 0.309	70	0.55

[a] $\log_{10}$ a = Y intercept; b = linear regression coefficient.

may have been introduced because of interactions between age and time of year. However, patterns were generally the same when each age was smoothed individually. Data from males ≥6 years of age exhibited large seasonal fluctuations in length and mass, with most growth occurring between November and February. Very little growth occurred during the breeding season (May–July); in fact, animals may have even de-

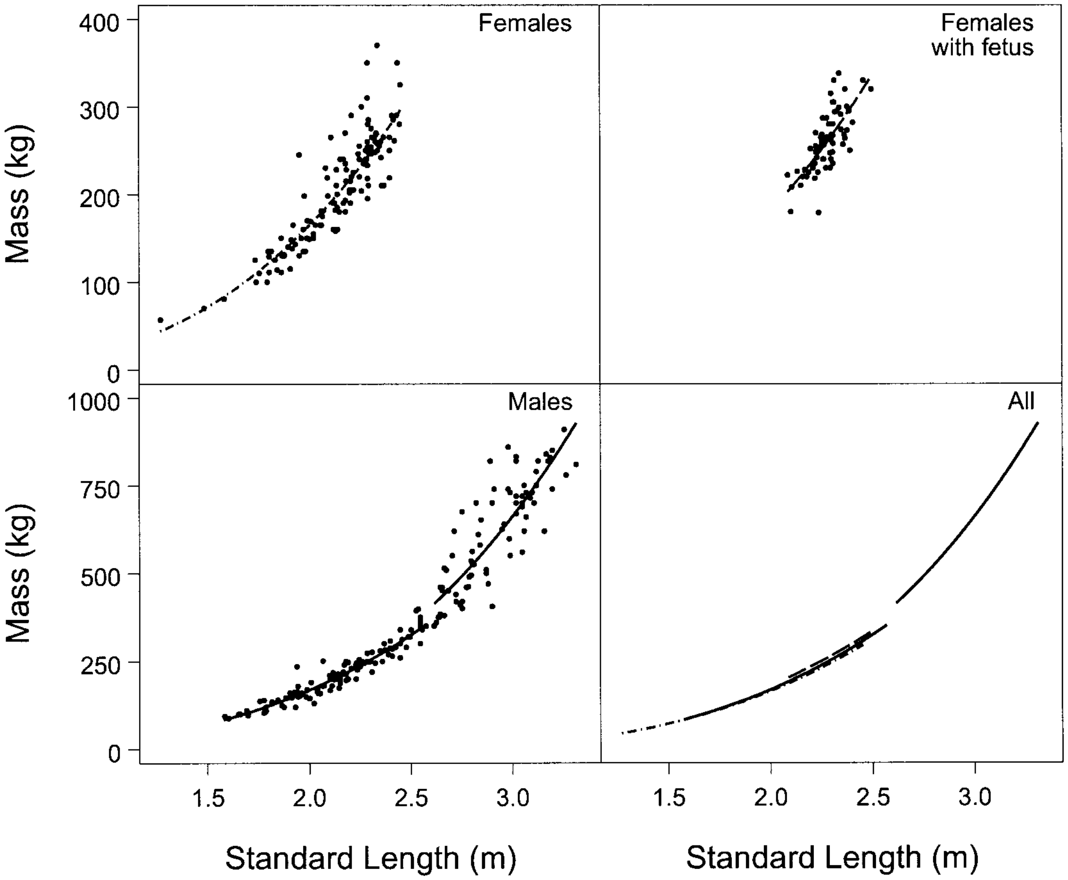

FIG. 5.—Mass–length relationships for Steller sea lion males (≥0.75 years old), females (≥0.75 years old), and females with a fetus. Parameter values of the fitted allometric models (lines) are given in Table 4.

creased in size. Young males and females (1–5 years old) also grew very little from April to June and may have decreased slightly in size during that time. Size of females ≥6 years old fluctuated very little during the year, although individuals collected in October and November were slightly longer and heavier than animals collected between February and May.

DISCUSSION

Cross-sectional data.—Growth of pinnipeds in the wild has invariably been assessed using cross-sectional data (Boyd et al. 1994; Bryden 1972; Garlich-Miller and Stewart 1998; Hammill et al. 1995; Innes et al. 1981; Lima and Páez 1995; McLaren 1993; Murie and Lavigne 1992; Olesiuk 1993; Rosas et al. 1993; Trites and Bigg 1996). Growth models derived from cross-sectional data represent mean size of collected individuals surviving to a given age during the collection period. Potential sources of bias are precision of assigned age, variation in birth date, accuracy of the aging technique, unequal body size representation within age classes, unequal sampling among months, unequal representation of ages, differential mortality related to size, and differential growth and survival rates related to environmental conditions (Innes et al. 1981; Leberg et al. 1989; McLaren 1993).

The first 3 potential sources of bias—pre-

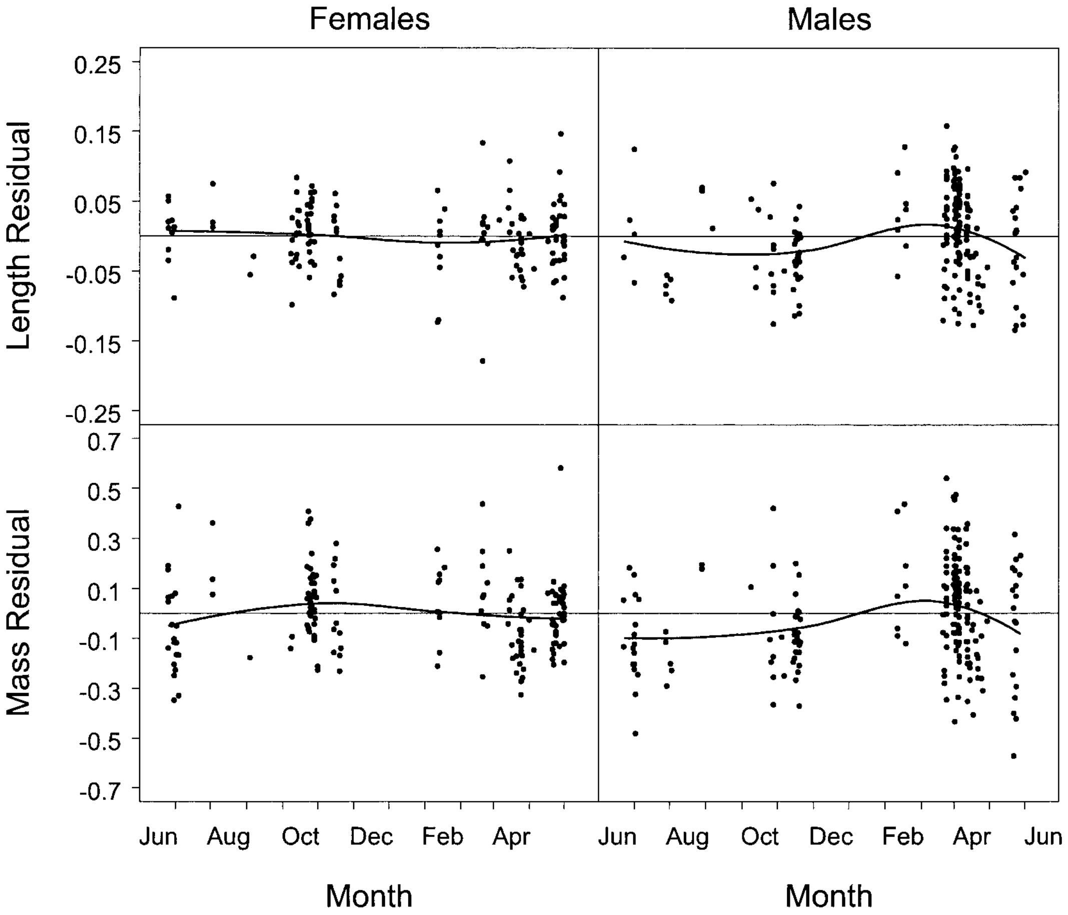

FIG. 6.—Seasonal variability in growth rate: residuals ([observed size − predicted size]/predicted size) of the fitted Richards models (Figs. 3 and 4; Table 2) by day of the year for male and female (without a fetus) Steller sea lions. Line is a locally weighted regression (see Materials and Methods).

cision of assigned age (e.g., nearest day or nearest month), variation in birth date (in the wild), and accuracy of the aging technique—are related to the aging of animals. The precision of assigned ages and variation in birth date have little effect on the fitting of growth models (Leberg et al. 1989). However, inaccurate aging techniques result in individuals being assigned to the wrong age class and can bias model parameter estimates and increase their variance (Leberg et al. 1989). We used dental cementum annuli to determine age. This is a common method for aging pinnipeds and has been shown to be accurate to within ±1 year for Steller sea lions, so we assumed that this bias was minimal (Fiscus 1961; C. H. Fiscus, in litt.; Scheffer 1950; Spalding 1964).

The next 2 potential sources of bias—unequal size representation within age classes and unequal sampling among months—are related to sampling selectivity within age classes. Size selectivity can be a problem with polygynous, sexually dimorphic species such as the Steller sea lion (McLaren 1993). Large, breeding male Steller sea lions are strongly territorial, resulting in segregation of smaller nonbreeding males from rookery areas during the breeding season (Mathisen et al. 1962; Thorsteinson and Lensink 1962; Zadal'skii 1997). Size bias of the sampled

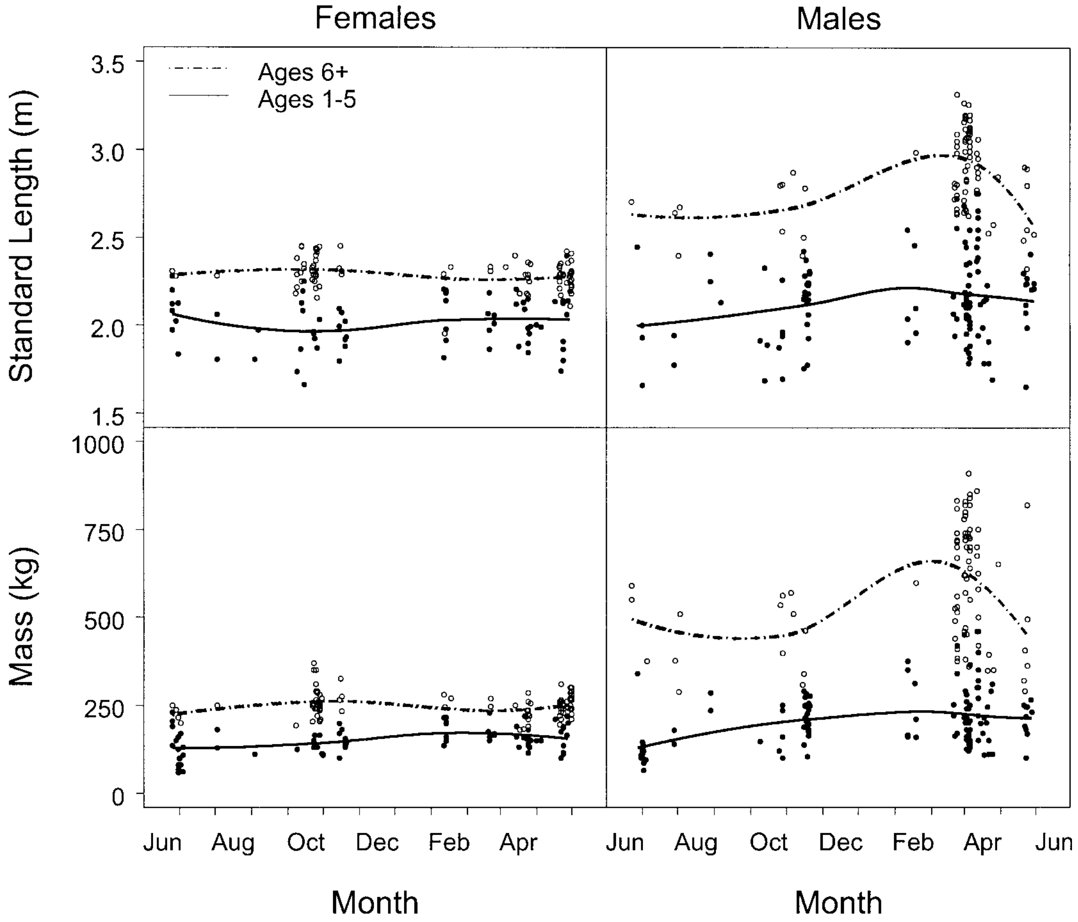

FIG. 7.—Seasonal growth in body size: length and mass by day of the year for male and female (without a fetus) Steller sea lions. Lines are locally weighted regressions (see Materials and Methods).

animals should be small because they were collected from rookeries, haulouts, and coastal waters. However, some bias may exist in the data on adult males because no adult males were taken from rookeries during the breeding season. If nonterritorial males were smaller than territorial males of the same age, our size-at-age models would have underestimated the mean size of socially mature males (males ≥9 years of age able to hold territories). However, adult males sampled during the breeding season are only a small proportion of the total sample of adult males so the effect of this bias on the fitted size-at-age models was probably small. This bias also may have influenced observed seasonal size patterns by exaggerating the decrease in body size during the breeding season (late May–early July; Fig. 7).

Selectivity by time of the year is a problem when animals undergo seasonal size fluctuations, as is the case with many pinniped species including the Steller sea lion (Ashwell-Erickson and Elsner 1981; Boyd and Duck 1991; Bryden 1972; Costa et al. 1986; Nordøy and Blix 1988; P. F. Olesiuk and M. A. Bigg, in litt.; Renouf et al. 1993; Ryg et al. 1990; Schusterman and Gentry 1971; Sergeant 1973; Trites and Bigg 1996). The majority of animals in our study were sampled between February and May, and October and November, although juveniles were collected more equally among seasons than were adults (Figs. 2 and 7). Thus, the size-at-age models were biased toward size at these times of the year, especially for older age classes.

The 6th potential source of bias is sampling selectivity among ages. Unequal sampling of a population with respect to age may bias the asymptotic-size parameter of growth models (Leberg et al. 1989). Older males and females constituted a small proportion of the total sample in our study, largely because they made up a relatively small proportion of the population. However, a reasonable sample of animals from this age group was present, so this bias likely did not affect the size-at-age models.

The last 2 potential sources of bias—differential mortality related to size and differential growth and survival rates related to environmental conditions—are more difficult to assess. An interaction between size and survival is likely. For example, rapidly growing juveniles or subadults may survive better than slowly growing individuals of the same age. This would result in an excess of large individuals among young adults (McLaren 1993). Furthermore, because of environmental variation over time, all generations may not have been exposed to the same environmental conditions. Varying environmental conditions could produce generational size differences (Innes et al. 1981). For example, using the same specimens we used, Calkins et al. (1998) showed that female Steller sea lions were larger in the 1970s than in the 1980s. This difference was probably a result of undernutrition. Unfortunately, not enough data are available to determine the exact effect of these 2 sources of bias. At best, our size-at-age models represent the average size of animals born during a specific period (mid- to late 1900s).

Mathematical growth models.—The usefulness of mathematical growth models has been questioned (Aldrich and Lawler 1996; Zach 1988). No single equation adequately describes growth of pinnipeds over the entire life cycle, and commonly used growth models fail to describe seasonal patterns of growth (McLaren 1993; Trites and Bigg 1996). However, by reducing the complex physical growth process to a few parameters that describe the nonlinear effect of age on size, growth models allow comparisons of growth patterns between sexes, populations, and species (Brown et al. 1976; McLaren 1993; Pruitt et al. 1979). Residual variances in these models of growth can be used to assess variability of size within populations and species, including seasonal size fluctuations (McLaren 1993).

Most mathematical growth models were formulated originally based on fundamental postulates about growth processes, but few data are available to support these theories (Pruitt et al. 1979; Richards 1959; Ricker 1979; von Bertalanffy 1938). Thus, selection of appropriate models is based on goodness-of-fit and convenience (Ricker 1979). The 3-parameter Pütter, von Bertalanffy, logistic, and Gompertz growth models are special cases of the 4-parameter Richards model (Table 1—Richards 1959). Some authors have suggested that the Richards model should be used because it is more flexible than 3-parameter models, is better at detecting changes in growth patterns due to environmental conditions, and produces less biased estimates of growth when the true growth pattern does not conform to a 3-parameter model (Brisbin et al. 1987; Leberg et al. 1989). Others have contended that simpler models are easier to interpret, do not have problems with parameter correlation, and often describe data just as well as the Richards model (Zach 1988). In our study, the Richards model provided the best fit in all cases. This was not unexpected because it is the most flexible of the models tested (4 parameters). However, the simpler models also described data well (Appendix I), and we encountered some problems with parameter correlation with the Richards model. Nevertheless, the Richards model was useful, especially when the growth pattern deviated from the predetermined shape of the 3-parameter models, as occurred with growth of mass in males.

Sexual size differences.—Female length and mass exhibited asymptotic growth, with growth rate declining with increasing age. Laws (1956) found that length at puberty, as a percentage of final size, was remarkably constant among female pinnipeds at 87%. The length of female Steller sea lions reached 87% of its asymptote during the 3rd year of life. This corresponds with the earliest evidence of female sexual maturity (Pitcher and Calkins 1981), as suggested by Laws (1956). Mass did not reach 87% of asymptotic mass until the 12th year of life. This is intriguing and suggests that females continue to accrete mass after they have stopped growing in length.

Growth in length and mass of males was different from the growth of females. Growth in length of males was asymptotic, but growth rate was relatively constant up to about 6 years of age. Thus, males sustained a higher rate of growth in length for a longer period of time than did females. Body length reached 87% of asymptotic length during the 7th year of life. Males are believed to reach sexual maturity between 3 and 8 years of age with the majority maturing between 5 and 7 years of age (Perlov 1971; Pitcher and Calkins 1981; Thorsteinson and Lensink 1962). This suggests that most males mature sexually before reaching 87% of body length. However, although the males may be physiologically mature, they usually are not socially mature and able to hold a territory until the age of 9 years or older (average age of harem bulls is 10 or 11 years), when they have reached 87% of asymptotic length (Pitcher and Calkins 1981; Thorsteinson and Lensink 1962).

Males exhibited a growth spurt in mass with a maximal rate of growth at 7.5 years of age. Such a growth spurt has been noted in other polygynous pinniped species (Boyd et al. 1994; Bryden 1972; Lander 1981; McLaren 1993; Trites and Bigg 1996). The rate of growth in mass was maximal shortly after the mean age of physiologic sexual maturity, suggesting that the growth spurt coincides with puberty. Perlov (1971) described a rapid increase in the weight of the Steller sea lion baculum and testes between 5 and 7 years of age. Miller et al. (2000) also described rapid bacular growth between 5 and 7 years of age in the Steller sea lion. This corresponds with the period of rapid growth in body mass that we observed. Concurrent growth spurts in bacular size and body size at sexual maturity also have been described for the Cape fur seal (*Arctocephalus p. pusillus*—Oosthuizen and Miller 2000) and the harp seal (*Pagophilus groenlandicus*—Miller et al. 1998). Our results do not agree with Bryden's (1972) suggestion that the growth spurt does not occur until social maturity.

Other workers have suggested that a growth spurt may also occur in length at the time of sexual or social maturity (Bryden 1972; McLaren 1993; Scheffer and Wilke 1953). We found only weak evidence of a growth spurt in length in males from the collection in our study. Therefore, during the pubertal growth spurt in mass, the allometric relationship between length and mass changed abruptly. Adult males were much heavier per unit length than were younger males. Other studies also have failed to detect such a growth spurt in length in species that exhibit a growth spurt in mass (McLaren 1993; Payne 1979).

McLaren (1993) modeled a growth spurt in the male Steller sea lion by using 2 consecutive size-at-age models. We chose to model the growth of mass in males using 1 size-at-age model. Data for some species of sexually dimorphic pinnipeds suggest that growth of males (which undergo growth spurts) is described better by 1, rather than 2, sigmoid models (Boyd et al. 1994; Lander 1981; Payne 1979). We modeled the change in the allometric relationship between length and mass at puberty using 2 consecutive power equations. We could have described the relationship between length and mass using 1 equation (e.g., exponential equation), but our goal was to simply describe the difference between pre- and postpubertal allometry (Pasternack and Gianutsos 1969).

Sexual size differences are greater in otariids than in any other mammals, with males averaging 3 times the size of females (Weckerly 1998). The sexual size differences are believed to be a result of their polygynous mating systems (intense male–male competition) and sexual selection (Trivers 1972). Body length first differed significantly between the sexes at 3 years of age, and mass initially differed at 2 years of age. Our failure to detect a significant size difference before these ages was likely a result of low statistical power because male and female Steller sea lions have been shown to differ in size at birth (Brandon et al. 1996; Merrick et al. 1995). Rate of growth in length declined much later in males than females, resulting in males being 1.3 times as long as females by 12 years of age. The growth spurt in mass of males produced a very large difference between the sexes, with males being 2.6 times as heavy as females by 12 years of age. The sexual size difference in the Steller sea lion is achieved through a longer period of growth in length and a pubertal growth spurt in mass of males.

Although some sources state that the mass of an adult male Steller sea lion is about 1 tonne or 900–1,000 kg (e.g., King 1983), we found an average mass of 681 kg for males aged 12 years and older. This corresponds to about 1,500 pounds (average mass of adult males listed in Wynne 1993). The maximal recorded mass in data we used was 910 kg (~2,000 pounds).

Pregnancy.—Females with a fetus averaged 3 cm longer and 28 kg heavier than other females of the same age. They also weighed more per unit length. The mass difference was mainly due to the mass of the fetus, placenta, and other physiologic changes associated with pregnancy. The length difference probably reflects this additional mass extending the vertebral column during measurement, as has been suggested for northern fur seals (Trites and Bigg 1996). The difference in the allometric relationship between mass and length is mainly due to the additional mass associated with pregnancy but also may be a result of females that weigh less per unit length having a lower probability of carrying a fetus to term (Pitcher et al. 1998).

The additive model described the female data best, suggesting that the change in mass associated with pregnancy (including fetal mass) was a constant amount and independent of maternal age and size. However, the proportional model described the data almost as well. Pup mass was correlated positively with maternal mass in southern elephant seals (*Mirounga leonina*), and all mothers had the same mass-to-length relationship, suggesting that longer mothers also gave birth to larger pups (Arnbom et al. 1994). Pup size (mass and length) also was correlated positively with maternal age in northern fur seals, although pup size was correlated negatively with older maternal ages (Trites 1991). Size and age of the mother probably influenced size of the fetus (especially near parturition), but our data and analyses were inadequate to determine this. The main intention of our analysis was to control for the additional size of a female carrying a fetus rather than to determine the exact nature of this size difference.

Seasonality.—Strong seasonality was evident in the growth of mass of males ≥6 years of age. Most growth occurred between November and March; little growth occurred during the breeding season and in late summer (May–September); in fact, animals may have decreased in size. These results are consistent with previous studies of seasonal size fluctuations in wild and captive adult male Steller sea lions (Nitto et al. 1998; P. F. Olesiuk and M. A. Bigg, in litt.). Changes in mass are probably a result of an increase in blubber content before the breeding season; this blubber provides a source of energy during fasting and additional body size for territorial competition (P. F. Olesiuk and M. A. Bigg, in litt.; Pitcher et al. 2000). Adult males of other otariid species also exhibit seasonal fluctuations in blubber content related to their reproductive strategy (Boyd and Duck 1991; Schusterman and Gentry 1971). Males >9 years of age grew very little in body mass so these seasonal changes in body mass are not changes in growth per se, but males aged 6–8 years were growing rapidly in mass so they exhibited seasonal fluctuations in growth rate.

These seasonal changes in body mass of adult male Steller sea lions may be associated with seasonal changes in food consumption. Kastelein et al. (1990) found that the food consumption of a captive adult male Steller sea lion was less than its average monthly food consumption between April and September (when we found a low rate of growth in mass), and greater than its average monthly food consumption between November and March (when we found a high rate of growth in mass).

When size was plotted by day of the year (Fig. 7), a sharp decrease in size seemed apparent during May. This can be explained by sampling bias. No adult males were taken from rookeries during the breeding season, so older males sampled in May were probably smaller individuals who were unable to acquire or maintain a territory. However, male Steller sea lions that hold territories fast during their tenancy, which lasts about 40 days (Gentry 1970), and this results in substantial loss of mass (P. F. Olesiuk and M. A. Bigg, in litt.). The observed seasonal fluctuations in body mass of young males (<6 years old) suggest that nonterritorial males also may undergo seasonal changes in body mass. Thus, all males possibly exhibited some decrease in body mass during the breeding season, but the observed decrease in body mass would have been exaggerated by the sampling bias. Also, nonterritorial males possibly did not differ substantially in size from territorial males. If this was the case and the body mass of nonterritorial males decreased during the breeding season, then the observed decrease in body mass in May would be close to the actual decrease in body mass of adult males during the breeding season.

Interestingly, seasonal fluctuations in length, similar to the seasonal fluctuations in mass, were detected in adult males. Trites and Bigg (1996) found seasonal length fluctuations in northern fur seals and suggested that these fluctuations might be due to a gravity phenomenon related to the amount of time spent in the water, changes in body-water content, or the displacement of body mass during measurement. Of the 3 hypotheses, only the latter 2 are probable for Steller sea lions. Unlike northern fur seals, Steller sea lions do not undergo a long migration, so they do not spend an extended period of time in the water when their bodies might expand (gravity phenomenon). However, male Steller sea lions do spend more time at sea during the winter, when adult male and juvenile body sizes were greatest. A change in body-water content is likely and has been shown for adult male Steller sea lions (P. F. Olesiuk and M. A. Bigg, in litt.). Mass displacement during standard length measurement, while animals were on their back, also is possible. Although some animals were measured while on their belly (dorsal standard length), those measurements were converted to standard length using an equation developed from animals that were measured on their backs, so those data would be subject to the same phenomenon. Most likely, both of these factors contributed to the observed seasonal fluctuations in body length.

Adult females (≥6 years of age) that were not carrying a fetus did not exhibit distinct seasonal fluctuations in length or mass. Weak evidence existed that mass was greater in October–November than in the spring (April–May). This may be because females that weigh less per unit length have a lower probability of carrying a fetus to term (Pitcher et al. 1998). In the autumn (October–November), all females collected were classified as ''not carrying a fetus.'' However, females collected late in gestation (April–May) that were not carrying a fetus were smaller individuals who were unable to maintain their pregnancy during winter.

Males and females <6 years of age grew very little during the breeding season and may have slightly decreased in size. Seasonal fluctuations in juvenile pinniped growth rate and size are less well documented but also may involve an increase in mass or fat content before the breeding season and a decrease during the breeding season (Ryg et al. 1990; Trites and Bigg 1996). Our data are consistent with this pattern. Pitcher et al. (2000) found that the sculp mass (mass of skin and blubber) of male Steller sea lions <5 years old was a greater proportion of body mass during the winter–spring than during the summer–autumn, suggesting animals were in better condition before the breeding season than during or after the breeding season. Evidence also exists that captive juvenile Steller sea lions experience seasonal changes in growth rate synchronous with those found in this study and that these fluctuations may be associated with inherent seasonality in food consumption related to growth and moulting (Nitto et al. 1998; A. W. Trites and D. A. S. Rosen, in litt.).

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Appendix I

Parameter estimates (±*SE*) for models (Table 1) describing the growth of Steller sea lions (standard length, m, and mass, kg, at age in years). Samples (*n*) were: male length, 203; female length, 222; male mass, 217; female mass, 250.[a]

Sex	Model	A	k	t_0
Length (m)				
Male	Pütter	3.376 ± 0.090	0.140 ± 0.015	−3.964 ± 0.462
	von Bertalanffy	3.298 ± 0.073	0.173 ± 0.016	−8.336 ± 0.793
	Logistic	3.200 ± 0.055	0.241 ± 0.018	0.385 ± 0.148
	Gompertz	3.268 ± 0.068	0.190 ± 0.016	−1.259 ± 0.199
	Richards	3.061 ± 0.054		
Female	Pütter	2.323 ± 0.011	0.369 ± 0.029	−2.374 ± 0.325
	Pütter (additive)	2.310 ± 0.012	0.368 ± 0.030	−2.434 ± 0.340
	Pütter (proportional)	2.310 ± 0.013	0.370 ± 0.030	−2.422 ± 0.338
	von Bertalanffy	2.321 ± 0.011	0.392 ± 0.031	−4.731 ± 0.510
	von Bertalanffy (additive)	2.308 ± 0.012	0.391 ± 0.031	−4.808 ± 0.533
	von Bertalanffy (proportional)	2.309 ± 0.012	0.392 ± 0.031	−4.788 ± 0.529
	Logistic	2.317 ± 0.011	0.438 ± 0.034	−1.172 ± 0.258
	Logistic (additive)	2.305 ± 0.012	0.436 ± 0.035	−1.247 ± 0.273
	Logistic (proportional)	2.305 ± 0.012	0.437 ± 0.035	−1.238 ± 0.271
	Gompertz	2.320 ± 0.011	0.404 ± 0.032	−1.726 ± 0.288
	Gompertz (additive)	2.308 ± 0.012	0.402 ± 0.032	−1.795 ± 0.303
	Gompertz (proportional)	2.308 ± 0.012	0.403 ± 0.032	−1.785 ± 0.301
	Richards	2.338		
	Richards (additive)	2.324		
	Richards (proportional)	2.324		
Mass (kg)				
Male	Pütter	1,120.759 ± 134.201	0.077 ± 0.015	0.334 ± 0.224
	von Bertalanffy	854.765 ± 47.933	0.182 ± 0.018	−2.133 ± 0.448
	Logistic	744.448 ± 24.698	0.394 ± 0.026	5.857 ± 0.250
	Gompertz	808.919 ± 37.354	0.235 ± 0.020	4.622 ± 0.264
	Richards	681.112 ± 16.254		
Female	Pütter	289.322 ± 6.389	0.212 ± 0.021	−0.740 ± 0.266
	Pütter (additive)	279.550 ± 6.690	0.198 ± 0.021	−1.030 ± 0.304
	Pütter (proportional)	276.738 ± 6.364	0.208 ± 0.021	−0.949 ± 0.291
	von Bertalanffy	284.135 ± 5.588	0.267 ± 0.025	−3.398 ± 0.516
	von Bertalanffy (additive)	274.653 ± 5.892	0.247 ± 0.024	−3.955 ± 0.587
	von Bertalanffy (proportional)	272.316 ± 5.676	0.258 ± 0.025	−3.765 ± 0.560
	Logistic	278.249 ± 4.822	0.378 ± 0.034	2.468 ± 0.166
	Logistic (additive)	268.895 ± 5.113	0.345 ± 0.032	2.348 ± 0.177
	Logistic (proportional)	267.061 ± 5.006	0.358 ± 0.033	2.274 ± 0.174
	Gompertz	282.250 ± 5.330	0.295 ± 0.027	1.260 ± 0.168
	Gompertz (additive)	272.840 ± 5.633	0.272 ± 0.026	1.064 ± 0.184
	Gompertz (proportional)	270.667 ± 5.453	0.283 ± 0.027	1.042 ± 0.184
	Richards	294.542		
	Richards (additive)	287.829 ± 9.979		
	Richards (proportional)	283.698 ± 8.997		

[a] A = asymptotic size; K = fitted parameter indicative of growth rate; t_0 = fitted time parameter; m = Richards shape parameter; S_0 = size at time 0; T = growth period indicative of growth rate; b = size difference (additive model) or proportional size difference (proportional model).

APPENDIX I.—Extended.

m	S_0	T	b	r^2
				0.876
				0.878
				0.880
				0.878
7.121 ± 3.163	1.635 ± 0.048	31.990 ± 2.465		0.883
				0.778
			0.029 ± 0.013	0.783
			0.012 ± 0.006	0.783
				0.777
			0.029 ± 0.013	0.782
			0.012 ± 0.006	0.782
				0.775
			0.028 ± 0.014	0.780
			0.012 ± 0.006	0.779
				0.777
			0.029 ± 0.013	0.781
			0.012 ± 0.006	0.781
−3.075	7.2E-05	−15.773		0.781
−3.218	0	−17.107	0.032	0.787
−3.203	0.004	−16.894	0.014	0.786
				0.809
				0.825
				0.840
				0.830
8.041 ± 3.392	101.148 ± 9.087	12.365 ± 0.890		0.850
				0.759
			27.127 ± 4.197	0.794
			0.109 ± 0.019	0.790
				0.757
			26.972 ± 4.227	0.792
			0.108 ± 0.019	0.788
				0.752
			27.033 ± 4.291	0.786
			0.108 ± 0.019	0.782
				0.756
			26.953 ± 4.243	0.790
			0.108 ± 0.019	0.787
−0.484	0.002	5.935		0.759
−0.690 ± 0.187	1.2E-04 ± 2.6E-19	4.225 ± 1.821	27.554 ± 4.201	0.795
−0.653 ± 0.185	0.002 ± 0.000	4.393 ± 1.631	0.112 ± 0.019	0.792