

Abstract—The growth rate of Steller sea lion (*Eumetopias jubatus*) pups was studied in southeast Alaska, the Gulf of Alaska, and the Aleutian Islands during the first six weeks after birth. The Steller sea lion population is currently stable in southeast Alaska but is declining in the Aleutian Islands and parts of the Gulf of Alaska. Male pups (22.6 kg [± 2.21 SD]) were significantly heavier than female pups (19.6 kg [± 1.80 SD]) at 1–5 days of age, but there were no significant differences among rookeries. Male and female pups grew (in mass, standard length, and axillary girth) at the same rate. Body mass and standard length increased at a faster rate for pups in the Aleutian Islands and the western Gulf of Alaska (0.45–0.48 kg/day and 0.47–0.53 cm/day, respectively) than in southeast Alaska (0.23 kg/day and 0.20 cm/day). Additionally, axillary girth increased at a faster rate for pups in the Aleutian Islands (0.59 cm/day) than for pups in southeast Alaska (0.25 cm/day). Our results indicate a greater maternal investment in male pups during gestation, but not during early lactation. Although differences in pup growth rate occurred among rookeries, there was no evidence that female sea lions and their pups were nutritionally stressed in the area of population decline.

Neonatal growth of Steller sea lion (*Eumetopias jubatus*) pups in Alaska

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Sea lion (order Carnivora, family Otariidae) pups depend entirely on milk for neonatal growth (Bonner, 1984). Studies of sea lions and fur seals have shown that if a pup does not obtain enough milk from its mother, it will exhibit poor body condition (i.e., reduced lean mass and total lipid mass for a given age or standard length) and a reduced growth rate (Trillmich and Limberger, 1985; Ono et al., 1987). Poor body condition and reduced growth rate, in turn, may have lifelong consequences because neonatal growth is an important factor in determining adult size and survival (Bryden, 1968; Innes et al., 1981; Calambokidis and Gentry, 1985; Albon et al., 1992; Baker and Fowler, 1992; Gaillard et al., 1997; Boltnev et al., 1998; Tveraa et al., 1998; Burns, 1999). Because of their large size, aggressive behavior, sensitivity to disturbance, and the remote location

of their rookeries, less is known about the early growth of Steller sea lions (SSL) than of most other pinniped (seals, sea lions, and walrus) species. Higgins et al. (1988) measured body mass of SSL pups on Año Nuevo Island in California but only reweighed five pups to measure growth rates. Merrick et al. (1995) weighed SSL pups at a number of locations throughout the Gulf of Alaska and the Aleutian Islands but did not reweigh them to assess individual growth rates.

Genetic studies show that there are distinct eastern and western populations of SSL (Bickham et al., 1996, 1998) (Fig. 1). The eastern population comprises animals in California, Oregon, British Columbia, and southeast Alaska. The western population comprises animals in the Gulf of Alaska, the Aleutian Islands, the Bering Sea, the Commander Islands, Kamchatka, and the Kuril Islands. A severe popu-

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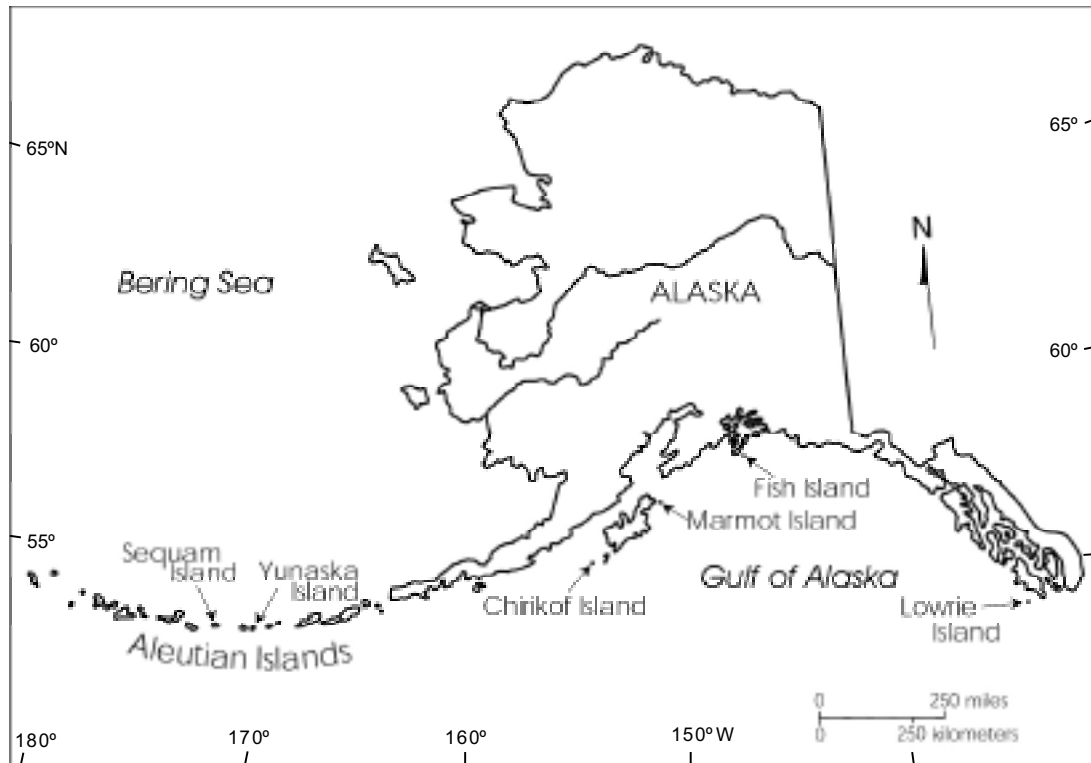


Figure 1

Study sites for Steller sea lions (*Eumetopias jubatus*) in Alaska. The Lowrie Island rookery in southeast Alaska has a stable population but rookeries at Fish, Marmot and Chirikof Islands in the Gulf of Alaska and Yunaska and Seguam Islands in the Aleutian Islands are areas where the population of Steller sea lions has declined.

lation decline (>80%) occurred in the western population between the 1970s and the 1990s. In 1997, these population changes led to the reclassification of the western population from “threatened” to “endangered” and a classification of the eastern population as “threatened” under the Endangered Species Act (U.S. Federal Register 62:24345–24355).

One hypothesis for the decline in population of SSLs is a decrease in food availability or quality in the Gulf of Alaska and the Aleutian Islands (Pascual and Adkison, 1994; York, 1994; Calkins et al., 1999; NMFS^{1,2}). If females are unsuccessful in obtaining sufficient food, pups will develop more slowly or die because of a decrease in milk supply. To examine the potential effects

of food availability on pup development, we measured growth rates of male and female pups from stable and declining populations of SSL in Alaska from 1990 to 1997. Our null hypothesis was that there was no difference in pup growth rates among rookeries in southeast Alaska, the Gulf of Alaska, and the Aleutian Islands. The alternative hypothesis was that pups grew at a faster rate in southeast Alaska, the area of stable population. However, our results showed that pups grew faster in the area of declining population during the first six weeks after birth. In addition, females invested more energy in male pups at all locations during gestation, but not during early lactation.

Materials and methods

Animals and study sites

From 1990 to 1997, SSL pups were studied at locations in southeast Alaska, the Gulf of Alaska, and the Aleutian Islands (Fig. 1 and Table 1). At Lowrie Island (54°51'N, 133°32'W) in southeast Alaska, measurements were made in 1993, 1994, and 1997. The rookery at Lowrie Island is in the area of the stable population (Calkins et al., 1999). In the Gulf of Alaska, measure-

¹ NMFS (National Marine Fisheries Service). 1992. Recovery plan for the Steller sea lion (*Eumetopias jubatus*), 92 p. Prepared by the Steller Sea Lion Recovery Team for the National Marine Fisheries Service, Silver Spring, MD. [Available from the National Marine Mammal Laboratory, 7600 Sandpoint Way, NE, Seattle, Washington 98115.]

² NMFS (National Marine Fisheries Service). 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population, 61 p. Prepared by the National Marine Mammal Laboratory, Alaska Fisheries Science Center. [Available from the National Marine Mammal Laboratory, 7600 Sandpoint Way, NE, Seattle, Washington 98115.]

Table 1
Locations, dates, and the number of Steller sea lion (*Eumetopias jubatus*) pups captured (*n*).

	Location	Dates	<i>n</i>
Stable population	Lowrie Island (1993)	26 May–5 June	25
		15–19 June	5
		3 July	1
	Lowrie Island (1994)	15–22 June	28
		24–30 June	9
		13–14 July	3
	Lowrie Island (1997)	5–12 June	25
		16–29 June	11
		9–10 June	20
Declining population	Fish Island (1995)	24–26 June	13
		13–14 July	12
		27 June	8
	Marmot Island (1990)	30 June	11
		27 June	21 ¹
	Marmot Island (1991)	15 July	11 ²
		11–17 June	20
	Marmot Island (1994)	27–28 June	14
		7 July	11
		18 July	4
	Chirikof Island (1993)	8–16 June	16
		22–24 June	12
		4 July	5
8–16 June		16	
Yunaska and Seguam Islands (1997)	22–24 June	12	
	4 July	5	

¹ Nine known-age pups.

² Six known-age pups.

ments were made in 1990, 1991, and 1994 on Marmot Island (58°12'N, 151°50'W), in 1993 on Chirikof Island (55°10'N, 155°8'W) and in 1995 on Fish Island (59°53'N, 147°20'W). On the Aleutian Islands of Seguam (52°30'N, 172°30'W) and Yunaska (52°45'N, 170°45'W), pups were studied in 1997. Data from Seguam and Yunaska Islands were combined because the islands are geographically close and can be considered part of one rookery complex. Rookeries in the Gulf of Alaska and the Aleutian Islands are in the area of declining population, although the rookery on Fish Island has not shown as precipitous a decline. Samples could not be obtained from all rookeries in all years because of logistical constraints and the need to minimize disturbance to rookeries. However, concurrent data were obtained from the declining and stable populations in 1993, 1994, and 1997.

Only pups that had an attached umbilical cord or an unhealed umbilicus were selected for study. The freshness of the umbilical cord was used as a rough estimate of age between 1 and 5 days (Davis and Brandon³).

Choosing only pups with fresh umbilical cords minimized the age bias (Trites, 1993) that occurs when pups are captured at different times and rookeries (Table 1).

Although pups were not selected by sex, sex was noted and used as a factor in analyses. Body mass (BM), standard length (SL), axillary girth (AG) (Am. Soc. Mammalogists, 1967) and body composition were measured for each pup. BM was measured to the nearest kilogram with a mechanical spring scale (Chatillon 160, Ametek, FL) on Marmot Island in 1990 and 1991 and on Lowrie Island in 1993. Body mass of pups at all other sites and years was measured to the nearest tenth of a kilogram by using an electronic scale (Rice Lake Weighing Systems, Rice Lake, WI; Ohaus I-20W, Ohaus, Pine Brook, NJ). Standard length was measured as a straight line from tip-of-nose to tip-of-tail, ventral surface down. Pups were restrained by hand and marked for later identification with hair bleach (Lady Clairol Maxi Blond, Clairol, Inc.) and with flipper tags attached in the axillary area of the fore-flippers.

Body composition was measured by using the labeled water method (Nagy 1975; Nagy and Costa, 1980; Costa, 1987; Bowen and Iverson, 1998). In this study, water labeled with a stable isotope of hydrogen (deuterium)

³ Davis, R. W. and A. A. Brandon. Unpubl. data. [Data are on file at Texas A&M University, 5007 Avenue U, Galveston, Texas 77551.]

was used to estimate total body water (TBW in kg and %TBW as a percentage of BM). Background concentration of deuterium was determined from blood samples taken from pups that were subsequently injected intramuscularly with 10 mL deuterium oxide (D_2O) (99% enriched, Cambridge Isotope Laboratories, Andover, MA). After a two-hour equilibration period (Costa, 1987), blood samples were taken to determine the dilution of injected deuterium in total body water.

Pups were recaptured at approximately two-week intervals over periods ranging in length from 18 to 38 days (average measurement period was 29.6 days) (Table 1) and were weighed, measured, and a blood sample was taken from each pup. Similar protocols were used at all rookeries, except Marmot Island in 1990 and 1991, when only BM and SL were measured, and the age of pups was not estimated. Therefore, no growth rates were obtained from these data.

Labeled water sample analysis

Blood samples were centrifuged in the field in serum separator tubes, and the serum was transferred to cryovials that were frozen at $-20^{\circ}C$ until analysis. Isotope-ratio mass spectrometry was used to determine the ratio of deuterium (2H) to hydrogen (H) (Laboratory of Biochemical and Environmental Studies at University of California, Los Angeles, CA). The hydrogen-isotope dilution space was calculated from this ratio by using Equation 3 in Schoeller et al. (1980). However, the hydrogen-isotope dilution space has been shown to underestimate TBW in a number of pinniped species (Reilly and Fedak, 1990; Arnould et al., 1996b), leading Bowen and Iverson (1998) to develop a single predictive equation to estimate %TBW from hydrogen-isotope dilution space in pinnipeds for which data on the accuracy of the hydrogen-isotope method are lacking. The equation

$$\%TBW = 0.003 + 0.968 H\text{-dilution space} \quad (1)$$

was used in the present study to correct the overestimated %TBW by 3.3% (Bowen and Iverson, 1998, Eq. 5). Percent total body lipid (%TBL, as a percentage of BM) was calculated by using predictive equations derived from the relationship between %TBW and %TBL for Antarctic fur seals (Arnould et al., 1996b):

$$\%TBL = 66.562 - 0.845 \%TBW. \quad (2)$$

%TBL was then compared between male and female pups and among rookeries.

Statistical analyses

Statistics were performed by using Systat (version 11, SPSS, Inc, Chicago, IL), and by first treating each study site and year as a separate "location," then combining data for multiple years at a location (e.g., Marmot Island and Lowrie Island) when no significant interannual differences were found. Significance was determined

at $P \leq 0.05$. Data were examined for heteroscedasticity (unequal variances) before analysis (Zar, 1984). All *post hoc* pairwise comparisons were made with the Tukey multiple comparison test. Data from the first capture (1–5 days of age) were analyzed for comparison by location and sex by using two-way ANOVA. Pup growth rate was estimated by performing a linear regression for each pup and extrapolating to $t = 0$ to estimate birth mass. Differences among means of pup growth rate and birth mass were then analyzed by using two-way ANOVA to determine differences by location and sex.

Results

Neonatal size

There were no significant differences by rookery in pup mass at 1–5 days of age (Table 2) and no significant interaction between rookery and sex. The only significant difference in SL of 1–5 day old pups was that both genders were significantly longer on Seguam and Yunaska Islands than on Fish Island ($P = 0.0395$). Pups on Chirikof Island had significantly smaller AG than pups on Lowrie, Fish, and Seguam and Yunaska Islands ($P < 0.02$). Male and female pups were significantly different for all three morphometric measurements. Overall, male pups averaged 22.6 kg (± 2.21 SD, $n = 71$) and female pups averaged 19.6 kg (± 1.80 SD, $n = 74$) at first capture (1–5 days of age).

There was no significant difference by rookery or sex and no significant interaction between rookery and sex in %TBW or %TBL of pups at first capture. When all pups at all rookeries were combined ($n = 116$), %TBW was 72.1% of BM (± 3.17 SD) and %TBL was 5.6% of BM (± 2.68 SD). Male pups had a significantly greater absolute TBW than female pups ($P < 0.0001$), as would be expected because of the difference in BM at birth. There was a significant correlation between TBW and BM (Pearson $r = 0.945$, $P < 0.001$, $n = 116$; $TBW \text{ (kg)} = 0.6895 \times BM + 0.6618$).

Neonatal growth

Growth rates were treated as linear over the period monitored; there were not enough data to determine if growth was nonlinear. Male and female pups on the same rookery grew at the same rate (in BM, SL, and AG) during the first six weeks after birth (Fig. 2). When compared by rookery, BM increased at a faster rate for pups on Chirikof Island ($P = 0.0005$) and on Seguam and Yunaska Islands ($P = 0.0002$) than on Lowrie Island (Fig. 3 and Table 3). The increase in BM for pups on Fish Island did not differ significantly from that at other rookeries. Marmot Island pups grew significantly more slowly than pups on Seguam and Yunaska Islands ($P = 0.0382$) but did not differ significantly from growth of pups at other rookeries.

Standard length increased at a faster rate for pups on Chirikof Island ($P = 0.0068$) and Seguam and Yu-

naska Islands ($P=0.0050$) than it did for pups on Lowrie Island (Table 3). Growth in SL was also faster on Chirikof ($P=0.0383$) and Seguam and Yunaska Islands ($P=0.0230$) than on Fish Island, whereas the increase in SL on Marmot Island did not differ significantly from the other rookeries. The increase in AG was significantly greater on Seguam and Yunaska Islands ($P=0.0021$) and Marmot Island ($P=0.0364$) than on Lowrie Island. There was no significant interaction between rookery and sex in the growth rate of BM, SL, and AG.

Body mass at birth extrapolated to $t = 0$ from growth rates did not differ by rookery. There was no significant interaction between rookery and sex, but extrapolated birth mass did differ by sex ($P<0.0001$). Male pups at all rookeries averaged 22.4 kg (± 2.36 SD, $n=39$), whereas female pups averaged 18.7 kg (± 2.08 SD, $n=35$). These extrapolated birth masses were similar to the average BM measured on the rookery for male (22.6 kg) and female (19.6) pups 1–5 days old. There was no correlation between extrapolated birth mass and growth rate (Pearson $r=-0.09$, $P=0.45$).

Table 2

Body mass (BM), standard length (SL), and axillary girth (AG) of neonatal (1–5 day old) Steller sea lion (*Eumetopias jubatus*) pups in the stable (Lowrie Island) and declining (Fish Is., Marmot Is., Chirikof Is., Seguam Is., Yunaska Is.) populations (mean \pm SD). An asterisk (*) indicates significant differences from all other sites, and † indicates a significant difference between two sites. Standard length from Fish Is. was significantly different from SL on Seguam and Yunaska Is. Axillary girth on Chirikof Is. was significantly different from AG at all other sites. In all cases, males were significantly larger than females. There were no significant interannual differences; therefore data from all years at Lowrie Is. were combined.

Location	n	BM (kg)		SL (cm)		AG (cm)	
		male	female	male	female	male	female
Lowrie Is. (1993–97)	39M	22.1	19.5	98.3	94.1	64.9	64.3
	41F	± 2.20	± 1.67	± 4.56	± 3.96	± 3.33	± 5.01
Fish Is. (1995)	11M	22.6	19.2	96.2†	93.3†	68.5	64.0
	9F	± 1.69	± 2.39	± 26.76	± 6.39	± 2.96	± 4.00
Marmot Is. (1994)	3M	21.7	20.2	101.7	97.4	65.5	61.8
	6F	± 1.80	± 2.42	± 1.53	± 2.67	± 2.78	± 5.38
Chirikof Is. (1993)	11M	23.21	19.02	99.1	94.9	62.7*	60.1*
	9F	± 2.59	± 1.05	± 5.24	± 2.40	± 3.52	± 2.15
Aleutian Is. (Seguam and Yunaska Is.) (1997)	7M	24.2	20.5	101.4†	96.3†	67.7	63.9
	9F	± 1.97	± 1.88	± 4.29	± 2.55	± 3.50	± 3.66

Table 3

Steller sea lion (*Eumetopias jubatus*) pup growth from 0 to 40 days of age (mean \pm SD). There were no significant differences between male and female pups. BM=body mass; SL = standard length; AG=axillary girth. Underlining indicates that there were no significant differences within an underlined grouping (e.g., for body mass growth rate, C was significantly different from L, and A was significantly different from M and L).

Location	n	BM growth rate (kg/day)	SL growth rate (cm/day)	AG growth rate (cm/day)
Lowrie Is. (L)	26	0.23 \pm 0.176	0.20 \pm 0.322	0.25 \pm 0.244
Fish Is. (F)	13	0.35 \pm 0.171	0.22 \pm 0.183	0.41 \pm 0.235
Marmot Is. (M)	6	0.28 \pm 0.141	0.22 \pm 0.287	0.59 \pm 0.510
Chirikof Is. (C)	17	0.45 \pm 0.126	0.47 \pm 0.171	0.47 \pm 0.187
Aleutian Is. (A) (Seguam and Yunaska Is.)	12	0.48 \pm 0.168	0.53 \pm 0.163	0.59 \pm 0.257
ANOVA results		<u>L M F C A</u>	<u>L F M C A</u>	<u>L F C M A</u>

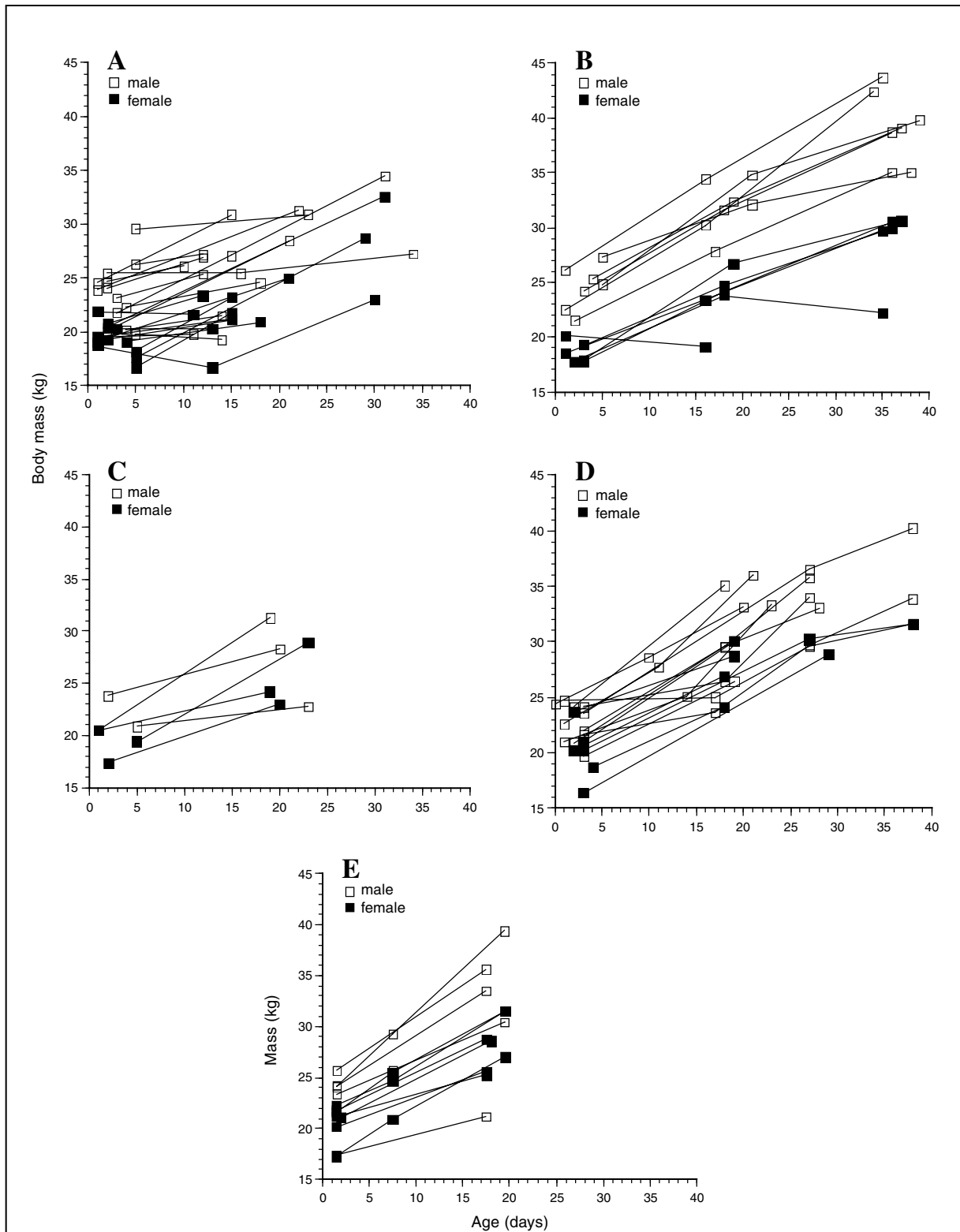


Figure 2

Change in body mass of individual Steller sea lion (*Eumetopias jubatus*) pups captured on (A) Lowrie Island in 1993, 1994, and 1997, (B) Fish Island in 1995, (C) Marmot Island in 1994, (D) Chirikof Island in 1993, and (E) Yunaska and Seguam Islands in 1997.

Discussion

Compared to other species of sea lions and fur seals, SSL pups are large, although this species produces smaller pups in relation to adult size than do smaller otariids (Kovacs and Lavigne, 1992; McLaren, 1993). In the present study, male pups averaged 22.6 kg and female pups averaged 19.6 kg at 1–5 days of age, which is in the range of birth masses reported in the literature. Two studies conducted before the recent population decline reported 17 kg for male pups at birth (Scheffer, 1945) and a range of 9.1–21.8 kg for male and female pups (Mathisen et al., 1962). Late in the population decline, studies reported a range of 16–23 kg for pups at birth in Alaska (Calkins and Pitcher, 1982) and an extrapolated birth mass of 17.9 kg for five pups for which growth rates were measured in California (Higgins et al., 1988).

This is the first, large-scale (in terms of sample size and geographic area) longitudinal study of growth in Steller sea lion pups. Growth rates reported in our study are the highest absolute growth rates reported for any sea lion or fur seal. This is to be expected because adult SSLs are the largest otariids (Kovacs and Lavigne, 1992). The growth rate of 0.38 kg/day measured for five SSL pups at Año Nuevo Island in California (Higgins et al., 1988) falls within the range of average growth rates measured in the present study (0.23–0.48 kg/day). The only other measurement of pup growth in SSLs was conducted on captive pups that were already

several months old. In terms of growth rate in relation to size at birth, SSL pups gained 1–2.3% of their birth weight per day (Lowrie Island and Seguam and Yunaska Islands, respectively, based on an average birth mass of 21.1 kg), which was faster than the relative growth rates reported for other otariid species (Kovacs and Lavigne, 1992, calculated from Table 1), except for northern fur seals. In contrast, seals (order Carnivora, family Phocidae) exhibit faster growth rates (1.3–5.6 kg/day or 8–26% birth weight per day) (Stewart and Lavigne, 1980; Bowen et al., 1985; Kovacs and Lavigne, 1985; Bowen et al., 1987; Bowen et al., 1992; Campagna et al., 1992). Although adult SSLs are larger than many species of phocid seals, phocids have much shorter lactation periods and their pups grow at a more accelerated rate than do otariids.

Male-female differences

Male pups weighed 15% more than females at birth, indicating a difference in maternal investment during gestation, which has been found in other otariids including Antarctic fur seals (Doidge et al., 1984; Lunn and Boyd, 1993; Goldsworthy, 1995; Boyd, 1996), South American fur seals (*Arctocephalus australis*) (Lima and Páez, 1995), California sea lions (Ono and Boness, 1996), and southern sea lions (*Otaria byronia*) (Cappozzo et al., 1991). These results are consistent with the predictions of Maynard-Smith's (1980) theory on sexual investment. Steller sea lion adults are extremely sexually dimorphic: females weigh 263 kg on average (maximum of approximately 350 kg); males weigh more than twice as much (average of 566 kg, maximum of approximately 1120 kg) (Calkins and Pitcher, 1982). In view of this dimorphism and the fact that size is more important to male fitness than to female fitness in a polygynous species (McCann, 1981) such as the SSL, theory predicts that males would be heavier than females at birth. Northern fur seal females with male fetuses are in poorer condition than mothers with female fetuses (Trites, 1992), and male fetuses grow at a faster rate than female fetuses (Trites, 1991), indicating that mothers invest more in male offspring during gestation.

However, there were no male-female differences in neonatal growth (BM, SL, and AG) rate in SSL during the first six weeks after birth. In a species as sexually dimorphic as SSL, one would expect males to grow at a faster rate than females during development. However, this difference may not occur until the animals are older. There is some evidence that male otariids undergo a sharp increase in growth rate near sexual maturity (McLaren, 1993; Bester and Van Jaarsveld, 1994), after females have already reached sexual maturity and their growth has slowed.

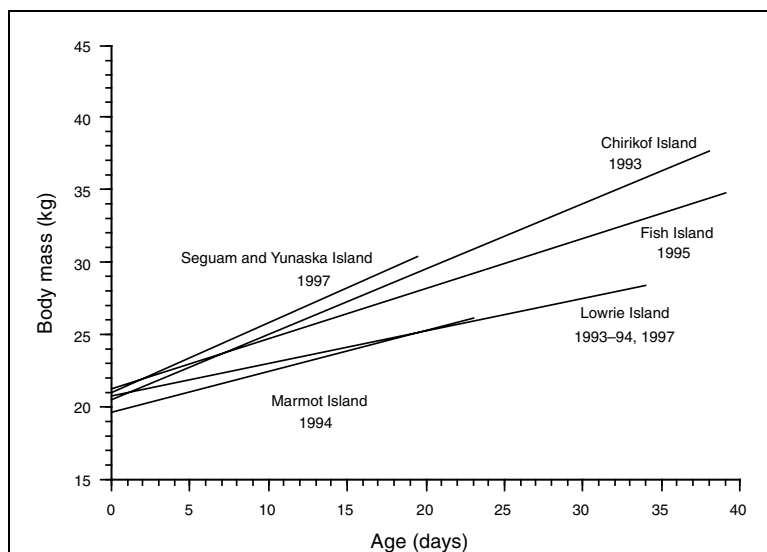


Figure 3

Summary of Steller sea lion (*Eumetopias jubatus*) pup growth (body mass) during the first six weeks after birth for all five rookeries. The length of each line indicates the length of the study period at that location. Pups from Seguam, Yunaska, and Chirikof Islands, in the declining population, grew significantly faster than pups from Lowrie Island, in the stable population. Pups from Seguam and Yunaska Islands also grew significantly faster than pups from Marmot Island.

Conflicting results have been reported in other growth studies of otariids. Several studies reported that male pups grew faster than female pups (Antarctic fur seals: Payne, 1979; Doidge et al., 1984; Antarctic and Subantarctic fur seals: Kerley, 1985; New Zealand fur seals: Mattlin 1981). However, cross-sectional data on growth rate were used in these studies. Conversely, longitudinal data, considered to be more accurate, demonstrate no differences in neonatal growth rate between male and female Antarctic fur seal pups (Doidge and Croxall, 1989; Lunn et al., 1993; Lunn and Arnould, 1997); Goldsworthy (1995), however, is the exception. Ono and Boness (1996) collected longitudinal growth data on California sea lion pups and found that males grew faster than females, but they found no other evidence of differential maternal investment. In phocids, most studies have found no difference in neonatal male and female growth rates, regardless of whether the data were longitudinal or cross sectional (Stewart and Lavigne, 1980; Innes et al., 1981; Bowen et al., 1992). This is true for species with extreme sexual dimorphism such as elephant seals (McCann et al., 1989; Campagna et al., 1992). The only other study where growth rates for SSL pups were measured did not have a large enough sample size for a comparison between males and females (Higgins et al., 1988). No differences between male and female pups were found for suckling behavior or maternal attendance behavior (Higgins et al., 1988).

Total body lipid

Average %TBL of neonatal pups was low (5.6% BM). Steller sea pups are born with small energy stores and normally fast for short periods (about one day) while their mothers make foraging trips to sea. There have been few measurements of lipid content in otariid neonates. Jonker and Trites (2000) found a blubber content of 9.7% BM in five SSL pups in the first month after birth. However, this measurement does not correspond directly to body fat content because they measured blubber content by weighing the sculp (skin plus blubber) and then calculating the fraction of sculp that was blubber by measuring skin and blubber thicknesses. Using the same labeled water method as in the present study, Arnould et al. (1996b) found a %TBL of 9.4% BM in four Antarctic fur seal pups in the first month after birth. In a similar study of one-day-old Antarctic fur seal pups, Arnould et al. (1996a) found a %TBL of 7.0% BM for female pups and 4.9% BM for male pups. Also using labeled water, Oftedal et al. (1987a) found an average %TBL of 5% BM for neonatal California sea lion pups.

Arnould et al. (1996b) suggested two explanations for the higher lipid content that they found in Antarctic fur seal pups in comparison to California sea lion pups (Oftedal et al. 1987b). First, in colder habitats, a larger subcutaneous lipid store may be necessary for thermoregulation. The data here do not support that explanation. SSL live in a colder habitat than California sea lions, but have a similar %TBL. The more

likely explanation is that larger lipid stores are found in species in which pups normally fast longer while their mothers are foraging. Steller sea lion pups have the smallest lipid stores and shortest fasting periods (Brandon, 2000) of the three species.

Differences in pup size among rookeries

Although male and female pups differed significantly in size, there were no significant differences in pup size at birth among the rookeries studied. Rookery location should have less influence on pup size at birth than on neonatal growth because maternal foraging range is much greater during gestation than during lactation (Merrick and Loughlin, 1997). This greater maternal foraging range during gestation reduces, among rookeries, variation in maternal size and feeding conditions (quantity and quality of prey available) during gestation, both of which have been shown to influence pup birth mass in pinnipeds (Calambokidis and Gentry, 1985; Kovacs and Lavigne, 1986; Trites, 1991; Trites 1992). The lack of a difference in pup BM at birth among rookeries could also be explained by the fact that females that are "successful" (i.e., carry their fetuses to term) have a significantly better body condition than females that do not carry their fetuses to term (Pitcher et al., 1998). As a consequence of our study design, only those females that were successful were used, and therefore our sample was biased toward females in the population with better body condition. In addition, gestation is less energetically expensive than early lactation; therefore differences in food availability would have less of an effect during gestation (Robbins and Robbins, 1979; Albon et al., 1983; Oftedal, 1984).

Although most pup morphometrics at first capture did not differ among rookeries, growth parameters differed significantly (Table 3). Growth rates of pups on Seguam and Yunaska Islands (0.48 kg/day) and on Lowrie Island (0.23 kg/day) represented the extremes, whereas growth rates of pups on Chirikof, Marmot, and Fish Islands fell between these two extremes. In general, faster growth rates occurred in the west and slower growth rates in the east. In terms of mass, Seguam and Yunaska Islands and Chirikof Island pups grew twice as fast as Lowrie Island pups. A concurrent study of the attendance patterns of lactating females (Brandon, 2000) showed that foraging trip duration decreased from east (25.6 hours on Lowrie Island) to west (an average of 9.4 hours on Chirikof and Seguam Islands). Therefore, it is possible that the higher growth rates in SSL pups in the western Gulf of Alaska and Aleutian Islands resulted from shorter periods of fasting while females were foraging at sea (Arnould et al., 1996a; Goldsworthy, 1995).

Is food limiting growth in Steller sea lion pups in the area of population decline?

If the cause of the population decline were decreased food availability, which is one of the leading hypotheses

(Pascual and Adkison, 1994; York, 1994; NMFS²), one might expect the animals in the declining population to show signs of nutritional stress compared to those in the stable population. The results for pup size and growth give no indication of food stress during early lactation. In fact, pups from the declining population on Seguam, Yunaska, and Chirikof Islands grew faster than pups from the stable population on Lowrie Island during the first six weeks. Similar results were also found in a study of pup BM (Merrick et al., 1995), in which pups were weighed on rookeries from Oregon to the Aleutian Islands in late June and early July from 1987 to 1994. Although the pups' ages were unknown, weighing date was used as a covariate in the analysis. Merrick et al. (1995) found a continuous increase in pup BM from Oregon to southeast Alaska and to the Aleutian Islands. These investigators also concluded that pup BM was on average greater in the declining population.

In most other studies of declining populations or differences among rookeries, such contradictory results have not been seen. A study of California sea lion pups during an ENSO (El Niño Southern Oscillation) event revealed lower pup growth during the period of food stress (Boness et al., 1991). Trillmich and Limberger (1985) have also seen clear effects of low food availability during an ENSO in Galapagos fur seals and sea lions. Antarctic fur seals are affected in predictable ways (increased pup mortality and increased female foraging time) during times of decreased food availability (Costa et al., 1989). Hood and Ono (1997) found that in the declining California population of SSLs, pups spent less time suckling when adult females made longer foraging trips in 1992 than in 1973 when the population was larger. The longer foraging trips suggested less abundant food resources.

Considering the results for SSL pup growth in light of the population decline, we suggest three alternative hypotheses: 1) food availability was never a factor in the population decline; 2) food availability caused the overall decline, but lactating females and their pups were not affected during early lactation; or 3) our study was conducted when pups and lactating females were no longer experiencing decreased food availability.

Faster rates of pup growth may be normal for the Aleutian Islands and western Gulf of Alaska despite the population decline. The declining and stable populations are genetically distinct (Bickham et al., 1996), and perhaps the differences seen in our study are normal differences between the two populations. It is impossible to determine if growth and foraging behavior have changed over time because historical data on maternal investment are sparse. Juveniles rather than neonates may be the affected age class in the declining population (Merrick et al., 1988), whereas lactating females are feeding on either different prey or age classes and not experiencing decreased food availability. York (1994) constructed a population model for SSLs in Alaska and concluded that the current population decline could be accounted for by increased juvenile mortality.

Alternatively, because our study was performed late in the decline, the higher growth rates could be the result of lower population density and less competition for food in the declining population. Trites and Bigg (1992) reported larger body sizes in northern fur seal populations during a period of decline. The northern fur seal population in the Pribilof Islands in the Bering Sea increased from the early 1900s to the 1950s. During this period, adult body size decreased. From 1950 to the 1970s the population declined and there was a concurrent increase in individual body size (Trites and Bigg, 1992). Scheffer (1955) hypothesized that increased body size was due to decreased competition for food, which in turn would be due to the lower population density. It is possible that the same density-dependent effects are occurring in the declining SSL population because our study was performed late in the decline, after the original cause may have abated. More information will be needed to determine the cause of the SSL decline and whether it is related to availability of food, especially for different age classes, and to different times of the year.

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