GROWTH AND BIOENERGETIC MODELS FOR STELLER SEA LIONS (*EUMETOPIAS JUBATUS*) IN ALASKA

by

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ABSTRACT

The primary goal of my study was to develop a bioenergetic model to predict the food requirements of Steller sea lions (*Eumetopias jubatus*). An important component of the bioenergetic model was a physical growth model. Growth models were constructed using morphometric measurements of males (≥ 1 year old), females (≥ 1 year old), and pregnant females with a foetus that had been shot on rookeries, haulouts, and in the coastal waters of southeastern Alaska, the Gulf of Alaska and along the Bering Sea ice edge between 1976 and 1989. A Richards model best described age related growth in body length and mass. Males grew (in length) over a longer period than females and exhibited a growth spurt in mass which coincided with sexual maturity. Sexual dimorphism in both body length and mass was significant by 3 years of age. The average predicted standard lengths of males and females older than 12 years were 3.04 m and 2.32 m respectively, while the average predicted weights were 681 kg and 273 kg respectively. 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.

The bioenergetic model was used to estimate the food requirements of the Alaskan Steller sea lion population in the 1990's and to examine how these food requirements varied seasonally and spatially. Input included age/sex-specific energy requirements, population size/composition, and diet composition/energy content by date and region of Alaska. Error in model predictions was calculated using uncertainty in parameter values and Monte Carlo simulation methods. Food requirements were generally lowest in the summer and highest in the winter and spring mainly due to changes in activity budgets and the energy content of the diet. The mean daily food requirement of pregnant females was only marginally greater than the mean daily food requirement of non-pregnant females of the same age, but the mean daily food requirement of females nursing pups was about 70% greater than females of the same age without pups. Per capita population food requirements differed by up to 12% among regions of Alaska due to differences in the energy content of the diet. Steller sea lion predation was small relative to total walleye pollock natural mortality, but accounted for a large part of total Atka mackerel natural mortality. Of the bioenergetic, population, and diet parameters, uncertainty in bioenergetic parameters resulted in the largest error in model predictions. The model provided both a quantitative estimate of the Alaskan Steller sea lion population's food requirements and direction for future research.

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CHAPTER I: GENERAL INTRODUCTION

Steller sea lions (*Eumetopias jubatus*) range from southern California, around the Pacific rim, to northern Japan (King 1983). A mitochondrial DNA study by Bickham et al. (1996) found that the species was comprised of two genetically distinct stocks, an eastern stock and a western stock (division near 144^o west longitude). The historical centre of abundance was the western Gulf of Alaska and the Aleutian Islands (western stock), but between 1980 and 1992 the Alaskan population of Steller sea lions decreased by over 70% (Loughlin *et al.* 1992; Trites and Larkin 1996). This resulted in the listing of Steller sea lions as threatened under the United States of America endangered species legislation in 1990 (National Marine Fisheries Service 1992). The status of the western stock was upgraded to endangered in 1995 (National Marine Fisheries Service 1995). Alverson (1992) identified at least four possible causes of this population decline: 1) bycatch in commercial fisheries, 2) indiscriminate shooting, 3) commercial harvest, and 4) nutritional deficiency. Additional possible causes included disease, parasites, predation, and pollution.

Recently, a lot of Steller sea lion research has focused on the hypothesis that a nutritional deficiency was the cause of the decline. Two pieces of evidence supporting this hypothesis are: 1) a decrease in female Steller sea lion body size between the 1970’s and the 1980’s in the Gulf of Alaska (Calkins *et al.* 1998); and 2) a negative correlation between diet diversity and the rate of population decline among seven regions of Alaska (Merrick *et al.* 1997). A nutritional deficiency may have been the result of a reduction in the abundance, availability and/or quality of prey (Alverson 1992). These hypothesized changes in the prey base may have been a result of natural changes in the ecosystem and/or commercial fishing activity.

The primary goal of my study was to develop a bioenergetic model to predict the food requirements of Steller sea lions. Estimates of marine mammal food consumption are a prerequisite for assessing interactions between marine mammals and their ecosystems including fisheries (Beverton 1985; Trites *et al.* 1997). In the case of Alaskan Steller sea lions, estimates of their prey requirements are central to evaluating the nutritional stress hypothesis. It is difficult to quantify marine mammal food consumption directly so bioenergetic models are commonly used to estimate food requirements indirectly (e.g., Olesiuk 1993; Mohn and Bowen 1996; Stenson *et al.* 1997). In addition to providing quantitative estimates of food consumption, bioenergetic models can be used to examine the sensitivity of food consumption estimates to uncertainty in parameter values. They can also be used to explore specific physiological and ecological questions (Hiby and Harwood 1985; Shelton *et al.* 1997).

One of the primary building blocks of a bioenergetic model is a growth curve showing how size changes with age and time of year. Surprisingly there are no comprehensive descriptions of growth for Steller sea lions, despite the large number of morphometric measurements that have been recorded for this species. Thus, my first task was to construct growth curves for Steller sea lions (Chapter II).

Chapter III describes a bioenergetic model for Steller sea lions. The model is used to answer the following questions: 1) How much food do Steller sea lions currently consume?; 2) How does food consumption vary seasonally?; and 3) How does food consumption vary by region of Alaska? Chapter III also describes the sensitivity of the model predictions to uncertainty in model parameters.

CHAPTER II: PHYSICAL GROWTH OF STELLER SEA LIONS

Introduction

Studies of physical growth offer insight into pinniped energetics, life histories, sociobiology, and environmental conditions (Laws 1956; Bryden 1972; Innes *et al.* 1981; Lavigne *et al.* 1982; McLaren 1993). Growth is often assessed by fitting mathematical equations to cross-sectional[1] measurements of body lengths and mass (Innes *et al.* 1981; Trites 1991; Murie and Lavigne 1992; McLaren 1993; Olesiuk 1993; Rosas *et al.* 1993; Boyd *et al.* 1994; Hammill *et al.* 1995; Lima and Páez 1995; Garlich-Miller and Stewart 1998). These 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 of growth models 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 the food requirements of marine mammals (Markussen *et al.* 1992; Olesiuk 1993; Boyd *et al.* 1994).

Size and age of Steller sea lions (*Eumetopias jubatus*) have been reported in previous studies (Scheffer 1945; Fiscus 1961; Thorsteinson and Lensink 1962; Spalding 1964; Calkins and Pitcher 1982; Loughlin and Nelson 1986; Olesiuk and Bigg 1987; Calkins and Goodwin 1988; Merrick *et al.* 1995; Brandon *et al.* 1996; Isono 1998). However, McLaren (1993) and Calkins *et al.* (1998) were the only ones who used a model to describe growth.

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[1] Cross-sectional meaning individuals of different ages are sampled from a population, and each individual is measured only once (Fitzhugh 1976)

McLaren (1993) analyzed length data sets from three different geographic locations in the North Pacific Ocean. Calkins *et al.* (1998) described growth (mass and length) of female Alaskan Steller sea lions that were less than fourteen years old. No study has used a model to describe mass growth of females older than fourteen years, or for males of any age. In addition, only one study has assessed seasonal fluctuations in size (mass) and it was focused on adult males (Olesiuk and Bigg 1987).

The first objective of my study was to use growth models to describe body length and mass at age of Alaskan Steller sea lions of all ages and of both sexes. The second objective was to describe the relationship between length and mass using allometric models. The third objective was to assess seasonal fluctuations in body growth.

Materials and Methods

The data I used were from Steller sea lions that were shot intermittently from 1976 to 1989 on rookeries, haulouts, and in coastal waters of southeastern Alaska, the Gulf of Alaska and along the Bering Sea ice edge during earlier research studies (Calkins and Pitcher 1982; Calkins and Goodwin 1988; Castellini and Calkins 1993). Animals were brought aboard a vessel, weighed and measured for standard and/or dorsal standard length[2]. The animals were later necropsied. Age in years was estimated by counting cementum annuli of the second upper premolar teeth (Calkins and Pitcher 1982). Age in days was estimated assuming 15 June as the mean date of birth (Pitcher and Calkins 1981; Calkins *et al.* 1998). Ovaries and uteri were collected from females and examined to determine reproductive status (Calkins and Pitcher 1982; Calkins and Goodwin 1988). Females were originally classified as pregnant, not pregnant, or unknown (Calkins and Pitcher 1982; Calkins and Goodwin 1988). For the purpose of my study, females were reclassified as either pregnant with foetus or other (not pregnant or pregnant with no foetus). Since Steller sea lions exhibit delayed implantation (of the blastula) and little foetal growth occurs before February, only pregnant females collected after 1 February were reclassified as pregnant with foetus. Females younger than 3 years of age were assumed to not be pregnant as female sexual maturity before this age is rare (Harrison 1969; Pitcher and Calkins 1981).

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[2] Standard length is the straight-line length from nose to tail while an animal is on its back, and dorsal standard length is the same measurement while the animal is on its stomach (McLaren 1993).

A total of 235 males, 200 females, and 81 females with foetus were measured for body mass and/or length. When only dorsal standard length (*DSL*) was measured, I estimated standard length (*SL*) using an equation developed from Steller sea lions in the sample with both DSL and SL measurements:

[2.1] $$SL = 0.98734DSL + 57.58$$ ($p<0.0001$, $r^2 = 0.97$)

where SL and DSL are in millimetres (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, and outliers (unusually large or small measurements).

Growth in mass and length with age were examined using several mathematical growth models (Table 2.1). Only data from animals older than 0.75 years of age were used. Growth patterns of foetuses and pups are different from growth patterns of older animals and no single equation adequately describes the growth of pinnipeds over the entire life cycle (McLaren 1993). Including pup data or ‘anchoring’ the models at the beginning of growth or parturition biases growth models. For females, an extra parameter (*b*) was added to the models to control for the presence or absence of a foetus (Table 2.1). Depending on the model, this parameter produced either an additive size effect (additive female model) or a multiplicative size effect (proportional female model) due to the presence of a foetus. Growth models were fit using non-linear, least squares regression (*Nonlin*, SYSTAT 5.0). Goodness of fit was evaluated using the coefficient of

Table 2.1. 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 which 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 one of the first five models, b is the size difference (additive model) or the proportional size difference (proportional model) between females with and without a foetus, and F is a foetus presence/absence dummy variable (1 = present, 0 = not present).

Model	Equation	References
Pütter (also monomolecular, Brody)	$S_t = A\left(1 - e^{-k(t-t_0)}\right)$	von Bertalanffy (1938); Ricker (1979) (cites Pütter 1920)
von Bertalanffy	$S_t = A\left(1 - e^{-k(t-t_0)}\right)^3$	von Bertalanffy (1938); Ricker (1979)
logistic (also autocatalytic)	$S_t = \dfrac{A}{1 + e^{-k(t-t_0)}}$	Ricker (1979) (cites Verhulst 1838)
Gompertz	$S_t = Ae^{-e^{-k(t-t_0)}}$	Ricker (1979) (cites Gompertz 1825)
Richards	$S_t = \left[A^{1-m} - \left(A^{1-m} - S_0{}^{1-m}\right)e^{\frac{-2t(1+m)}{T}}\right]^{\frac{1}{1-m}}$	Richards (1959); Leberg (1989)
Additive female	[base model] + bF	
Proportional female	[base model]$(1 + bF)$	

determination (r^2) and by comparing the fitted models to robust locally weighted regressions or ‘smooths’ of the data (*Lowess*, S-Plus 3.3) (Cleveland 1979). The significance of the extra parameter (*b*) in the female models was tested using Student’s *t* test (Zar 1996). The age at which sexual dimorphism became significant was determined by comparing mean size (length and mass) for each age (year) using Student’s *t* test (SYSTAT).

The relationships between mass (*M*) and length (*L*) were examined by linearizing the allometric relationship:

[2.2] $M = aL^b$

so that

[2.3] $\log M = \log a + b \log L$

and fitting this equation using linear, least-squares regression (*Lm*, S-Plus 3.3).

The residuals of the fitted size (mass and length) at age models ([observed size – predicted size] / predicted size) were smoothed (*Lowess*, S-Plus 3.3) to examine seasonal patterns of growth. Also, the mass and length of males and females were plotted by day of the year and smoothed (*Lowess*, S-Plus 3.3) to further examine seasonal size fluctuations. For the latter analysis, data were grouped into two age groups (ages 1-5 and ages≥6) to boost sample size.

Results

Sampling Bias and Outliers

Juveniles aged 1 to 3 years (males and females) were collected at higher numbers than any other age group (Fig. 2.1). Only 17% of males collected were older than 10 years of age and only 10% of females (without a foetus) were older than 15 years. Most females with a foetus (87%) were collected between 4 and 14 years of age. With respect to time of year, most animals were collected from February to May, and from October to November (89%) (Fig. 2.2). A small number of animals were collected from June to September, but no animals were collected in January or December.

One male datum (10 mo) was an outlier with respect to mass at age and length at age, suggesting the age was incorrectly recorded. This datum was excluded from size at age analyses. In addition, data from 3 males, 9 females, and 1 female with a foetus were outliers with respect to length at age and mass versus length, suggesting the length measurements may have been wrong. These outliers were excluded from further length analyses. Finally, a datum from a very old female (30 y) was an outlier on all plots and was excluded from all analyses.

Length at Age Models

All of the growth models described the data well (see Appendix 1 for details). 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 2.2).

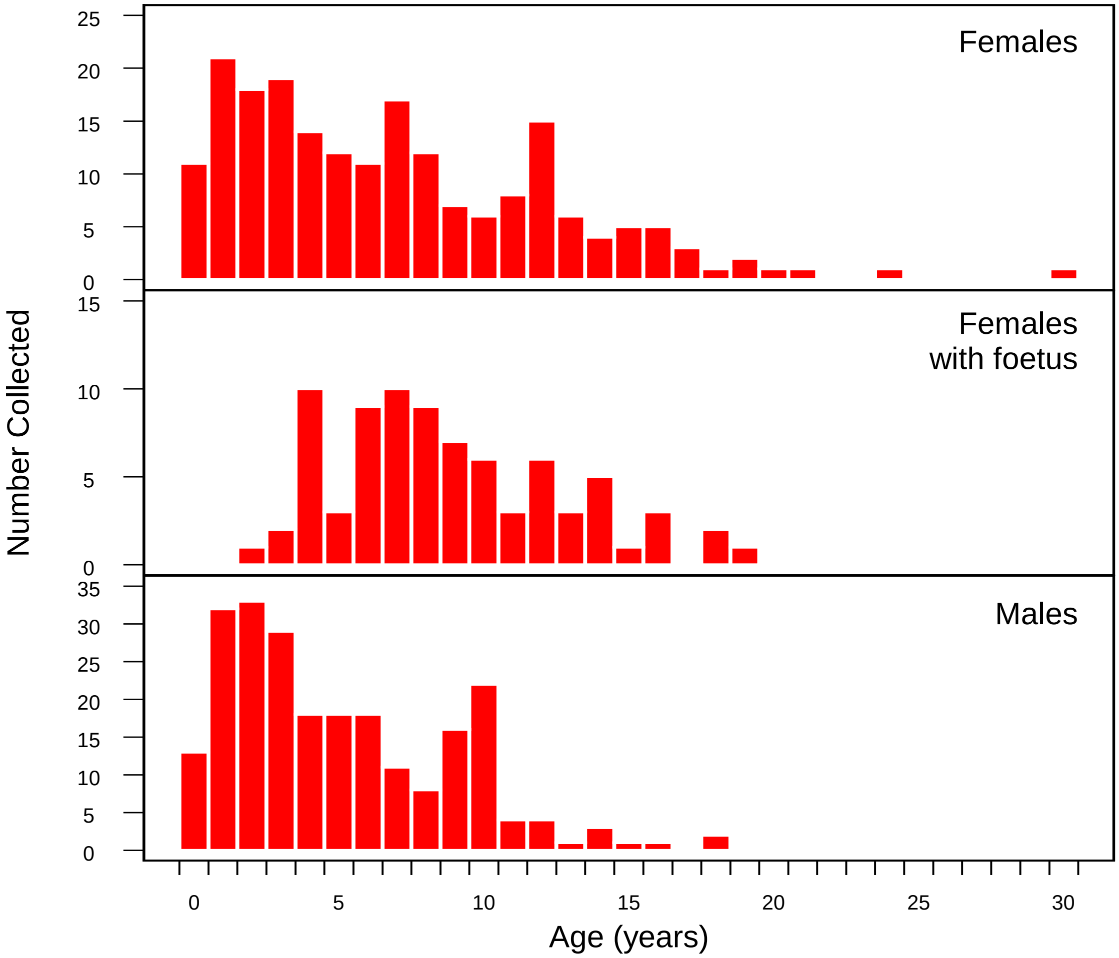


Figure 2.1. Age frequencies of Steller sea lions collected in Alaska from 1976 to 1989.

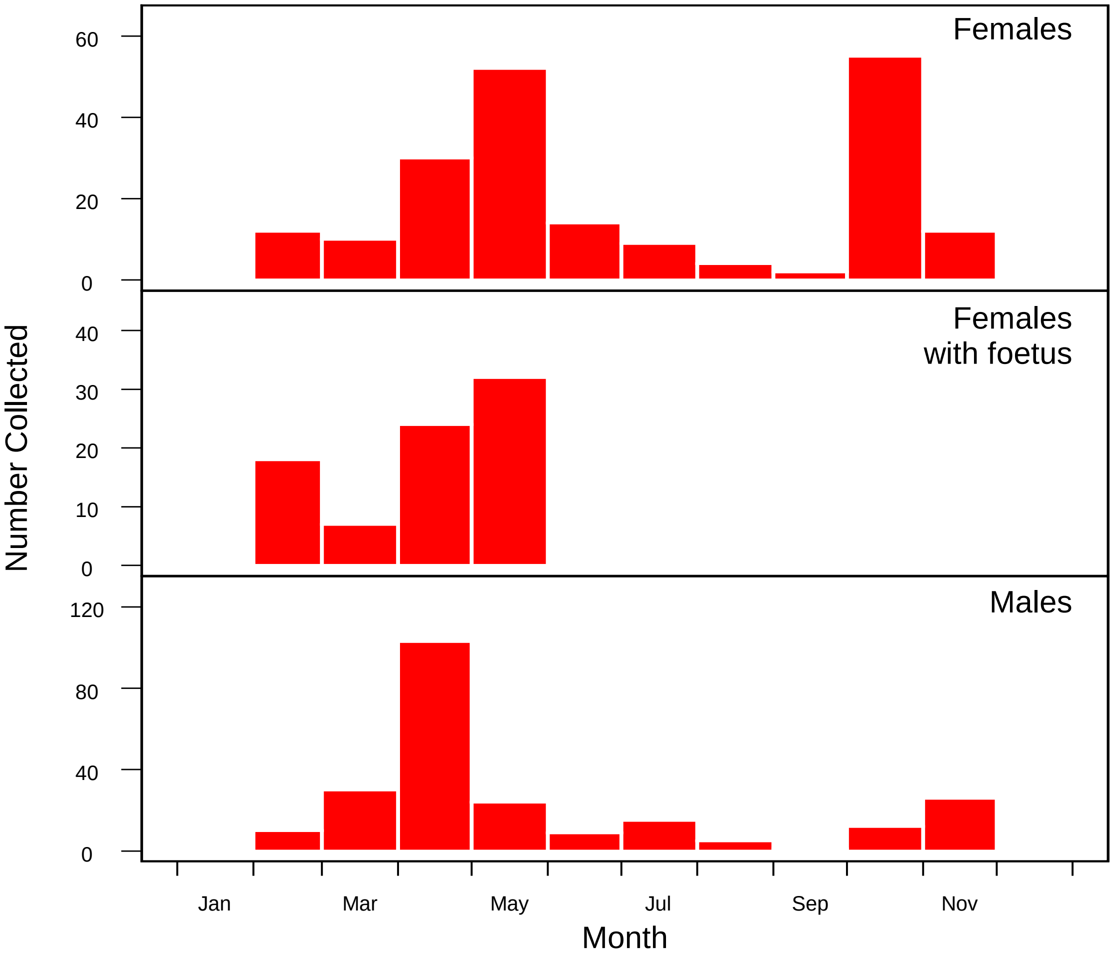


Figure 2.2. Sampling date frequencies for Steller sea lions collected in Alaska from 1976 to 1989.

Table 2.2. Parameter estimates (± *S.E.*) for Richards models describing the growth of Steller sea lions (standard length and mass at age (years)). The female model is the additive model with the Richards model as the base model (Table 2.1). Data used were from animals aged 0.75 years and older.

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	217
Female (additive)	2.324	-3.218	0.001	-17.107	0.032	0.787	250
Mass (kg)							
Male	681.112 ± 16.254	8.041 ± 3.392	101.148 ± 9.087	12.365 ± 0.890		0.850	203
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	222

With the female Richards models, I was unable to obtain standard errors of the parameter estimates due to parameter correlation. Growth in body length with age was asymptotic for males and females (Fig. 2.3, Table 2.3). Female growth rate declined with age, with length reaching 90% of maximum by 4 years of age. The extra parameter (*b*) was significant in the additive and proportional female models ($p<0.05$) indicating females with a foetus were longer than other females of the same age. The additive model was chosen over the proportional model as the r^2 was higher, but the difference was marginal (Appendix 1). The presence of a foetus increased body length by 0.032 m (Fig. 2.3, Table 2.3). Growth in male length increased to a maximum rate at 4 years, afterwhich it decreased with age. The maximum growth rate (m d^{-1}) was 6% greater than the growth rate at 2 years of age. Male body length did not reach 90% of maximum until about 7.5 years of age. The data did not reveal significant sexual dimorphism in length until the third year of life (males = 2.200 m ± 0.138 *S.D.*, females = 2.019 m ± 0.106 *S.D.*; $p<0.001$).

Both the male and female length at age models failed to accurately predict birth length (Fig. 2.3). The female model predicted a birth length of 0.001 m which is much lower than 0.94 m, the observed mean length of newborn female Steller sea lions from various locations in Alaska (Brandon *et al.* 1996). The male model predicted a birth length of 1.635 m which is much higher than the observed 0.98 m (Brandon *et al.* 1996). Thus, the female length at age model overestimated the average growth rate during the first year of life, and the male model underestimated the average growth rate of animals

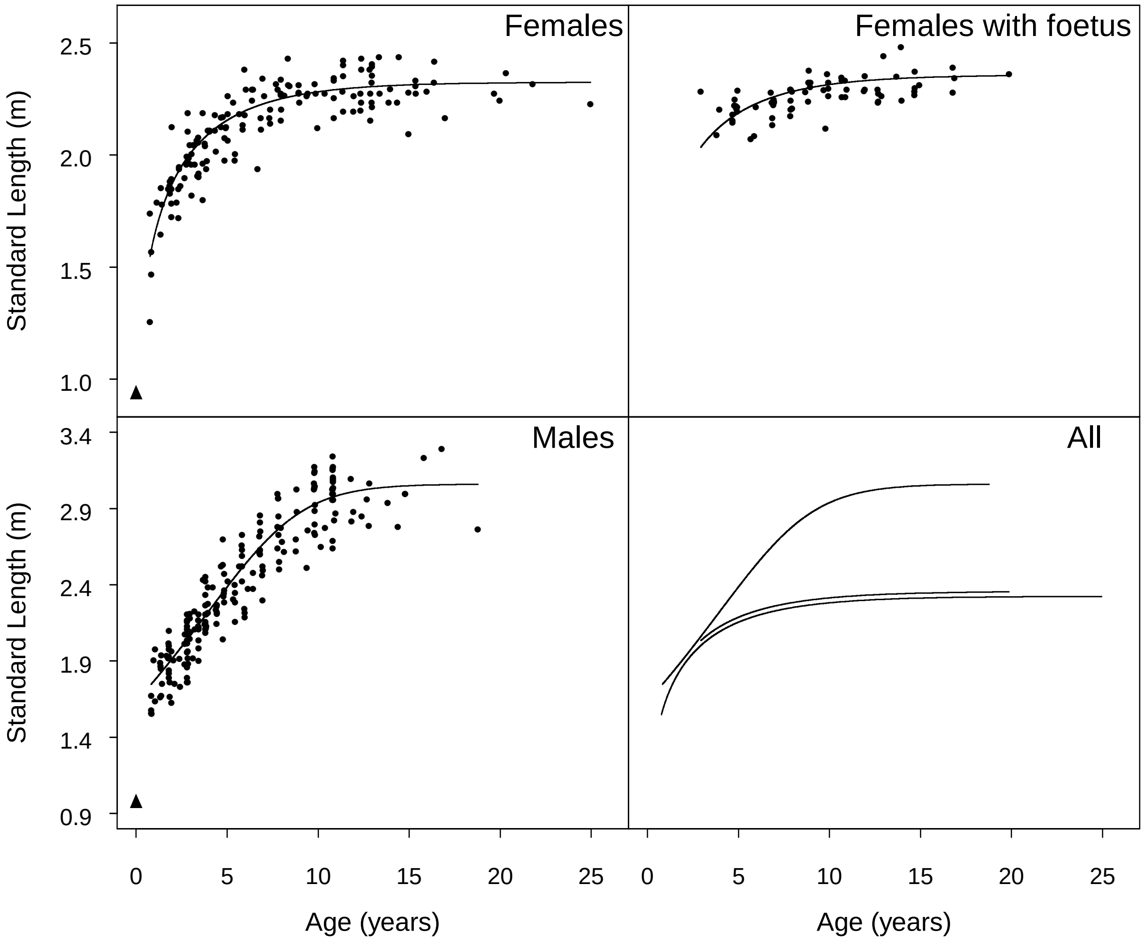


Figure 2.3. Standard length of Steller sea lion males (≥ 0.75 year old), females (≥ 0.75 year old), and females with a foetus by age. Parameter values of the fitted Richards models (lines) are in Table 2.2. Triangles are mean lengths of newborn (0 – 5 days old) Steller sea lions from various locations in Alaska from Brandon *et al.* (1996).

Table 2.3. Standard length and mass at age of Steller sea lions (age 0 is birth, 15 June). Sizes at birth are mean sizes (length and mass) of newborn (0 – 5 days old) Steller sea lions from various locations in Alaska from Brandon *et al.* (1996). All other sizes were calculated from fitted Richards growth models (Table 2.2).

Age (y)	Standard Length (m)			Mass (kg)		
	Male	Female	Female with foetus	Male	Female	Female with foetus
0	0.98	0.94	-	22.4	19.5	-
1	1.77	1.64	-	124.5	88.6	-
2	1.92	1.88	1.91	153.2	128.0	155.6
3	2.07	2.01	2.04	188.6	156.2	183.8
4	2.23	2.09	2.13	232.1	178.0	205.6
5	2.39	2.15	2.19	285.6	195.4	223.0
6	2.54	2.20	2.23	351.2	209.7	237.2
7	2.67	2.23	2.26	430.4	221.4	249.0
8	2.78	2.25	2.28	520.6	231.3	258.8
9	2.87	2.27	2.30	604.9	239.5	267.1
10	2.94	2.28	2.31	656.0	246.5	274.0
11	2.98	2.29	2.32	674.6	252.4	280.0
12	3.01	2.30	2.33	679.6	257.4	285.0
13	3.03	2.30	2.34	680.7	261.7	289.3
14	3.04	2.31	2.34	681.0	265.4	292.9
15	3.05	2.31	2.34	681.1	268.5	296.1
16	3.05	2.32	2.35	681.1	271.2	298.8
17	3.06	2.32	2.35	681.1	273.5	301.1
18	3.06	2.32	2.35	681.1	275.5	303.1
19	-	2.32	2.35	-	277.2	304.8
20	-	2.32	-	-	278.7	-
21	-	2.32	-	-	279.9	-
22	-	2.32	-	-	281.0	-
23	-	2.32	-	-	282.0	-
24	-	2.32	-	-	282.8	-

less than a year old. This resulted in an apparent convergence of male and female body sizes from ages 0.75 to 2 years and a divergence thereafter (Fig. 2.3).

Mass at Age Models

As with body length, all growth models described the mass data well (Appendix 1). The Richards model was again chosen over the other growth equations based on its r^2 value and its similarity to the locally weighted regressions (Table 2.2). I was unable to obtain standard errors for the parameter estimates of the female Richards model without the extra parameter (*b*), but was able to obtain them when the extra parameter was included. Growth in body mass with age was asymptotic for males and females (Fig. 2.4, Table 2.3). Annual increases in female mass declined with age, with body mass reaching 90% of maximum by 13 years of age. As with the female length models, the extra parameter (*b*) was significant in the additive and proportional models ($p<0.05$). The additive model was chosen for its higher r^2 value, although the r^2 was similar to the proportional model (Appendix 1). Females with a foetus were 27.6 kg heavier on average than other females of the same age (Fig. 2.4, Table 2.3). Male mass growth rate increased with age to a maximum during the seventh year of life, afterwhich it decreased with age. The growth rate (kg d^{-1}) at 7.5 years of age was approximately three times that at 2 years of age. Male body mass was 90% of maximum at about 9 years of age. The data did not reveal a significant sexual dimorphism in mass at age 1, but did show a significant difference in the second year of life (males = 173.9 kg ± 36.0 *S.D.*, females = 143.8 kg ± 34.8 *S.D.*; $p<0.01$).

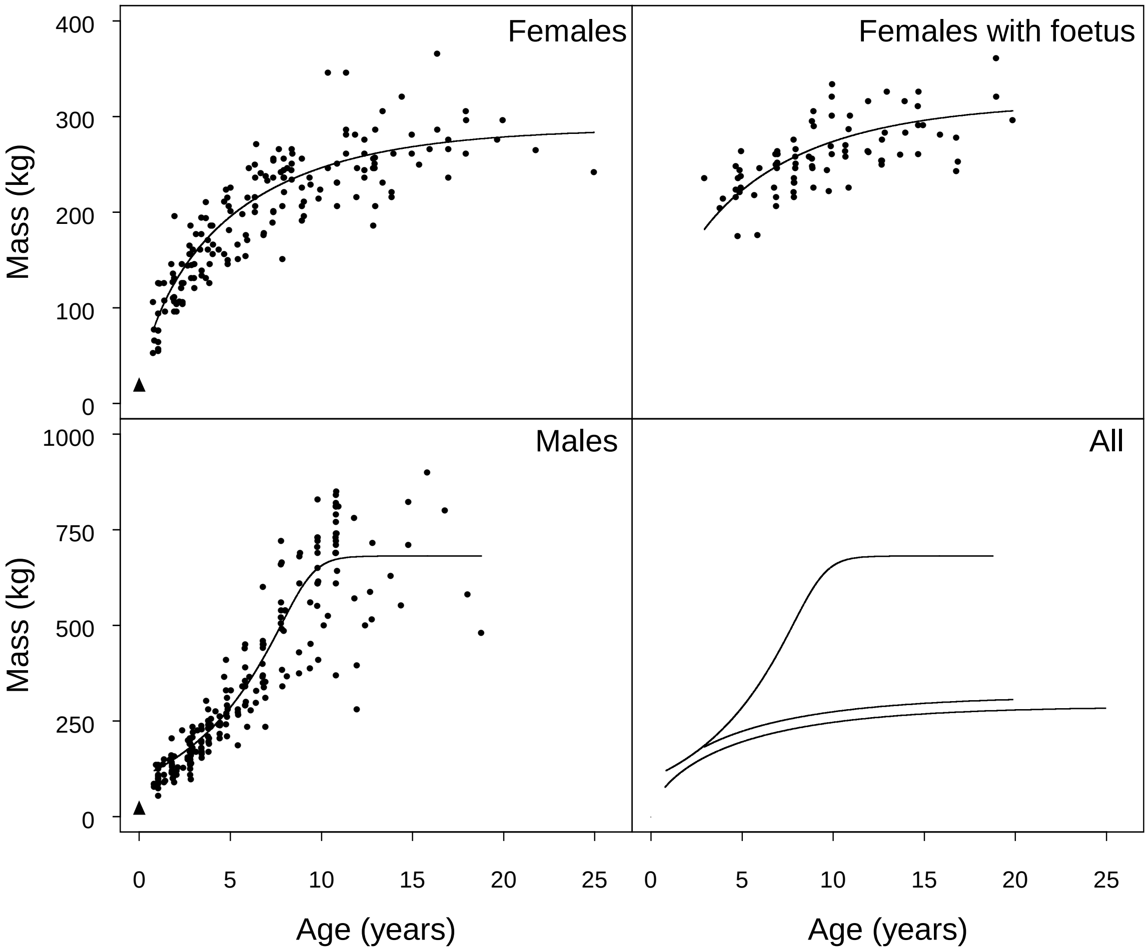


Figure 2.4. Mass of Steller sea lion males (≥ 0.75 year old), females (≥ 0.75 year old), and females with a foetus by age. Parameter values of the fitted Richards models (lines) are in Table 2.2. Triangles are mean weights of newborn (0 – 5 days old) Steller sea lions from various locations in Alaska from Brandon *et al.* (1996).

As with length (Fig. 2.3), the male and female mass at age models failed to accurately predict birth weight (Fig. 2.4). The female model predicted an obviously inaccurate birth weight of 0 kg. In contrast, the observed mean weight of newborn female Steller sea lions from various locations in Alaska was 19.5 kg (Brandon *et al.* 1996). The male model predicted a birth weight of 101.1 kg, which is over four times the observed 22.4 kg (Brandon *et al.* 1996). Thus, the female mass at age model overestimated the average growth rate during the first year of life, and the male model underestimated the average growth rate of animals less than 1 year old. As with the length at age models, this resulted in an apparent convergence of male and female body mass from ages 0.75 to 2 years and a divergence thereafter (Fig. 2.4).

Mass – Length Relationships

The relationship between body mass and standard length was described well by the allometric model for females with and without foetuses (Table 2.4, Fig. 2.5). However, the model tended to overestimate mass at smaller lengths, and underestimate mass at larger lengths. For males, there was a change in the mass-length relationship around 2.6 m (Fig. 2.5) such that I divided the male length data into two groups (less than and greater than 2.6 m) and fit two separate allometric models. Both described their respective data well (Table 2.4, Fig. 2.5). Males greater than 2.6 m long were heavier per unit length than shorter males. Males (<2.6 m long) and females were similar in weight for a given length, while females with a foetus were slightly heavier per unit length.

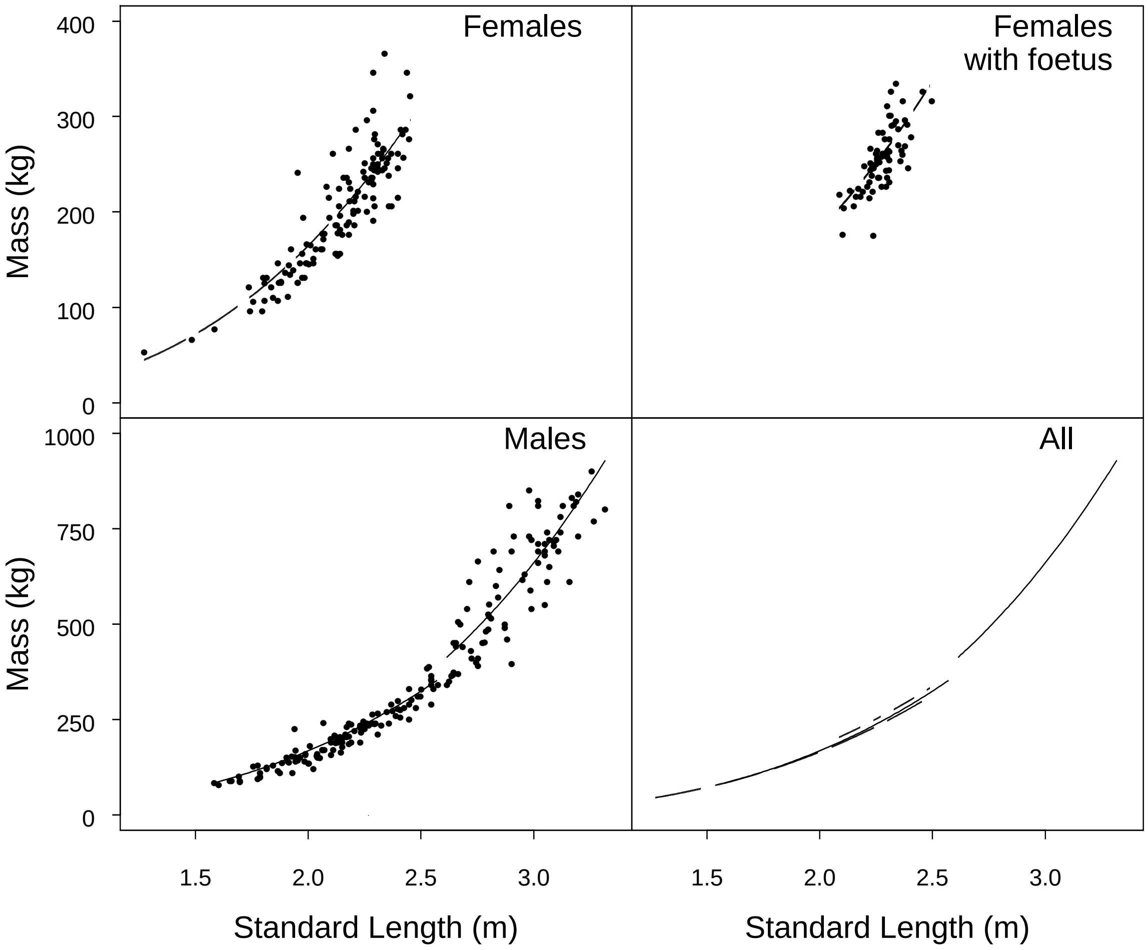


Figure 2.5. Mass – length relationships for Steller sea lion males (≥ 0.75 year old), females (≥ 0.75 year old), and females with a foetus. Parameter values of the fitted allometric models (lines) are in Table 2.4.

Table 2.4. Allometric models ($M = aL^b$) fit to mass (M in kg) and standard length (L in m) data for Steller sea lions (≥ 0.75 years old). r^2 is from linear least squares regression of $\log M = \log a + b \log L$.

Class	Parameter		n	r^2
	a	*b*		
Male < 2.6 m	21.87	2.945	118	0.92
Male > 2.6 m	15.69	3.405	75	0.71
Female	13.63	2.894	129	0.84
Female with foetus	26.00	2.792	70	0.55

Seasonal Growth Patterns

Deciphering exact seasonal patterns of growth was complicated by a lack of animals sampled in December and January, and low sample sizes in June – September. Despite these shortcomings, the residuals of the fitted growth models indicated seasonal variability in growth rate (other than that inherent to the models), especially for males (Fig. 2.6). The length residual smooth for females without foetuses did not deviate much from 0 (± 1%) suggesting seasonal variability in female length growth rate was low. The female mass residual smooth was within ± 5% throughout the year with observed mass higher than predicted mass in October – November and lower than predicted during April and May. The smooths of the male length and mass residuals exhibited a distinct seasonal pattern. Observed length and mass was higher than predicted in February and March, and lower than predicted in the breeding season (May-July) and October and November. This indicates that the average male growth rate (length and mass) was higher than predicted by the models between November and February, and lower than predicted during May and June. The smooth of the male length residuals was within ± 3%, while the smooth of the male mass residuals was within ± 10 % throughout the year.

The patterns exhibited by the residual smooths were supported when size was plotted by day of the year and smoothed (Fig. 2.7). By grouping the data into two age classes, bias may have been introduced due to interactions between age and time of year. However, the patterns were generally the same when each age was smoothed individually. Data from males over six years of age exhibited large seasonal fluctuations in length and mass, with the majority of growth (length and mass) occurring between November and February. Very little growth occurred during the breeding season (May-July); in fact, the animals may have even decreased in size. Young males and females (1-5 years old) also grew very little from April-June (length and mass) and may have slightly decreased in size during this time. Size (length and mass) of females over the age of 6 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.

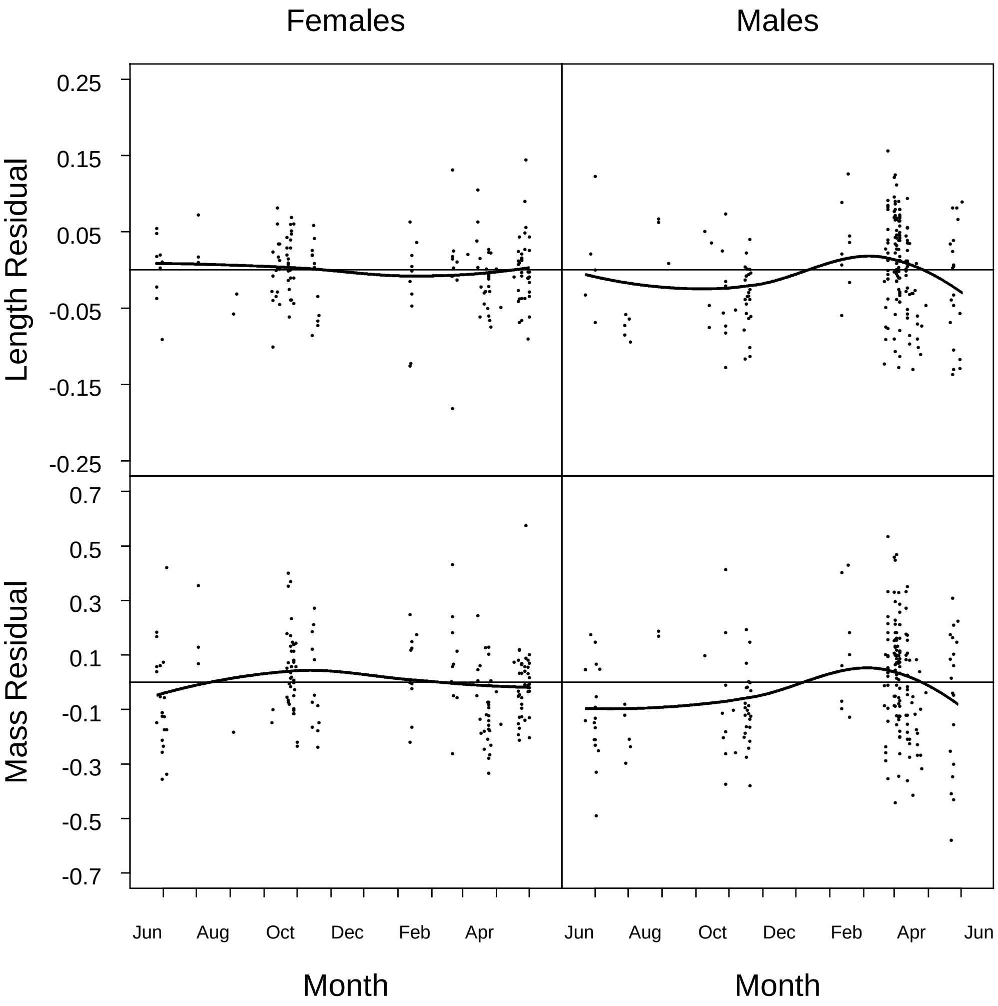


Figure 2.6. Residuals ([observed size – predicted size])/predicted size) of the fitted Richards models (Figs. 2.3 and 2.4, Table 2.2) by day of the year for male and female (without a foetus) Steller sea lions. Residuals were smoothed using a locally weighted regression (*Lowess*, S-Plus 3.3).

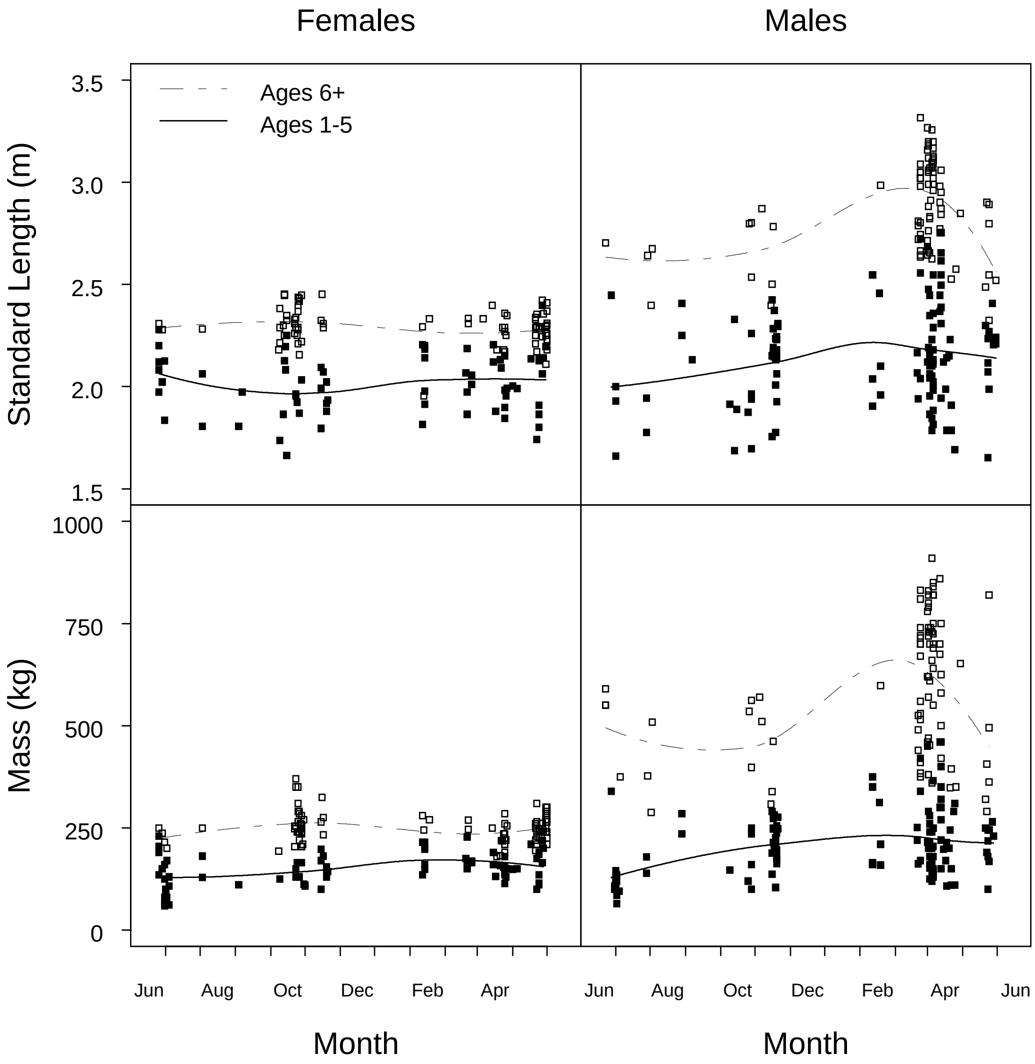


Figure 2.7. Size by day of the year for male and female (without a foetus) Steller sea lions. Data were smoothed by age group (ages 1-5 and ages 6+) using a locally weighted regression (*Lowess*, S-Plus 3.3).

Discussion

Cross Sectional Data

Growth of pinnipeds in the wild has generally been assessed using cross-sectional data (Bryden 1972; Innes *et al.* 1981; Murie and Lavigne 1992; McLaren 1993; Olesiuk 1993; Rosas *et al.* 1993; Boyd *et al.* 1994; Hammill *et al.* 1995; Lima and Páez 1995; Trites and Bigg 1996; Garlich-Miller and Stewart 1998). 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: 1) precision of assigned age, 2) variation in birth date, 3) accuracy of the aging technique, 4) unequal size representation within age classes, 5) unequal sampling among months, 6) unequal representation of ages, 7) differential mortality related to size, and 8) differential growth and survival rates related to environmental conditions (Innes *et al.* 1981; Leberg *et al.* 1989; McLaren 1993).

The first three potential sources of bias – precision 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 this can bias model parameter estimates and increase their variance (Leberg *et al.* 1989). The age determination technique used dental cementum annuli. This is the common method for aging pinnipeds and has been shown to be accurate for Steller sea lions, so I assumed this bias was minimal (Scheffer 1950; Fiscus 1961; Spalding 1964).

The next two 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 especially be a problem with polygynous, sexually dimorphic species like the Steller sea lion (McLaren 1993). Large, breeding bull Steller sea lions are strongly territorial, resulting in the segregation of smaller non-breeding males from rookery areas during the breeding season (Mathisen *et al.* 1962; Thorsteinson and Lensink 1962; Kastelein and Weltz 1990; Zadal'skii 1997). Size bias of the sampled animals should be small because they were collected from rookeries, haulouts, and coastal waters. However, there may be some bias in the adult male data since no adult males were taken from rookeries during the breeding season. This bias would have a negligible effect on the size at age models, but may influence the observed seasonal size patterns.

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 (Schusterman and Gentry 1971; Bryden 1972; Sergeant 1973; Ashwell-Erickson and Elsner 1981; Costa *et al.* 1986; Anderson and Fedak 1987b; Olesiuk and Bigg 1987; Nordøy and Blix 1988; Ryg *et al.* 1990; Boyd and Duck 1991; Renouf *et al.* 1993; Trites and Bigg 1996). The majority of animals in my study were sampled between February and May, and October and November, although juveniles were collected more equally among seasons than adults (Figs. 2.2 and 2.7). Thus, the size at age models were biased toward size at these times of the year, especially for older age classes.

The sixth 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 were less represented in the collection than young animals so this may have slightly biased the growth models.

The last two 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, fast growing juveniles or sub-adults may survive better than slow growing individuals of the same age. This would result in an excess of large individuals among young adults (McLaren 1993). Furthermore, due to 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, Calkins *et al.* (1998) have shown that female Steller sea lions, from this collection, were larger in the 1970's than in the 1980's. This difference was probably a result of undernutrition. Unfortunately there are not enough data to determine the exact effect of these two sources of bias. At best, my size at age models represent the average size of animals born during a specific period (mid to late 1900's).

Mathematical Growth Models

Growth of pinnipeds has often been described using mathematical growth models (Innes *et al.* 1981; Trites 1991; Murie and Lavigne 1992; McLaren 1993; Olesiuk 1993; Rosas *et al.* 1993; Boyd *et al.* 1994; Hammill *et al.* 1995; Lima and Páez 1995; Garlich-Miller and Stewart 1998). The usefulness of mathematical growth models has been questioned (Zach 1988; Aldrich and Lawler 1996). No single equation adequately describes the 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; Pruitt *et al.* 1979; McLaren 1993). The residual variances of these growth models can be used to assess variability of size within populations and species, including seasonal size fluctuations (McLaren 1993).

Most mathematical growth models were originally formulated based on fundamental postulates about growth processes, but there is little data to support these theories (von Bertalanffy 1938; Richards 1959; Pruitt *et al.* 1979; Ricker 1979). Thus, selection of appropriate models is based on goodness of fit and convenience (Ricker 1979). The three parameter Pütter, von Bertalanffy, logistic, and Gompertz growth models are special cases of the four parameter Richards model (Table 2.1; Richards 1959). Some authors have suggested that the Richards model should be used as it is more flexible than three 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 three 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 *et al.* 1984; Zach 1988). In my study, the Richards model provided the best fit in all cases. This was not unexpected as it is the most flexible of the models tested (four parameters). However, the simpler models also described the data well (Appendix 1) and I 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 three parameter models as occurred with male mass growth.

Physical Growth with Age

Female length and mass exhibited asymptotic growth, with growth rate declining with increasing age. Laws (1956) found the length at puberty, as a percentage of final size, was remarkably constant among female pinnipeds at 87%. Female length reached 87% of its maximum (asymptote) during the third year of life. This corresponds with the earliest evidence of female sexual maturity as suggested by Laws (Pitcher and Calkins 1981). Mass did not reach 87% of maximum until the twelfth year of life. Females with a foetus were 3 cm longer and 28 kg heavier than other females of the same age. They also weighed more per unit length. The length difference probably reflects the weight of the foetus, placenta, and other physiological changes associated with pregnancy extending the vertebral column during measurement as has been suggested for northern fur seals (Trites and Bigg 1996).

The additive model described the female data best, which suggested the weight change associated with pregnancy (including the weight of the foetus) was a constant amount, independent of maternal age and size. However, the proportional model described the data almost as well. Pup mass was positively correlated with maternal mass in southern elephant seals, and all mothers had the same mass/length relationship suggesting longer mothers also gave birth to larger pups (Arnbom *et al.* 1994). Pup size (mass and length) was also positively correlated with maternal age in northern fur seals, although the relationship became negative at older ages (Trites 1991). The size and age of the mother probably influenced the size of the foetus (especially near parturition), but my data and analyses were inadequate to determine this. The main intention of my analysis was to control for the additional size of a female carrying a foetus. It was not intended to determine the exact nature of this size difference.

Male length growth with age was asymptotic, and growth rate was relatively constant up to about 6 years of age. Body length reached 87% of maximum during the seventh year of life. Males are believed to reach sexual maturity between 3 and 8 years of age (majority between 5 and 7) (Thorsteinson and Lensink 1962; Pitcher and Calkins 1981). This suggests the majority of male Steller sea lions mature sexually before reaching 87% of body length. However, while 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 (when they have reached 87% of maximum length) (Thorsteinson and Lensink 1962). Sexual bimaturation is common in sexually dimorphic species with members of the larger sex maturing at older ages (Stamps and Krishnan 1997).

The pattern of mass growth with age was different for males and females. Male mass growth rate increased up to 7.5 years of age, then decreased as they became older. This growth spurt has been shown in males of other polygynous pinniped species (Bryden 1972; Lander 1981; McLaren 1993; Boyd *et al.* 1994; Trites and Bigg 1996). Mass growth rate appeared maximal around the mean age of physiological sexual maturity, suggesting the growth spurt coincides with puberty. Sociological maturity for male Steller sea lions – the average age of harem bulls – is 10 or 11 years (Thorsteinson and Lensink 1962; Pitcher and Calkins 1981). My results refute Bryden's (1972) suggestion that the growth spurt does not occur until sociological maturity.

McLaren (1993) modeled the growth spurt of a male Steller sea lion using two consecutive equations. However, data for some species of sexually dimorphic pinnipeds suggest that growth of males (which undergo growth spurts) is described better by one, rather than two sigmoid models (Payne 1979; Lander 1981; Boyd *et al.* 1994). Some have suggested that growth spurts may also occur in length at the time of sexual or sociological maturity (Scheffer and Wilke 1953; Bryden 1972; McLaren 1993). However, I found only weak evidence of a length growth spurt in the Steller sea lion data I examined. Other studies have failed to detect a length growth spurt for male pinnipeds that undergo a mass growth spurt (Payne 1979; McLaren 1993). Because male length growth rate did not undergo a pronounced acceleration like mass growth rate, adult males were heavier per unit length than younger males.

Although some sources state that the weight of an adult male Steller sea lion is approximately 1 tonne (e.g., King 1983), I found an average weight of 681 kg for males aged 12 years and older. This corresponds to approximately 1500 lbs (average weight of adult males listed in Wynne 1993). The maximum recorded weight in the data I used was 910 kg.

Sexual dimorphism in length was significant at three years of age, and sexual dimorphism in mass was significant at two years of age. Male length growth rate did not begin to decline until much later than female length growth rate resulting in males being 1.3 times longer than females by 12 years of age. The male mass growth spurt produced a larger mass difference between the sexes, with males being 2.6 times heavier than females by 12 years of age. Otariid seals are the most sexually dimorphic mammals, with males averaging three times the size of females (Weckerly 1998). The degree of sexual dimorphism in the Steller sea lion is similar to other otariids, and is achieved through both a longer male length growth period and a male mass growth spurt at puberty.

The extreme sexual dimorphism in the Steller sea lion is a result of the polygynous mating system and sexual selection. Males generally do not have the opportunity to copulate until they acquire a breeding territory so there is intense male-male competition for territories (Gisiner 1985). Larger males are more successful at acquiring and maintaining a territory (Mathisen *et al.* 1962; Gentry 1970). The ability to hold a territory begins to fade around 12 years of age, with an estimated male longevity of only 14 years (compared to female longevity of 24 y) (Thorsteinson and Lensink 1962; Trites and Pauly 1998). The reduced longevity (relative to females) is probably a result of increased mortality associated with their reproductive strategy (Trivers 1972; Clinton and Le Boeuf 1993). Selection should favour large body size and therefore rapid growth during their relatively short lifespan (Trivers 1972).

Neither the female nor male size at age models accurately predicted birth length and mass. Specifically, the female models underestimated newborn size and the male models overestimated newborn size. My size at age models can not be used to estimate the length or mass of Alaskan Steller sea lions less than one year old. If growth was linear during the first year of life, female pups would have grown about 1.9 mm and 0.2 kg per day to reach the sizes predicted by the models at 1 year of age (using mean newborn sizes from Brandon *et al.* (1996)). Male pups would have grown 2.2 mm and 0.3 kg per day. These estimates are consistent with rates reported for Steller sea lion pup growth during the first forty days of life (range from 1.7-4.7 mm d^{-1} and 0.2-0.45 kg d^{-1}) (Higgins *et al.* 1988; Brandon *et al.* 1996). Data from Spalding (1964) and Calkins and Pitcher (1982) suggest this growth rate is sustained up to at least nine months of age. Steller sea lions may nurse their pups for one year or more (Pitcher and Calkins 1981). This extended nursing period (compared to other pinnipeds) may account for the high growth rate throughout the first year of life.

Seasonality

Seasonal mass fluctuations are common in adult pinnipeds. With phocids, both adult males and females accumulate blubber before the breeding season to meet the high energetic demands of mating and lactation when they eat little or no food (Sergeant 1973; Ashwell-

Erickson and Elsner 1981; Costa *et al.* 1986; Nordøy and Blix 1988; Ryg *et al.* 1990; Renouf *et al.* 1993). Otariid males exhibit similar fluctuations in mass related to the breeding season, with changes in both blubber mass and water content of core tissue (Schusterman and Gentry 1971; Olesiuk and Bigg 1987; Boyd and Duck 1991; Trites and Bigg 1996; Nitto *et al.* 1998). This seasonal fattening before the breeding season provides both a source of energy during the fast and additional body size for territorial competition (Olesiuk and Bigg 1987).

Strong seasonality was evident in the mass growth of older males (> 6 years of age). The majority of growth occurred sometime between November and March and little growth occurred during the breeding season and late summer (May – September). When size was plotted by day of the year (Fig. 2.7), there appeared to be a sharp decrease in size 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 the 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 mass loss (Olesiuk and Bigg 1987).

A captive study of Steller sea lions documented a seasonal pattern of food consumption, associated with this mass change. Kastelein *et al.* (1990) found that the food consumption of an adult male was less than average between April and September, and greater than average between November and March. Their results suggest adult male food consumption is highest during the time of the year when I found mass growth rate to be highest.

It is interesting that similar seasonal fluctuations in length were detected in adult males. Trites and Bigg (1996) found seasonal length fluctuations in northern fur seals, and suggested they may be due to: 1) a gravity phenomenon related to the amount of time spent in the water; 2) changes in body water composition; or 3) the displacement of body mass during measurement. Of the three hypotheses, only the latter two are probable for Steller sea lions. Unlike northern fur seals, Steller sea lions do not undergo a long distance migration, so they do not spend an extended period of time in the water when their bodies might expand (gravity phenomenon). A change in body water composition is likely, and has been shown for adult male Steller sea lions (Olesiuk and Bigg 1987). Mass displacement during standard length measurement, while animals were on their back, is also possible. Although some animals were measured while on their belly (dorsal standard length), these measurements were converted to standard length using an equation developed from animals that were measured on their backs, so these data would be subject to the same phenomenon. Most likely, both of these factors contributed to the observed seasonal fluctuations in body length.

Older females that were not carrying a foetus (>6 years of age) did not exhibit distinct seasonal fluctuations in length or mass. There was weak evidence that mass was greater in October and November than in the spring (April - May). This may be due to females, that weigh less per unit length, having a lower probability of carrying a fetus to term (Pitcher *et al.* 1998). In the fall (October and November) all of the females collected were classified as 'not carrying a foetus'. However, females collected late in gestation (April and May) that were not carrying a foetus were smaller individuals who were unable to maintain their pregnancy during the winter.

Seasonal fluctuations in juvenile pinniped growth rate and size are less well documented, but may also involve an increase in mass or fat content before the breeding season, and a decrease thereafter (Ryg *et al.* 1990; Trites and Bigg 1996). My data are consistent with this pattern. Males and females less than 6 years of age grew very little during the breeding season, and may have slightly decreased in size. There is also evidence that captive juvenile Steller sea lions experience seasonal changes in growth rate synchronous with those found in this study and these fluctuations may be associated with inherent seasonality in food consumption related to growth and moulting (Nitto *et al.* 1998, Trites and Rosen, unpubl. data).

Summary

Morphometric measurements were used to describe growth of Steller sea lions (*Eumetopias jubatus*). Growth models were constructed for males (≥ 1 year old), females (≥ 1 year old), and pregnant females with a foetus that had been shot on rookeries, haulouts, and in the coastal waters of southeastern Alaska, the Gulf of Alaska and along the Bering Sea ice edge between 1976 and 1989. The Richards model best described age related growth in body length and mass. Females with foetuses were an average 3.2 cm longer and 27.6 kg heavier than females of the same age without foetuses. Males grew (in length) over a longer period than females and exhibited a growth spurt in mass which coincided with sexual maturity. Sexual dimorphism in both body length and mass was significant by 3 years of age. The average predicted standard lengths of males and females older than 12 years were 3.04 m and 2.32 m respectively, while the average predicted weights were 681 kg and 273 kg respectively. The maximum recorded weight 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 to 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.

CHAPTER III: A BIOENERGETIC MODEL FOR ESTIMATING FOOD REQUIREMENTS OF STELLER SEA LIONS

Introduction

Since the late 1970’s, the Alaskan population of Steller sea lions has decreased in number by over 70% (Loughlin *et al.* 1992; Trites and Larkin 1992). One of the leading hypotheses regarding the cause of this decline is nutritional deficiency caused by human or natural reductions in the abundance, availability and/or quality of prey (Alverson 1992; Merrick *et al.* 1997; Calkins *et al.* 1998). Central to evaluating the nutritional stress hypothesis, is the need to understand the food requirements of Steller sea lions. Food consumption estimates are also a prerequisite for assessing interactions between marine mammals and fisheries (Beverton 1985; Trites *et al.* 1997).

It is difficult to observe food consumption directly because marine mammals feed at sea. Nevertheless, there are several ways to estimate the amount of food they consume. One method, stomach content analysis (Murie and Lavigne 1991; Ohizumi and Miyazaki 1998), provides a direct measure of food consumption, but requires logistically difficult stomach lavage techniques or the sacrifice of a large number of animals. Stomach content analysis also requires knowledge of feeding frequency and stomach passage rates (Davis and Warren 1971; Elliott and Persson 1978). To date, stomach contents of Steller sea lions have only been used to identify diet composition rather than the quantity of food consumed (Mathisen *et al.* 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966; Pitcher 1981; Calkins and Goodwin 1988; Calkins 1998).

A second method for estimating the food consumption of wild marine mammal populations is to infer wild feeding rates from feeding rates of captive marine mammals (Sergeant 1973; Innes *et al.* 1987; Nordøy *et al.* 1995). Unfortunately, food requirements and food availability may not be the same for wild and captive animals (Naumov and Chekunova 1980). Furthermore, sample size is usually low in captive studies with only a few age and sex classes represented. A study by Kastelein *et al.* (1990) documented the food consumption of 11 captive Steller sea lions of both sexes and various ages throughout the year.

A third method for estimating the food consumption of marine mammals is bioenergetic modelling. Bioenergetics is the study of energy flow and transformation in biological systems. Biological systems are governed by the laws of thermodynamics and can be considered open systems (exchange energy and matter) (Wiegert 1968; Galluci 1973). As a result, biological systems reach steady states (not equilibrium) where energy influx is equal to energy efflux. In reality, a true steady state is never reached in nature, but in the long term any biological system must be in energy balance (Klekowski and Duncan 1975). For an individual organism, this is illustrated by the expression:

$$[3.1] \quad \textit{Consumption} = \textit{Feces} + \textit{Urine} + \textit{Respiration} + \textit{Production}$$

where *Consumption* is consumed energy, *Feces* is energy in feces, *Urine* is energy in urine, *Respiration* is energy used for work (degraded to heat), and *Production* is deposited energy (tissue growth, fat storage, eggs, sperm, embryos, exuviae, etc.) (Klekowski and Duncan 1975).

Most organism-level bioenergetic models are some form of the above equation. They are generally used to estimate one component, given estimates of the other components. For example, bioenergetic models have been used to estimate growth (both positive and negative) of organisms given different feeding regimes, activity levels, and environmental conditions (e.g., Kitchell and Stewart 1977; Øritsland 1990). Bioenergetic models have also been used to estimate energy or food consumption (*Consumption* in Eq. 3.1) for a range of taxa including crustaceans (Luxmoore 1985), fish (Kerr 1982; Rice and Cochran 1984; Wahl and Stein 1991), birds (Nichols *et al.* 1995; Derby and Lovvorn 1997), and small mammals (McNab 1963).

The energy consumption of marine mammals has frequently been estimated using bioenergetic models (Hinga 1979; Naumov and Chekunova 1980; Ashwell-Erickson and Elsner 1981; Doidge and Croxall 1985; Hiby and Harwood 1985; Lavigne *et al.* 1985; Worthy 1987a; Øritsland and Markussen 1990; Härkönen and Heide-Jørgensen 1991; Markussen and Øritsland 1991; Ryg and Øritsland 1991; Markussen *et al.* 1992; Olesiuk 1993; Ugland *et al.* 1993; Mohn and Bowen 1996; Stenson *et al.* 1997). These models range in detail from simple equations (few parameters) representative of an average individual's annual energy consumption to detailed energy budgets (many parameters) for each age/sex class and day of the year. In most of these studies, individual energy consumption has been multiplied by population size to estimate population energy consumption, and converted to food consumption using data on diet composition and the energetic density of prey.

In addition to providing quantitative estimates of food consumption, bioenergetic models have several other uses. First, bioenergetic models can be used to examine the sensitivity of food consumption estimates to uncertainty in parameter values (Olesiuk 1993; Mohn and Bowen 1996; Shelton *et al.* 1997). This provides a measure of confidence in the model predictions and direction for future research. Second, bioenergetic models can be used to explore specific physiological and ecological questions. For example, Innes *et al.* (1981) examined the effect of a change in body size on the food consumption of a harp seal population, and Hiby and Harwood (1985) examined the relationship between population size and *per capita* food consumption for a hypothetical grey seal population.

The first objective of my study was to develop a generalized bioenergetic model for Steller sea lions, and to apply this model to answer such questions as: 1) How much food do Steller sea lions currently consume?; 2) How does food consumption vary seasonally?; and 3) How does food consumption vary by region of Alaska? The second objective was to calculate confidence limits for the estimates of food consumption based on the error structure of the model parameters. The third objective was to examine the sensitivity of the model predictions to uncertainty in different groups of model parameters.

Methods

Model Structure

The model was built using Microsoft Visual Basic 5.0, and was structured along the lines proposed by Lavigne *et al.* (1982) as follows. First, gross energy consumption was calculated for each age, sex, reproductive status (immature, mature, and pregnant), and day of the year using the following framework (bioenergetic model):

$$[3.2] \quad GEC = \frac{P + (A * BM)}{E_{HIF} * E_{f+u}}$$

where GEC is gross energy consumption, E_{f+u} is fecal and urinary digestive efficiency (metabolizable energy as a proportion of gross energy), E_{HIF} is the efficiency of utilization of metabolizable energy (or 1 – heat increment of feeding as a proportion of metabolizable energy), P is production or energy deposition, BM is basal metabolism, and A is an activity multiplier. These terms in Eq. 3.2 are, in fact, groups of parameters. For example, P is composed of body composition parameters, body mass, and the energy content of tissues.

Next, population composition was determined using:

$$[3.3] \quad N_{i+1,j,t+1} = N_{i,j,t} * s_{i,j}$$

where N is number of individuals, i is age (years), j is sex, t is time (years) – during the breeding season, and s is annual survival rate; and

$$[3.4] \quad N_{0,t} = \sum N_{i,f,t} * fec * mat_{i-1,f}$$

where N_0 is number of pups, f is female, *fec* is fecundity (number of pups born per sexually mature female per year), and *mat* is the proportion of animals that are sexually mature at a given age. The population simulation ended when the finite rate of population change (λ) stabilized. The stable age distribution, or proportion of individuals of each age, was then calculated and multiplied by total population size to obtain the numbers of individuals of each age and sex alive during the breeding season.

To account for mortality throughout the year, the numbers of individuals of each age and sex that were alive during the breeding season were multiplied by $\frac{1}{\ln(s_{i,j})}\left[e^{\ln(s_{i,j})}-1\right]$ to obtain the effective numbers of individuals of each age and sex that were alive for an entire year. This assumes that the number alive declines exponentially throughout the year. For the oldest age class, the number of individuals alive during the breeding season was multiplied by $[(1 + s_{i,j}) / 2]$ to obtain the effective number of individuals that were alive for the entire year. This assumes a linear decline in numbers throughout the year.

The numbers of animals (by age and sex) that were sexually mature were determined by multiplying the numbers alive by the proportions, $mat_{i,j}$. The number that were pregnant was determined by multiplying the number of mature females by $\frac{1}{\ln(fec)}\left[e^{\ln(fec)}-1\right]$. This assumes that all sexually mature females are pregnant in early gestation (Pitcher *et al.* 1998), and that the number of pregnancies declines exponentially throughout the year.

Finally, food consumption was calculated for animals older than 1 year using the framework (diet model):

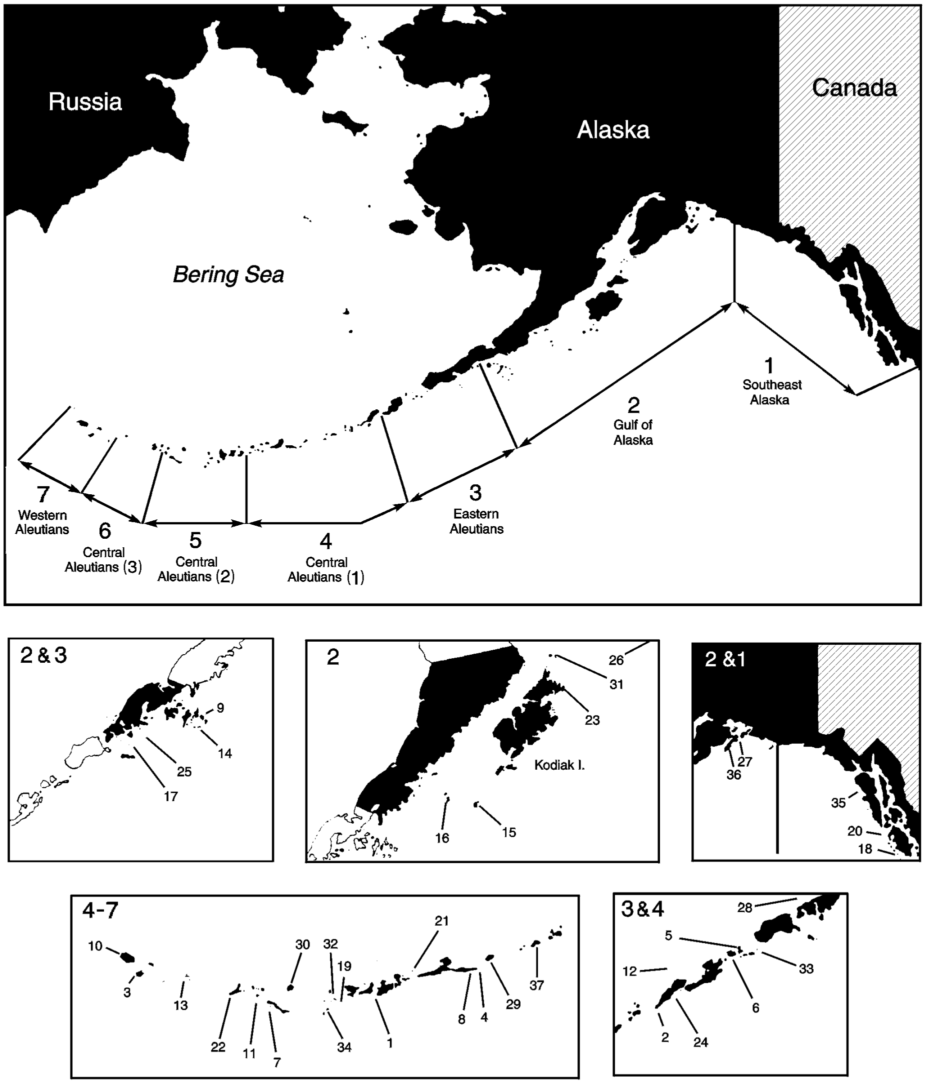
$$[3.5] \quad BC_i = \frac{GEC * prey_i}{ED_{diet}}$$

where BC_i is the biomass consumed of prey category i, $prey_i$ is the proportion of prey category i in the diet (biomass), and ED_{diet} is the mean weighted (by $prey_i$) energetic density of the diet. I assumed that pups (<1 year old) obtained all energy through nursing, therefore, their energy demands were included in their mothers' *GEC*. Female-offspring bonds usually last less than one year with weaning occurring just prior to or during the breeding season (Sandegren 1970; Pitcher and Calkins 1981; Porter and Trites in review). Prey species were grouped into seven categories as defined by Merrick *et al.* (Merrick *et al.* 1997) (Table 3.1). The annual amount of food consumed by the population was calculated by summing daily food consumption for the entire year for each age, sex, and reproductive status; and then multiplying these annual food consumption estimates by the effective number of individuals of each age, sex, and reproductive status in the population.

The Alaskan population of Steller sea lions was divided into seven regions (Fig. 3.1) based on previous population surveys and diet composition studies (Merrick *et al.* 1997; Sease and Loughlin 1999). The annual amount of food consumed by the population was calculated for each area.

Table 3.1. Steller sea lion prey species categories as defined by Merrick *et al*. (1997).

Prey Category	Prey Species	
	Common Name	Scientific Name
Gadids	walleye pollock	*Theragra chalcogramma*
	Pacific cod	*Gadus macrocephalus*
	Pacific hake	*Merluccius productus*
	other gadids	Gadidae
Pacific Salmon	Pacific Salmon	*Oncorhynchus* spp.
Small Schooling Fish	capelin	*Mallotus villosus*
	Pacific herring	*Clupea pallasi*
	eulachon	*Thaleichthys pacificus*
	Pacific sand lance	*Ammodytes hexapterus*
Flatfish	arrowtooth flounder	*Atheresthes stomias*
	rock sole	*Lepidopsetta bilineatus*
	other pleuronectids	Pleuronectidae
Other Demersal Fish	sculpins	Cottidae
	rockfish	*Sebastes* spp.
	pricklebacks	Stichaeidae
	skates	*Raja* spp.
	sharks	
	lamprey	*Lampetra* sp.
Atka Mackerel	Atka mackerel	*Pleurogrammus monopterygius*
Cephalopods	squid	
	octopus	



1.5 Adak
2.4 Adugak
3.7 Agattu
4.4 Agligadak
5.3 Akun
6.3 Akutan
7.5 Amchitka
8.4 Amlia
9.2 Atkins
10.7 Attu
11.5 Ayugadak
12.4 Bogoslof
13.6 Buldir
14.2 Chernabura
15.2 Chirikof
16.2 Chowiet
17.3 Clubbing Rocks
18.1 Forrester
19.5 Gramp Rock
20.1 Hazy
21.4 Kasatochi
22.6 Kiska
23.2 Marmot
24.4 Ogchul
25.3 Pinnacle Rock
26.2 Pye (Outer)
27.2 Seal Rocks
28.3 Sea Lion Rock
29.4 Seguam
30.5 Semisopochnoi
31.2 Sugarloaf
32.5 Tag
33.3 Ugamak
34.5 Ulak
35.1 White Sisters
36.2 Wooded
37.4 Yunaska

Figure 3.1. Steller sea lion rookeries in the seven study areas of Alaska (adapted from Merrick et al. (1997) and Sease and Loughlin (1999)). Number prefixes of names designate the rookery; suffixes identify the areas in which the rookeries are found. Note: Amchitka, Kiska, and Agattu Islands have two rookeries each for a total of 40 rookeries (Table 3.2).

Monte Carlo simulations were used to incorporate parameter uncertainty into annual population food consumption estimates. In each run of the model, parameter values were randomly selected from sampling distributions (uniform, triangular, or normal) that described their uncertainty. Thus, each run of the model produced one estimate of annual population food consumption, and multiple runs produced a distribution of consumption estimates.

Three types of parameter sampling distributions were used: uniform, triangular, and normal. Uniform parameter sampling distributions were defined by upper and lower limits (e.g., 0.1 – 0.3), with every value between the limits having an equal probability of being sampled. Triangular sampling distributions were defined by a median, an upper limit and a lower limit (e.g., 0.15, 0.1 – 0.3). Half of the values sampled were less than the median and half were greater than the median. Between the median and the limits, the probability of a value being sampled was directly proportional to its distance from the median. Normal sampling distributions were defined by a mean and standard deviation (e.g., 0.2 ± 0.05). The computer routine used to sample the normal distribution was from Box and Muller (1958). For sampling normally distributed proportions, a *z*-transformation (Zar 1996) was used to bound the proportions at 0 and 1.

A sensitivity analysis of the model was performed by systematically incorporating uncertainty in each of the main parameter groups (bioenergetics, diet, population), one at a time, while holding the other parameters constant at their mean/median values. The model was then run with uncertainty in all parameters. The model was also run systematically incorporating uncertainty in all possible pairs of parameter groups to examine interaction effects (Rose 1983). A further sensitivity analysis was performed on the three main bioenergetic parameter groups (efficiency, metabolism, production; Eq. 3.2) where diet and population parameters were held constant.

Parameters

Bioenergetic

Bioenergetic parameter values are summarized in Table 3.2 and discussed and justified in detail in Appendix 2. Bioenergetic parameters include fecal and urinary digestive efficiency, efficiency of utilization of metabolizable energy, production (body growth), basal metabolism, and activity metabolism. Key assumptions and decisions drawn for each of these groups of parameters are briefly outlined as follows.

I used a fecal digestive efficiency of 0.90-0.96, and a urinary digestive efficiency of 0.90-0.93 for animals older than 1 year (Appendix 2; Keiver *et al.* 1984; Ronald *et al.* 1984; Fisher *et al.* 1992; Mårtensson *et al.* 1994; Lawson *et al.* 1997; Rosen and Trites 2000). This yields estimates of fecal and urinary digestive efficiency (E_{f+u}; Eq. 3.2) of 0.81-0.89 given that E_{f+u} is the product of fecal digestive efficiency and urinary digestive efficiency. Pup fecal and urinary digestive efficiency (which is metabolizable energy as a proportion of gross energy) ranged from 0.95-0.96 (Oftedal and Iverson 1987).

Table 3.2. Main bioenergetic parameter values (sources are in the text and Appendix 2).

Name	Symbol	Equation	Value	Details
fecal and urinary digestive efficiency	E_{f+u}	3.2	0.95-0.96	pup fecal and urinary
			0.90-0.96	non-pup fecal
			0.90-0.93	non-pup urinary
efficiency of utilization of metabolizable energy (1 – heat increment of feeding as proportion of metabolizable energy)	E_{HIF}	3.2	0.85-0.90	maintenance
			0.75-0.95	lipid deposition
			0.45-0.56	protein deposition
total energetic efficiency of energy deposition during gestation	substituted for E_{HIF}	3.2	0.20, 0.10-0.70	
total energetic efficiency of energy deposition during lactation	substituted for E_{HIF}	3.2	0.775, 0.60-0.95	
fetal mass	M	3.6-8	Eq. 3.7	male
			Eq. 3.8	female

Table 3.2 cont.

Name	Symbol	Equation	Value	Details
birth mass	M_b	3.6-8	22.4 ± 2.03 kg	male
			19.5 ± 1.80 kg	female
Postnatal mass	M	3.6	see Chapter 2 and text; Richards multipliers:	
			1.00 ± 0.20	males
			1.00 ± 0.16	females
Proportion of body growth that is lipid	p_{lip}	3.6	0.023 ± 0.0434	fetus
			1.0	newborn pup (first few weeks)
			0.07-0.14	adult
Proportion of body growth that is lean	p_{lean}	3.6	0.977 ± 0.0434	fetus
			0.0	newborn pup (first few weeks)
			0.86-0.93	adult
Proportion of lean body growth that is water	p_w	3.6	0.742 ± 0.033	fetus
			0.66-0.73	postnatal

Table 3.2 cont.

Name	Symbol	Equation	Value	Details
Proportion of energy deposited during gestation represented by fetus			0.80	
basal metabolism	*BM*	3.2, 3.9	2.5-3.5 × Eq. 3.9	newborn
			1.75-2.25 × Eq. 3.9	1 year of age
			Eq. 3.9	>8 years old
Proportion of time spent on land	*land*	3.10	1.0	0 – 1 month old
			0.435, 0.24-0.63	immature (>1 year old)
			1.0	mature female: 12-22 June
			0.60, 0.53-0.67	mature female: 23 June
			0.30, 0.23-0.37	mature female: 26 July
			0.185, 0.10-0.27	mature female: 1 November – 11 June
			1.0	mature male: 29 May-10 July
			0.30, 0.15-0.45	mature male: rest of year

Table 3.2 cont.

Name	Symbol	Equation	Value	Details
Proportion of time spent in the water	$water$	3.10	0.0	0 – 1 month old
			0.565, 0.37-0.76	immature (>1 year old)
			0.0	mature female: 12-22 June
			0.40, 0.33-0.47	mature female: 23 June
			0.70, 0.63-0.77	mature female: 26 July
			0.815, 0.73-0.90	mature female: 1 November – 11 June
			0.0	mature male: 29 May-10 July
			0.70, 0.55-0.85	mature male: rest of year
land metabolic rate multiplier	A_{land}	3.10	3, 2.5-3.5	breeding males
			1.2, 1.0-1.4	all other animals
water metabolic rate multiplier	A_{water}	3.10	4.0, 2.5-5.5	all animals

The efficiency of utilization of metabolizable energy (E_{HIF}; Eq. 3.2) equals 1 minus the heat increment of feeding as a proportion of metabolizable energy intake (Appendix 2). Heat increment of feeding equaled 0.10-0.15 (E_{HIF} = 0.85-0.90) for maintenance energy requirements and 0.05-0.25 (E_{HIF} = 0.75-0.95) and 0.44-0.55 (E_{HIF} = 0.45-0.56) for fat and protein growth energy requirements respectively (Ashwell-Erickson and Elsner 1981; Gallivan and Ronald 1981; Webster 1983; Blaxter 1989; Markussen *et al.* 1994; Rosen and Trites 1997). For pregnancy and lactation energy deposition requirements (fetus, placenta, uterine tissue, and milk), I used total energetic efficiencies of 0.20, 0.10-0.70 for gestation and 0.775, 0.60-0.95 for lactation (Appendix 2; Oftedal 1985; Blaxter 1989; Robbins 1993).

Production (P; Eq. 3.2) is mainly growth in body mass and was calculated as the amount of energy invested in body mass (P_t) per day:

[3.6] $$P_t = \Delta M * [\, p_{lip} * ED_{lip} + p_{lean} * (1 - p_w) * ED_{pro}\,]$$

where ΔM is the daily body mass growth increment, p_{lip} is the proportion of new body mass that is lipid, ED_{lip} is the energetic density of lipid (39330 kJ kg^{-1}; Schmidt-Nielsen 1990), p_{lean} is the proportion of new body mass that is lean tissue, p_w is the proportion of lean tissue that is water, and ED_{pro} is the energetic density of protein (17991 kJ kg^{-1}; Schmidt-Nielsen 1990). The sum of p_{lip} and p_{lean} was 1.

Body mass (M in kg) of fetuses was calculated from the following equations:

[3.7] $$M_t = \frac{(M_b/0.936)}{\left(1 + e^{-13.256(t-0.502)}\right)}$$ for males

and

[3.8] $$M_t = \frac{\left(M_b/0.952\right)}{\left(1+e^{-13.916(t-0.49)}\right)}$$ for females

where t is age in years (0 = implantation, assumed to be 15 October), and M_b is birth mass (Appendix 2). By setting the asymptote of these models as a multiple of birth mass, it allowed me to incorporate uncertainty in fetal mass through uncertainty in birth mass. This assumed the pattern of fetal growth (or shape of the growth curve) was independent of birth mass. I used birth masses of 22.4 ± 2.03 kg for males and 19.5 ± 1.80 kg for females (E. Brandon, pers. comm.).

Mass of animals from one to two years of age was calculated using the male and non-pregnant female Richards growth models developed in Chapter 2. Uncertainty was incorporated into the Richards growth models by using gross multipliers of 1 ± 0.20 for males and 1 ± 0.16 for females (Appendix 2). Changes in mass between birth and 1 year of age were assumed to be linear. The mass of animals older than two years of age was calculated at one year intervals using the Richards growth models. I then assumed that all growth occurred during a seasonal growth period during which time, growth was linear (Chapter 2). I assumed the seasonal growth period started between 1 August and 15 September and ended between 1 March and 15 April (uniform sampling distributions).

The composition of fetal tissue growth (p_{lip}, p_{lean}, and p_w) was assumed to be the same as newborn Steller sea lion body composition: $p_{lip} = 0.023 \pm 0.0434$, $p_{lean} = 0.977 \pm 0.0434$, and $p_w = 0.742 \pm 0.033$ (E. Brandon, pers. comm.). After parturition, growth was assumed to be entirely lipid ($p_{lip} = 1.0$), until body composition reached adult proportions of lipid and lean tissue. After this point, the composition of growth was assumed to be the same as adult body composition: p_{lip} = 0.07-0.14, p_{lean} = 0.86-0.93, and p_w = 0.66-0.73 (Olesiuk and Bigg 1987; Davis *et al.* 1996; Pitcher and Calkins in press).

A second component of P (Eq. 3.2) is growth of the placenta and uterus of pregnant females. I assumed that the fetus represented 80% of the energy retained by the gravid uterus and that the other 20% was uterine tissue, placenta, etc. (Oftedal 1985; Robbins 1993). I also assumed the additional uterine energy was deposited linearly over the gestation period.

Basal metabolism (BM in kJ d^{-1}; Eq. 3.2) of animals older than 8 years was calculated from the equation:

[3.9] $$BM = 292.88M^{0.75}$$

where M is body mass in kg (Kleiber 1975). I assumed basal metabolic rate declined linearly from birth (2.5-3.5 × Eq. 3.9) to 1 year of age (1.75-2.25 × Eq. 3.9), and from 1 year to 8 years of age (Rosen and Trites 1997, D. Rosen unpubl. data).

The energetic cost of activity was incorporated using a multiplier of basal metabolic rate (A; Eq. 3.2) for each sex, sexual status (immature or mature), and day of the year according to:

[3.10] $$A = land * A_{land} + water * A_{water}$$

where *land* is the proportion of time spent on land, A_{land} is a multiplier of basal metabolic rate for land, *water* is the proportion of time spent in the water, and A_{water} is a multiplier of basal metabolic rate for water. The sum of the proportion of time on land and in the water is 1.

I effectively assumed that active metabolic rate was proportional to body mass$^{0.75}$ by assuming active metabolism was a constant multiple of basal metabolic rate. Active metabolism is the energy that organisms expend to overcome forces (e.g., drag when swimming). It is also a function of the distance travelled and the time to cover that distance (speed). Thus, active metabolic rate is a product of many factors such as foraging behaviour and the distance to feeding areas. In homeotherms, the rate of energy expenditure may also be related to the need to generate heat through activity to maintain body temperature (thermoregulation). Each of these factors scale with body mass in different ways. The question is what is the scaling exponent between active metabolic rate and body mass when all these factors are combined.

Nagy (1987) found that, interspecifically, field metabolic rate (total metabolism) scaled with body mass to the power of 0.8 which is very close to 0.75 (the scaling factor for basal metabolic rate). For the sake of simplicity, I assumed active metabolic rate was a constant multiple of basal metabolic rate (i.e., active metabolic rate scaled with body mass$^{0.75}$). Several other recent marine mammal bioenergetic models have also assumed that active metabolic rate is a constant multiple of basal metabolic rate (Olesiuk 1993; Mohn and Bowen 1996; Stenson et al. 1997). Note, however, that estimates of mass specific energy requirements will be overestimated for younger animals relative to older, larger animals if active metabolic rate, in fact, scales with body mass to a power greater than 0.75.

Conversely, if active metabolic rate scales with body mass to a power less than 0.75 then the energy requirements of younger animals relative to older animals will be underestimated.

Immature animals, older than 1 year, spent a constant mean proportion of their time at sea throughout the year (*water* = 0.565, 0.37-0.76) (Merrick and Loughlin 1997; Swain and Calkins 1997; Trites and Porter in review). I also assumed that pups less than 1 month old spent all of their time on land (*water* = 0) (Scheffer 1945), and that the mean percentage of time spent at sea increased linearly from 1 month to 1 year of age. The proportion of time pups spent at sea each day was then described by a triangular distribution with an increasing median and upper and lower limits equal to ±35% of the median (which corresponds to the limits of the immature sampling distribution as a percentage of the immature median).

I assumed mature females were entirely on land from 12 June to 22 June: the perinatal period (*water* = 0) (Gentry 1970; Higgins *et al.* 1988; Milette 1999). Starting on the first day of foraging trips (23 June), mature females spent 0.40, 0.33-0.47 of their time at sea (*water*). This proportion increased linearly to 0.70, 0.63-0.77 on 26 July (Higgins *et al.* 1988; Swain 1996; Merrick and Loughlin 1997; Milette 1999). It then increased linearly from this point to 0.815, 0.73-0.90 on 1 November (Swain 1996; Merrick and Loughlin 1997; Trites and Porter in review). Mature females continued to spend this proportion of time at sea through to the next breeding season.

I assumed mature males were entirely on land from 29 May to 10 July while holding breeding territories (*water* = 0) (Gentry 1970). For the rest of the year, I assumed mature males spent a constant mean proportion of their time at sea each day (*water* = 0.70, 0.55-0.85).

I used a land multiplier of basal metabolic rate (A_{land}) of 1.2, 1.0-1.4 for all animals except breeding males on territories (Ashwell-Erickson and Elsner 1981; Worthy 1987b). For breeding males I used A_{land} = 3, 2.5-3.5 (Anderson and Fedak 1987a; Boyd and Duck 1991). I used a water multiplier of basal metabolic rate (A_{water}) of 4.0, 2.5-5.5 for all animals (Costa and Gentry 1986; Costa *et al.* 1989; Reilly and Fedak 1991; Castellini *et al.* 1992; Hindell *et al.* 1992; Arnould and Boyd 1996, R. Andrews unpubl. data).

Population

Rates of survival (*s*; Eq. 3.3), female maturity (*mat*; Eq. 3.4) and fecundity (*fec*; Eq. 3.4) were taken from life tables by Trites and Larkin (1992) and York (1994) (Table 3.3). Median female annual survival rates were multiplied by 1.017 to obtain a finite rate of population increase (λ) of 1.0 (population neither increasing or decreasing). In order to incorporate uncertainty, annual survival rates were then sampled from uniform distributions with upper and lower limits equal to the medians ± 0.05. The fecundity rate used was 0.53-0.73 pups/female per year. Maturity rates of females aged 3-5 years were sampled from uniform distributions with upper and lower limits equal to the

Table 3.3. Median annual survival (*s*, Eq. 3.3) and maturity (*mat*, Eq. 3.4) rates for Steller sea lions by sex and age. Survival rates and female maturity rates are from life tables by Trites and Larkin (1992) and York (1994). Female survival rates were multiplied by 1.017 to obtain a finite rate of population increase (λ) of 1.0. Male maturity rates were estimated from Pitcher and Calkins (1981).

Age	Probability of Survival to Next Age		Proportion Mature at Age	
	Male	Female	Male	Female
0	0.520	0.671	0	0
1	0.650	0.824	0	0
2	0.780	0.915	0	0
3	0.860	0.946	0.2	0.321
4	0.870	0.924	0.4	0.57
5	0.850	0.910	0.6	0.83
6	0.831	0.899	0.8	1
7	0.814	0.890	1	1
8	0.798	0.882	1	1
9	0.782	0.874	1	1
10	0.768	0.867	1	1
11	0.754	0.861	1	1
12	0.740	0.855	1	1
13	0.727	0.850	1	1
14	0	0.845	1	1
15		0.841		1
16		0.836		1
17		0.832		1
18		0.828		1
19		0.824		1
20		0.821		1
21		0.817		1
22		0		1

medians ± 0.1. I assumed the earliest age of male sexual maturity was 3 years (median of 20% mature at 3) and that the proportion of males which were sexually mature increased linearly with age so that all males were mature by 7 years of age (Pitcher and Calkins 1981) (Table 3.3). Maturity rates of males aged 3-6 years were sampled from uniform distributions with upper and lower limits equal to the medians ± 0.1. Male and female longevity were assumed to be 14 and 22 years respectively (Trites and Pauly 1998). I assumed the sex ratio at birth was 1:1. This life table model (median values) produced a population sex ratio of 1.98 females per male and a ratio of 0.205 pups per adult during the breeding season (17% of population was pups).

Total breeding season population size in each area was estimated using pup count data from the U.S. National Marine Fisheries Service and Alaska Department of Fish and Game surveys done in June and July 1998 (Table 3.4) (Sease and Loughlin 1999). I assumed that the actual number of pups born could have been as much as 10% greater than the number counted due to pups being hidden during the surveys, pup mortality before the survey dates, and births after the survey dates (Trites and Larkin 1996). I also assumed that pups represented 17% of the total population size based on the life table model. Thus,

$$[3.11] \quad Total\ \ population = \frac{1.10 \times pups\ counted}{0.17}$$

In order to incorporate uncertainty, population sizes were randomly sampled from uniform distributions with upper and lower limits equal to ±10% of the total population size estimates in Table 3.4.

Table 3.4. Number of Steller sea lions counted on rookeries in Alaska in 1998 (Sease and Loughlin 1999) and total breeding season population size estimates obtained using Eq. 3.11. Areas are defined in Fig. 3.1.

Area	Number of Rookeries	Geographic Range	Number Counted			Estimated Median Total Breeding Season Population Size
			Non-Pups	Pups	Total	
Southeast Alaska	3	Forrester – White Sisters	6608	4234	10842	27394
Gulf of Alaska	9	Seal Rocks – Chernabura	4751	2971	7722	19222
Eastern Aleutian Islands	6	Pinnacle Rock – Akutan	3806	2340	6146	15140
Central Aleutian Islands 1	8	Bogoslof – Kasatochi	1946	1297	3243	8392
Central Aleutian Islands 2	8	Adak – Ayugadak	2907	1729	4636	11187
Central Aleutian Islands 3	3	Kiska – Buldir	845	355	1200	2297
Western Aleutian Islands	3	Agattu – Attu	1892	681	2573	4406
All	40	Forrester – Attu	22755	13607	36362	88038

Diet

The median proportion of biomass that each prey species category represented in the diet ($prey_i$; Eq. 3.5) is shown for each region in Table 3.5 and discussed in detail in Appendix 3. In order to incorporate uncertainty associated with these estimates, $prey_i$ were randomly sampled from triangular distributions with medians from Table 3.5 and upper and lower limits equal to ±20% of the medians. These proportions were then standardized so that they summed to 1 for a given diet. Lacking seasonal diet information, I set diet composition to be constant year-round from the western Aleutian Islands to the Gulf of Alaska (Table 3.5). But data were available to set two diet compositions for Southeast Alaska: a 'summer' diet commencing between 1 December and 31 May and a 'winter' diet commencing sometime between 1 August and 30 September (uniform distributions). I assumed the same diet composition for both sexes and all ages.

The energetic density of each diet (ED_{diet}; Eq. 3.5) was calculated from:

$$[3.12] \quad ED_{diet} = \sum_{i=1}^{7} prey_i ED_{prey_i}$$

where $ED_{prey,i}$ is the energetic density of prey species category i. The energetic densities of the seven prey categories are shown in Table 3.6 and discussed in detail in Appendix 3. For all prey categories, except small schooling fish, I assumed one energetic density for the entire year. For small schooling fish I assumed different summer and winter energetic densities, corresponding in time with the dates of the Southeast Alaska diet composition.

Table 3.5. Diet composition (median percent biomass contribution of each prey species category in the diet; $prey_i$, Eq. 3.5) of Steller sea lions in Alaska. Gulf of Alaska to western Aleutian Islands values are based on split-sample frequency of occurrence data from Merrick *et al*. (1997), and Southeast Alaska values are based on split-sample frequency of occurrence data from Trites and Calkins (unpubl. data) (Appendix 3). Prey categories are defined in Table 3.1 and areas are defined in Fig. 3.1.

Area	Prey Category						
	Gadids	Pacific Salmon	Small Schooling Fish	Flatfish	Other Demersal Fish	Atka Mackerel	Cephalopods
Southeast Alaska							
Summer	31.0	19.4	23.2	10.2	14.6	0.0	1.6
Winter	57.3	6.2	16.6	10.5	2.0	0.0	7.3
Gulf of Alaska	66.5	20.3	6.1	3.9	0.0	0.3	2.9
Eastern Aleutian Islands	32.9	17.3	7.7	1.8	7.3	30.7	2.3
Central Aleutian Islands 1	40.2	21.8	3.3	0.0	5.4	29.4	0.0
Central Aleutian Islands 2	9.7	4.7	0.0	0.0	2.2	69.7	13.7
Central Aleutian Islands 3	3.2	0.5	0.0	0.0	4.9	84.2	7.1
Western Aleutian Islands	6.9	4.6	0.0	0.0	4.6	77.3	6.7

Table 3.6. Energetic density of prey categories ($ED_{prey,i}$, Eq. 3.12). Prey categories are defined in Table 3.1 and sources are in Appendix 3.

Prey Category	Energetic Density (kJ g^{-1})
Gadids	4.0, 3.0 – 5.0
Pacific Salmon	5.0 – 9.0
Small Schooling Fish	summer: 8.5, 6.0 – 11.0
	winter: 5.0, 4.0 – 6.0
Flatfish	3.0 – 5.0
Other Demersal Fish	3.0 – 6.0
Atka Mackerel	3.0 – 6.0
Cephalopods	4.0 – 6.0

Results

Daily Individual Energy/Food Requirements

Daily energy requirements (per individual) varied throughout the year, due primarily to changes in activity budgets (proportion of time spent on land and in the water) (Fig. 3.2). Pups exhibited an initial drop in daily energy requirement following the period of rapid lipid deposition, and a gradual increase thereafter as they grew in size and spent progressively more time in the water. The minimum daily energy requirements of nursing were 29.3 ± 4.83 MJ for male pups and 24.6 ± 4.00 MJ for female pups (2 weeks after parturition), while the maximum daily energy requirements were 117 ± 29.2 MJ and 90.4 ± 20.7 MJ respectively (just prior to weaning). Near the end of a pup's first year of life, the energy required by a 10 year old to nurse a pup was approximately equal to her own energy requirement. In other words, a 10 year old female nursing a pup in the spring had to consume twice as much energy as a female of the same age without a pup.

Immature animals exhibited little change in daily energy requirement throughout the year given that they were assumed to spend a constant proportion of time in the water. A slight increase in energy needs occurred during the fall to spring growth period, but the difference between the minimum and maximum daily energy requirements for immature, 3 year olds was only 14% for males and 7% for females (late July: males – 93.2 ± 21.5 MJ, females – 81.5 ± 16.6 MJ; early March: males – 107 ± 24.0 MJ, females – 87.3 ± 17.7 MJ). This suggests the amount of energy they required for growth was small relative to their total energy requirement.

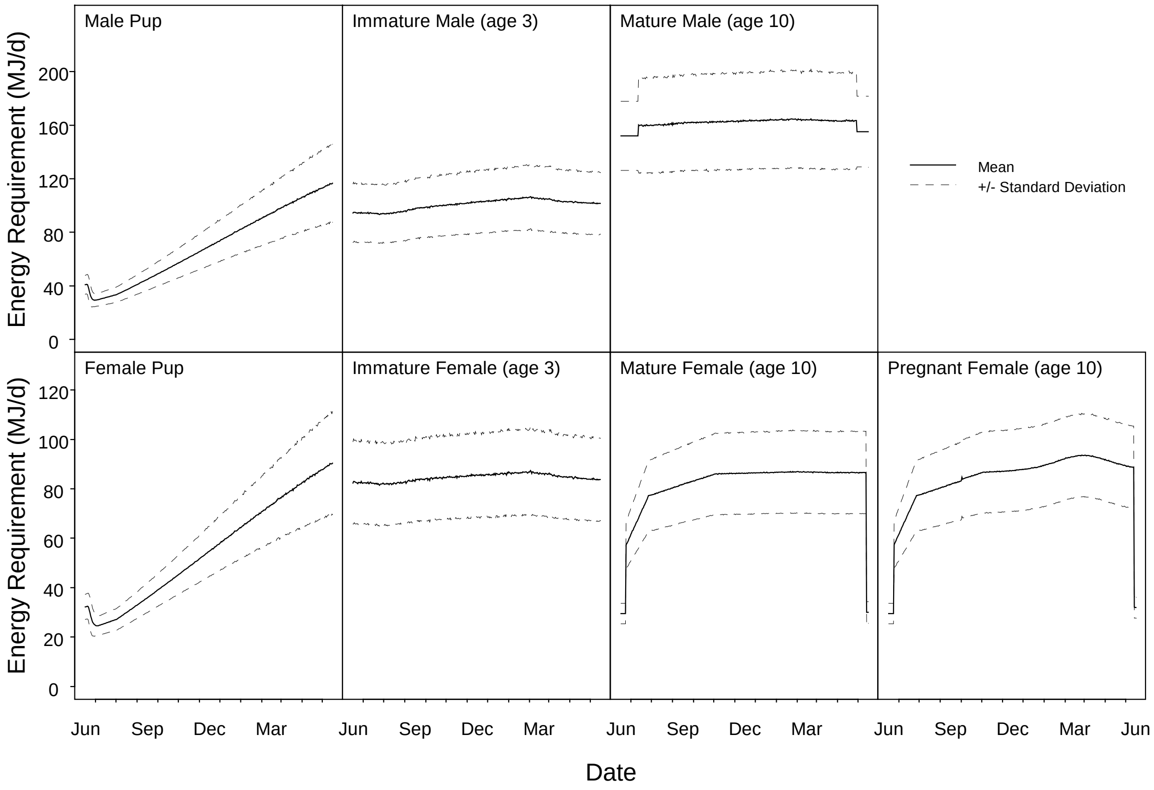


Figure 3.2. Individual energy requirements by day of the year. Pup energy requirements represent the amount of energy a female would require to support a pup. Standard deviations were obtained using Monte Carlo simulations (1000 runs). Note: these are plots of energy requirements, not energy consumption. For example, mature males do not consume energy during the breeding season fast.

Mature males also exhibited little variation in energy requirement throughout the year (maximum for a 10 year old male: 165 ± 36.5 MJ/d). The most substantial change was a drop in energy requirement during the breeding season while they were maintaining territories (minimum for a 10 year old: 152 ± 25.8 MJ/d).

The daily energy requirement of mature females was more variable than males, due to their more variable activity budget. It increased from the breeding season through November as the mature females spent progressively more time in the water, and then remained relatively constant until the following breeding season. During the breeding season, mature female energy requirements were low while primarily on land (minimum for a 10 year old: 29.5 ± 4.16 MJ/d). Pregnant females required additional energy for gestation. The additional daily energy requirement was greatest from mid-February to early May when fetal growth was maximum. However, the peak daily energy requirement (late March) for pregnant 10 year olds (93.6 ± 16.9 MJ) was only 8% greater than the daily energy requirement of non-pregnant 10 year olds at the same time of year (86.9 ± 16.7 MJ). This suggests the energetic cost of gestation is small relative to total female energy requirements.

Daily food requirements (per individual) essentially tracked daily energy requirements for all regions between the Gulf of Alaska and the western Aleutian Islands. This was because diet compositions were assumed to be constant year-round in these regions. Although the amount of food required per unit energy was higher in the fall and winter than at other times of the year due to changes in the energetic density of small schooling fishes, the difference was relatively small. For example, in the eastern Aleutians, where the contribution of small schooling fishes to the diet was highest (excluding Southeast Alaska), the amount of food required per unit energy was only 6% greater in early November than in late July for a 14 year old male.

For Southeast Alaska, daily food requirements (per individual) did not always track daily energy requirements (i.e., compare Figs. 3.2 and 3.3). In other words, the amount of food required per unit energy changed throughout the year due to changes in diet composition. The summer diet had a lower proportion of gadids, and higher proportions of Pacific salmon and small schooling fish that resulted in a higher energetic density than the winter diet. As a result, less food biomass was required to meet energetic demands during the summer than in the winter.

For nursing pups, this seasonal diet change resulted in an asymptotic increase in maternal food requirements throughout their first year. During the first few months, food requirements increased concurrent with an increase in energy requirements and a decrease in the energetic density of the diet (summer to winter). As a pup approached the end of its first year of life (spring), the mother required less food per unit energy because the energetic content of the diet increased (back to the summer diet). This caused the daily food requirements to level out. At the beginning of June, a pregnant, 10 year old female (in Southeast Alaska) nursing an 11 month old pup needed to consume

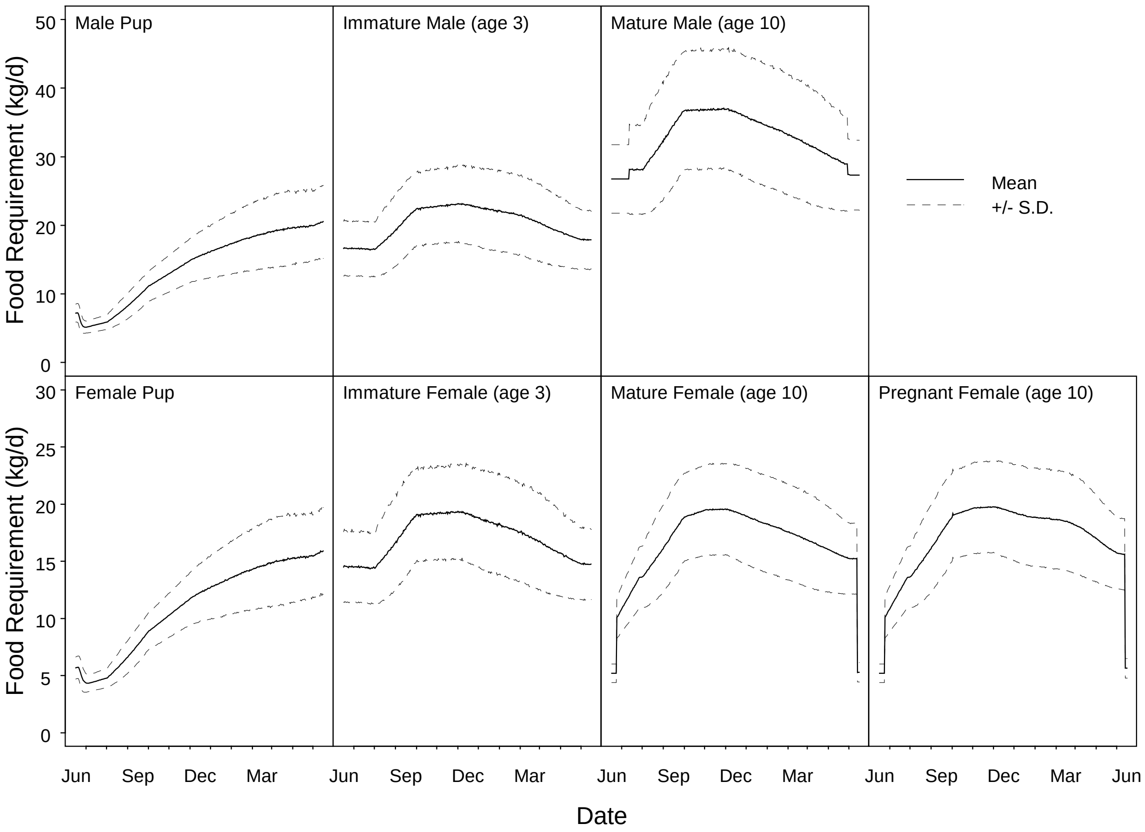


Figure 3.3. Individual food biomass requirements by day of the year for the Southeast Alaska region. Pup food requirements represent the amount of food a female would require to support a pup. Standard deviations were obtained using Monte Carlo simulations (1000 runs). Note: these are plots of food requirements, not food consumption. For example, mature males do not consume food during the breeding season fast.

15.7 ± 3.12 kg of food per day of food for herself and an additional 15.5 ± 3.65 kg d^{-1} to nourish a female pup or 19.9 ± 5.14 kg d^{-1} for a male pup.

For all non-pups (Southeast Alaska), the seasonal diet change resulted in a similar pattern of daily food requirements throughout the year. In general, daily food requirements were highest in October and November and lowest in July and August corresponding to the ‘winter’ and ‘summer’ diet composition periods respectively. The diet change obscured most of the effects of changing daily energy requirements on daily food requirements. The maximum daily food requirements (Southeast Alaska) occurred in late October and early November when immature, 3 year old males and females required 23.2 ± 5.60 kg and 19.4 ± 4.11 kg respectively, and mature, 10 year old males and females required 37.1 ± 8.67 kg and 19.6 ± 3.96 kg respectively. The maximum daily food requirement for a pregnant, 10 year old female nursing a pup was 33 – 37 kg (late March).

Mean daily food requirements increased for males and females from 1 to 3 years of age (Fig. 3.4). These increases were due to increasing maintenance and activity costs associated with rapidly increasing body size. Males continued to grow rapidly up to about 9 years of age with concurrent increases in food requirements. Daily food requirements beyond the age of 10 years were relatively constant from one year to the next.

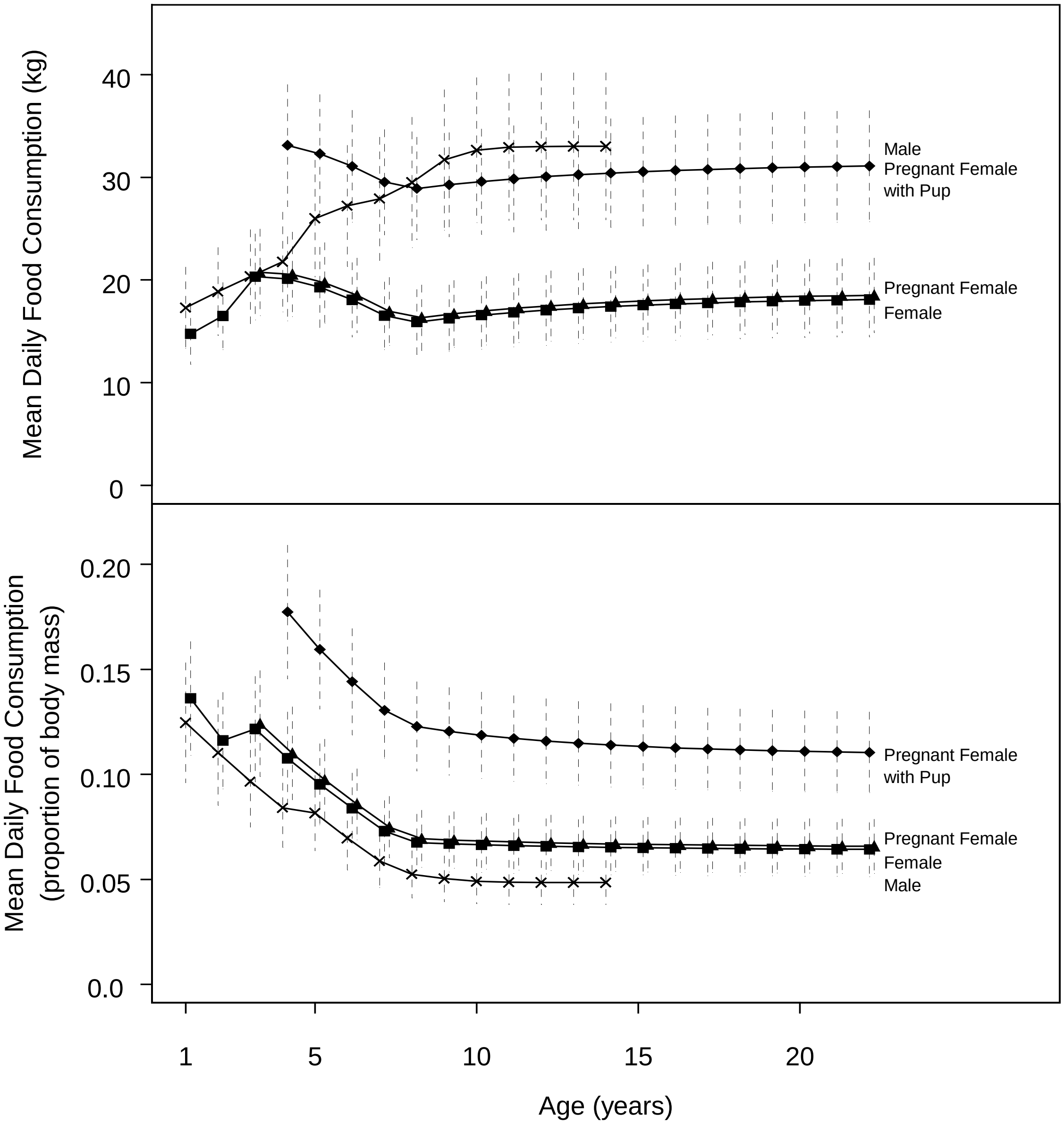


Figure 3.4. Mean daily individual food biomass requirements (top) and mean daily individual food biomass requirements as a proportion of body mass (bottom) by age for the Southeast Alaska region. For the purpose of this figure, it was assumed males and females mature at 3 and 5 years of age respectively. Error bars represent ± 1 *S.D.* (obtained using Monte Carlo simulations – 1000 runs). For the bottom panel, average body masses for each year of life were used.

In contrast to the male pattern, mean female daily food requirements declined from ages 3 to 8, afterwhich they increased gradually through the end of the female lifespan. The decrease in mean daily food requirement during the first few years of maturity was due to a decreasing basal metabolic rate (and therefore activity metabolic rate). In the model, basal metabolic rate was elevated for animals less than 8 years old, and decreased with age. By age 4, female growth rate had declined substantially, so increasing body size had a relatively smaller effect than the decreasing basal metabolic rate. However, the body size effect obscured the effect of basal metabolic rate for males that grew rapidly during this time. The gradual increase in mean female daily food requirements after age 8 was due to a gradual increase in body size, as females continue to grow throughout their lives. The mean daily food requirement of pregnant females was only marginally greater than the mean daily food requirement of non-pregnant females of the same age. But the mean daily food requirement for females with pups was about 70% greater than females of the same age without pups.

Mean daily food requirements, when expressed as a proportion of body mass, generally decreased with age for males and females, especially for animals less than 8 years old (Fig. 3.4). This was due to the relationship between body size and basal metabolism (Eq. 3.9, and see text). Smaller animals required more energy (and therefore food) for metabolism per unit body mass than larger animals. The only exception to this trend was an increase in food requirements per unit body mass from ages 2 to 3 for females (the assumed period of maturation for females in Fig. 3.4). Changes in the activity budget with maturity (increased time in the water) resulted in an increase in the amount of food required per unit body mass. With males, maturity (assumed to be from ages 4 to 5 in Fig. 3.4) slowed the rate of decrease in mean daily food requirements with age due to an increase in the amount time spent in the water. Food requirements per unit body mass were relatively constant with age beyond 8 years. The maximum mean daily food requirements (as a proportion of body mass) for the Southeast Alaska population were 0.12 ± 0.03 (*S.D.*) for males (age 1), 0.14 ± 0.03 for females (age 1), and 0.18 ± 0.03 for pregnant females (age 4) with pups. The minimum mean daily food requirements (as a proportion of body mass) were 0.05 ± 0.01, 0.06 ± 0.01, and 0.11 ± 0.02 for males (age 14), females (age 22), and pregnant females with pups (age 22) respectively.

Annual Population Food Requirements

Annual food requirements for the entire population are shown for Southeast Alaska by sex and age class (Fig. 3.5). Despite differences in diet and population size among the regions of Alaska, the general patterns of population food requirements with age were similar for all regions since population structure (age composition, maturity and reproductive rates) was assumed to be the same for all regions. The model shows that the annual population food requirements of males decreased with age (Fig. 3.5) due to the male survival schedule (Table 3.3). In each age class, there were fewer individuals than in the previous age class, resulting in decreased food requirements. Although individual male food requirements increased with age (Fig. 3.4), the relatively high mortality rates obscured this effect at the population level.

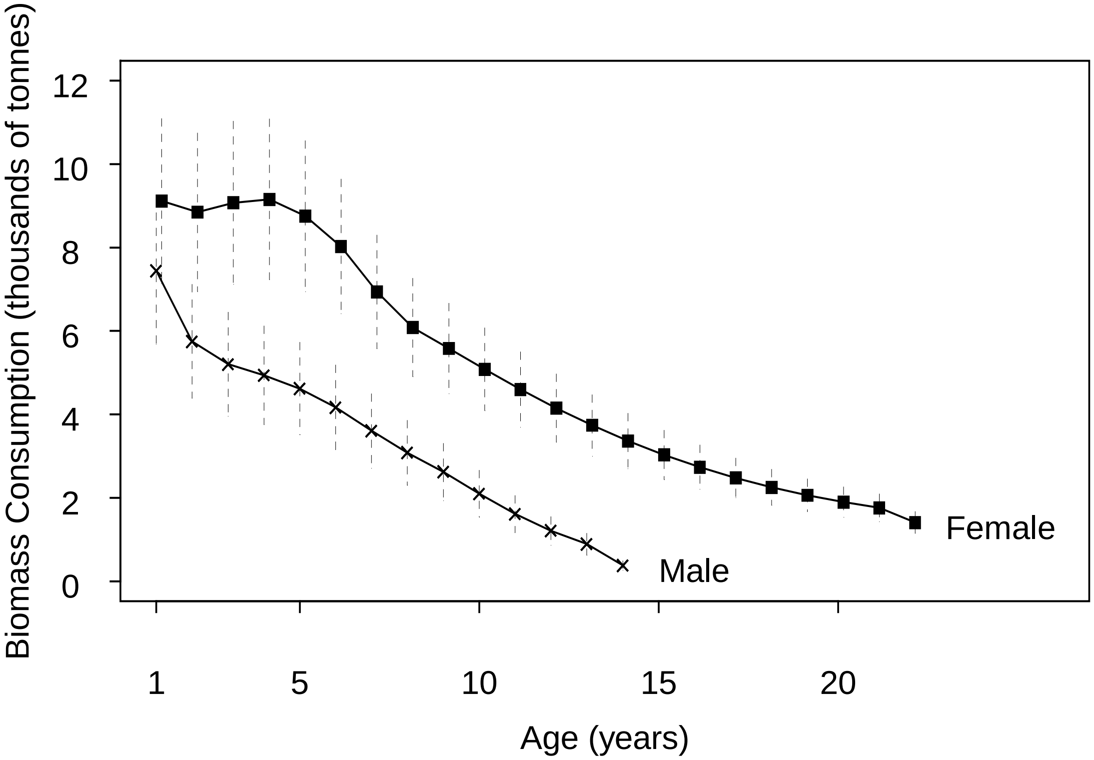


Figure 3.5. Annual population food biomass consumption by sex and age class for the Southeast Alaska region. Error bars represent ± 1 *S.D.* (obtained using Monte Carlo simulations – 1000 runs).

Annual food requirements for the female population dropped from ages 1 to 2, and increased from ages 2 to 4 (Fig. 3.5). The initial drop reflects the relatively high mortality of young animals, while the subsequent rise reflects the maturation of females through ages 3 and 4 (Table 3.3). Mature females and females with pups have higher food requirements than immature females. Thus, the food requirements of age classes 3 and 4 increased as the proportion of females that were mature/with pups increased. Individual female food requirements (excluding reproduction) also increased from ages 2 to 4 (Fig. 3.4) reinforcing this trend in population food requirements. Beyond the age of 4, food requirements drop in parallel with the survival schedule.

Total annual population food requirements varied among regions, as expected, due to differences in diet and population size. The Southeast Alaska population consumed the most prey biomass on an annual basis ($1.58\times10^5 \pm 2.91\times10^4$ tonnes) and the central Aleutian Islands 3 population consumed the least ($1.48\times10^4 \pm 3.10\times10^3$ tonnes) (Fig. 3.6). The coefficient of variation for total annual population food biomass requirements ranged between 18% (Southeast Alaska – eastern Aleutians) and 21% (central Aleutians 3) (Table 3.7). The mean annual food requirement per individual alive during the breeding season ranged from 5763 ± 1061 kg (Southeast Alaska) to 6455 ± 1349 kg (central Aleutians 3): a 12% difference (Table 3.7). The Steller sea lion population from Southeast Alaska through the central Aleutians 1 consumed less biomass per individual alive during the breeding season on an annual basis than did Steller sea lions from the central Aleutians 2 through the western Aleutians. This trend was due to a higher proportion of more energetic prey species (Pacific salmon, small schooling fish) in

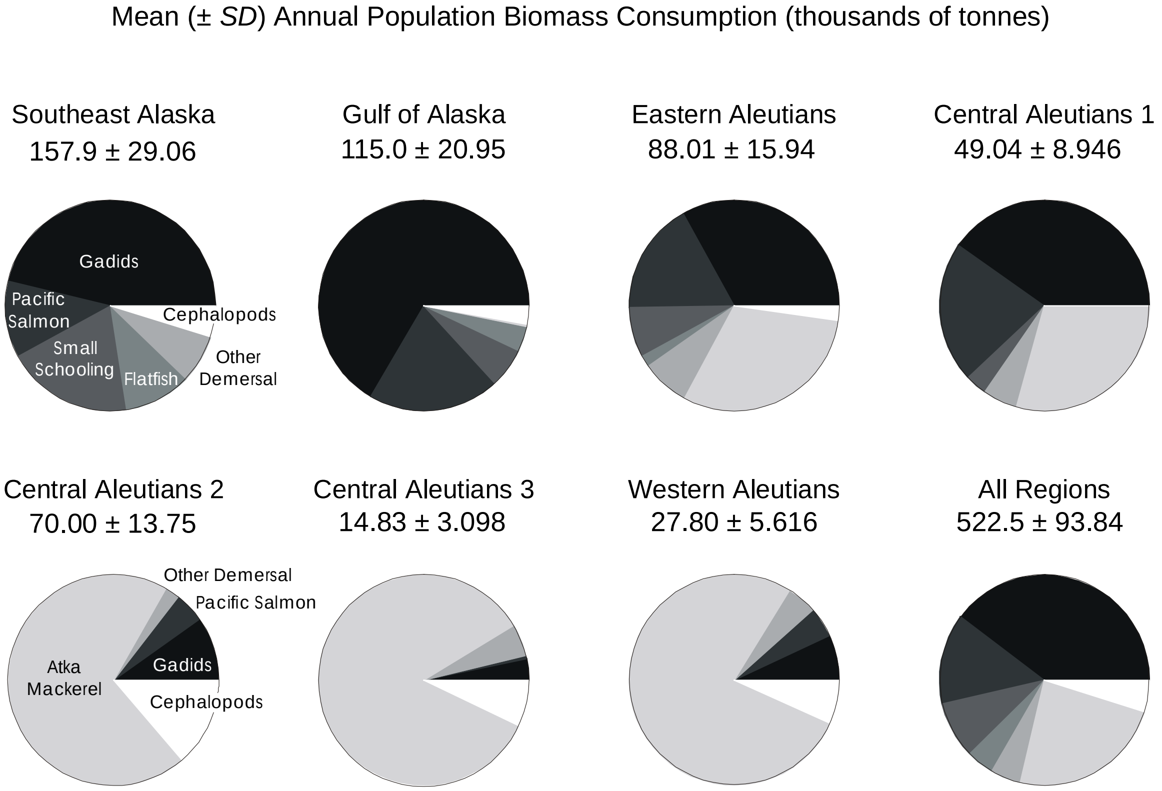


Figure 3.6. Total annual population food biomass requirements and mean diet composition (proportional contribution of each species to the diet by biomass) for the seven regions of Alaska (as defined in Fig. 3.1). Standard deviations were obtained using Monte Carlo simulations (1000 runs).

Table 3.7. Annual population food biomass consumption by region of Alaska. Standard deviations were obtained using Monte Carlo simulations (1000 runs).

Area	Population Consumption (thousands of tonnes)			Consumption per individual alive during the breeding season (kg)	
	Mean	*S.D.*	*C.V.*	Mean	*S.D.*
Southeast Alaska	157.9	29.1	0.18	5763	1061
Gulf of Alaska	115.0	21.0	0.18	5982	1090
Eastern Aleutian Islands	88.0	15.9	0.18	5813	1053
Central Aleutian Islands 1	49.0	8.95	0.18	5843	1066
Central Aleutian Islands 2	70.0	13.7	0.20	6257	1229
Central Aleutian Islands 3	14.8	3.10	0.21	6455	1349
Western Aleutian Islands	27.8	5.62	0.20	6310	1275

the diet of Steller sea lions from Southeast Alaska through the central Aleutians 1 (Table 3.5, Fig. 3.6). The greatest annual biomass consumption of a single prey species category among all areas was $7.64\times10^4 \pm 1.42\times10^4$ tonnes of gadids in the Gulf of Alaska (Fig. 3.7). Gadids were consumed in a similar amount in Southeast Alaska ($7.29\times10^4 \pm 1.66\times10^4$ tonnes). The second ranked prey species category for biomass consumption was Atka mackerel, of which the central Aleutian Islands 2 population consumed the greatest amount ($4.87\times10^4 \pm 9.62\times10^3$ tonnes).

Sensitivity Analysis

The sensitivity analysis was conducted on the model describing the Southeast Alaska region. Patterns of sensitivity would have been similar among regions. Of the three main parameter groups (bioenergetics, diet, population), annual population food requirement estimates were most sensitive to the uncertainty in bioenergetic parameters, with a resulting *C.V.* of 16% (Fig. 3.8, Table 3.8). Uncertainty in diet and population parameters had much smaller effects on variability of the estimates (*C.V.* = 6%). When uncertainty was incorporated in all three main parameter groups, the resulting distribution of annual population food requirement estimates was positively skewed and significantly different from normal ($p<0.001$) (Table 3.8). Thus, the distributions of all food requirement estimates produced by my model tended to be positively skewed due to the multiplicative relationships between some model parameters. Only incorporating uncertainty in population parameters resulted in platykurtosis due to the dominant effect of error in total population size which was sampled from a uniform distribution.

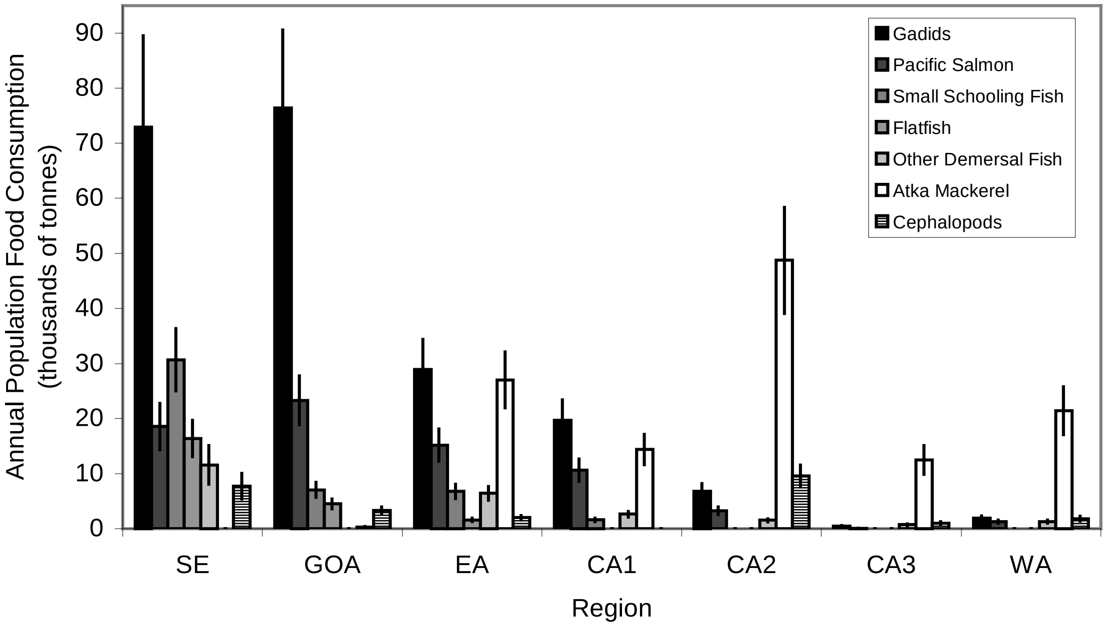


Figure 3.7. Total annual population food biomass requirements by prey species for the seven regions of Alaska (as defined in Fig. 3.1). Error bars represent ± 1 *S.D.* (obtained using Monte Carlo simulations – 1000 runs).

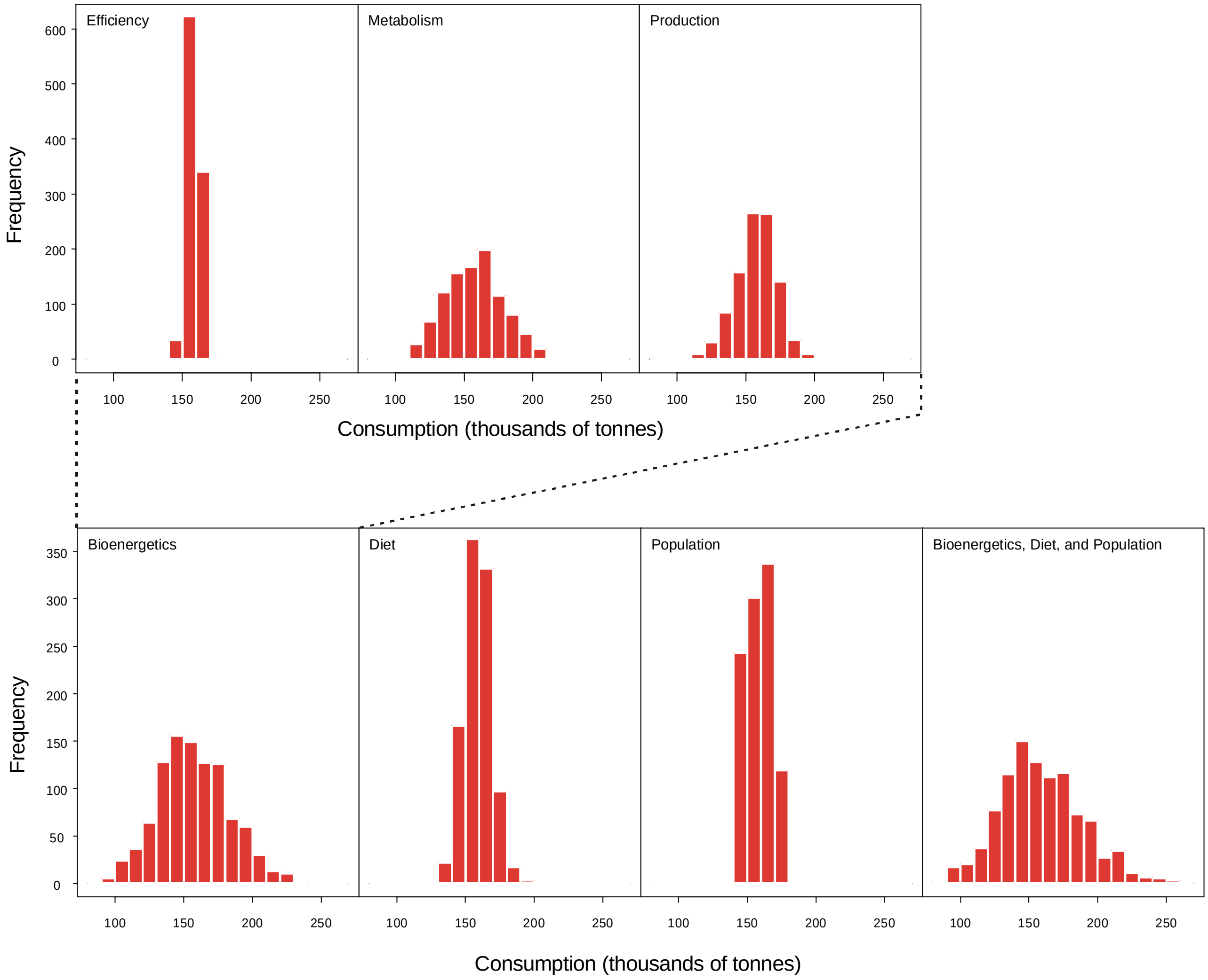


Figure 3.8. Sensitivity analysis results. Total annual population food biomass requirement estimates for the Southeast Alaska region obtained using Monte Carlo simulations (1000 runs) incorporating the indicated sources of parameter uncertainty.

Table 3.8. Sensitivity analysis of total annual population food biomass requirement estimates for the Southeast Alaska region. Analysis was performed using Monte Carlo simulation (1000 runs). p-value is from Kolmogorov-Smirnov goodness of fit test for normality (S-Plus for Windows 3.3). A significant p-value (e.g., <0.05) indicates that the distribution is significantly different from a normal distribution. Skew and kurtosis were calculated using Microsoft Excel 97. Positive skew means the right tail of the distribution is extended (mean>median) and negative skew means the left tail of the distribution is extended (mean<median). Positive kurtosis indicates a leptokurtic distribution and negative kurtosis indicates a platykurtic distribution.

Parameter Group(s) in which Uncertainty was Incorporated	Mean	Median	*S.D.*	Minimum	Maximum	*C.V.*	p-value	Skew	Kurtosis
Main Parameter Groups									
Bioenergetics	1.57E+08	1.57E+08	2.52E+07	9.15E+07	2.61E+08	0.16	0.087	0.186	0.052
Diet	1.58E+08	1.58E+08	1.00E+07	1.30E+08	1.91E+08	0.06	0.084	0.246	-0.018
Population	1.58E+08	1.58E+08	9.30E+06	1.40E+08	1.76E+08	0.06	0.000	-0.018	-1.137
Bioenergetics, Diet	1.58E+08	1.56E+08	2.67E+07	8.54E+07	2.60E+08	0.17	0.006	0.226	-0.034
Bioenergetics, Population	1.57E+08	1.55E+08	2.69E+07	8.22E+07	2.43E+08	0.17	0.016	0.282	-0.129
Diet, Population	1.58E+08	1.58E+08	1.39E+07	1.26E+08	2.02E+08	0.09	0.026	0.215	-0.341
Bioenergetics, Diet, Population	1.58E+08	1.55E+08	2.91E+07	8.54E+07	2.72E+08	0.18	0.000	0.374	0.033

Table 3.8 cont.

Parameter Group(s) in which Uncertainty was Incorporated	Mean	Median	*S.D.*	Minimum	Maximum	*C.V.*	p-value	Skew	Kurtosis
Bioenergetic Parameter Groups									
Efficiency	1.58E+08	1.58E+08	4.41E+06	1.46E+08	1.71E+08	0.03	0.093	0.112	-0.275
Metabolism	1.58E+08	1.58E+08	2.03E+07	1.08E+08	2.07E+08	0.13	0.117	0.041	-0.581
Production	1.57E+08	1.57E+08	1.45E+07	9.44E+07	2.03E+08	0.09	0.239	-0.163	0.333
Efficiency, Metabolism	1.58E+08	1.58E+08	2.09E+07	1.06E+08	2.15E+08	0.13	0.281	0.057	-0.451
Efficiency, Production	1.57E+08	1.57E+08	1.53E+07	9.26E+07	2.06E+08	0.10	0.217	-0.118	0.364
Metabolism, Production	1.57E+08	1.55E+08	2.49E+07	8.77E+07	2.34E+08	0.16	0.034	0.167	-0.295
Efficiency, Metabolism, Production	1.57E+08	1.57E+08	2.52E+07	9.15E+07	2.61E+08	0.16	0.087	0.186	0.052

Of the bioenergetic parameter groups (efficiency, metabolism, and production), annual population food requirement estimates were most sensitive to uncertainty in metabolism (*C.V.* = 13%) and production (*C.V.* = 9%) parameters (Fig. 3.8, Table 3.8). Uncertainty in efficiency parameters had only a small effect on the variability of the estimates (*C.V.* = 3%). In general, incorporating error in each bioenergetic parameter group resulted in normally distributed estimates of population food requirements.

Discussion

Bioenergetic Models

Models have frequently been used to estimate the amount of food that marine mammal populations consume (Hinga 1979; Naumov and Chekunova 1980; Ashwell-Erickson and Elsner 1981; Doidge and Croxall 1985; Hiby and Harwood 1985; Lavigne *et al.* 1985; Worthy 1987a; Øritsland and Markussen 1990; Härkönen and Heide-Jørgensen 1991; Markussen and Øritsland 1991; Ryg and Øritsland 1991; Markussen *et al.* 1992; Olesiuk 1993; Ugland *et al.* 1993; Mohn and Bowen 1996; Stenson *et al.* 1997). However many of these and other bioenergetic models have serious shortcomings due to: 1) unassessed and underassessed terms; 2) inaccurate approximations of terms; and 3) uniqueness or specificity of the studies (Davies and Hatcher 1998).

Correcting for omitted or underestimated terms often results in markedly different conclusions (Davies and Hatcher 1998). Components of marine mammal energy budgets that have commonly been omitted in past studies include reproduction, molting, and thermoregulation (Olesiuk 1993; Mohn and Bowen 1996; Stenson *et al.* 1997). Of these three omissions, I incorporated reproduction, but did not incorporate molting or thermoregulation. Energy expenditure during the molt is low for pinnipeds and molting may even be associated with a reduction in basal metabolism (Ashwell-Erickson and Elsner 1981; Worthy *et al.* 1992). Therefore, it is unlikely that the omission of molting in my model resulted in an underestimate of energy requirements. Thermoregulatory costs are also probably low. Marine mammals have many thermoregulatory adaptations for existence in extreme environments (Irving 1969). A mature Steller sea lion probably does not need to generate body heat in excess of the heat produced from feeding and basal and active metabolism to maintain its body temperature. A younger, less developed animal may have increased thermoregulatory costs, but several studies on phocid pups (post-weaning) and juveniles found they had thermoneutral zones within the range of environmental temperatures experienced in the wild (Ashwell-Erickson and Elsner 1981; Boily and Lavigne 1996; Hansen and Lavigne 1997b; Hansen and Lavigne 1997a). Newborn pups, however, have very little blubber, and probably require additional energy for thermoregulation; but given the high pup basal metabolic rate assumed in my model, the omission of thermoregulatory costs probably had a minimal effect.

The second major criticism of bioenergetic models is that inaccurate approximations are often used for parameter values. Particular problems include extrapolations from captive to wild animals, estimation of certain difficult parameters (e.g., activity budgets, demographic parameters), and variation in parameters with age/size, time, and space (Davies and Hatcher 1998). One way to address these inaccuracies, is to include error terms for all model parameters estimates. Another is to use fewer parameters (with increased precision) as has been done in some recent marine mammal bioenergetic models (e.g., Mohn and Bowen 1996; Stenson *et al.* 1997).

I developed a relatively complex (and hopefully realistic) Steller sea lion model to examine seasonal and spatial patterns of food consumption. All model parameters had error estimates and were sampled/resampled using Monte Carlo techniques similar to those used in two previous marine mammal bioenergetic models (i.e., Mohn and Bowen 1996; Stenson *et al.* 1997). In general, the less accurately a parameter value was known, the wider the range of possible values that I considered. I also tended to use uniform sampling distributions for parameters that lacked information. Thus, using sampling distributions that described the uncertainty in parameter values reduced the bias related to inaccurate parameter estimates.

The third major criticism of bioenergetic models is that they are of limited comparative value because they apply to a single set of unique conditions and do not have flexibility to consider energy budgets that vary in time and space (Davies and Hatcher 1998). In the case of my Steller sea lion model, my results are unique in space (Alaska) and time (1990’s), and may not be directly applicable to Steller sea lions from other parts of their range, or from different time periods. Estimates of food consumption are affected by components of the energy budget like growth and diet composition, which have been demonstrated to vary in space and over time (Merrick *et al.* 1997; Calkins *et al.* 1998). However, my bioenergetic model could easily be adapted to another Steller sea lion population, and to other pinniped species, and contains insights that are useful for comparison within and among species.

Sensitivity Analysis

Rather than examine the sensitivity of mean model predictions to standardized deviations in each parameter value (e.g., 10% perturbations), I examined the sensitivity of the error in model predictions to the error in each group of parameter value estimates. The larger the error in a parameter estimate, the larger the effect of uncertainty in that parameter on the error in food requirement estimates. Similarly, the stronger the effect of a parameter value on mean model predictions, the larger the effect of uncertainty in that parameter on the error in food requirement estimates.

Of the three main parameter groups (bioenergetic, diet, and population), uncertainty in bioenergetic parameters produced the most error in annual population food requirements. Uncertainty in diet and population parameters had much smaller effects. Of the bioenergetic parameter groups (efficiency, metabolism, and production), uncertainty in metabolism parameters had the largest effect on the error in annual population food requirements, but uncertainty in production parameters also had a strong effect. The sensitivity of the error in model predictions to uncertainty in metabolism parameters was due to the strong effect of activity costs on energy requirements and the large error in activity budget and activity metabolism parameter estimates.

Sensitivity analyses of models provide direction for future research by highlighting key parameters that have strong effects on model predictions. Setting priorities depends on the sensitivity of mean model predictions to perturbations in parameter values, and current knowledge of that parameter's value (or the error in parameter estimates). My results suggest that the largest improvements in precision of food requirement estimates can be obtained through future studies on Steller sea lion bioenergetics, especially activity costs. These findings are contrary to the suggestion that pinniped bioenergetics are well understood, and researchers should focus on obtaining better diet and population data (Lavigne 1994). I am not suggesting that better diet and population data are not needed, but there is still a lack of important bioenergetic information for Steller sea lions that is needed to refine estimates of food requirements.

Individual Energy/Food Requirements

Food and energy requirements of individual Steller sea lions varied with time of year and may have slightly biased estimates of total population needs. This is because the effective number of animals that were alive for an entire year was calculated and then multiplied by the annual food/energy requirement per individual. In reality, however, more animals are alive at the beginning of the year than at the end of the year, which when combined with seasonal variation in food/energy requirements, introduced a slight bias in total consumption. This approach would only produce accurate estimates of population food/energy requirements if daily requirements were constant throughout the year. My estimates of population requirements are slightly high because food and energy requirements tended to be greater later in the year especially for pups and mature females.

Trends in energy requirements throughout the year mirrored the relative importance of different components of the energy budget. By far, the largest proportion of energy requirements was activity costs. For example, energy requirements were low during the breeding season while animals were on land. As the year progressed, their energy requirements increased as pups and mature females spent progressively more time in the water. Most pinniped bioenergetic models have shown activity costs to be the largest component of the energy budget (e.g., Boyd *et al.* 1994).

Growth was a relatively small component of energy requirements. Immature animals which were growing rapidly showed only a minor increase in energy requirements during the seasonal growth period (~5-15%). Other pinniped bioenergetic modeling studies have also found the energy required directly for growth to be small in comparison to total energy requirements (Innes *et al.* 1981; Olesiuk 1993). However, the elevated basal metabolism of juveniles is related to growth, and inclusion of this energetic cost would increase the relative importance of growth.

Reproduction also influenced seasonal patterns of individual energy requirements. Pregnancy produced an increase in mature female energy requirements near the end of gestation (spring), but the increase was small relative to total energy requirements (maximum difference ~ 8%). Lactation, on the other hand, produced a large increase in energy requirements. The additional energy required to nurse a pup increased throughout the lactation period and was equal to the mother's own energy requirement by spring. This agrees with the general mammalian pattern: lactation is much more expensive in terms of energy than pregnancy (Oftedal 1985; Costa *et al.* 1986). The maximum daily individual energy requirement among all sex/age classes was approximately 200 MJ for pregnant, lactating females late in gestation. This is equivalent to 47,800 kilocalories per day. Reproduction is thus very costly for female Steller sea lions nursing a pup.

Trade-offs among reproduction, growth, and survival are central to life history theory (Stearns 1992). The large energetic cost of raising a pup probably plays a key role in physiological trade-offs for female Steller sea lions. For example, Pitcher et al. (1998) found that the proportion of lactating female Steller sea lions that were pregnant in late gestation was lower than the proportion of non-lactating females that were pregnant. This suggests that there is a trade-off between nursing a pup through its first year of life and giving birth to a pup the next year. This trade-off may be most important for young females who require more energy per unit body mass than older females. Young females must also allocate energy to body growth and the age at which they first give birth is probably partially related to the trade-off between nursing a pup and attaining some critical body size (e.g., for survival).

My model predicted that during the two weeks following parturition, a female had to consume an average of 35.3 MJ/d to nurse a male pup and 29.6 MJ/d to nurse a female pup. Using the median values for maternal efficiency, this corresponds to 23.4 MJ and 19.5 MJ of milk per day, respectively. Using milk intake and energy intake rates from Davis et al. (1996), the energetic density of Steller sea lion milk was approximately 14 kJ/ml during the first four weeks postpartum. Thus, my model predicted that newborn male pups required 1.67 L milk/d and female pups required 1.39 L milk/d. This agrees with previous estimates of pup milk consumption rates. Higgins et al. (1988) found that newborn (<25 kg) Steller sea lion pups on Año Neuvo Island, California consumed approximately 1.5-1.6 L of milk per day, which encompasses my average estimate of 1.53 L d^{-1}. Davis et al. (1996) found slightly higher rates of milk consumption (and energy consumption) for Alaskan Steller sea lion pups less than two weeks old (1.7-2.1 L/d). Using the same milk energetic density as above, my model predicted that at one year of age, a male pup would need 5.50 L milk/d and a female would need 4.26 L milk/d. However, the energetic density of milk may change during the lactation period as it does in other pinniped species (Arnould and Hindell 1999; Debier *et al.* 1999).

The energy required for lactation may be less than predicted by the model if pups begin foraging before 1 year of age. In some otariid species, pups accompany their mothers on foraging trips and begin to feed on prey before they are weaned (Trillmich 1986a; Trillmich 1986b). Independent feeding would reduce the amount of the milk the mother needed to produce. It is unknown if Steller sea lion pups forage on prey prior to weaning. Steller sea lion pups make trips to sea in the winter and spring (prior to weaning), but Porter and Trites (in review) suggest that these trips are separate from their mothers, and may not be foraging trips.

In general, total daily metabolism (gross energy requirement minus energy deposited or lost as waste) estimated by the model was approximately 3-4 times basal metabolic rate except during periods of particularly low (breeding season) or high (mature females in winter and spring) energy expenditure. These results are similar to observed field metabolic rates (or sustained metabolic rates) of mammals in general (Nagy 1987; Peterson *et al.* 1990). The highest metabolic rate predicted by the model was that of a pregnant, lactating female prior to the breeding season (5 times basal metabolic rate). This level of energy expenditure is similar to the sustained metabolic rate of human athletes participating in the Tour de France bicycle race (Peterson *et al.* 1990).

Assuming that diet is constant throughout the year results in seasonal patterns of food requirements that are similar to seasonal patterns of energy requirements. In Southeast Alaska, where diet is known to change seasonally, seasonal change in the energetic density of the diet resulted in maximum daily food requirements in October and November and minimum daily food requirements in the summer (May - August) for all non-pups. This pattern generally obscured seasonal trends in energy requirements. Thus, changes in the energetic density of the diet can have large effects on the amount of food Steller sea lions need to eat. The mean annual food biomass requirement per individual was 12% greater in the Central Aleutian Islands 3 (diet with lowest energetic density) than in Southeast Alaska (diet with highest energetic density).

The effect of diet on food requirements, can be further illiustrated by considering two diets – one of entirely gadids (walleye pollock, Pacific cod) and one of entirely small schooling fish (herring, sandlance). Based only on caloric differences between prey types, a 10 year old male would require an average of 26.1 ± 6.11 kg of small schooling fish per day

(4% of body mass), but would require 40.9 ± 8.93 kg of gadids (6% of body mass) – a 57% increase in prey biomass requirements. A 10 year old female’s (pregnant, no pup) average daily food requirement would increase by a similar percentage with a diet shift from small schooling fish to gadids (13.7 ± 2.94 kg to 21.2 ± 4.22 kg or 5 to 8% of body mass). These differences are based only on differences in caloric value of prey types, and may in fact be much higher if differences in digestibilities are taken into account (Rosen and Trites in press).

A large animal may be able to compensate for changes in prey biomass requirements, but immature or recently weaned animals may be more susceptible to changes in prey biomass requirements because they need to consume more food per unit body mass than adult animals. Juvenile animals may also be more susceptible to changes in prey biomass requirements due to foraging constraints (e.g., dive depth; Merrick 1995). A 1 year old male would require an average of 13.8 ± 3.40 kg of small schooling fish per day (10% of body mass), but would require an average of 21.7 ± 5.03 kg of gadids (16% of body mass). A 1 year old female would need 11.8 ± 2.60 kg of small schooling fish (11% of body mass) or 18.5 ± 3.75 kg of gadids (17% of body mass). Although animals prey on more than one species category in nature, which would buffer the effects of changes in diet composition, differences in the energetic density of prey can have large effects on prey biomass requirements, especially for young animals.

Fiscus and Baines (1966) suggested that the maximum capacity of a 2 year old male Steller sea lion stomach was approximately 10% of the animal’s body weight. My model predicted that immature animals and lactating females require more than 10% of their body weight in food per day. If animals are generally not feeding on a daily basis (see below) then individuals would frequently have to consume biomass in excess of 10% of their body weight. If a 1 year old animal was preying solely on gadids and was feeding every other day, it would need to consume an average of over 30% of its body weight in food during a foraging trip. This is much greater than its suggested stomach capacity. However, pinnipeds have very fast digestive passage rates (Helm 1984). The majority of a meal may be passed through the stomach in 5 hours (Markussen 1993). Pinnipeds also have a very long small intestine which may act as a storage compartment during foraging trips (Krockenberger and Bryden 1994). These two characteristics would allow an animal to consume a large amount of food on a foraging trip, and then digest/absorb the food over a longer period (including its time on land).

It is important to note that the results of my model are estimates of food requirements and not estimates of food consumption. On an annual basis, food consumption would equal food requirements, but on a daily basis, animals would not always consume the food they needed to meet their energy demands. Two important examples are breeding males holding territories and females with pups during the perinatal period.

During the breeding season, bulls remain on territories and fast, spending very little time in the water, if any (Gisiner 1985). Pregnant females arrive on breeding rookeries an average of about 3 days before giving birth. After parturition, they remain on land with their pups for an average of about 7-9 days (perinatal period) (Gentry 1970; Higgins *et al.* 1988;

Milette 1999). Thus, breeding males and females have to store energy prior to the fast and/or replace lost energy after the fast. The food 'required' during the breeding season is actually consumed at a different time of year.

In general, the rate of food consumption for most animals is probably not constant on a daily basis. Steller sea lions, especially lactating females, exhibit cyclic behaviour consisting of foraging trips to sea followed by periods onshore. Onshore intervals average from 8-28 hours in length for adult females and 11-25 hours for immature animals (Higgins *et al.* 1988; Merrick 1995; Swain 1996; Swain and Calkins 1997; Trites and Porter in review). Thus, animals frequently go without food for a day or more and must therefore consume more food on foraging trips than would be expected from daily food requirements.

Extended fasting periods may have slightly biased my estimates of food requirements for breeding males and females. Steller sea lion bulls, like other otariid males, store energy prior to the breeding season fast in the form of blubber, and then rely on these energy stores during the fast (Schusterman and Gentry 1971; Olesiuk and Bigg 1987; Boyd and Duck 1991; Trites and Bigg 1996, Chapter 2). Steller sea lion females may also store some energy prior to arriving on the rookeries to give birth. Storing and remobilizing energy, may be less efficient than directly utilizing the energy in food. If this is the case, I would have underestimated their food requirements. However, if there is a difference in efficiency, it is probably small and would have a negligible effect on my estimates of food requirements. Fasting may also have biased my estimates of food requirements in the opposite direction. A study on captive Steller sea lions showed that juveniles had the ability to depress their metabolic rate during periods of reduced energy intake (Rosen and Trites 1998). If fasting adults have a depressed metabolic rate then I would have overestimated food requirements. However, due to the relatively short period of time that they fast, the effect would have been small.

Population Food Requirements

The coefficients of variation (*C.V.*) of total annual population food requirement estimates ranged from 18-21% for the seven regions of Alaska. While these *C.V.*'s are relatively low, they still reflect considerable uncertainty in my estimates of food requirements, which must be considered if used in other analyses (e.g., comparative analyses, management decisions).

Annual prey biomass consumption varied by region of Alaska (Figs. 3.6 and 3.7) mainly due to differences in population size, but also as a result of differences in diet composition (previous section). Gadids and Atka mackerel were the top two prey categories in terms of biomass consumption. Gadids dominated the diet in the eastern areas (Southeast Alaska and Gulf of Alaska) while Atka mackerel dominated the diet in the western areas (central Aleutians 2 to western Aleutians).

Walleye pollock were the main gadids consumed by Steller sea lions in the 1990's (Merrick *et al.* 1997). Projected exploitable (adult) walleye pollock biomass in 1999 was 7.38×10^5 tonnes in the Gulf of Alaska, 1.06×10^5 tonnes in the Aleutian Islands (1998), 4.03×10^5 tonnes in the Aleutian basin, and 7.04×10^6 tonnes in the eastern Bering sea

(Witherell 1999) for a total of 8.29×10^6 tonnes in these four regions. Assuming juvenile pollock biomass was 18% of total pollock biomass (Trites *et al.* 1999), there was an estimated 1.81×10^6 tonnes of juvenile pollock in 1999. The annual adult walleye pollock natural mortality rate is about 25% ($M = 0.30$ year^{-1}) (Witherell 1998). The annual juvenile mortality rate is between 10 and 96% ($M = 0.1\text{-}3.2$ year^{-1}) depending on age (Livingston 1993; Livingston and Methot 1998). These estimates of stock sizes and natural mortality rates combine to produce estimates of 2.07×10^6 tonnes of adult pollock and 1.46×10^6 tonnes of juvenile pollock dying naturally each year (assuming median juvenile M). The most recent pollock catch statistic data are 8.98×10^4 tonnes in the Gulf of Alaska in 1997 ($\cong$ 12% of the 1999 exploitable biomass in the Gulf of Alaska), and 1.02×10^6 tonnes in the eastern Bering sea in 1998 ($\cong$ 14% of the 1999 exploitable biomass in the eastern Bering sea) (DiCosimo 1998; Witherell 1998). The mean model estimate of gadid consumption by Steller sea lions was $2.07\times10^5 \pm 3.96\times10^4$ tonnes per year. This represents about 6% of the total estimated pollock biomass dying naturally per year or 19% of the total biomass removed per year by commercial fisheries. Thus, estimated total walleye pollock biomass consumption by Steller sea lions in Alaska is less than that taken by the fishery, and is small relative to total pollock natural mortality. Livingston (1993) also estimated that the pollock biomass taken by sea lions in the eastern Bering sea in 1985 was small relative to that taken by the fishery, and remarked that cannibalism of adults on juveniles was the greatest source of mortality for walleye pollock.

Projected exploitable biomass of Atka mackerel in 1999 in the Bering sea and Aleutian Islands was 5.95×10^5 tonnes (Witherell 1999). No estimates were available for the

Gulf of Alaska Atka mackerel stock although the population is much smaller. The estimated annual natural mortality for Atka mackerel is 25% ($M = 0.30$) (Witherell 1998) which corresponds to 1.49×10^5 tonnes of exploitable biomass dying naturally each year in the Bering sea and Aleutian Islands. Recent catch statistics were 5.58×10^4 tonnes for the Bering sea/Aleutian Islands in 1998 ($\cong$ 9% of the 1999 exploitable biomass in the Bering sea/Aleutian Islands), and 330 tonnes for the Gulf of Alaska in 1997 (DiCosimo 1998; Witherell 1998). Estimated Steller sea lion consumption of Atka mackerel for all regions of Alaska was $1.24\times10^5 \pm 2.39\times10^4$ tonnes per year (83% of estimated Atka mackerel biomass dying naturally in Bering Sea and Aleutian Islands). Thus, Steller sea lions remove more Atka mackerel biomass than the fishery per year, and Steller sea lion predation accounts for a large amount of natural Atka mackerel mortality. As with pollock, other fish species (e.g., Pacific cod) are also important predators on Atka mackerel (Yang 1997).

Inferences about prey availability and competition for prey between fisheries and Steller sea lions should be made with caution given that the fish that are caught in fisheries may not be the same fish that Steller sea lions are consuming. For example, the pollock fishery targets fish older than 3 years, but Steller sea lions generally prey on pollock younger than 3 years old and tend not to consume large pollock (>60 cm) (Calkins and Goodwin 1988). Thus, there may only be minor overlap between the pollock taken by humans and pollock taken by Steller sea lions.

Caution should also be used when making inferences about competition and prey availability even when estimates of prey biomass and catch are specific to sea lions and fisheries. Spatial and temporal distributions of prey (and fishing) at the local scale determine the availability of food resources for Steller sea lions. Estimates of total prey abundance are not enough to make inferences about the food that is available to Steller sea lions. For example, if estimates of the amount of food that Steller sea lions require were less than the estimated available prey biomass (minus the prey taken by fisheries), it would not necessarily mean Steller sea lions had enough to eat. Sea lions may not have access to all of the prey due to local differences between their foraging space/time and the spatial/temporal distribution of the fish. Local prey densities encountered by Steller sea lions are more relevant than absolute abundance when assessing prey availability.

Conclusion

I constructed a bioenergetic computer model to estimate the food requirements of Steller sea lions. The model, like all models, is a simplified or abstract representation of the real system. However, models aid in the conceptualization of complex systems and can be used to predict properties of real systems that are difficult or impossible to measure (Hall and Day 1977; Keen and Spain 1992). It has been difficult to measure the food consumption of wild Steller sea lions, so my model provides the first comprehensive estimates of food requirements. There were also unexpected, emergent predictions from my model that were not intuitive. For example, the energetic importance of body size is not the direct cost of growth but rather the indirect effect of body size on metabolic rate. However, the most important value of my model is not its predictions *per se*, but rather the interplay between the model predictions and future research on the real system. My model has generated many hypotheses which can now be tested through field studies. For example, a new stomach temperature telemetry method may allow researchers to quantify the amount of food wild animals consume (R. Andrews, pers. comm.). Estimates of food consumption obtained in the wild could then be used to validate the model predictions and generate new hypotheses regarding discrepancies between the model and field estimates.

My model is one abstraction of the food consumption of a population of Steller sea lions. Other modeling approaches could be taken in the future to further explore Steller sea lion predation and physiology. It is important to consider other levels in the heirarchy of systems in nature (Hall and Day 1977). For example, Steller sea lion predation could be modeled as a function of prey availability on local spatial and temporal scales. My model predicted food requirements based on set diet compositions, but diet varies as a function of prey availability. It is well documented that pinnipeds are opportunistic feeders (Olesiuk 1993; Ugland *et al.* 1993). At low levels of prey abundance, opportunistic feeders may abandon a food source and turn to a more abundant species (Beverton 1985). Several authors have emphasized the need for behavioural information before key questions can be answered about marine mammal – fisheries interaction (Beverton 1985; Härkönen and Heide-Jørgensen 1991; Markussen and Øritsland 1991; Olesiuk 1993). Härkönen and Heide-Jørgensen (1991) go so far as to say “additional effort and resources spent on refining knowledge about the purely quantitative aspects of seals’ predation will not necessarily lead to the kind of insights sought concerning predator-prey dynamics and ecological cause and effect relations.”

Another interesting future modeling exercise would be to explore what happens to a Steller sea lion population that does not obtain the required amount of food. Theoretically, at some prey abundance, individuals are unable to meet their energy requirement. At this point, organisms may alter their behaviour to reduce their energy requirement. Organisms may also have physiological mechanisms which reduce their energy requirement (e.g. metabolic depression). At some critical level of energy consumption, organisms can no longer maintain normal function and/or growth and must draw upon reserves (starvation). Several bioenergetic simulation models have been built to explore the effects of starvation on pinnipeds (Worthy 1987a; Øritsland and Markussen 1990). The emphasis of these models was individual survival. In addition to increased mortality, population level effects of starvation may include increased age at maturity (delayed growth) and reduced reproductive success (Eberhardt and Siniff 1977; Bowen *et al.* 1981).

Summary

Estimates of marine mammal food requirements are critical for understanding the relationships between marine mammals and their ecosystems (including fisheries). An interactive bioenergetic computer model was constructed to determine the food requirements of the Alaskan Steller sea lion population in the 1990's. Input included age/sex-specific energy requirements, population size/composition, and diet composition/energy content by date and region of Alaska. Error in model predictions was calculated using uncertainty in parameter values and Monte Carlo simulation methods. Food requirements were generally lowest in the summer and highest in the winter and spring mainly due to changes in activity budgets and the energy content of the diet. The mean daily food requirement of pregnant females was only marginally greater than the mean daily food requirement of non-pregnant females of the same age, but the mean daily food requirement of females nursing pups was about 70% greater than females of the same age without pups. Per capita population food requirements differed by up to 12% among regions of Alaska due to differences in the energy content of the diet. Steller sea lion predation was small relative to total walleye pollock natural mortality, but accounted for a large part of total Atka mackerel natural mortality. Of the bioenergetic, population, and diet parameters, uncertainty in bioenergetic parameters resulted in the largest error in model predictions. The model provided both a quantitative estimate of the Alaskan Steller sea lion population's food requirements and direction for future research.

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APPENDIX 1: COMPARISON OF GROWTH MODELS

Table A1.1. Parameter estimates (± *S.E.*) for growth models (Table 2.1) describing the growth of Steller sea lions (standard length (m) and mass (kg) at age (years)). Sample sizes (n) were: male length - 217, female length - 250, male mass - 203, female mass - 222.

Sex	Model	A	k	t_0	m	S_0	T	b	r^2
Length									
Male	Pütter	3.376 ± 0.090	0.140 ± 0.015	-3.964 ± 0.462					0.876
	von Bertalanffy	3.298 ± 0.073	0.173 ± 0.016	-8.336 ± 0.793					0.878
	Logistic	3.200 ± 0.055	0.241 ± 0.018	0.385 ± 0.148					0.880
	Gompertz	3.268 ± 0.068	0.190 ± 0.016	-1.259 ± 0.199					0.878
	Richards	3.061 ± 0.054			7.121 ± 3.163	1.635 ± 0.048	31.990 ± 2.465		0.883
Female	Pütter	2.323 ± 0.011	0.369 ± 0.029	-2.374 ± 0.325					0.778
	Pütter (additive)	2.310 ± 0.012	0.368 ± 0.030	-2.434 ± 0.340				0.029 ± 0.013	0.783
	Pütter (proportional)	2.310 ± 0.013	0.370 ± 0.030	-2.422 ± 0.338				0.012 ± 0.006	0.783
	von Bertalanffy	2.321 ± 0.011	0.392 ± 0.031	-4.731 ± 0.510					0.777
	von Bertalanffy (additive)	2.308 ± 0.012	0.391 ± 0.031	-4.808 ± 0.533				0.029 ± 0.013	0.782
	von Bertalanffy (proportional)	2.309 ± 0.012	0.392 ± 0.031	-4.788 ± 0.529				0.012 ± 0.006	0.782
	Logistic	2.317 ± 0.011	0.438 ± 0.034	-1.172 ± 0.258					0.775
	Logistic (additive)	2.305 ± 0.012	0.436 ± 0.035	-1.247 ± 0.273				0.028 ± 0.014	0.780
	Logistic (proportional)	2.305 ± 0.012	0.437 ± 0.035	-1.238 ± 0.271				0.012 ± 0.006	0.779
	Gompertz	2.320 ± 0.011	0.404 ± 0.032	-1.726 ± 0.288					0.777
	Gompertz (additive)	2.308 ± 0.012	0.402 ± 0.032	-1.795 ± 0.303				0.029 ± 0.013	0.781
	Gompertz (proportional)	2.308 ± 0.012	0.403 ± 0.032	-1.785 ± 0.301				0.012 ± 0.006	0.781
	Richards	2.338			-3.075	7.2E-05	-15.773		0.781
	Richards (additive)	2.324			-3.218	0.001	-17.107	0.032	0.787
	Richards (proportional)	2.324			-3.203	0.004	-16.894	0.014	0.786

Table A1.1 cont.

Sex	Model	*A*	*k*	t_0	*m*	S_0	*T*	*b*	r^2
Mass									
Male	Pütter	1120.759 ± 134.201	0.077 ± 0.015	0.334 ± 0.224					0.809
	von Bertalanffy	854.765 ± 47.933	0.182 ± 0.018	-2.133 ± 0.448					0.825
	Logistic	744.448 ± 24.698	0.394 ± 0.026	5.857 ± 0.250					0.840
	Gompertz	808.919 ± 37.354	0.235 ± 0.020	4.622 ± 0.264					0.830
	Richards	681.112 ± 16.254			8.041 ± 3.392	101.148 ± 9.087	12.365 ± 0.890		0.850
Female	Pütter	289.322 ± 6.389	0.212 ± 0.021	-0.740 ± 0.266					0.759
	Pütter (additive)	279.550 ± 6.690	0.198 ± 0.021	-1.030 ± 0.304				27.127 ± 4.197	0.794
	Pütter (proportional)	276.738 ± 6.364	0.208 ± 0.021	-0.949 ± 0.291				0.109 ± 0.019	0.790
	von Bertalanffy	284.135 ± 5.588	0.267 ± 0.025	-3.398 ± 0.516					0.757
	von Bertalanffy (additive)	274.653 ± 5.892	0.247 ± 0.024	-3.955 ± 0.587				26.972 ± 4.227	0.792
	von Bertalanffy (proportional)	272.316 ± 5.676	0.258 ± 0.025	-3.765 ± 0.560				0.108 ± 0.019	0.788
	Logistic	278.249 ± 4.822	0.378 ± 0.034	2.468 ± 0.166					0.752
	Logistic (additive)	268.895 ± 5.113	0.345 ± 0.032	2.348 ± 0.177				27.033 ± 4.291	0.786
	Logistic (proportional)	267.061 ± 5.006	0.358 ± 0.033	2.274 ± 0.174				0.108 ± 0.019	0.782
	Gompertz	282.250 ± 5.330	0.295 ± 0.027	1.260 ± 0.168					0.756
	Gompertz (additive)	272.840 ± 5.633	0.272 ± 0.026	1.064 ± 0.184				26.953 ± 4.243	0.790
	Gompertz (proportional)	270.667 ± 5.453	0.283 ± 0.027	1.042 ± 0.184				0.108 ± 0.019	0.787
	Richards	294.542			-0.484	0.002	5.935		0.759
	Richards (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
	Richards (proportional)	283.698 ± 8.997			-0.653 ± 0.185	0.002 ± 0.000	4.393 ± 1.631	0.112 ± 0.019	0.792

APPENDIX 2: DISCUSSION OF BIOENERGETIC PARAMETERS

Fecal and Urinary Digestive Efficiency (E_{f+u})

Not all of the energy in food is available to an organism for metabolism and deposition (Eq. 3.1). Some of the gross energy in food is lost in feces and urine. Apparent digestible energy is defined as gross energy minus fecal energy, and is referred to as digestive efficiency when expressed as a proportion of gross energy (Lavigne *et al.* 1982). Metabolizable energy is apparent digestible energy minus urinary energy (Lavigne *et al.* 1982). Urinary digestive efficiency can be defined as the proportion of apparent digestible energy that is metabolizable energy, while fecal digestive efficiency can be defined as the proportion of gross energy that is apparent digestible energy. Fecal and urinary digestive efficiency (E_{f+u}) is the product of fecal digestive efficiency and urinary digestive efficiency (Eq. 3.2).

Fecal digestive efficiency varies with prey type and composition. In general, diets with lower energetic content result in lower fecal digestive efficiencies (Brekke and Gabrielsen 1994; Lawson *et al.* 1997). This may be due to a negative correlation between the energetic density of a meal and gastric emptying rate (Hunt and Stubbs 1975; Grove *et al.* 1985). Several studies have looked at the fecal digestive efficiency of captive pinnipeds and found values ranging from about 0.92-0.97 for fish prey and 0.72-0.83 for crustacean prey (Keiver *et al.* 1984; Ronald *et al.* 1984; Fisher *et al.* 1992; Mårtensson *et al.* 1994; Lawson *et al.* 1997). Rosen and Trites (2000) found the average fecal digestive efficiency of juvenile Steller sea lions ranged from 0.904-0.954 for diets of squid, salmon, pollock, and herring. Although digestive efficiency was correlated with prey energetic density, differences among prey species were small. I therefore did not incorporate changes in fecal digestive efficiency with prey species in the model, and used a fecal digestive efficiency of 0.90-0.96.

Urinary digestive efficiency of pinnipeds has not been studied as much as fecal digestive efficiency. Keiver *et al*. (1984) found the proportion of apparent digestible energy in urine was 0.069-0.095 energy for captive juvenile harp seals on a herring diet. Ronald *et al*. (1984) found urinary energy was 0.079 of the gross energy in food for a captive grey seal on a herring diet. This corresponded to about 0.085 of apparent digestible energy (using their fecal digestive efficiency of 0.074). I used a urinary digestive efficiency of 0.90-0.93.

Fecal and urinary digestive efficiency is probably higher for pups whose diet consists entirely of milk. Oftedal and Iverson (1987) suggest the metabolizable energy in milk is about 0.95-0.96 of gross energy. I used a pup fecal and urinary digestive efficiency of 0.95-0.96.

Efficiency of Utilization of Metabolizable Energy (E_{HIF})

Metabolizable energy is the gross energy in food minus the energy lost in feces and urine (Lavigne *et al.* 1982). Not all metabolizable energy is available to an organism for maintenance, activity, deposition, etc. Some metabolizable energy is degraded to heat through ingestion, digestion, absorption, the processing of food energy into usable forms, and synthesis in body tissues (turnover and net accretion) (Webster 1983; Blaxter 1989).

This increase in heat production (or metabolism) after a meal has been given several names including specific dynamic action/effect (e.g., Kriss *et al.* 1934; Jobling 1983) and heat increment of feeding (e.g., Rosen and Trites 1997). For the purpose of this paper, I chose the more general term, heat increment of feeding (Webster 1983). The majority of the heat increment of feeding can be attributed to protein synthesis (Webster 1981; Jobling 1983).

The heat increment of feeding is usually presented as a percentage or proportion of gross or metabolizable energy intake. In my model, the efficiency of utilization of metabolizable energy term (E_{HIF}, Eq. 3.2) is 1 minus the heat increment of feeding as a proportion of metabolizable energy intake. Most marine mammal bioenergetic models have treated the heat increment of feeding as a constant proportion of metabolizable or gross energy intake (e.g., Lavigne *et al.* 1985; Worthy 1987a; Olesiuk 1993; Boyd *et al.* 1994; Mohn and Bowen 1996). Often the value used was from a study by Gallivan and Ronald (1981) which found the heat increment of feeding to be approximately 0.17 of gross energy intake for a captive adult harp seal. Three other captive pinniped studies have found the heat increment of feeding (as a percentage of gross energy intake) to be somewhat lower: 0.047-0.057 for three juvenile harbour seals (Ashwell-Erickson and Elsner 1981), 0.051-0.090 for four juvenile harbour seals (Markussen *et al.* 1994), and 0.099-0.124 for six juvenile Steller sea lions (Rosen and Trites 1997).

The proportion of metabolizable (or gross) energy lost as the heat increment of feeding has been shown to vary with meal size and composition, nutritional state (maintenance or growing), composition of growth (if the animal is growing), and core body/prey temperature differential (Kriss *et al.* 1934; Ashwell-Erickson and Elsner 1981; Webster 1983; Blaxter 1989; Beamish and Trippel 1990; Wilson and Culik 1991; Markussen *et al.* 1994; Rosen and Trites 1997). At least two marine mammal bioenergetic models have incorporated a variable heat increment of feeding. One, applied to harp seals, calculated heat increment of feeding (as a percentage of metabolizable energy intake) of different diets using 0.20 of protein energy intake and 0.10 of lipid energy intake (Ugland *et al.* 1993). A ringed seal model by Ryg and Øritsland (1991) incorporated a variable heat increment of feeding with respect to the composition of growth. They used separate efficiencies for fat (0.90) and protein (0.44) synthesis (inefficiency of synthesis is part of the heat increment of feeding).

In my model I allowed the heat increment of feeding to vary with nutritional state (maintenance or growing) and the composition of growth. First I divided the energy requirements into maintenance energy requirements (activity and basal metabolism) and growth energy requirements (energy deposition). I then used separate heat increments of feeding for maintenance and growth energy requirements. Blaxter (1989) states that the heat increment of feeding at maintenance (and below maintenance) ranges from 0.02-0.23 of metabolizable energy for simple stomached species depending on the diet composition. He further states that humans, dogs, and rats consuming average diets below maintenance have heat increments of feeding around 0.10-0.15. I used a heat increment of feeding at maintenance of 0.10-0.15 of metabolizable energy (E_{HIF} from Eq. 3.2 = 0.90-0.85). Above maintenance, or during energy deposition (growth), the proportion of energy lost as the heat increment of feeding is greater, and its magnitude depends on the composition of growth

(Webster 1983; Blaxter 1989). This increase in the heat increment of feeding is a result of the inefficiency of tissue synthesis. Webster (1983) states that deposition efficiencies are 0.75 for fat and 0.45 for protein. Blaxter (1989) points out that these efficiencies depend on the dietary source of energy, and suggests the efficiencies of fat and protein synthesis may be slightly higher (0.78-0.95 for fat and 0.56 for protein). I used fat and protein synthesis efficiencies of 0.75-0.95 and 0.45-0.56 respectively. Thus, the heat increment of feeding for growth energy requirements was between 0.05 and 0.55 of metabolizable energy (E_{HIF} = 0.45-0.95) and depended on the proportions of energy deposition that were fat and protein.

For reproducing females, the heat increment of feeding also includes the inefficiency of synthesis (energy deposition) during gestation (fetus, placenta, uterine tissue) and lactation (milk). I am not aware of any studies that looked at the heat increment of feeding with respect to pregnancy or lactation in marine mammals. Extrapolating from studies done with other species is complicated due to differences in methodology (Blaxter 1989). Because of these difficulties, I took a more general approach. Rather than guess at the efficiencies of synthesis during gestation and lactation, I used total energetic efficiencies for pregnancy and lactation which incorporate the inefficiency of synthesis, but may also include fetal/uterine maintenance costs and changes in maternal basal metabolism (*see Energetic Efficiency of Reproduction section below*).

Production (*P*)

The main component of production (*P*, Eq. 3.1) was growth in body mass (*M*, Eqs. 6,7, and 8). The equations used for calculating fetal body mass (Eqs. 7,8) were logistic growth models fit to fetal mass at age data. The data used in fitting these curves were mass at implantation (0 kg), mean masses from 4.5 – 7.5 months of age at intervals of one month (Calkins and Pitcher 1982), and mean birth mass from various locations in Alaska (Brandon *et al.* 1996). Implantation was assumed to be 15 October (Pitcher and Calkins 1981). The models were fit using weighted (by sample size) nonlinear least-squares regression. Several other models were tested (linear, von Bertalanffy, Gompertz), but the logistic model provided the best fit (highest r^2).

Postnatal growth in body mass was generally modeled according to the male and non-pregnant female Richards growth models from Chapter 2, except during the first year of life. Pinniped growth is generally linear until weaning (McLaren 1993), so I assumed growth was linear until 1 year of age. Uncertainty was incorporated into the Richards growth models using gross multipliers with means equal to 1 and standard deviations calculated from the residuals ((observed – predicted)/predicted) of the fitted Richards models (Chapter 2). For animals older than 2 years, I assumed all growth occurred during a seasonal growth period (Chapter 2) during which time, body mass increased linearly. Although seasonal growth models have been developed for other species (e.g., Cloern and Nichols 1978) there is not enough Steller sea lion morphometric data to parameterize a complex seasonal growth model. Thus, linear growth periods were used to approximate seasonal growth patterns. Based on the results of Chapter 2 and data from captive juvenile Steller sea lions (Trites and Rosen, unpubl. data) it was assumed the seasonal growth period started between 1 August and 15 September and ended between 1 March and 15 April.

In addition to growth in mass, the model incorporated changes in the composition of growth (proportion lipid, lean, and water) with age (p_{lip}, p_{lean}, and p_w, Eq. 3.6). Newborn Steller sea lion body composition was based on data from pups aged 0 – 5 days from various locations in Alaska (E. Brandon, pers. comm.). After parturition, growth was assumed to be entirely lipid, until body composition reached adult proportions. Pinniped pups are generally born with very little body fat, and early postnatal development is mainly blubber deposition which enables them to maintain homeothermy (Lavigne *et al.* 1982). A study by Trites and Jonker (in press) supports this assumption of rapid lipid growth early in life for Steller sea lions. They found 5 dead pups, aged 3 to 14 days (which were apparently healthy at the time of death), had an average of 10% blubber (by weight) which is near the adult proportion.

Adult female Steller sea lion lipid content (after parturition) has been found to average 7-9% of total body mass (Davis *et al.* 1996). Blubber averaged about 11% of total body mass for a sample of adult male Steller sea lions (although it changed seasonally), and 10-14% of total body mass for a sample of male and female Steller sea lions of various ages (Olesiuk and Bigg 1987; Pitcher and Calkins). I used an adult lipid proportion of body mass of 7-14% (proportion lean body mass ranged from 86-93%). I used an adult lean tissue water content of 66-73% (Olesiuk and Bigg 1987; Davis *et al.* 1996).

Basal Metabolism (*BM*)

Basal metabolic rate (of homeotherms) is defined as the metabolic rate of a mature, post-absorptive individual at rest in thermoneutral conditions (Kleiber 1975). It is the minimum amount of energy needed by an organism to sustain normal body function. For mammals, basal metabolism (BM in kJ d^{-1}, Eq. 3.2) can be estimated from the allometric equation:

[3.9] $BM = 292.88M^{0.75}$

where M is body mass in kg (Kleiber 1975). Although some have suggested marine mammals have higher basal metabolic rates than other mammals (Irving 1969; Schmidt-Nielsen 1990), Lavigne *et al*. (1986) argued that under true basal conditions, marine mammal metabolic rates are not significantly different from other mammals'. In the model, basal metabolism of individuals older than 8 years was calculated using Eq. 3.9.

By definition, the term 'basal metabolism' does not apply to growing animals (young animals) or reproducing animals (pregnant, lactating), but for the purpose of this paper I used the term 'basal metabolic rate' to refer to the metabolic rate of any post-absorptive individual at rest in thermoneutral conditions. This has also been referred to as standard metabolic rate, but the term 'standard metabolic rate' has also been applied under different conditions (Gessaman 1973).

The basal metabolic rate of growing animals is generally greater than predicted by Eq. 3.9 because growing animals have a greater capacity for cell synthesis and turnover (Webster 1983). Growing animals also sustain greater energy expenditure over time than non-growing animals, resulting in a greater capacity alimentary system which has greater maintenance costs (increased basal metabolism) (Speakman and McQueenie 1996). Immature, growing pinnipeds have basal metabolic rates ranging from 1.5 to 3 times the predicted rate (Eq. 3.9), with an average of about 2 (Matsuura and Whittow 1973; Miller 1978; Lavigne *et al.* 1986; Worthy 1987b; Hansen *et al.* 1995). In general, basal metabolic rate decreases rapidly during the first year of life, then declines more gradually after one year of age to reach the predicted level at sexual or physical maturity (Ashwell-Erickson and Elsner 1981).

During the first two months of life, captive Steller sea lion pups raised at the Vancouver Aquarium had basal metabolic rates approximately 3 – 3.75 times predicted (Rosen unpubl. data). Mean field metabolic rate of five Steller sea lion pups (less than 2 months old) measured in the wild was approximately 2.5 times predicted basal metabolic rate which suggested basal metabolic rate was lower than 2.5 times predicted basal metabolic rate (Higgins *et al.* 1988). Captive juvenile Steller sea lions aged 1 year had a mean resting metabolic rate around 2 times predicted basal metabolic rate (Rosen unpubl. data) and juveniles aged 1.8 – 2.8 years had a mean resting metabolic rate about 1.6 times predicted basal metabolic rate (Rosen and Trites 1997). I used a basal metabolic rate at birth of 2.5 – 3.5 times predicted basal metabolic rate (Eq. 3.9), and a basal metabolic rate at 1 year of age of 1.75 – 2.25 times predicted basal metabolic rate. I assumed basal metabolic rate declined linearly from birth to 1 year of age, and from 1 year to 8 years of age.

Pregnancy and lactation may also increase basal metabolism resulting in higher basal metabolic rates than predicted. These changes in basal metabolism may be a result of the additional basal metabolism of the uterus and fetus (during pregnancy) and/or other changes in maternal basal metabolism (Robbins 1983; Blaxter 1989). For example, Speakman and

McQueenie (1996) found that both pregnancy and lactation resulted in elevated basal metabolic rates for rats, mainly due to an increase in the mass of the alimentary tract, and the resulting maintenance requirement. There has been only one pinniped study, that I am aware of, that measured the basal metabolic rate of females in relation to pregnancy or lactation. This study, by Hedd *et al*. (1997), found a decrease in basal metabolic rate of two captive harp seals during gestation. This decrease was not due to pregnancy *per se*, rather seasonal changes in basal metabolism; but pregnancy did not seem to produce a substantial increase in basal metabolic rate. Due to the uncertainty regarding this topic, I did not incorporate specific changes in basal metabolism related to pregnancy or lactation in the model. Instead, I took a more general approach and used total energetic efficiencies for pregnancy and lactation which incorporate possible changes in maternal basal metabolism, but also incorporate the inefficiencies of energy deposition (part of the heat increment of feeding) (*see Energetic Efficiency of Reproduction section below*).

Energetic Efficiency of Reproduction

Due to uncertainty regarding the efficiency of energy deposition (part of the heat increment of feeding) and maternal basal metabolism with respect to pregnancy and lactation, I took a general approach and used total energetic efficiencies for gestation and lactation. Total energetic efficiency is the proportion of the additional metabolizable energy required for pregnancy or lactation (above normal maintenance requirements) that is deposited as the products of gestation (fetus, placenta, uterine tissue) or milk. Theoretically these efficiencies may change with the amount of energy deposited, but I assumed they were constant.

The total energetic efficiency of pregnancy may be related to synthesis of the fetus, synthesis of maternal tissue, maintenance of the gravid uterus, and changes in maternal basal metabolism (Blaxter 1989). Oftedal (1985) suggested the total energetic efficiency of gestation was about 0.13, although it may be greater if energy is derived from maternal stores. Robbins (1993) states that only 0.10 to 0.20 of the additional energy required for pregnancy is retained as new tissue. Despite these low estimates, some bioenergetic models have used higher values for the efficiency of gestation. A golden-mantled ground squirrel study by Kenagy *et al*. (1989) used a value of 0.75 and a harbour seal study by Olesiuk (1993) used a value of 0.70. Given this uncertainty, I used a total efficiency of energy deposition during gestation (fetus, placenta, uterine tissue) of 0.20, 0.10-0.70.

The total energetic efficiency of lactation may be related to synthesis of milk, synthesis of maternal tissue and changes in maternal basal metabolism. Oftedal (1985) and Blaxter (1989) suggest the total energetic efficiency of lactation is about 0.60-0.85 depending on whether the milk energy is derived from food energy or maternal tissue. However, there is evidence that lactation does not substantially increase overall metabolism (which includes the inefficiency of synthesis and basal metabolism) in pinnipeds. Costa and Gentry (1986) and Costa *et al*. (1986) found little difference between the field metabolic rates of lactating and non-lactating female northern fur seals and northern elephant seals respectively; although, these studies did not control for activity levels. Given this uncertainty, I used a total efficiency of energy deposition during lactation (milk) of 0.775, 0.60-0.95.

Activity (*A*)

Voluntary physical activity requires energy in addition to basal metabolism. For pinnipeds, this includes activity on land and in the water. In the model, the energetic cost of activity was incorporated using a multiplier of basal metabolic rate (*A*; Eqs. 2 and 10), which was a function of time spent on land/at sea (*land*, *water*, Eq. 3.10) and metabolic rate multipliers for land and sea (A_{land}, A_{water}, Eq. 3.10)

The proportion of time immature Steller sea lions spend on land and in the water has been documented in several studies. Following birth (assumed to be 15 June; Pitcher and Calkins 1981), pups remain entirely on land for about one month, afterwhich they begin to play in the water and swim in surge channels (Scheffer 1945). Merrick and Loughlin (1997) found that 5 winter (November – May) young of the year spent 37.5 % of their time at sea. One yearling female spent an average of 61.1% of her time in the water (June – September) and one yearling male spent an average of 57.6% of his time in the water (Swain and Calkins 1997). Swain and Calkins (1997) also found that a 2 year old winter (January – May) male spent an average of 75.5% of his time in the water, and a 1-2 year old winter female spent an average of 37.6% of her time in the water. Trites and Porter (in review) found that winter (January – April) immatures (pups and yearlings) spent an average of 54% of their time at sea.

I assumed that immature animals, older than 1 year, spent a constant mean proportion of their time at sea throughout the year (56.5%, 37-76%). I also assumed that pups less than 1 month old spent all of their time on land, and that the mean percentage of time spent at sea increased linearly from 1 month to 1 year of age.

The proportion of time mature Steller sea lions spend on land and in the water has also been documented in a number of studies. Pregnant females arrive on breeding rookeries and give birth from mid-May to mid-July, with the majority of births occurring in early to mid-June (Pitcher and Calkins 1981). Females arrive an average of about 3 days before birth (Gentry 1970). After parturition, females remain on land with their pups for an average of about 7-9 days (perinatal period) (Higgins *et al.* 1988; Milette 1999). After the perinatal period they periodically go to sea on foraging trips. A study on Año Nuevo Island, California found that during the first week of foraging trips, Steller sea lion mothers spent about 40% of their time away from the rookery which increased to about 70% by the fifth week (Higgins *et al.* 1988). The standard error of these percentages was approximately 3.5%. Three other studies support Higgins *et al.*'s findings. Milette (1999) found that 116 lactating females spent an average of 41.1 ± 5.83% *S.E.* of their time at sea between the end of the perinatal period and early August, and this percentage increased with pup age. Merrick and Loughlin (1997) found three groups of summer (June – July) adult females with pups spent 50.0, 52.5, and 58.1% of their time at sea respectively. Swain (1996) found that for 11 summer (May – July) adult females with pups, the average percentage of time spent at sea ranged from 34.7 to 65.6%, and one adult female without a pup spent 46.7% of her time at sea.

Adult females with pups spend less time on land during the winter. Merrick and Loughlin (1997) found that 5 winter (November – May) adult females with pups spent an average of 89.9% of their time at sea. Swain (1996) found one winter (January – May) adult female spent an average of 85.7% of her time at sea. Trites and Porter (in review) found winter (January – April) lactating females spent an average of 73% of their time at sea.

For the model, I assumed mature females were entirely on land from 12 June to 22 June. Starting on the first day of foraging trips (23 June), mature females spent 40%, 33-47% of their time at sea. This percentage increased linearly to 70%, 63-77% on 26 July. It then increased linearly from this point to 81.5%, 73-90% on 1 November. Mature females continued to spend this percentage of time at sea through to the next breeding season. Although this pattern was chosen based on data from mature females with pups, I applied it to all mature females. Almost all mature females copulate every year and must therefore spend time on a rookery or haulout during the breeding season (Pitcher and Calkins 1981). Also, data from Swain (1996) suggest the amount of time spent on land by females with and without pups, may not be different, at least during the summer.

Breeding males are present on rookeries from mid-May to late July, and the majority of breeding occurs in June (Thorsteinson and Lensink 1962; Pitcher and Calkins 1981). During this time, males remain on their territories and fast, spending very little time in the water, if any (Gentry 1970). The mean length of territory tenance is 43 days (Gentry 1970). No studies have looked at the proportion of time mature, non-breeding males spend on land during the breeding season, or the proportion of time males spend on land the rest of the year. For the model I assumed mature males were entirely on land from 29 May to 10 July. For the rest of the year, I assumed mature males spent a constant mean percentage of their time at sea each day (70%, 55 – 85%). The lower and upper limits roughly correspond to the median values for immatures and mature females respectively. As with females, I applied this pattern to all mature males, not just breeding males. Male Steller sea lions attain sexual maturity several years before they are able to hold a breeding territory (Thorsteinson and Lensink 1962). It is possible that mature, non-breeding males spend more time in the water during the breeding season than breeding males. However, this period is short and given the uncertainty in the male activity budget for the rest of the year, using one activity pattern for all mature males probably has a minimal effect.

On land, pinnipeds are generally inactive spending most of the time resting and sleeping. As a result, activity metabolism on land (A_{land}) is low. Ashwell-Erickson and Elsner (1981) measured the metabolic rate of sleeping, resting, and active harbour and spotted seals (2 months – 4 years old) in air. They found sleep reduced metabolic rate by 10 – 40% from basal levels, while activity (alert, agonistic) increased metabolic rate by 20 – 80% from basal metabolic levels. The animals were post-absorptive, so these metabolic rates did not include the heat increment of feeding. Worthy (1987b) also found that sleep reduced metabolic rate (average 40.8% reduction) in young harp and grey seals. These two studies suggest metabolic rate on land (excluding heat increment of feeding) may be similar to basal metabolic rate when animals spend a substantial amount of time sleeping and resting. Some pinniped bioenergetic modelling studies have used basal metabolic rate as the metabolic rate on land (Olesiuk 1993; Ugland *et al.* 1993). I used a metabolic rate on land of 1.2, 1.0 – 1.4 times basal metabolic rate.

An exception to low land activity costs may be breeding males. During the breeding season, male Steller sea lions actively defend territories (Gentry 1970) and this may increase energy expenditure. Boyd and Duck (1991) found that the field metabolic rate of breeding, fasting male Antarctic fur seals was about 3.3 times predicted basal metabolic rate. Breeding male grey seals, another polygynous, territorial pinniped, had an estimated field metabolic rate of 4.8 times predicted basal metabolic rate during the breeding season when they fast (Anderson and Fedak 1987a). However, this was calculated with assumptions about the energy content of mass loss that may have been incorrect. The actual field metabolic rate may have been closer to 3 times predicted basal metabolic rate (Boyd and Duck 1991). Olesiuk and Bigg (1987) documented seasonal blubber changes in adult male Steller sea lions and estimated the maximum length of territory tenance assuming a metabolic rate of 2-3 times predicted basal metabolic rate. Their estimate was similar to the observed length of territory tenance suggesting their assumed metabolic rate was correct. I used a breeding male metabolic rate of 3, 2.5 – 3.5 times basal metabolic rate.

In the water, pinniped activity also includes swimming (cruising, diving, and foraging). The energetic cost of swimming (A_{water}) has been the subject of a number of past studies, and can be indirectly calculated from hydrodynamic studies (Williams 1987; Fish 1992). This is done by calculating the drag force at a given speed from theoretical equations using data on properties such as drag coefficient. The metabolic energy expenditure necessary to overcome this force is then calculated using data on efficiencies (e.g., propeller and aerobic efficiency). These estimates, together with data on swim speeds in the wild, can be used to calculate the energetic cost of swimming for wild pinnipeds.

Stelle (1997) performed a hydrodynamic analysis on captive juvenile Steller sea lions, and predicted swimming metabolic rates of 1630 W for a female, and 2360 W for a male (using average drag coefficients) at a speed of 1.4 body lengths per second (the predicted speed for minimum cost of transport for California sea lions; Feldkamp 1987). Assuming 0.020083 kJ (ml O_2)$^{-1}$, and using body weights back-calculated from power input in units of ml O_2 min^{-1} kg^{-1} and W, these swimming metabolic rates correspond to approximately 14 and 17 times predicted basal metabolic rate, respectively. Assuming juveniles have a basal metabolic rate twice the predicted rate, these swimming metabolic rates are 7 to 8.5 times actual basal metabolic rate. Unfortunately, metabolic rates of wild Steller sea lions can not be estimated in this way because the swim speeds of free swimming animals are not well documented.

A second approach to estimating the energetic cost of swimming is to measure swimming metabolic rate of captive or wild animals directly. Several studies have measured the swimming metabolic rate of captive pinnipeds (commonly measured using respirometry). Ashwell-Erickson and Elsner (1981) measured the swimming metabolic rates of young, captive harbour and spotted seals and found values ranging from 0.91 to 2.2 times the measured resting metabolic rates. Feldkamp (1987) measured the metabolic rate of captive California sea lions swimming at various speeds, and found the minimum cost of transport was 0.12 ml O_2 kg^{-1} m^{-1} at a relative speed of 1.4 body lengths s^{-1} (1.8 m s^{-1}). This corresponded to about 2 times the measured resting metabolic rate or 2.8 times predicted basal metabolic rate. Williams *et al*. (1991) also measured swimming metabolic rates and heart rates of captive California sea lions and estimated a maximum swimming metabolic rate of at least 5 times the measured resting metabolic rate.

As with hydrodynamic studies, data from captive studies can be used along with data on swim speeds in the wild to estimate average swimming metabolic rate in the wild. For example, Ponganis *et al*. (1990) used the speed-metabolic rate relationship developed by Feldkamp (1987), along with their own swim speed data from field studies to estimate the average swimming metabolic rate of several otariid species. They concluded average swimming metabolic rate in the wild was about 1.3 times their assumed resting metabolic rate (or 5.9 times predicted basal metabolic rate, not including the heat increment of feeding). Note, however, that their assumed resting metabolic rate was probably high as it was extrapolated from immature animals.

The swimming metabolic rates of wild pinnipeds have also been measured directly. Wild swimming metabolic rate has commonly been measured using oxygen-18 doubly-labelled water. If animals are foraging, estimates of energy expenditure obtained in this way include the heat increment of feeding, and are therefore higher than the actual energetic cost of swimming. Costa and Gentry (1986) found the field metabolic rate of northern fur seal mothers on foraging trips (at sea) averaged about 2.5 times their assumed standard metabolic rate (or 5.5 times predicted basal metabolic rate). Their assumed standard metabolic rate was from juvenile animals and may therefore have been an overestimate. Costa *et al*. (1989) found the mean at-sea field metabolic rate of female Antarctic fur seals on foraging trips was 6.7 times predicted basal metabolic rate. However, Arnould *et al*. (1996) found mean at-sea metabolic rate of females of the same species was only 4.6 times predicted basal metabolic rate. The field metabolic rate of a male, harbour seal during the breeding season (who spend about two-thirds of their time in the water) was 6.0 times predicted basal metabolic rate (Reilly and Fedak 1991). Studies on deep-diving phocid species have produced much lower estimates of activity costs. For example, Castellini *et al*. (1992) found average field, diving metabolic rates (measured using respirometry) of Weddell seals were between 1.4 and 2 times predicted basal metabolic rate. Diving metabolic rate was not significantly different from resting metabolic rate. Hindell *et al* (1992) suggest southern elephant seals may reduce their metabolism below the resting rate during dives that exceed their aerobic dive limit (part of the classic ‘dive response’). Russ Andrews (unpubl. data) found the average field metabolic rate of lactating, female Steller sea lions (summer) ranged from 3.1 to 4.9 times predicted basal metabolic rate. The measurement period included time on land, so assuming metabolic rate is lower on land than in the water, the average field metabolic rate in water may be higher than these values. However, these values also included the heat increment of feeding so activity metabolism was lower than the observed field metabolic rates.

Based on the above, I used one metabolic rate (excluding the heat increment of feeding) in the water for all animals (4.0, 2.5 – 5.5 times basal metabolic rate).

APPENDIX 3: DISCUSSION OF DIET PARAMETERS

Diet Composition (*prey$_i$*)

In the past, Alaskan Steller sea lion diet composition was generally assessed through stomach content analyses (Mathisen *et al.* 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966; Pitcher 1981; Calkins and Goodwin 1988). These studies demonstrated that diet changed over time and varied with location and time of year. There may also be differences in diet between sexes and among age classes. The most recent diet data for Alaskan Steller sea lions are from scat collections done in the early 1990's (Merrick *et al.* 1997, Trites and Calkins unpubl. data). Merrick *et al*. (1997) collected scat from the western Aleutian Islands to the central Gulf of Alaska from 1990 to 1993. Collections were done mainly on breeding rookeries during the last week of June or first week of July. As a result, these scats were primarily from adult females. Trites (unpubl. data) collected scat in Southeast Alaska during the winter of 1993 (late October – early November) and the summers of 1994 and 1995 (June – July). Scats were collected on rookeries and non-breeding haul-outs. These two studies covered most of the range of Steller sea lions in Alaska. The only area not covered by these two studies was the eastern Gulf of Alaska. I assumed the diet composition of Steller sea lions in the eastern Gulf of Alaska was the same as the diet of Steller sea lions in the central and western Gulf of Alaska.

Two limitations of the diet data are incomplete sampling coverage by time of the year and by sex/age class. Merrick *et al*. (1997) collected scat during the summer, and Trites (unpubl. data) collected scat in the summer and winter. Neither study collected scat during the spring or fall. Lacking other data, I assumed diet composition was constant year-round from the western Aleutian Islands to the Gulf of Alaska (Table 3.5). I assumed two diet compositions for Southeast Alaska: a 'summer' diet and a 'winter' diet (Table 3.5). I assumed the summer diet commenced sometime between 1 December and 31 May and the winter diet commenced sometime between 1 August and 30 September (uniform distributions). The majority of the scat collected by Merrick *et al*. (1997) and Trites (unpubl. data) were from adult females, although some scat was collected on non-breeding haulouts which would be predominantly juvenile and sub-adult male scat. Although there does appear to be a difference in diet between rookeries and haulouts (Trites unpubl. data), it is difficult to translate this difference into specific sex or age differences. As a result, I used one diet composition (combined rookery and haulout data) for both sexes and all ages.

In addition to sampling limitations, there are at least two other potential biases associated with using scat data to assess diet composition. The first potential bias is the possibility that some of the consumed prey species are not present in the scat samples. Cartilaginous fish or fish with small or fragile bony structures may be completely digested and not evident in scat (Olesiuk *et al.* 1990). For example, in captive harbour seal feeding trials, the number of hard parts recovered in scat ranged from 1.08 per smelt to 7.27 per salmon (Cottrell *et al.* 1996; Cottrell and Trites in review). Thus, there was a greater chance of an individual smelt being missed compared to an individual salmon. However, small fish are likely consumed in larger numbers which would increase the likelihood of detecting their presence in scat (A. Trites pers. comm.).

The second potential source of bias arises from using frequency of occurrence data to estimate the percent biomass each prey species represents in the diet. Frequency of occurrence is calculated by dividing the number of samples in which a prey species occurs by the total number of occurrences of all prey species in all samples. This proportion can then be used as the percent biomass that the prey species represents in the diet. This technique assumes that all prey species are consumed in equal quantities, which overestimates the importance of prey consumed in small quantities, and underestimates the importance of prey consumed in large quantities. To avoid this bias, it is best to perform a volumetric analysis (e.g., estimate prey size from otolith size), but otoliths are usually not available from Steller sea lion scat (Merrick *et al.* 1997).

Another way to reduce this bias is to use the split-sample frequency of occurrence method (Olesiuk *et al.* 1990). This technique assumes that the prey identified in a scat sample represent all the prey consumed in a meal, and that all prey species comprising a meal are consumed in equal quantities. Thus, a prey species that occurs alone in a scat sample is considered more important than a species that occurs with other species. Both Merrick *et al*. (1997) and Trites (unpubl. data) present split-sample frequency of occurrence data, so these data were used as the median percent biomass each prey species represented in the diet ($prey_i$ in Eq. 3.5 and 12; Table 3.5). In order to incorporate uncertainty associated with these estimates, the percent biomass each prey species represented in a given diet was randomly sampled from a triangular distribution with upper and lower limits equal to ± 20% of the median.

Energetic Density of Prey ($ED_{prey,i}$)

In addition to diet composition, the model also required the energetic density of each prey species (energy content per unit mass, $ED_{prey,i}$ in Eq. 3.12). The energy content of fish is generally determined using bomb calorimetry and depends on the chemical composition of the fish, especially lipid content (Perez 1994). Thus, energetic density may vary with age (older fish store more lipid), season (feeding or fasting), and reproductive status (spawning) (Harris *et al.* 1986; Smith *et al.* 1988; Paul *et al.* 1998a; Paul *et al.* 1998b). The energetic densities of some Alaskan/North Pacific fish species are presented in Table A3.1.

Gadids consumed by Steller sea lions were primarily walleye pollock (Merrick *et al.* 1997). The length of pollock consumed by Steller sea lions averages approximately 20 – 30 cm long (juvenile pollock), although there is a lot of variation (Pitcher 1981; Calkins and Goodwin 1988; Calkins 1998). Pollock of this size (and Pacific cod) have energetic densities around 3 – 5 kJ g wet weight^{-1}, and do not exhibit marked changes in energetic density throughout the year (Table A3.1). I used a sampling distribution of 4.0, 3.0 – 5.0 kJ g^{-1} for gadids in the summer and winter (where summer and winter were defined as in diet composition).

Small schooling fish consumed by Steller sea lions were mainly Pacific herring or Pacific sand lance, but capelin and eulachon were also eaten (Merrick *et al.* 1997). In the summer, mature small schooling fish have energetic densities between 6 and 11 kJ g^{-1} (Table A3.1). However, data for herring suggest energetic density drops during the over-winter fast to around 6 kJ g^{-1} (Table A3.1). I used sampling distributions of 8.5, 6.0 – 11.0 kJ g^{-1} and 5.0, 4.0 – 6.0 kJ g^{-1} for small schooling fish in the summer and winter respectively.

Data were also available for the energetic densities of flatfish, other demersal fish, and cephalopods (Table A3.1). I used sampling distributions of 3.0 – 5.0 kJ g^{-1}, 3.0 – 6.0 kJ g^{-1}, and 4.0 – 6.0 kJ g^{-1} for these three prey categories respectively (summer and winter). There were less data available for the energetic densities of Pacific salmon and Atka mackerel. I could only find whole body energetic density estimates for juvenile Atka mackerel (Table A3.1). This was unfortunate as salmon and Atka mackerel are dominant prey categories west of Southeast Alaska (Merrick *et al.* 1997). I used sampling distributions of 5.0 – 9.0 kJ g^{-1} and 3.0 – 6.0 kJ g^{-1} for the energetic densities of Pacific salmon and Atka mackerel respectively (summer and winter).

Table A3.1. Energetic densities of some Alaskan/North Pacific fish species. Where necessary, calories converted to Joules assuming 4.184 J cal^{-1} (Schmidt-Nielsen 1990).

Prey Species	Energetic Density (kJ g wet mass $^{-1}$)	Details (location, time of year, age, size)	Source
walleye pollock	4.64	Bering Sea and/or Gulf of Alaska; summer and winter (no difference); 43 – 53 cm	Perez (1994)
	2.73	Gulf of Alaska, eastern Aleutian Islands; summer; age 0; 5.4 – 8.7 cm	Van Pelt et al. (1997)
	5.90	Bering Sea	Miller (1978)
	3.5 – 3.6	Prince William Sound; spring/summer; ages 0 & 2	Anthony and Roby (1997)
	3.99 (winter), 6.25 (summer)	Gulf of Alaska; summer and winter; juveniles; <100 g	Harris et al. (1986)

Table A3.1 cont.

Prey Species	Energetic Density (kJ g wet mass $^{-1}$)	Details (location, time of year, age, size)	Source
	3.68 – 4.03 (ripe), 3.26 – 3.41 (spent)	Gulf of Alaska; March and April; adults (ripe in March and spent in April); approx. 95 cm	Smith et al. (1988)
	2.7 (summer), 3.6 (fall), 3.4 – 4.0 (spring)	Prince William Sound; summer, fall, and spring; age 0 (metamorphosis in May); <11 cm	Paul et al. (1998b)
Pacific cod	3.93		Perez (1994)
	2.94	Gulf of Alaska, eastern Aleutian Islands; summer; juveniles	Van Pelt et al. (1997)
	2.8 – 3.4	Prince William Sound; spring/summer; ages 0 & 1	Anthony and Roby (1997)
	4.00 – 4.30 (March), 3.33 – 3.38 (July), 3.60 – 4.92 (November)	Gulf of Alaska; spring – early winter; adults (spawn in April)	Smith et al. (1990)

Table A3.1 cont.

Prey Species	Energetic Density (kJ g wet mass $^{-1}$)	Details (location, time of year, age, size)	Source
tomcod	2.8	Prince William Sound; spring/summer; age 0	Anthony and Roby (1997)
capelin	7.03	Bering Sea and/or Gulf of Alaska; summer	Perez (1994)
	3.54 – 4.84	Gulf of Alaska, eastern Aleutian Islands; summer; ages 1 & 2	Van Pelt et al. (1997)
	5.48	Bering Sea	Miller (1978)
	3.8	Prince William Sound; spring/summer; adults	Anthony and Roby (1997)
Pacific herring	8.58	Bering Sea and/or Gulf of Alaska; summer	Perez (1994)

Table A3.1 cont.

Prey Species	Energetic Density (kJ g wet mass $^{-1}$)	Details (location, time of year, age, size)	Source
Pacific herring	4.0 – 7.1	Prince William Sound; spring/summer; ages 0 – 2	Anthony and Roby (1997)
	fall: 5.7 – 8.0 (ages 0,1), 9.4 – 10.2 (ages>2); spring: 4.4 (ages 0,1), 5.2 – 6.3 (ages>2)	Prince William Sound; spring and fall; ages 0 – 7 (fast during winter)	Paul et al. (1998a)
	5.2 (early winter), 3.4 – 3.8 (spring)	Gulf of Alaska; winter and spring; age 0 (fast during winter); approx. 8 – 9 cm	Paul and Paul (1998)
eulachon	11.00	Bering Sea and/or Gulf of Alaska; spring and summer	Perez (1994)
Pacific sand lance	3.18 – 5.67	Gulf of Alaska, eastern Aleutian Islands; summer; ages 0 – 2	Van Pelt et al. (1997)
	4.2 – 6.3	Prince William Sound; spring/summer; ages 0 – 2	Anthony and Roby (1997)

Table A3.1 cont.

Prey Species	Energetic Density (kJ g wet mass $^{-1}$)	Details (location, time of year, age, size)	Source
arrowtooth flounder	5.15	Bering Sea and/or Gulf of Alaska; summer and winter	Perez (1994)
yellowfin sole	May: 3.33 (juveniles), 3.47 (adults); June: 4.44 (juveniles), ≈4.5 (adults) (approx. linear change between these months)	Gulf of Alaska; year-round; adults (spawn in May & June) and juveniles	Paul et al. (1993)
sculpins (Cottidae)	3.51 – 5.19	Bering Sea and/or Gulf of Alaska; four species	Perez (1994)
	3.0 – 3.6	Prince William Sound; spring/summer; two species	Anthony and Roby (1997)
rockfish (*Sebastes* spp.)	5.77 – 6.23	Bering Sea and/or Gulf of Alaska; four species	Perez (1994)
	2.97	Gulf of Alaska, eastern Aleutian Islands; summer; juveniles	Van Pelt et al. (1997)

Prey Species	Energetic Density (kJ g wet mass $^{-1}$)	Details (location, time of year, age, size)	Source
squid	3.85 – 6.53	Bering Sea and/or Gulf of Alaska; five species	Perez (1994)
	3.81	Gulf of Alaska, eastern Aleutian Islands; Gonatidae; summer; 7.1 – 13.5 cm	Van Pelt et al. (1997)
Atka mackerel	4.02	Gulf of Alaska, eastern Aleutian Islands; summer; juveniles; 7.0 – 7.1 cm	Van Pelt et al. (1997)
pricklebacks (Stichaeidae)	4.4 – 4.5	Prince William Sound; spring/summer; two species	Anthony and Roby (1997)