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A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA

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ABSTRACT: A generalized bioenergetic model was used to estimate the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Inputs included age- and sex-specific energy requirements by date, population size and composition, and diet composition and energy content. Error in model predictions was calculated using uncertainty in parameter values and Monte Carlo simulation methods. Our model suggests that energy requirements of individuals were generally lowest in the summer breeding season (June to August) and highest in the winter (December to February) and spring (March to May) mainly due to changes in activity budgets. Predicted relative daily food requirements were highest for young animals (12 ± 3% SD and 13 ± 3% of body mass for 1 yr old males and females respectively) and decreased with age (5 ± 1% and 6 ± 1% of body mass for 14 yr old males and 22 yr old females respectively). The mean daily food requirement of pregnant females predicted by the model was only marginally greater than the predicted mean daily food requirement of non-pregnant females of the same age. However, the model suggested that the mean daily food requirement of females nursing pups was about 70% greater than females of the same age without pups. Of the 3 sets of model parameters (diet, population, and bioenergetic), uncertainty in diet and bioenergetic parameters resulted in the largest variation in model predictions. The model provides a quantitative estimate of the Steller sea lion population's food requirements and also suggests directions for future research.

KEY WORDS: Bioenergetic model · *Eumetopias jubatus* · Food consumption · Steller sea lion · Sensitivity analysis

INTRODUCTION

Since the late 1970s, the Alaskan population of Steller sea lions *Eumetopias jubatus* has decreased by over 70% (Loughlin et al. 1992, Trites & Larkin 1996). One of the leading hypotheses regarding the cause of this decline is nutritional deficiency caused by fishing of prey, or natural reductions in its abundance, availability and/or quality (Alverson 1992, Merrick et al. 1997, Calkins et al. 1998). Central to evaluating the nutritional stress hypothesis is the need to quantify the prey requirements of Steller sea lions. Prey 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 (Antonelis et al. 1987, Murie & Lavigne 1991, Ohizumi & 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. A second method is to infer wild feeding rates from feeding rates of captive marine mammals (Innes et al. 1987, Perez et al. 1990, Nordøy et al. 1995). A

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third method for estimating food consumption is bioenergetic modeling.

Biological systems are governed by the laws of thermodynamics and theoretically reach steady states where energy influx is equal to energy efflux (Wiegert 1968, Galluci 1973). In reality, a true steady state is never reached in nature, but in the long term any biological system must be in energy balance such that

$$\text{Consumption} = \text{Feces} + \text{Urine} + \text{Respiration} + \text{Production} \quad (1)$$

where 'Consumption' is energy ingested, 'Feces' and 'Urine' are energy egested, 'Respiration' is energy used for work (degraded to heat), and 'Production' is energy deposited as tissue growth, fat storage, eggs, sperm, embryos, exuviae etc. (Klekowski & Duncan 1975).

The energy consumption of marine mammals has frequently been estimated using bioenergetic models (Hinga 1979, Naumov & Chekunova 1980, Ashwell-Erickson & Elsner 1981, Doidge & Croxall 1985, Hiby & Harwood 1985, Lavigne et al. 1985, Worthy 1987a, Øritsland & Markussen 1990, Härkönen & Heide-Jørgensen 1991, Markussen & Øritsland 1991, Ryg & Øritsland 1991, Markussen et al. 1992, Olesiuk 1993, Ugland et al. 1993, Mohn & Bowen 1996, Stenson et al. 1997). These models range in detail from simple equations (with few parameters) representing an average individual's annual energy consumption, to detailed energy budgets (with many parameters) for each age- and sex-class and day of the year. In most of these studies, estimates of individual energy consumption have been multiplied by population size to estimate population energy consumption, and converted to estimates of 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, these models can be used to examine the sensitivity of food consumption estimates to uncertainty in parameter values (Olesiuk 1993, Mohn & Bowen 1996, Shelton et al. 1997). This provides a measure of confidence in the model predictions and also 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 & Harwood (1985) examined the relationship between population size and per capita food consumption for a hypothetical grey seal population.

The first objective of our study was to develop a generalized bioenergetic model for Steller sea lions in Alaska, and to apply this model to answer such questions as: (1) How do energy and food requirements vary with age, sex, and reproductive status? (2) How do energy and food requirements vary seasonally? (3) How much food does the entire Alaskan Steller sea lion population consume on an annual basis? Our second objective was to calculate confidence limits for the estimates of energy and food consumption based on the error structure of the model parameters. Our 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 structured along the bioenergetic scheme proposed by Lavigne et al. (1982). The model had 3 main components: (1) estimation of individual energy requirements (the bioenergetic component); (2) estimation of population size and composition (the population component); and (3) estimation of food requirements (the diet component). First, gross energy requirements were calculated for each age, sex, reproductive state (immature, mature, pregnant) and day of the year using the following framework (i.e. the bioenergetic model):

$$\text{GER} = \frac{P + (A \times \text{BM})}{E_{\text{HIF}} \times E_{\text{f+u}}} \quad (2)$$

where GER is gross energy requirement, P is production or energy deposition, A is an activity metabolic multiplier, BM is basal metabolism, E_{HIF} is the efficiency of utilization of metabolizable energy (or 1 minus the heat increment of feeding as a proportion of metabolizable energy), and $E_{\text{f+u}}$ is fecal and urinary digestive efficiency (metabolizable energy as a proportion of gross energy).

Next, population composition was determined using:

$$N_{i,j+1,t+1} = N_{ijt} s_{ij} \quad (3)$$

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

$$N_{0_t} = \sum_j (N_{\text{f}_{jt}} \times fec \times mat_{\text{f}_{j-1}}) \quad (4)$$

where N_0 is number of pups, N_f is number of females, fec is fecundity (number of pups born per sexually mature female per year), and $mat_{\text{f}_{j-1}}$ is the proportion of females of age j that are sexually mature at age j. 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. In reality, it is unlikely that the rate of change in population size is constant over time, and that the age structure is stable. However, we did not assume any change in population size and used estimates of survival and reproductive rates that by definition assume a stable age distribution (see 'Population parameters' below). Total breeding season population size was calculated by dividing pup counts by the proportion of the population comprised of pups.

To account for mortality throughout the year, the effective numbers of individuals of each age and sex that were alive for an entire year (N_{adjusted}) were calculated using:

$$N_{\text{adjusted}_{ijt}} = \frac{N_{ijt}(s_{ij} - 1)}{\ln(s_{ij})} \tag{5}$$

This assumes that the number of animals alive declines exponentially throughout the year. For the oldest age class, the number of individuals alive during the breeding season was multiplied by $0.5 \times (1 + s_{ij})$ 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_{ij} (proportion of individuals of sex i and age j that are sexually mature at age j). The numbers of animals of each age that were pregnant were determined using the numbers of mature females of each age and Eq. (5) substituting fec (Eq. 4) for s_{ij}. 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 requirements were calculated for animals ≥1 yr old using the diet model:

$$\text{BR}_i = \frac{\text{GER} \times prey_i}{\text{ED}_{\text{diet}}} \tag{6}$$

where BR_i is biomass requirement of prey category i, $prey_i$ is the proportion of total diet biomass comprised of prey category i, and ED_{diet} is the mean weighted (by $prey_i$) energetic density of the diet. We assumed that pups (<1 yr old) obtained all energy through nursing, therefore, their energy demands were included in their mothers' GER. Female-offspring bonds usually last <1 yr, with weaning occurring just prior to or during the breeding season (Sandegren 1970, Pitcher & Calkins 1981, Porter 1997). Prey species were grouped into 7 categories as defined by Merrick et al. (1997): Cephalopods (squid and octopus), Flatfish, Forage fish (small schooling fish species, e.g. Pacific herring and Pacific sandlance), Gadids (e.g. Pacific cod and walleye pollock), Hexagrammids (e.g. Atka mackerel), Salmon and Other. The amount of food consumed annually by the population was calculated by summing daily individual food requirements for the entire year for each age, sex, and reproductive state, and then multiplying these annual individual food requirement estimates by the effective number of individuals of each age, sex, and reproductive state in the population.

Model error. Monte Carlo simulations were used to incorporate parameter uncertainty into energy/food requirement estimates. In each run of the model, parameter values were randomly selected from assigned sampling distributions that best described their uncertainty. Thus, each run of the model produced 1 estimate of energy/food requirements, and multiple runs produced a distribution of requirement 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 to 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 to 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 & 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 individual parameters belonging to each of the main parameter groups (diet, population, bioenergetic), 1 group at a time, while holding the other parameters constant at their mean or median values. The model was then run with uncertainty in all parameters. The model was also run systematically incorporating uncertainty in parameters from all possible pairs of parameter groups, in order to examine interaction effects (Rose 1983). A further sensitivity analysis was performed on the 3 main bioenergetic parameter groups (efficiency, basal and activity metabolism, and production; Eq. 2) where diet and population parameters were held constant.

Bioenergetic parameters. Bioenergetic parameter values are summarized in Table 1 and discussed in detail in Winship (2000). 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.

Table 1. Bioenergetic parameter values used in the model (sources are in the text)

Name	Symbol	Equation	Value	Details
Fecal and urinary digestive efficiency	$E_{\mathrm{f+u}}$	(2)	0.95–0.96 0.81–0.89	Pup Non-pup: fecal = 0.90–0.96 Urinary = 0.90–0.93
Efficiency of utilization of metabolizable energy (1 – heat increment of feeding as proportion of metabolizable energy)	E_{HIF}	(2)	0.85–0.90 0.75–0.95 0.45–0.56	Maintenance Lipid deposition Protein deposition
Total energetic efficiency of energy deposition during gestation	Substituted for E_{HIF}	(2)	0.20, 0.10–0.70	
Total energetic efficiency of energy deposition during lactation	Substituted for E_{HIF}	(2)	0.775, 0.60–0.95	
Fetal mass	M	(7 to 9)	see Eq. 8 see Eq. 9	Male Female
Birth mass	M_{b}	(7 to 9)	22.4 ± 2.03 kg 19.5 ± 1.80 kg	Male Female
Postnatal mass	M	(7)	Winship et al. (2001) and see text; Richards multipliers: 1.00 ± 0.20 1.00 ± 0.16	 Males Females
Proportion of body growth that is lipid	p_{lip}	(7)	0.023 ± 0.0434 1.0 0.07-0.14	Fetus Newborn pup (first few wk) Adult
Proportion of lean body growth that is water	p_{w}	(7)	0.759 ± 0.0330 0.66–0.73	Fetus Postnatal
Proportion of energy deposited during gestation represented by fetus			0.80	
Basal metabolism	BM	(2 & 10)	2.5–3.5 × Eq. 10 1.75–2.25 × Eq. 10 Eq. 10	Birth 1 yr of age ≥8 yr of age
Proportion of time spent in the water	$water$	(11)	0.0 0.565, 0.37–0.76 0.0 0.40, 0.33–0.47 0.70, 0.63–0.77 0.815, 0.73–0.90 0.0 0.70, 0.55–0.85	0–1 mo old Immature (≥1 yr old) Mature female: 12–22 Jun Mature female: 23 Jun Mature female: 26 Jul Mature female: 1 Nov to 11 Jun Mature male: 29 May to 10 Jul Mature male: rest of year
Land metabolic rate multiplier	A_{land}	(11)	3, 2.5–3.5 1.2, 1.0–1.4	Breeding males All other animals
Water metabolic rate multiplier	A_{water}	(11)	4.0, 2.5–5.5	All animals

We assumed a fecal digestive efficiency of 0.90 to 0.96, and a urinary digestive efficiency of 0.90 to 0.93 for animals ≥1 yr old (Keiver et al. 1984, Ronald et al. 1984, Fisher et al. 1992, Mårtensson et al. 1994, Lawson et al. 1997, Rosen & Trites 2000a). This yields estimates of fecal and urinary digestive efficiency ($E_{\mathrm{f+u}}$; Eq. 2) of 0.81 to 0.89 given that $E_{\mathrm{f+u}}$ 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 to 0.96 (Oftedal & Iverson 1987).

The efficiency of utilization of metabolizable energy (E_{HIF}; Eq. 2) was defined as 1 minus the heat increment of feeding as a proportion of metabolizable energy intake. E_{HIF} equaled 0.85 to 0.90 (heat increment of feeding = 0.10 to 0.15) for maintenance energy requirements and 0.75 to 0.95 (heat increment of feeding = 0.05 to 0.25) and 0.45 to 0.56 (heat increment of feeding = 0.44 to 0.55) for fat and protein growth energy requirements respectively (Ashwell-Erickson & Elsner 1981, Gallivan & Ronald 1981, Webster 1983, Blaxter 1989, Markussen et al. 1994, Rosen & Trites 1997).

We used total energetic efficiencies (triangular sampling distribution) of 0.20 (0.10 to 0.70) for gestation and 0.775 (0.60 to 0.95) for lactation energy deposition requirements (fetus, placenta, uterine tissue and milk) (Oftedal 1985, Blaxter 1989, Robbins 1993). Total energetic efficiency is defined as 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.

Production (P; Eq. 2) is mainly growth in body mass and was calculated as the amount of energy invested in body mass per day:

$$P = \Delta M \left[p_{\text{lip}} \text{ED}_{\text{lip}} + (1 - p_{\text{lip}})(1 - p_{\text{w}}) \text{ED}_{\text{pro}} \right] \tag{7}$$

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 (39.330 kJ g^{-1}; Schmidt-Nielsen 1990), p_{w} is the proportion of lean tissue that is water, and ED_{pro} is the energetic density of protein (17.991 kJ g^{-1}; Schmidt-Nielsen 1990). We assumed that body mass was either lipid or lean tissue and that lean tissue was either protein or water.

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

$$M_t = \frac{(M_{\text{b}} / 0.936)}{(1 + \text{e}^{-13.256(t - 0.502)})} \tag{8}$$

for males, and

$$M_t = \frac{(M_{\text{b}} / 0.952)}{(1 + \text{e}^{-13.916(t - 0.49)})} \tag{9}$$

for females, where t is fetal age (d) divided by 365 (0 = implantation, assumed to be 1 October), and M_{b} is birth mass (Winship 2000). Setting the asymptote of these models as a multiple of birth mass allowed us 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. We used birth masses (±SD) of 22.4 ± 2.03 kg for males and 19.5 ± 1.80 kg for females (Davis et al. 1996).

Mass of animals from 1 to 2 yr of age was calculated using the male and non-pregnant female Richards growth models developed by Winship et al. (2001). Uncertainty was incorporated into the Richards growth models by using gross multipliers of 1.0 ± 0.20 for males and 1.0 ± 0.16 for females (Winship 2000). Changes in mass between birth and 1 yr of age were assumed to be linear. Winship et al. (2001) found that the majority of growth in body mass of Steller sea lions (non-pups) occurred during a seasonal growth period which started in late summer (August to September) and ended in the spring (March to April). Very little growth in body mass occurred during the breeding season (May to July). In order to incorporate this seasonality in growth, the mass of sea lions >2 yr old was calculated at 1 yr intervals using the Richards growth models from Winship et al. (2001). All growth between these ages was assumed to occur during a seasonal growth period during which growth was linear. We assumed the seasonal growth period started between 1 August and 15 September and ended between 1 March and 15 April (using uniform sampling distributions for start and end dates).

The composition of fetal tissue growth (p_{lip} and p_{w}) was assumed to be the same as newborn Steller sea lion body composition: $p_{\text{lip}} = 0.023 \pm 0.0434$ and $p_{\text{w}} = 0.759 \pm 0.0330$ (Davis et al. 1996). After parturition, growth was assumed to be entirely lipid ($p_{\text{lip}} = 1.0$), until body composition reached adult proportions of lipid and lean tissue. Thereafter, the composition of growth was assumed to be the same as adult body composition: $p_{\text{lip}} = 0.07$ to 0.14, and $p_{\text{w}} = 0.66$ to 0.73 (Olesiuk & Bigg 1987, Davis et al. 1996, Pitcher et al. 2000).

A second component of P (Eq. 2) is growth of the placenta and uterus of pregnant females. We 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). We also assumed that the additional uterine energy was deposited linearly over the gestation period.

Basal metabolism (BM in kJ d^{-1}; Eq. 2) of sea lions ≥8 yr old was calculated from Kleiber's (1975) predictive equation:

$$\text{BM} = 292.88 \times M^{0.75} \tag{10}$$

where M is body mass (kg). We assumed that the basal metabolic rates of juveniles were elevated and declined linearly from birth (2.5 to 3.5 × Eq. 10) to 1 yr of age (1.75 to 2.25 × Eq. 10), and from 1 yr of age to 8 yr of age (Rosen & Trites 1997, D.A.S.R. unpubl. data). The elevated basal metabolic rate of juveniles is properly termed 'resting metabolic' rate since only adult animals meet basal requirements as defined by Kleiber (1975). However, for consistency we used the term 'basal metabolic rate'.

The energetic cost of activity was incorporated using a multiplier of basal metabolic rate (A; Eq. 2) for each sex, sexual state (immature or mature) and day of the year, according to:

$$A = \mathit{water} \times A_{\text{water}} + (1 - \mathit{water}) \times A_{\text{land}} \tag{11}$$

where *water* is the proportion of time spent in the water, A_{water} is a multiplier of basal metabolic rate for water, and A_{land} is a multiplier of basal metabolic rate for land. It was assumed that time was either spent on land or in the water.

Active metabolism is the energy that organisms expend to overcome forces (e.g. drag when swimming). It is also a function of the distance traveled 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 to maintain body temperature (thermoregulation). Each of these factors scale with body mass in different ways complicating 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 the scaling factor used here for basal metabolic rate (0.75). For the sake of simplicity, we effectively assumed that active metabolism was proportional to $M^{0.75}$ by assuming it to be a constant multiple of basal metabolic rate (Eq. 10). 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 & 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 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 (≥1 yr old spent a constant mean proportion of their time at sea throughout the year (*water* = 0.565, 0.37 to 0.76; Merrick & Loughlin 1997, Swain & Calkins 1997, Trites & Porter 2001). We assumed that pups <1 mo 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 mo to 1 yr 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).

We assumed mature females were entirely on land (*water* = 0) from 12 to 22 June, i.e. during the perinatal period (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 to 0.47) of their time at sea. This proportion increased linearly to 0.70 (0.63 to 0.77) on 26 July (Higgins et al. 1988, Swain 1996, Merrick & Loughlin 1997, Milette 1999). It then increased linearly from this point to 0.815 (0.73 to 0.90) on 1 November (Swain 1996, Merrick & Loughlin 1997, Trites & Porter 2001). Mature females continued to spend this proportion of time at sea through to the next breeding season.

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

We used an 'on land' multiplier of basal metabolic rate (A_{land}) of 1.2 (1.0 to 1.4) since activity levels on land are generally low and animals are often resting or sleeping (Ashwell-Erickson & Elsner 1981, Worthy 1987b). The only exception was breeding males on territories for which we assumed A_{land} = 3 (2.5 to 3.5) (Anderson & Fedak 1987, Boyd & Duck 1991). We used an 'in water' multiplier of basal metabolic rate

Table 2. Median annual survival (s_{ij}, Eq. 3) and maturity (mat_{ij}, Eq. 4) rates for Steller sea lions by sex and age. Survival rates and female maturity rates are from life tables by Trites & Larkin (1992) and York (1994). Female survival rates from these studies were multiplied by 1.017 to obtain a finite rate of population increase (λ) of 1.0. Male maturity rates were estimated from Pitcher & Calkins (1981)

Age (yr)	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

(A_{water}) of 4.0 (2.5 to 5.5) for all animals (Costa & Gentry 1986, Costa et al. 1989, Reilly & Fedak 1991, Castellini et al. 1992, Hindell et al. 1992, Arnould et al. 1996).

Population parameters. Rates of survival (s_{ij}; Eq. 3), female maturity ($mat_{\mathrm{f}j}$; Eq. 4) and fecundity (fec; Eq. 4) were taken from life tables that assumed a stable population (neither increasing or decreasing in size) of Steller sea lions (Table 2; Trites & Larkin 1992, York 1994). Median female annual survival rates from those studies were multiplied by 1.017 to obtain a finite rate of population increase (λ) of 1.0. Although the entire population of Steller sea lions in Alaska was declining in the late 1990s (the larger, western population was declining: Sease & Loughlin 1999; the smaller, eastern population was increasing: Calkins et al. 1999), there is no information available with which to determine the relationship between the demographics and the rate of change in size of a population of Steller sea lions. Thus, we used a life table that assumed a stable population. Since the population was declining, however, it may have had proportionally more older animals than we assumed, which would have resulted in an underestimation of population size and thus of the total food requirements of the population. In order to incorporate uncertainty, annual survival rates were sampled from uniform distributions with upper and lower limits equal to the medians ± 0.05. The fecundity rate used was 0.53 to 0.73 pups per female per year. Maturity rates of females aged 3 to 5 yr were sampled from uniform distributions with upper and lower limits equal to the medians ± 0.1. We assumed that the earliest age of male sexual maturity was 3 yr (median of 20% mature at 3 yr) and that the proportion of males which were sexually mature increased linearly with age so that all males were mature by 7 yr of age (Table 2; Pitcher & Calkins 1981). Maturity rates of males aged 3 to 6 yr 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 yr respectively (Trites & Pauly 1998). We assumed that 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 0.258 pups per adult (males and females) during the breeding season, such that pups comprised 20% of the population.

Total breeding season population size was estimated for Alaska using pup count data from the US National Marine Fisheries Service and Alaska Department of Fish and Game surveys done in June and July 1998 (Sease & Loughlin 1999). A total of 13607 pups were counted from SE Alaska through the western Aleutian Islands (excluding Walrus Island in the Pribilof Islands). We assumed that the actual number of pups born could have been as much as 20% 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 & Larkin 1996). The number of pups was therefore assumed to be 13607 to 16328. This results in a total breeding season population size estimate (pups and non-pups) of 66347 to 79615, assuming the median stable age structure (Table 2).

Diet parameters. The median percentage of biomass that each prey species category represented in the diet ($prey_i$; Eq. 6) was: Cephalopods 3.5%, Flatfish 3.1%, Forage 9.8%, Gadids 34.2%, Hexagrammids 23.2%, Other 7.4%, and Salmon 18.8%. This diet composition was calculated by applying the split-sample frequency of occurrence method (Olesiuk et al. 1990) to scat data reported by Merrick et al. (1997) and A. W. Trites & D. G. Calkins (unpub. data) for Alaska in the 1990s. Merrick et al. (1997) collected scat in 6 regions of Alaska from the western Aleutian Islands through the Gulf of Alaska; Trites & Calkins collected scat in SE Alaska. The diet composition we used here was a weighted average (by pup counts; Sease & Loughlin 1999) of the diet in these 7 regions of Alaska. The majority of these data were from breeding rookeries in the summer (June to August). We assumed that diet remained consistent throughout the year for both sexes and all ages, although we recognize that diet likely varies with age, sex, and season. Unfortunately data are not currently available to determine what these differences might be.

There are at least 2 potential biases associated with estimating diet from scats. First, it is possible that some of the prey species consumed are completely digested and are not present in the scat samples (Bowen 2000). Second, the split-sample frequency of occurrence technique used to estimate the proportions of prey consumed has several assumptions (Olesiuk et al. 1990). The validity of using split-sample frequencies of occurrence of prey to estimate the biomass composition of the diet depends on the validity of these assumptions. Olesiuk et al. (1990) and Olesiuk (1993) estimated the error associated with a key assumption of the split-sample frequency of occurrence technique (i.e. all prey categories in a scat are consumed in equal quantities) by calculating the minimum and maximum split-sample frequencies of occurrence of prey categories. We considered their estimates of this error to approximate the total potential error in estimating diet from scats. We randomly sampled the diet composition ($prey_i$) from triangular distributions with upper and lower limits equal to ±45% of medians ≥10%, or ±98% of medians <10%, where the limits approximated the maximum and

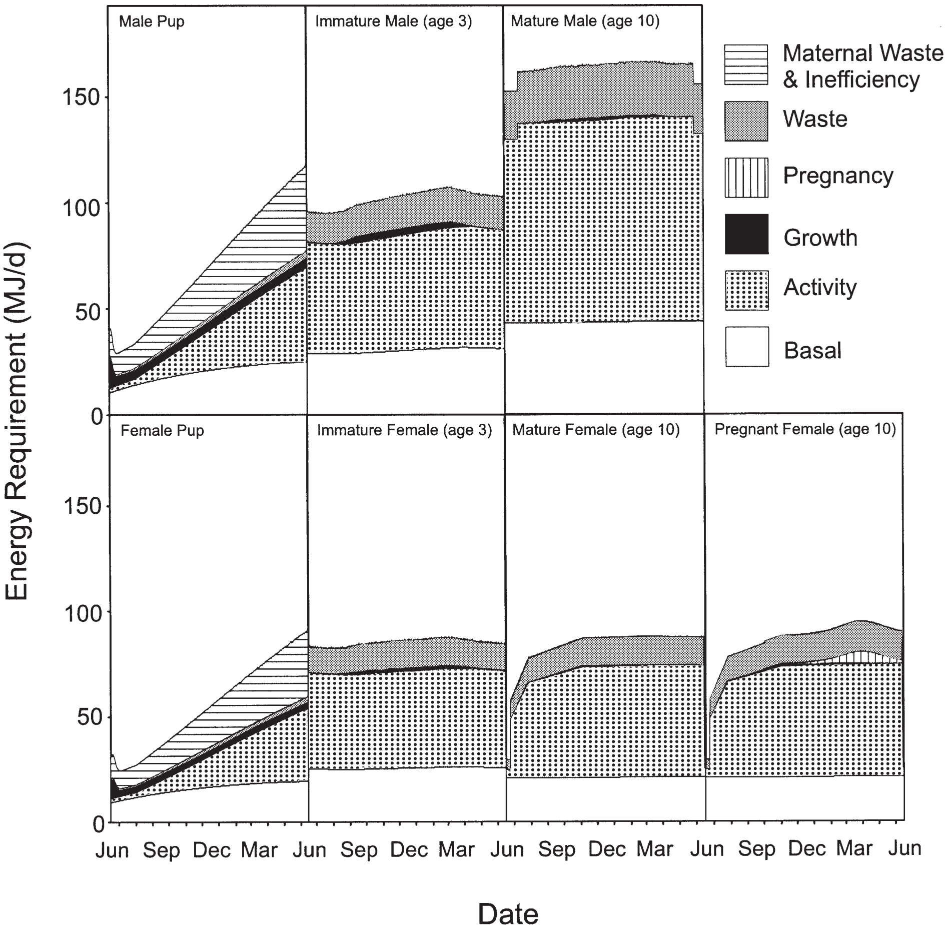

Fig. 1. Energy requirements of individual Steller sea lions by day of the year. The amount of metabolizable energy required for different components of the energy budget is shown along with the energy lost as waste (feces and urine). Total pup energy requirements represent the amount of energy a female would require to support a pup (i.e. total pup energy requirements include energy lost by the mother as waste and the inefficiency of milk synthesis). Note: these are plots of energy requirements, not energy consumption (e.g. mature males do not consume energy during the breeding season fast: late May to early July)

minimum split-sample frequencies of occurrence. These percentages were then standardized to sum to 100% for any given diet.

The energetic density of each diet (ED_{diet}; Eq. 6) was calculated from:

$$ED_{diet} = \sum_i prey_i ED_i \qquad (12)$$

where ED_i is the energetic density of prey species category i. The energetic densities (kJ g^{-1}) of the prey categories were: Cephalopods 4.0 to 6.0, Flatfish 3.0 to 5.0, Forage fish 7.5, (4.0 to 11.0), Gadids 4.0 (3.0 to 5.0), Hexagrammids 3.0 to 6.0, Salmon 5.0 to 9.0, and Other 3.0 to 6.0 (Miller 1978, Harris et al. 1986, Smith et al. 1988, 1990, Paul et al. 1993, 1998a,b, Perez 1994, Anthony & Roby 1997, Van Pelt et al. 1997, Paul & Paul 1998). For all prey categories, we assumed 1 energetic density for the entire year.

RESULTS

Daily energy/food requirements of individuals

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. 1, Table 3). 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 requirement (±SD) to nurse a male pup was 29 ± 4.6 MJ and to nurse a female pup was 25 ± 4.0 MJ (2 to 3 wk after parturition), while the maximum daily energy requirements were 118 ± 29.9 MJ and 91 ± 21.9 MJ respectively (just prior to weaning). Near the end of a pup's first year of life, the energy required by a 10 yr old

Table 3. Total energy requirements (GJ) of individual Steller sea lions (±SD) in each season. The seasons are: Summer (1 June to 31 August), Autumn (1 September to 30 November), Winter (1 December to 28 February), and Spring (1 March to 31 May). Fetus and pup energy requirements represent the amount of energy a female would require to support a fetus and a pup respectively. SD obtained using Monte Carlo simulations (1000 runs). Note: for a given age (or year of life) summer includes the first 2.5 mo (15 June to 31 August) and the last 2 wk (1 June to 14 June)

Age	Male				Female			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Fetus	0.035 ± 0.020	0.046 ± 0.020	0.210 ± 0.091	0.510 ± 0.212	0.026 ± 0.015	0.040 ± 0.017	0.193 ± 0.084	0.439 ± 0.185
Pup	4.34 ± 0.91	4.91 ± 0.96	7.06 ± 1.51	9.49 ± 2.10	3.48 ± 0.66	3.89 ± 0.69	5.52 ± 1.07	7.36 ± 1.48
1	7.76 ± 1.68	7.72 ± 1.67	7.76 ± 1.71	8.15 ± 1.73	6.37 ± 1.23	6.49 ± 1.27	6.69 ± 1.33	7.13 ± 1.38
2	8.20 ± 1.77	8.39 ± 1.80	8.66 ± 1.88	8.93 ± 1.88	7.18 ± 1.39	7.33 ± 1.42	7.54 ± 1.49	7.78 ± 1.49
3	8.84 ± 1.89	9.08 ± 1.92	9.35 ± 2.02	9.60 ± 2.00	7.76 ± 1.52	9.39 ± 1.91	9.62 ± 2.00	9.84 ± 1.98
4	9.46 ± 2.00	9.75 ± 2.04	10.02 ± 2.14	10.23 ± 2.11	7.80 ± 1.51	9.37 ± 1.88	9.47 ± 1.95	9.61 ± 1.91
5	11.15 ± 2.10	11.75 ± 2.51	12.04 ± 2.63	12.22 ± 2.53	7.57 ± 1.45	9.05 ± 1.80	9.06 ± 1.85	9.14 ± 1.80
6	11.69 ± 2.18	12.37 ± 2.61	12.63 ± 2.73	12.71 ± 2.61	7.15 ± 1.36	8.52 ± 1.68	8.46 ± 1.72	8.49 ± 1.66
7	12.06 ± 2.24	12.78 ± 2.68	12.96 ± 2.79	12.90 ± 2.64	6.59 ± 1.25	7.83 ± 1.53	7.72 ± 1.56	7.70 ± 1.49
8	12.51 ± 2.33	13.30 ± 2.79	13.74 ± 2.96	14.09 ± 2.88	6.16 ± 1.17	7.38 ± 1.44	7.50 ± 1.52	7.73 ± 1.50
9	13.85 ± 2.57	14.38 ± 3.03	14.54 ± 3.15	14.91 ± 3.05	6.31 ± 1.20	7.56 ± 1.48	7.66 ± 1.55	7.89 ± 1.53
10	14.60 ± 2.71	14.87 ± 3.15	14.78 ± 3.21	15.17 ± 3.11	6.45 ± 1.23	7.71 ± 1.51	7.80 ± 1.58	8.03 ± 1.56
11	14.86 ± 2.76	15.03 ± 3.18	14.84 ± 3.23	15.23 ± 3.12	6.56 ± 1.25	7.83 ± 1.53	7.92 ± 1.60	8.15 ± 1.58
12	14.93 ± 2.77	15.07 ± 3.19	14.85 ± 3.23	15.24 ± 3.12	6.65 ± 1.27	7.94 ± 1.55	8.02 ± 1.62	8.25 ± 1.60
13	14.95 ± 2.77	15.08 ± 3.20	14.85 ± 3.24	15.25 ± 3.13	6.73 ± 1.28	8.03 ± 1.57	8.10 ± 1.64	8.34 ± 1.62
14	14.95 ± 2.77	15.08 ± 3.20	14.85 ± 3.24	15.25 ± 3.13	6.80 ± 1.30	8.11 ± 1.59	8.17 ± 1.66	8.41 ± 1.63
15					6.86 ± 1.31	8.17 ± 1.60	8.23 ± 1.67	8.47 ± 1.65
16					6.91 ± 1.32	8.23 ± 1.61	8.29 ± 1.68	8.53 ± 1.66
17					6.95 ± 1.32	8.28 ± 1.62	8.33 ± 1.69	8.57 ± 1.66
18					6.99 ± 1.33	8.32 ± 1.63	8.37 ± 1.70	8.61 ± 1.67
19					7.02 ± 1.34	8.35 ± 1.63	8.40 ± 1.71	8.65 ± 1.68
20					7.05 ± 1.34	8.38 ± 1.64	8.43 ± 1.71	8.67 ± 1.68
21					7.07 ± 1.35	8.41 ± 1.65	8.46 ± 1.72	8.70 ± 1.69
22					7.09 ± 1.35	8.43 ± 1.65	8.48 ± 1.72	8.72 ± 1.69

female to nurse a pup was approximately equal to her own energy requirement, i.e. a 10 yr 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 requirements 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 yr olds was only 14% for males and 6% for females (late July — males: 95 ± 21.0 MJ, females: 83 ± 16.6 MJ; early March — males: 108 ± 24.4 MJ, females: 88 ± 18.0 MJ). This suggests the amount of energy that immature Steller sea lions required for growth was small relative to their total energy needs.

Mature males also exhibited little variation in energy requirements throughout the year (maximum for a 10 yr old male: 167 ± 36.4 MJ d^{-1}). The most substantial change was a drop in energy requirement during the breeding season while they were maintaining territories (minimum for a 10 yr old: 153 ± 26.6 MJ d^{-1}).

Daily energy requirements of mature females were less constant than for males because the activity budgets of females were more variable. The energy needs of mature females 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 because they were primarily on land (minimum for a 10 yr old: 29 ± 4.2 MJ d^{-1}). 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 a pregnant 10 yr old (94 ± 16.5 MJ) was only 8% greater than the daily energy requirement of a non-pregnant 10 yr old at the same time of year (87 ± 16.4 MJ). This suggests that the energetic cost of gestation is small relative to total female energy requirements.

Daily food requirements per individual simply tracked daily energy requirements (compare Figs. 1 & 2) because we assumed 1 diet composition, and therefore 1 diet energetic density, all year round. In other words, the amount of food required per unit energy did not change throughout the year due to the assumed constant diet composition.

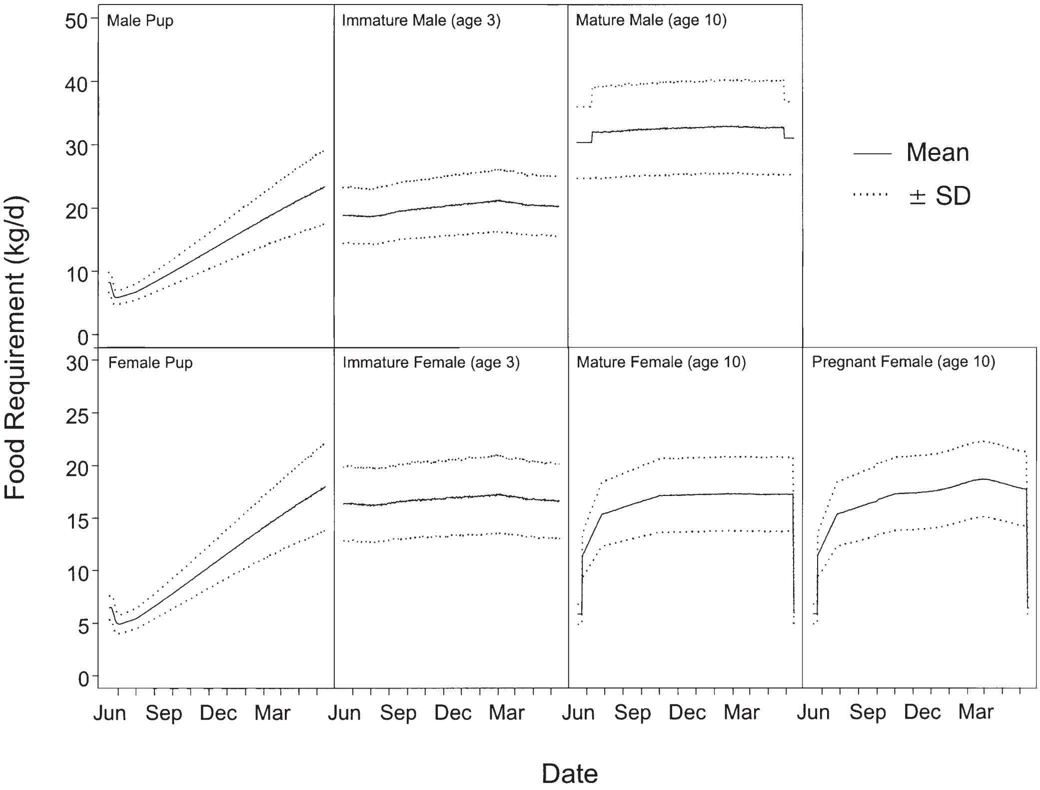

Fig. 2. Food biomass requirements of individual Steller sea lions in Alaska by day of the year. Pup food requirements represent the amount of food a female would require to support a pup. SD obtained using Monte Carlo simulations (1000 runs). Note: these are plots of food requirements, not food consumption (e.g. mature males do not consume food during the breeding season fast: late May to early July)

Maternal food requirements for nursing a pup increased throughout the pup's first year of life reflecting an increase in its energy requirements. Two weeks after parturition, a female needed to consume 6 ± 1.1 kg d^{-1} of food to nurse a male pup, and 5 ± 1.0 kg d^{-1} to nurse a female pup (based on the average Steller sea lion diet in all regions of Alaska in the 1990s). By the next breeding season, a female needed to consume 23 ± 5.7 kg d^{-1} to nourish a 1 yr old male or 18 ± 4.1 kg d^{-1} to nourish a 1 yr old female. A pregnant, 10 yr old female's own food requirement at that time was 18 ± 3.6 kg d^{-1}.

For all non-pups, daily food requirements were generally highest in winter and spring and lowest in summer. The maximum daily food requirements occurred in February, when immature 3 yr old males and females required 21 ± 5.0 kg and 17 ± 3.8 kg respectively, and mature 10 yr old males and females required 33 ± 7.4 kg and 17 ± 3.5 kg respectively. The maximum daily food requirement for a pregnant, 10 yr old female nursing a pup averaged 35 to 41 kg and occurred in early June.

Mean daily food requirements of males and females increased from 1 to 3 yr of age (Fig. 3). 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 yr of age, with concurrent increases in food requirements. Mean daily food requirements of males beyond the age of 10 yr were relatively constant from one year to the next.

In contrast to the male pattern, mean daily food requirements of females declined from ages 3 to 8 yr, after which they increased gradually to the end of the assumed female lifespan. The decrease in mean daily food requirements of females during the first few years of maturity was due to a decreasing basal metabolic rate. In the model, basal metabolic rate was elevated for animals <8 yr 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 effect of body size obscured the effect of basal metabolic rate for males that grew rapidly during this time. The gradual increase in mean daily food requirements of females after age 8 was due to a gradual increase in body size, as females continued to grow in body mass throughout their lives. The mean daily food requirement of pregnant females was only marginally greater

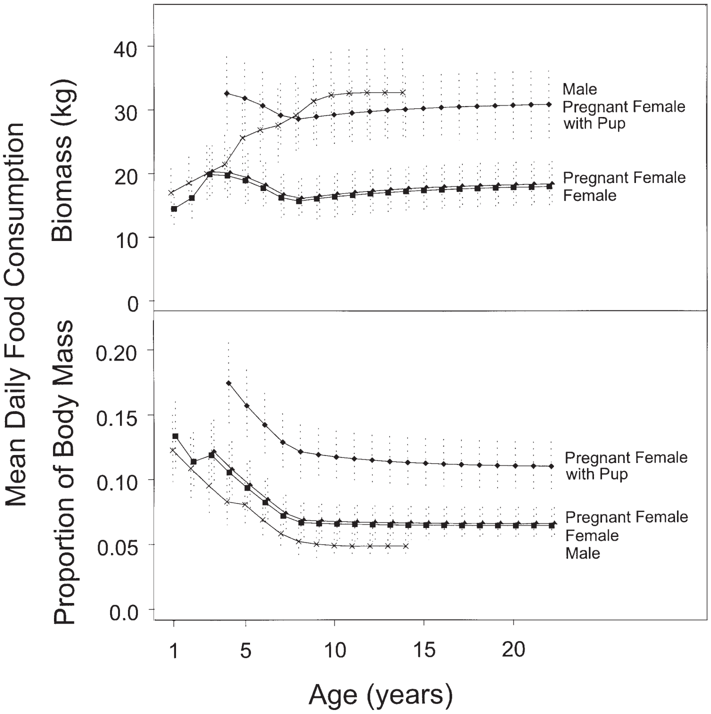

Fig. 3. Mean daily food biomass requirements of individuals (top) and mean daily food biomass requirements of individuals as a proportion of body mass (bottom) by age for Steller sea lions in Alaska, assuming that males and females mature at 3 and 5 yr of age respectively. Error bars represent ± SD, obtained using Monte Carlo simulations (1000 runs). For the bottom panel, average body masses for each year of life were used

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 for 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 <8 yr old (Fig. 3). This was due to the relationship between body size and basal metabolism (Eq. 10 and explanatory text in the same section). 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 yr for females (the assumed period of maturation for females, Fig. 3). Changes in the activity budget of females at maturity (i.e. 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 yr, Fig. 3) slowed the rate of decrease in mean daily food requirements with age, also due to an increase in the amount of time spent in the water. Food requirements per unit body mass of males and females were relatively constant with age beyond 8 yr. The maximum mean daily food requirements (as a percentage of body mass) were 12 ± 2.7% for males (age 1 yr), 13 ± 2.7% for females (age 1 yr), and 17 ± 3.1% for pregnant females (age 4 yr) with pups. The minimum mean daily food requirements (% body mass) were 5 ± 1.0%, 6 ± 1.3 %, and 11 ± 1.9% for males (age 14 yr), females (age 22 yr) and pregnant females with pups (age 22) respectively.

Annual population food requirements

The annual food requirements of the male segment of the population decreased with age (Fig. 4) due to the male survival schedule (Table 2). In each age class, there were fewer individuals than in the previous age class, resulting in decreased total food requirements. Although individual male food requirements increased with age (Fig. 3), the relatively high mortality rates obscured this effect at the population level.

Annual food requirements of the female segment of the population dropped from ages 1 to 2 yr, and increased from ages 2 to 4 yr (Fig. 4). 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 yr (Table 2). Mature females and females with pups have higher food requirements than immature females. Thus, the food requirements of ages 3 and 4 yr increased as the proportion of females that were

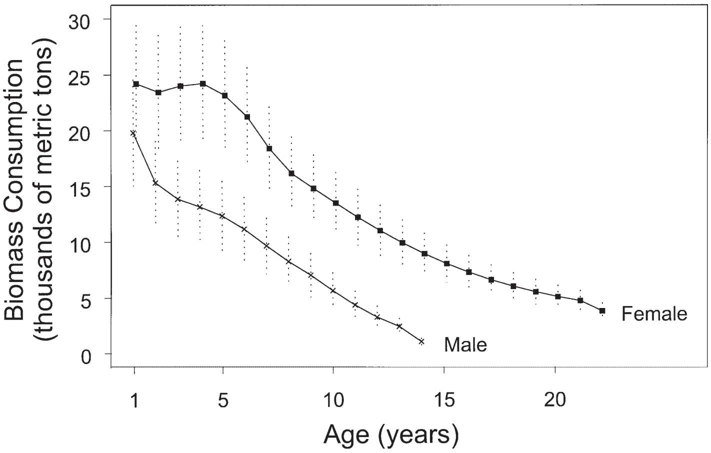

Fig. 4. Annual food biomass consumption by sex- and age-class for the Steller sea lion population in Alaska in 1998. Error bars represent ± SD obtained using Monte Carlo simulations (1000 runs)

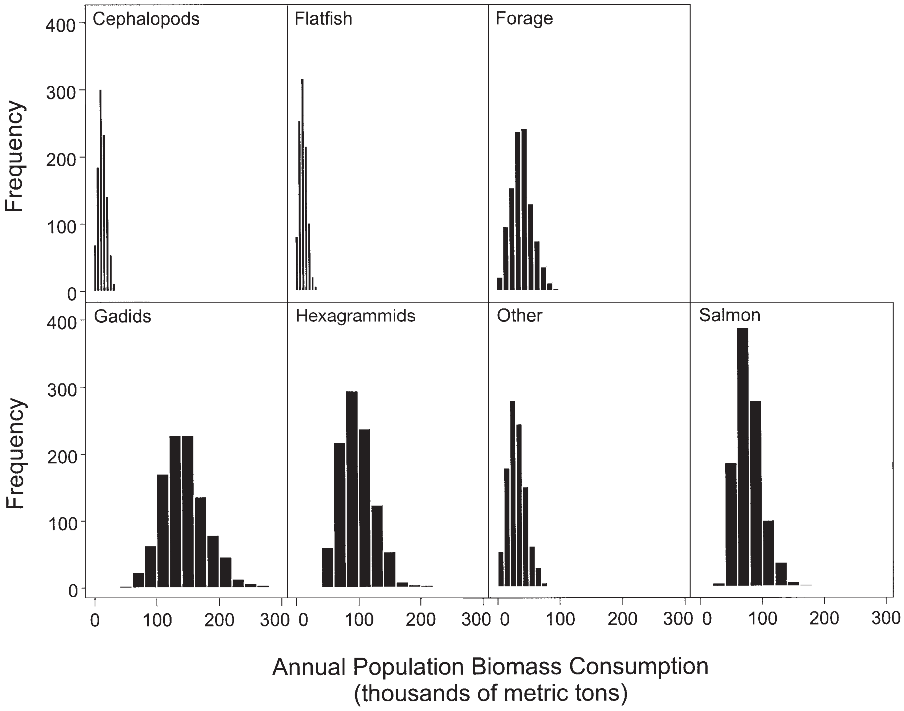

Fig. 5. Frequency distributions of estimates of annual biomass consumption of prey categories by the Steller sea lion population in Alaska in 1998. Distributions of estimates were obtained using Monte Carlo simulations (1000 runs)

mature or with pups increased. Food requirements of individual females (excluding reproduction) also increased from ages 2 to 4 yr (Fig. 3) reinforcing this trend in population food requirements. Beyond the age of 4 yr, food requirements dropped in parallel with the female survival schedule.

The entire 1998 Steller sea lion population in Alaska (total breeding season size = 73 570 ± 5350 animals) consumed an estimated $4.2 \pm 0.83 \times 10^5$ metric tons of food annually (Fig. 5, Table 4). The prey category consumed in the greatest quantity was gadids ($1.4 \pm 0.36 \times 10^5$ metric tons). Hexagrammids and salmon also accounted for a large proportion of total biomass consumption while the other prey categories were consumed in quantities $<4.1 \times 10^4$ metric tons. The coefficients of variation (CV) of these prey consumption estimates ranged from 0.25 to 0.46 and were larger for species that comprised a smaller proportion of the overall diet. This was due to the assumed larger error in the diet composition for species that comprised <10 % of diet biomass.

Sensitivity analysis

Of the 3 main parameter groups (diet, population, bioenergetic), estimates of total annual food consump-

Table 4. Annual biomass consumption (±SD) of prey categories by the Steller sea lion population in Alaska in 1998. SD obtained using Monte Carlo simulations (1000 runs). p-value is from Kolmogorov-Smirnov goodness-of-fit test for normality (Statistical Sciences 1995). A significant p-value (i.e. <0.05) indicates that the distribution is significantly different from a normal distribution

Prey category	Consumption (10^3 metric tons)								
	Mean	SD	CV	Median	Minimum	Maximum	Skew	Kurtosis	p-value
Cephalopods	14.6	6.71	0.46	13.9	0.726	46.9	0.46	0.26	<0.001
Flatfish	13.1	6.04	0.46	12.6	0.787	41.8	0.61	0.82	0.002
Forage fish	40.5	16.61	0.41	39.9	2.91	101	0.38	0.08	0.017
Gadids	144	35.64	0.25	141	55.2	279	0.47	0.46	0.001
Hexagramids	97.5	26.81	0.28	94.9	44.8	225	0.73	1.02	<0.001
Other	30.9	13.81	0.45	29.7	1.29	78.5	0.44	–0.10	0.001
Salmon	78.7	21.35	0.27	76.3	32.3	180	0.80	1.02	<0.001
Total	419	82.70	0.20	413	209	777	0.43	0.16	<0.001

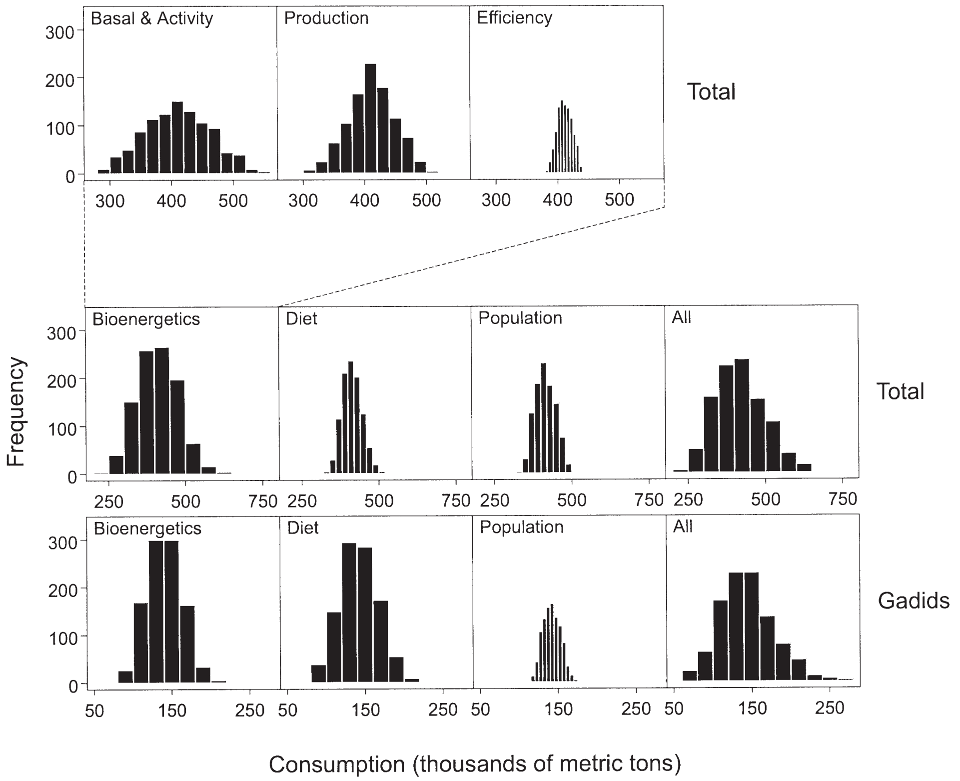

Fig. 6. Sensitivity analysis results. Frequency distributions of estimates of total annual biomass consumption and annual consumption of gadid biomass by the Steller sea lion population in Alaska in 1998 obtained using Monte Carlo simulations (1000 runs) incorporating the indicated sources of parameter uncertainty

Table 5. Sensitivity analysis of annual food biomass consumption estimates for the Steller sea lion population in Alaska in 1998. Analysis was performed using Monte Carlo simulation (1000 runs). p-value is from Kolmogorov-Smirnov goodness-of-fit test for normality (Statistical Sciences 1995). A significant p-value (i.e. <0.05) indicates that the distribution is significantly different from a normal distribution

Parameter group(s) in which uncertainty was incorporated	Mean	SD	CV	Median	Minimum	Maximum	Skew	Kurtosis	p-value
Total biomass									
Bioenergetics	410	66.4	0.16	410	223	638	0.17	−0.17	>0.100
Diet	414	31.7	0.08	412	327	526	0.30	0.01	0.069
Population	415	32.8	0.08	415	330	512	0.12	−0.51	0.003
Bioenergetics, Diet	412	74.3	0.18	409	204	686	0.37	0.21	0.019
Bioenergetics, Population	416	74.2	0.18	411	225	680	0.33	−0.06	0.012
Diet, Population	418	46.6	0.11	415	282	573	0.22	−0.05	>0.100
Bioenergetics, Diet, Population	419	82.7	0.20	413	209	777	0.43	0.16	<0.001
Efficiency	412	11.9	0.03	411	380	446	0.01	−0.46	>0.100
Metabolism	410	52.8	0.13	409	281	552	0.06	−0.51	>0.100
Production	411	38.6	0.09	411	278	554	−0.03	0.09	>0.100
Efficiency, Metabolism	411	54.6	0.13	410	278	573	0.06	−0.46	>0.100
Efficiency, Production	411	40.6	0.10	412	287	580	0.02	0.30	>0.100
Metabolism, Production	410	64.8	0.16	408	232	621	0.13	−0.33	0.055
Gadid biomass									
Bioenergetics	140	22.7	0.16	140	76.1	218	0.17	−0.17	>0.100
Diet	142	24.7	0.17	141	77.4	224	0.16	−0.17	>0.100
Population	142	11.2	0.08	142	113	175	0.12	−0.51	0.003
Bioenergetics, Diet	141	33.4	0.24	138	65.7	273	0.47	0.25	<0.001
Bioenergetics, Population	142	25.4	0.18	140	76.9	233	0.33	−0.06	0.012
Diet, Population	144	28.8	0.20	143	71.9	304	0.40	1.00	>0.100
Bioenergetics, Diet, Population	144	35.6	0.25	141	55.2	279	0.47	0.46	0.001

tion were most sensitive to the uncertainty in bioenergetic parameters, with a resulting CV of 16% (Fig. 6, Table 5). Uncertainty in diet and population parameters had much smaller effects on the variability of the estimates (CV = 8% for both). When uncertainty was incorporated in all parameters, the resulting distribution of annual population food consumption estimates was leptokurtic, positively skewed and significantly different from normal ($p < 0.001$; Table 5). Thus, the distributions of all food consumption estimates produced by our model tended to be leptokurtic and positively skewed (Table 4). The positive skew was likely due to the multiplicative relationships between some model parameters.

Of the bioenergetic parameter groups (efficiency, basal and activity metabolism and production), estimates of total annual food consumption were most sensitive to uncertainty in metabolism (CV = 13%) and production (CV = 9%) parameters (Fig. 6, Table 5). Uncertainty in efficiency parameters had only a small effect on the variability of the estimates (CV = 3%). In general, incorporating error in each bioenergetic parameter group resulted in normally distributed estimates of population food requirements.

Estimates of the biomass of individual prey categories consumed annually by the entire population were more sensitive to error in diet parameters than were estimates of total food consumption. For example, uncertainty in diet parameters resulted in a CV of 17% for estimates of annual gadid consumption, but a CV of only 8% for estimates of total annual food consumption (all prey categories combined; Table 5). This resulted in higher overall CVs for estimates of consumption of individual prey categories (0.25 to 0.46) relative to estimates of total food consumption (0.20; Table 4). Uncertainty in diet parameters had the largest effect on the CVs of estimates of consumption of prey categories that comprised only a small proportion of total diet biomass (e.g. uncertainty in diet parameters resulted in CVs of 46% for estimates of cephalopod and flatfish consumption).

DISCUSSION

We constructed a bioenergetic model to estimate the food requirements of Steller sea lions. Our 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 & Day 1977, Keen & Spain 1992). It has been difficult to measure the food consumption of wild Steller sea lions. Our model provides the first comprehensive estimates of their food requirements.

Bioenergetic models

Bioenergetic models have frequently been used to estimate the amount of food that marine mammal populations consume. However, Davies & Hatcher (1998) claim that many 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.

Correcting for omitted or underestimated terms often results in markedly different conclusions (Davies & Hatcher 1998). Components of marine mammal energy budgets that have commonly been omitted in past studies include reproduction, molting, and thermoregulation (e.g. Olesiuk 1993, Mohn & Bowen 1996, Stenson et al. 1997). Of these 3 omissions, we incorporated reproduction, but did not incorporate molting or thermoregulation. Energy expenditure during the molt in Steller sea lions and other otariids is not well understood. In phocids, the energetic cost of molting is low (Ashwell-Erickson & Elsner 1981, Worthy et al. 1992). We assumed large errors in metabolic rates in our model; therefore, unless the cost of molting is very high, the explicit inclusion of molting in our model would not result in substantially different predictions of energy requirements or estimates of the error in those predictions.

Thermoregulation is an important consideration and marine mammals have many thermoregulatory adaptations for existence in extreme environments (Irving 1969). The ranges of values we used for metabolic rates on land and at sea were determined from studies that measured the field metabolic rates of wild otariids. Thus, while we did not explicitly incorporate a cost of thermoregulation, the metabolic rates we used included the cost of thermoregulation. Newborn pups, however, have very little blubber, and probably have increased thermoregulatory costs. Studies have found that northern fur seal pups resting out of water were generally thermoneutral within the normal range of environmental air temperatures experienced by the pups, and had metabolic rates between 2 and 3× the basal metabolic rate predicted by Kleiber's relationship (Blix et al. 1979, Trites 1990, Donohue et al. 2000). We used similar values for the metabolic rates of Steller sea lion pups on land. Northern fur seal pups resting in water (5 to 20°C) had metabolic rates averaging 3.5 to 6× the basal metabolic rate predicted by Kleiber's relationship (Donohue et al. 2000) and one newborn pup resting in ice water had a metabolic rate as high as 10× the basal metabolic rate predicted by Kleiber's relationship (Blix et al. 1979). The latter study suggested that non-shivering thermogenesis may play an important role in thermoregulation in newborn northern fur seal pups. These resting values are less than or equal to the values we used for the total metabolic rates of pups in the water, suggesting that the water metabolic rates we assumed accounted for thermoregulatory costs.

The second major criticism of bioenergetic models is that they often use inaccurate approximations 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 & Hatcher 1998). One way to address these inaccuracies is to include error terms for all model parameter estimates. Another is to use fewer parameters (with increased precision) as has been done in some recent bioenergetic models for marine mammals (e.g. Mohn & Bowen 1996, Stenson et al. 1997).

We developed a relatively complex (and hopefully realistic) Steller sea lion model in order to examine seasonal patterns of food consumption. All model parameters had error estimates and were sampled/resampled using Monte Carlo techniques similar to those used in 2 previous bioenergetic models for marine mammals (i.e. Mohn & Bowen 1996, Stenson et al. 1997). In general, the less accurately a parameter value was known, the wider the range of possible values that we considered. We 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 & Hatcher 1998). In the case of our Steller sea lion model, our results are unique in space (Alaska) and time (1990s), 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, the design of our bioenergetic model allows it to be easily 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

The CVs of annual population food consumption estimates ranged from 25 to 46% for the 7 prey categories. These CVs reflect considerable uncertainty in our estimates of food requirements, which must be considered if used in other analyses (e.g. comparative analyses, management decisions).

Rather than examine the sensitivity of mean model predictions to standardized deviations in each parameter value (e.g. 10% perturbations), we examined the sensitivity of the error in model predictions to the error in each group of parameter values. 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 3 main parameter groups (i.e. diet, population and bioenergetic), uncertainty in bioenergetic parameters produced the most error in estimates of total annual food consumption. Uncertainty in diet and population parameters had smaller effects. However, uncertainty in diet parameters had a greater effect on the error in estimates of consumption of individual prey categories. This suggests that error in diet composition had a strong effect on estimates of consumption of individual prey categories, but the variability in energetic density among prey categories was too low for error in diet composition to substantially affect error in estimates of total biomass consumption.

Of the bioenergetic parameter groups (i.e. efficiency, metabolism and production), uncertainty in metabolism parameters had the largest effect on the error in estimates of annual food consumption by the population, 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 those parameter values (or the error in parameter estimates). Our results suggest that the largest improvements in precision of food requirement estimates can be obtained through future studies on Steller sea lion diet and bioenergetics (especially activity costs). Lavigne (1995) suggested that pinniped bioenergetics are well understood, and researchers should focus on obtaining better diet and population data. While we found that error in consumption estimates was relatively sensitive to error in diet parameters, we also found that error in consumption estimates was relatively sensitive to error in bioenergetic parameters. Better diet and population data are needed, but there is still a lack of important bioenergetic information for Steller sea lions that is needed to refine estimates of food requirements.

Model validation

Our bioenergetic model provided the first detailed estimates of the food requirements of Steller sea lions. However, the most important value of our model is not in its predictions per se, but rather in the interplay between the model predictions and future research on the real system. Our model has generated a number of hypotheses about food consumption that can be tested through field studies. Telemetry techniques are being developed to estimate consumption of free ranging animals from stomach temperature changes (e.g. Andrews 1998) and measures of gastric pH and motility. Other techniques are considering the reconstruction of diet (volume and weight) from scat samples. Such estimates of food consumption obtained in the wild could be used to validate the model predictions and generate new hypotheses regarding discrepancies between the model and field estimates. Studies which compare and contrast estimates of food consumption obtained using different methods are necessary to validate the accuracy of each individual method (Grémillet et al. 2000).

Energy requirements of individuals

Predicted energy requirements of individual Steller sea lions varied with time of year and may have slightly biased the 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 energy requirement per individual to obtain the total annual energy requirement for the population. 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 energy requirements, introduced a slight bias in total population requirement. The approach that we used to calculate total annual population energy requirement would only produce accurate estimates if daily requirements were constant throughout the year. Our estimate of population requirements are slightly biased upwards because energy requirements tended to be greater later in the year, especially for pups and mature females.

Our model suggested that 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, the energy requirements of pups and mature females increased as those animals 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).

Our model predicted that 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 (ca. 6 to 14 %). Other bioenergetic modeling studies for pinnipeds 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 if we had included this energetic cost in growth requirements it would have increased the relative importance of growth.

Reproduction also influenced seasonal patterns of individual energy requirements. Our model suggested that 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 energy requirement of an individual among all sexes and age-classes was approximately 200 MJ for pregnant, lactating females late in gestation. Reproduction is thus very costly for a female Steller sea lion.

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).

Our model predicted that during the 2 wk following parturition, a male pup had a mean milk consumption of 23 MJ d^{-1} and a female pup had to consume a mean of 19 MJ d^{-1}. Using milk intake and energy intake rates from Davis et al. (1996), the energetic density of Steller sea lion milk was ca. 14 kJ ml^{-1} during the first 4 wk postpartum. Thus, our model predicted that newborn male pups required 1.6 l milk d^{-1} and female pups required 1.4 l milk d^{-1}. 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, CA consumed ca. 1.5 to 1.6 l d^{-1}, which encompasses our average estimate of 1.5 l d^{-1}. Davis et al. (1996) found slightly higher rates of milk and energy consumption for Alaskan Steller sea lion pups <2 wk old (1.7 to 2.1 l d^{-1}). Using the same milk energetic density as above, our model predicted that at 1 yr of age, a male pup would need 5.5 l milk d^{-1} and a female would need 4.2 l milk d^{-1}. However, the energetic density of milk may change during the lactation period as it does in other pinniped species (Arnould & 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 yr 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,b). Independent feeding would reduce the amount of 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 Trites & Porter (2001) suggest that these trips are separate from their mothers, and may not be for foraging.

In general, total daily metabolism (gross energy requirement minus energy deposited or lost as waste) estimated by the model was ca. 3 to 4× basal metabolic rate, except during periods when energy expenditure is particularly low (i.e. breeding season) or high (i.e. for mature females in winter and spring). 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 (5× basal metabolic rate) was for a pregnant, lactating female prior to the breeding season. 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).

Food requirements of individuals

It is important to note that the predictions of our model are estimates of food requirements and not estimates of food consumption. On a seasonal or 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 ca. 3 d before giving birth. After parturition, they remain on land with their pups for an average of 7 to 9 d: the 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 prior to and/or after the breeding season. The patterns of daily food requirements during the breeding season (Fig. 2) are not the patterns of daily food consumption, and therefore do not accurately represent patterns of prey consumption or impact on the prey populations during the breeding season. No prey are consumed by breeding animals during their fasts and more prey are consumed prior to and/or after the breeding season than are 'required' at those times. Kastelein et al. (1990) found that the food intake of an adult male Steller sea lion in captivity was reduced during the breeding season and was greater than average from November through March. Their findings suggest that breeding males may acquire the energy needed for the breeding season fast during the winter and spring.

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 to 28 h in length for adult females and 11 to 25 h for immature animals (Higgins et al. 1988, Merrick 1995, Swain 1996, Swain & Calkins 1997, Milette 1999, Trites & Porter 2001). 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 our 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 & Gentry 1971, Olesiuk & Bigg 1987, Boyd & Duck 1991, Trites & Bigg 1996, Winship et al. 2001). 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, we 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 our estimates of food requirements. Fasting may also have biased our 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 & Trites 1999, 2000b). If fasting adult females have a depressed metabolic rate then we would have overestimated food requirements. However, due to the relatively short period of time that they fast, the effect would have been small.

Fiscus & Baines (1966) suggested that the maximum stomach capacity of a 2 yr old male Steller sea lion was ca. 10% of its body weight. Our model predicted that immature animals and lactating females require >10% of their body weight in food per day. In addition, if animals are generally not feeding on a daily basis then individuals would frequently have to consume biomass in excess of 10% of their body weight, which is greater than the 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 h (Markussen 1993). This would allow an animal to consume and process a large amount of food on a foraging trip.

The amount of prey biomass required by an individual on a daily basis also varies substantially with the energy content of the prey. The model predicted that 1 yr old males and females consuming our assumed diet required on average 12 ± 2.7% and 13 ± 2.7% of their body weight in food per day respectively. These food requirements dropped to 9 ± 2.6% of body weight (males and females) if we assumed that animals ate only forage fish, and increased to 16 ± 3.6% (males) and 17 ± 3.6% (females) if we assumed that animals ate only gadids. Thus, a juvenile animal consuming only gadids (e.g. walleye pollock) on a foraging trip would need to consume >80% more fish biomass than an animal consuming only forage fish (e.g. Pacific herring). An increase of gadids, and a decrease of forage fish in the prey base of Steller sea lions (which occurred prior to and during the population decline; Alverson 1992) may therefore result in an increase in the foraging effort of Steller sea lions which in turn may increase their vulnerability to predation or reduce their foraging efficiency (ratio of energy obtained to energy expended while foraging). It is also possible that young animals and females with nursing young consuming a diet of entirely low-energy prey may be unable to acquire and/or process enough food (i.e. 16 to 17% of body mass per day) to meet their energy requirements.

Food requirements of the population

Our model produced estimates of the annual prey requirements of the entire Alaskan Steller sea lion population by prey species category (Table 4, Fig. 5) that can be used in global-level or ecosystem-level modeling studies to examine the impact of Steller sea lions on their prey and competitors (Trites et al. 1997, 1999). Our findings can also assist in the conservation of Steller sea lions by estimating the amount of prey necessary to sustain a given population of Steller sea lions. However, the management applications of our estimates of annual prey requirements are limited to an annual, global-level or ecosystem-level scale because we used 1 average diet for all Steller sea lions in Alaska for the entire year. Interactions on finer spatial (e.g. regional) and temporal (e.g. seasonal) scales are also important as well as estimates of prey size-specific food requirements. For example, the model predicted that on average 6.4 ± 1.13 metric tons of prey were required per Steller sea lion per year. If the incidence of gadids in the diet of Steller sea lions from a particular region of Alaska was 50% (rather than 34%), the model predicted that 6.7 ± 1.17 metric tons of prey would be required per sea lion per year. These relationships remain to be determined as data become available.

CONCLUSION

The decline of Steller sea lions has prompted a wide range of studies to determine why the population has decreased in most regions of Alaska, and what might be done to assist its recovery. One of the more critical pieces of information needed to assist in this effort is an assessment of the amount of food that Steller sea lions require. Bioenergetic models, such as the one we constructed, are currently the only way to obtain reliable estimates of food consumption for this marine predator.

In addition to estimating food requirements, our model also provides insights into life history strategies of Steller sea lions. It predicts, for example, that the cost of carrying a fetus is greatest late in gestation (spring) when the cost of nursing a pup is also substantial. This may have bearing on the relatively high incidence of late-term abortions, especially during periods of nutritional stress (Pitcher et al. 1998). The model also predicts that young animals must consume significantly greater amounts of food than mature individuals (relative to body mass) to meet their daily needs. These findings suggest there is a greater potential for nutritional stress in juveniles. These findings also suggest greater potential stress on adult females during the spring. Thus, management for conservation should focus on young animals and springtime conditions.

Our model provides the first estimates of the food requirements of Steller sea lions in Alaska. It can be applied to other regions of the Steller sea lion range where estimates of population numbers and diet are available. The model may also be readily adapted to other species of pinnipeds, and may ultimately be useful in the allocation of marine resources between fisheries and sea lions.

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LITERATURE CITED

Alverson DL (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. Rev Aquat Sci 6:203–256

Anderson SS, Fedak MA (1987) The energetics of sexual success of grey seals and comparison with the costs of reproduction in other pinnipeds. In: Loudon ASI, Racey PA (eds) Reproductive energetics in mammals. Zool Soc London Symp 57. Oxford University Press, Oxford, p 319–341

Andrews RD (1998) Remotely releasable instruments for monitoring the foraging behaviour of pinnipeds. Mar Ecol Prog Ser 175:289–294

Anthony JA, Roby DD (1997) Proximate composition of some northeastern Pacific forage species. In: Forage fishes in marine ecosystems. Alaska Sea Grant College Program Report 97–01, University of Alaska Fairbanks, AK, p 725–729

Antonelis GA Jr, Lowry MS, DeMaster DP, Fiscus CH (1987) Assessing northern elephant seal feeding habits by stomach lavage. Mar Mamm Sci 3:308–322

Arnould JPY, Hindell MA (1999) The composition of Australian fur seal (*Arctocephalus pusillus doriferus*) milk throughout lactation. Physiol Biochem Zool 72:605–612

Arnould JPY, Boyd IL, Speakman JR (1996) The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. J Zool (Lond) 239:769–782

Ashwell-Erickson S, Elsner R (1981) The energy cost of free existence for Bering Sea harbor and spotted seals. In: Hood DW, Calder JA (eds) The Eastern Bering Sea shelf: oceanography and resources, Vol. 2. University of Washington Press, Seattle, WA, p 869–899

Beverton RJH (1985) Analysis of marine mammal-fisheries interaction. In: Beddington JR, Beverton RJH, Lavigne DM (eds) Marine mammals and fisheries. George Allen & Unwin, London

Blaxter KL (1989) Energy metabolism in animals and man. Cambridge University Press, Cambridge

Blix AS, Miller K, Keyes MC, Grav HJ, Elsner R (1979) Newborn northern fur seals (*Callorhinus ursinus*)—do they suffer from the cold? Am J Physiol 236:R322–R327

Bowen WD (2000) Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. Can J Fish Aquat Sci 57:898–905

Box GEP, Muller ME (1958) A note on the generation of random normal deviates. Ann Math Stat 29:610–611

Boyd IL, Duck CD (1991) Mass changes and metabolism in territorial male Antarctic fur seals (*Arctocephalus gazella*). Physiol Zool 64:375–392

Boyd IL, Arnbom TA, Fedak MA (1994) Biomass and energy consumption of the South Georgia population of southern elephant seals. In: Le Boeuf BJ, Laws RM (eds) Elephant seals: population ecology, behaviour, and physiology. University of California Press, Berkeley, CA, p 98–117

Calkins DG, Becker EF, Pitcher KW (1998) Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. Mar Mamm Sci 14:232–244

Calkins DG, McAllister DC, Pitcher KW, Pendleton GW (1999) Steller sea lion status and trend in Southeast Alaska: 1979–1997. Mar Mamm Sci 15:462–477

Castellini MA, Kooyman GL, Ponganis PJ (1992) Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. J Exp Biol 165:181–194

Costa DP, Gentry RL (1986) Free-ranging energetics of northern fur seals. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, NJ, p 79–101

Costa DP, Le Boeuf BJ, Huntley AC, Ortiz CL (1986) The energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. J Zool (Lond) 209:21–33

Costa DP, Croxall JP, Duck CD (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology 70:596–606

Davies MS, Hatcher AM (1998) The energy budget: a useful tool? Ann Zool Fennici 35:231–240

Davis RW, Brandon EAA, Adams TC, Williams TM, Castellini MA, Loughlin TR, Calkins DG (1996) Indices of reproductive effort, body condition and pup growth for Steller sea lions (*Eumetopias jubatus*) in Alaska. In: Steller sea lion recovery investigations in Alaska, 1992–1994. Wildlife Technical Bulletin 13, Alaska Department of Fish and Game, Anchorage, AK, p 53–61

Debier C, Kovacs KM, Lydersen C, Mignolet E, Larondelle Y (1999) Vitamin E and vitamin A contents, fatty acid profiles, and gross composition of harp and hooded seal milk through lactation. Can J Zool 77:952–958

Doidge CE, Croxall JP (1985) Diet and energy budget of the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, p 543–550

Donohue MJ, Costa DP, Goebel ME, Baker JD (2000) The ontogeny of metabolic rate and thermoregulatory capabilities of northern fur seal, *Callorhinus ursinus*, pups in air and water. J Exp Biol 203:1003–1016

Fiscus CH, Baines GA (1966) Food and feeding behaviour of Steller and California sea lions. J Mammal 47:195–200

Fisher KI, Stewart REA, Kastelein RA, Campbell LD (1992) Apparent digestive efficiency in walruses (*Odobenus rosmarus*) fed herring (*Clupea harengus*) and clams (*Spisula* sp.). Can J Zool 70:30–36

Gallivan GJ, Ronald K (1981) Apparent specific dynamic action in the harp seal (*Phoca groenlandica*). Comp Biochem Physiol A69:579–581

Galluci VF (1973) On the principles of thermodynamics in ecology. Ann Rev Ecol Syst 4:329–357

Gentry RL (1970) Social behavior of the Steller sea lion. PhD thesis, University of California, Santa Cruz

Gisiner RC (1985) Male territorial and reproductive behavior in the Steller sea lion, *Eumetopias jubatus*. PhD thesis, University of California, Santa Cruz

Grémillet D, Storch S, Peters G (2000) Determining food requirements in marine top predators: a comparison of three independent techniques in Great Cormorants, *Phalacrocorax carbo carbo*. Can J Zool 78:1567–1579

Hall CAS, Day JWJ (1977) Systems and models: terms and basic principles. In: Hall CAS, Day JWJ (eds) Ecosystem modeling in theory and practice: an introduction with case histories. John Wiley & Sons, New York, p 5–36

Härkönen T, Heide-Jørgensen M-P (1991) The harbour seal *Phoca vitulina* as a predator in the Skagerrak. Ophelia 34: 191–207

Harris RK, Nishiyama T, Paul AJ (1986) Carbon, nitrogen and caloric content of eggs, larvae, and juveniles of the walleye pollock, *Theragra chalcogramma*. J Fish Biol 29:87–98

Helm RC (1984) Rate of digestion in three species of pinnipeds. Can J Zool 62:1751–1756

Hiby AR, Harwood J (1985) The effects of variation in population parameters on the energy requirements of a hypothetical grey seal population. In: Beddington JR, Beverton JH, Lavigne DM (eds) Marine mammals and fisheries. George Allen & Unwin, London, p 337–343

Higgins LV, Costa DP, Huntley AC, Le Boeuf BJ (1988) Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus*. Mar Mamm Sci 4:44–58

Hindell MA, Slip DJ, Burton HR, Bryden MM (1992) Physiological implications of continuous, prolonged, and deep dives of the southern elephant seal (*Mirounga leonina*). Can J Zool 70:370–379

Hinga KR (1979) The food requirements of whales in the southern hemisphere. Deep-Sea Res A26:569–577

Innes S, Stewart REA, Lavigne DM (1981) Growth in Northwest Atlantic harp seals *Phoca groenlandica*. J Zool (Lond) 194:11–24

Innes S, Lavigne DM, Earle WM, Kovacs KM (1987) Feeding rates of seals and whales. J Anim Ecol 56:115–130

Irving L (1969) Temperature regulation in marine mammals. In: Andersen HT (ed) The biology of marine mammals. Academic Press, New York, p 147–174

Kastelein RA, Vaughan N, Wiepkema PR (1990) The food consumption of Steller sea lions (*Eumetopias jubatus*). Aquat Mamm 15:137–144

Keen RE, Spain JD (1992) Computer simulation in biology: a BASIC introduction. Wiley-Liss, New York

Keiver KM, Ronald K, Beamish FWH (1984) Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (*Phoca groenlandica*). Can J Zool 62:769–776

Kleiber M (1975) The fire of life: an introduction to animal energetics. Robert E. Krieger, Huntington, NY

Klekowski RZ, Duncan A (1975) Physiological approach to ecological energetics. In: Grodzinski W, Klekowski RZ, Duncan A (eds) Methods for ecological bioenergetics, IBP Handbook No. 24. Blackwell Scientific Publications, Oxford, p 15–64

Lavigne DM (1995) Ecological interactions between marine mammals, commercial fisheries and their prey: unravelling the tangled web. Technical Report 95–02. International Marine Mammal Association, Guelph

Lavigne DM, Barchard W, Innes S, Øritsland NA (1982) Pinniped bioenergetics. In: Mammals in the seas: small cetaceans, seals, sirenians, and sea otters, Vol. 4. FAO Fisheries Series 5, FAO, Rome, p 191–235

Lavigne DM, Innes S, Stewart REA, Worthy GAJ (1985) An annual energy budget for north-west Atlantic harp seals. In: Beddington RJH, Beverton RJH, Lavigne DM (eds) Marine mammals and fisheries. George Allen & Unwin, London, p 319–336

Lawson JW, Miller EH, Noseworthy E (1997) Variation in assimilation efficiency and digestive efficiency of captive harp seals (*Phoca groenlandica*) on different diets. Can J Zool 75:1285–1291

Loughlin TR, Perlov AS, Vladimirov VA (1992) Range-wide survey and estimation of total number of Steller sea lions in 1989. Mar Mamm Sci 8:220–239

Markussen NH (1993) Transit time of digesta in captive harbour seals (*Phoca vitulina*). Can J Zool 71:1071–1073

Markussen NH, Øritsland NA (1991) Food energy requirements of the harp seal (*Phoca groenlandica*) population in the Barents and White Seas. In: Sakshaug E, Hopkins CCE, Øritsland NA (eds) Proc Pro Mare Symp Polar Mar Ecol, Trondheim, Norway, 12–16 May 1990. Polar Res 10:603–608

Markussen NH, Ryg M, Lydersen C (1992) Food consumption of the NE Atlantic minke whale (*Balaenoptera acutorostrata*) population estimated with a simulation model. ICES J Mar Sci 49:317–323

Markussen NH, Ryg M, Øritsland NA (1994) The effect of feeding on the metabolic rate in harbour seals (*Phoca vitulina*). J Comp Physiol B164:89–93

Mårtensson PE, Nordøy ES, Blix AS (1994) Digestibility of crustaceans and capelin in harp seals (*Phoca groenlandica*). Mar Mammal Sci 10:325–331

Merrick RL (1995) The relationship of the foraging ecology of Steller sea lions (*Eumetopias jubatus*) to their population decline in Alaska. PhD thesis, University of Washington, Seattle

Merrick RL, Loughlin TR (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can J Zool 75:776–786

Merrick RL, Chumbley MK, Byrd GV (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Can J Fish Aquat Sci 54:1342–1348

Milette LL (1999) Behaviour of lactating Steller sea lions (*Eumetopias jubatus*) during the breeding season: a comparison between a declining and stable population in Alaska. MSc thesis, University of British Columbia

Miller LK (1978) Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. MMC-75/08. US Marine Mammal Commission, Washington, DC

Mohn R, Bowen WD (1996) Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. Can J Fish Aquat Sci 53:2722–2738

Murie DJ, Lavigne DM (1991) Food consumption of wintering harp seals, *Phoca groenlandica*, in the St. Lawrence estuary, Canada. Can J Zool 69:1289–1296

Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol Monogr 57:111–128

Naumov AG, Chekunova VI (1980) Energy requirements of pinnipeds (Pinnepedia). Oceanology 20:348–350

Nordøy ES, Mårtensson PE, Lager AR, Folkow LP, Blix AS (1995) Food consumption of the Northeast Atlantic stock of harp seals. In: Blix AS, Walløe L, Ulltang Ø (eds) Developments in marine biology 4: whales, seals, fish and man. Elsevier Science, Amsterdam, p 255–260

Oftedal OT (1985) Pregnancy and lactation. In: Hudson RJ, White RG (eds) Bioenergetics of wild herbivores. CRC Press, Boca Raton, FL, p 215–238

Oftedal OV, Iverson SJ (1987) Hydrogen isotope methodology for measurement of milk intake and energetics of growth in suckling young. In: Huntley AC, Costa DP, Worthy GAJ, Castellini MA (eds) Approaches to marine mammal energetics. Soc Mar Mammal Spec Publ 1, Lawrence, KS, p 67–96

Ohizumi H, Miyazaki N (1998) Feeding rate and daily energy intake of Dall's porpoise in the northeastern Sea of Japan. Proc NIPR Symp Polar Biol 11:74–81

Olesiuk PF (1993) Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. Fish Bull 91:491–515

Olesiuk PF, Bigg MA (1987) Seasonal changes in condition of male Steller sea lions, *Eumetopias jubatus*. Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, BC, Canada (unpubl. ms.)

Olesiuk PF, Bigg MA, Ellis GM, Crockford SJ, Wigen RJ (1990) An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can Tech Rep Fish Aquat Sci 1730

Øritsland NA, Markussen NH (1990) Outline of a physiologically based model for population energetics. Ecol Model 52:267–288

Paul AJ, Paul JM (1998) Comparisons of whole body energy content of captive fasting age zero Alaskan Pacific herring (*Clupea pallasi* Valenciennes) and cohorts over-wintering in nature. J Exp Mar Biol Ecol 226:75–86

Paul AJ, Paul JM, Smith RL (1993) The seasonal changes in somatic energy content of Gulf of Alaska yellowfin sole, *Pleuronectes asper*. J Fish Biol 43:131–138

Paul AJ, Paul JM, Brown ED (1998a) Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi* Valenciennes 1847) relative to age, size and sex. J Exp Mar Biol Ecol 223:133–142

Paul AJ, Paul JM, Smith RL (1998b) Seasonal changes in whole-body energy content and estimated consumption rates of age 0 walleye pollock from Prince William Sound, Alaska. Estuar Coast Shelf Sci 47:251–259

Perez MA (1994) Calorimetry measurements of energy value of some Alaskan fishes and squids. NOAA Tech Memo NMFS-AFSC-32

Perez MA, McAlister WB, Mooney EE (1990) Estimated feeding rate relationship for marine mammals based on captive animal data. NOAA Tech Memo NMFS F/NWC-184

Peterson CC, Nagy KA, Diamond J (1990) Sustained metabolic scope. Proc Natl Acad Sci USA 87:2324–2328

Pitcher KW, Calkins DG (1981) Reproductive biology of Steller sea lions in the Gulf of Alaska. J Mammal 62: 599–605

Pitcher KW, Calkins DG, Pendleton GW (1998) Reproductive performance of female Steller sea lions: an energetics based reproductive strategy? Can J Zool 76:2075–2083

Pitcher KW, Calkins DG, Pendleton GW (2000) Steller sea lion body condition indices. Mar Mamm Sci 16:427–436

Porter B (1997) Winter ecology of Steller sea lions (*Eumetopias jubatus*) in Alaska. MSc thesis, University of British Columbia, Vancouver

Reilly JJ, Fedak MA (1991) Rates of water turnover and energy expenditure of free-living male common seals (*Phoca vitulina*). J Zool (Lond) 223:461–468

Robbins CT (1993) Wildlife feeding and nutrition, 2nd edn. Academic Press, San Diego

Ronald K, Keiver KM, Beamish FWH, Frank R (1984) Energy requirements for maintenance and faecal and urinary losses of the grey seal (*Halichoerus grypus*). Can J Zool 62: 1101–1105

Rose KA (1983) A simulation comparison and evaluation of parameter sensitivity methods applicable to large models. In: Lauenroth WK, Skogerboe GV, Flug M (eds) Analysis of ecological systems: state-of-the-art in ecological modelling, Vol. 5. International Society for Ecological Modelling, Copenhagen, and Elsevier Scientific, Amsterdam, p 129–140

Rosen DAS, Trites AW (1997) Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. Comp Biochem Physiol A118:877–881

Rosen DAS, Trites AW (1999) Metabolic effects of low-energy diet on Steller sea lions, *Eumetopias jubatus*. Physiol Biochem Zool 72:723–731

Rosen DAS, Trites AW (2000a) Digestive efficiency and dry matter digestibility of Steller sea lions fed herring, pollock, squid, and salmon. Can J Zool 78:1–6

Rosen DAS, Trites AW (2000b) Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. Can J Zool 78:1243–1250

Ryg M, Øritsland NA (1991) Estimates of energy expenditure and energy consumption of ringed seals (*Phoca hispida*) throughout the year. In: Sakshaug E, Hopkins CCE, Øritsland NA (eds) Proc Pro Mare Symp Polar Mar Ecol, Trondheim, Norway, 12–16 May 1990. Polar Res 10: 595–601

Sandegren FE (1970) Breeding and maternal behavior of the Steller sea lion (*Eumetopias jubatus*) in Alaska. MSc thesis, University of Alaska, Fairbanks, AK

Scheffer VB (1945) Growth and behaviour of young sea lions. J Mammal 26:390–392

Schmidt-Nielsen K (1990) Animal physiology: adaptation and environment, 4th edn. Cambridge University Press, Cambridge

Schusterman RJ, Gentry RL (1971) Development of a fatted male phenomenon in California sea lions. Dev Psychobiol 4:333–338

Sease JL, Loughlin TR (1999) Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1997 and 1998. NOAA Tech Memo NMFS-AFSC-100

Shelton PA, Warren WG, Stenson GB (1997) Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption, Part I: uncertainty in consumption estimates associated with population size, residency, energy requirement and diet. J Northwest Atl Fish Sci 22:303–315

Smith RL, Paul AJ, Paul JM (1988) Aspects of energetics of adult walleye pollock, *Theragra chalcogramma* (Pallas), from Alaska. J Fish Biol 33:445–454

Smith RL, Paul AJ, Paul JM (1990) Seasonal changes in energy and the energy cost of spawning in Gulf of Alaska Pacific cod. J Fish Biol 36:307–316

Statistical Sciences (1995) S-Plus guide to statistical and mathematical analysis, version 3.3. StatSci Division, Mathsoft, Seattle, WA

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Stenson GB, Hammill MO, Lawson JW (1997) Predation by harp seals in Atlantic Canada: preliminary consumption estimates for Arctic cod, capelin and Atlantic cod. J Northwest Atl Fish Sci 22:137–154

Swain U (1996) Foraging behaviour of female Steller sea lions in Southeast Alaska and the eastern Gulf of Alaska. In: Steller sea lion recovery investigations in Alaska, 1992–1994. Wildlife Technical Bulletin 13. Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, p 135–166

Swain U, Calkins DG (1997) Foraging behaviour of juvenile Steller sea lions in the northeastern Gulf of Alaska: diving and foraging trip duration. In: Pitcher K (ed) Steller sea lion recovery investigations in Alaska, 1995–1996. Alaska

Department of Fish and Game, Division of Wildlife Conservation, Anchorage, p 92–106

Trillmich F (1986a) Attendance behavior of Galapagos fur seals. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, NJ, p 168–185

Trillmich F (1986b) Attendance behavior of Galapagos sea lions. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, NJ, p 196–208

Trites AW (1990) Thermal budgets and climate spaces: the impact of weather on the survival of Galapagos (*Arctocephalus galapagoensis* Heller) and northern fur seal pups (*Callorhinus ursinus* L.). Funct Ecol 4:753–768

Trites AW, Bigg MA (1996) Physical growth of northern fur seals (*Callorhinus ursinus*): seasonal fluctuations and migratory influences. J Zool (Lond) 238:459–482

Trites AW, Christensen V, Pauly D (1997) Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. J Northwest Atl Fish Sci 22:173–187

Trites AW, Larkin PA (1992) The status of Steller sea lion populations and the development of fisheries in the Gulf of Alaska and Aleutian Islands. Fisheries Centre, University of British Columbia, Vancouver (unpubl. rep.)

Trites AW, Larkin PA (1996) Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? Aquat Mamm 22: 153–166

Trites AW, Pauly D (1998) Estimating mean body masses of marine mammals from maximum body lengths. Can J Zool 76:886–896

Trites AW, Porter B (2001) Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. J Zool (Lond) 256:547–556

Trites AW, Livingston PA, Vasconcellos MC, Mackinson S, Springer AM, Pauly D (1999) Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. Fisheries Centre Res Rep 7(1). Fisheries Centre, University of British Columbia, Vancouver

Ugland KI, Jødestøl KA, Aspholm PE, Krøyer AB, Jakobsen T (1993) Fish consumption by invading harp seals off the Norwegian coast in 1987 and 1988. ICES J Mar Sci 50: 27–38

Van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some North Pacific forage fishes. Comp Biochem Physiol A118:1393–1398

Webster AJF (1983) Energetics of maintenance and growth. In: Girardier L, Stock MJ (eds) Mammalian thermogenesis. Chapman & Hall, London

Wiegert RG (1968) Thermodynamic considerations in animal nutrition. Am Zool 8:71–81

Winship AJ (2000) Growth and bioenergetic models for Steller sea lions (*Eumetopias jubatus*) in Alaska. MSc thesis, University of British Columbia, Vancouver

Winship AJ, Trites AW, Calkins DG (2001) Growth in body size of the Steller sea lion. J Mammal 82:500–519

Worthy GAJ (1987a) Ecological energetics of harp and gray seals: implications from a simulation model. In: Huntley AC, Costa DP, Worthy GAJ, Castellini MA (eds) Approaches to marine mammal energetics. Soc Mar Mammal Spec Publ 1, Allen Press, Lawrence, KS, p 227–246

Worthy GAJ (1987b) Metabolism and growth of young harp and grey seals. Can J Zool 65:1377–1382

Worthy GAJ, Morris PA, Costa DP, Le Boeuf BJ (1992) Moult energetics of the northern elephant seal (*Mirounga angustirostris*). J Zool (Lond) 227:257–265

York AE (1994) The population dynamics of northern sea lions, 1975–1985. Mar Mamm Sci 10:38–51

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice-Hall, Englewood Cliffs, NJ

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