Abstract—The effects of seasonal and regional differences in diet composition on the food requirements of Steller sea lions (*Eumetopias jubatus*) were estimated by using a bioenergetic model. The model considered differences in the energy density of the prey, and differences in digestive efficiency and the heat increment of feeding of different diets. The model predicted that Steller sea lions in southeast Alaska required 45–60% more food per day in early spring (March) than after the breeding season in late summer (August) because of seasonal changes in the energy density of the diets (along with seasonal changes in energy requirements). The southeast Alaska population, at 23,000 (±1660 SD) animals (all ages), consumed an estimated 140,000 (±27,800) t of prey in 1998. In contrast, we estimated that the 51,000 (±3680) animals making up the western Alaska population in the Gulf of Alaska and Aleutian Islands consumed just over twice this amount (303,000 [±57,500] t). In terms of biomass removed in 1998 from Alaskan waters, we estimated that Steller sea lions accounted for about 5% of the natural mortality of gadids (pollock and cod) and up to 75% of the natural mortality of hexagrammids (adult Atka mackerel). These two groups of species were consumed in higher amounts than any other. The predicted average daily food requirement per individual ranged from 16 (±2.8) to 20 (±3.6) kg (all ages combined). Per capita food requirements differed by as much as 24% between regions of Alaska depending on the relative amounts of low–energy-density prey (e.g. gadids) versus high–energy-density prey (e.g. forage fish and salmon) consumed. Estimated requirements were highest in regions where Steller sea lions consumed higher proportions of low–energy-density prey and experienced the highest rates of population decline.

Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require?

Arliss J. Winship

Andrew W. Trites

Department of Zoology and Marine Mammal Research Unit
Fisheries Center, Room 18, Hut B-3
University of British Columbia
6248 Biological Sciences Road
Vancouver, British Columbia, Canada, V6T 1Z4
E-mail address (for A. J. Winship): winship@zoology.ubc.ca

Nutritional stress may account for the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska (Alverson, 1992), which have declined by over 70% in the last 20–25 years (Loughlin et al., 1992; Trites and Larkin, 1996). Merrick et al. (1997) found a negative correlation between Steller sea lion diet diversity and the rate of population change among six regions of Alaska in the early 1990s. The greatest rates of population decline occurred in areas with low diet diversity, where Steller sea lions predominantly preyed on either walleye pollock or Atka mackerel. Steller sea lions from areas that did not experience a decline, or experienced a lower rate of decline, preyed on both walleye pollock and Atka mackerel along with several other groups of prey species.

Merrick et al. (1997) suggested that the relationship between diet diversity and the rate of population decline reflected differences in the efficiency with which Steller sea lions could find, capture, and handle different numbers of prey categories. However, the energy content of the diet may also have a substantial effect on the foraging efficiency of Steller sea lions. Steller sea lions consuming a low diversity diet of primarily low–energy-density species (e.g. gadids) need to consume more prey biomass than Steller sea lions eating a more diverse diet including high–energy-density species (e.g. forage fish, salmon) to obtain the same amount of energy. Thus, it may be more difficult for Steller sea lions consuming a diet of low-energy content to meet their energy requirements or to forage efficiently than it would be for animals consuming prey of high-energy content.

The overall goal of our study was to estimate the amount of prey required by Steller sea lions in Alaska during the 1990s using a previously developed bioenergetic model (Winship et al., 2002). Our first objective was to examine how daily food biomass requirements were affected by seasonal differences in the energy density of the diet of Steller sea lions in southeast Alaska. Our second objective was to use the same model to compare the food requirements of Steller sea lions among seven regions of Alaska during the 1990s (regions based on Merrick et al., 1997, and Sease and Loughlin, 1999; Fig. 1). Our third objective was to use data from 1998 to compare estimates of Steller sea lion prey consumption with fisheries catches and estimates of prey stock sizes (and natural mortality rates).

Methods

Model structure

The bioenergetic model that we used is described in detail by Winship et al. (2002). In brief, gross energy requirements were calculated for individuals of each age, sex, reproductive status (immature, mature, pregnant), and day of the year by using information on Steller sea lion energetics (basal metabolic rates, active metabolic rates, activity budgets, body growth and composition, digestive efficiency and the
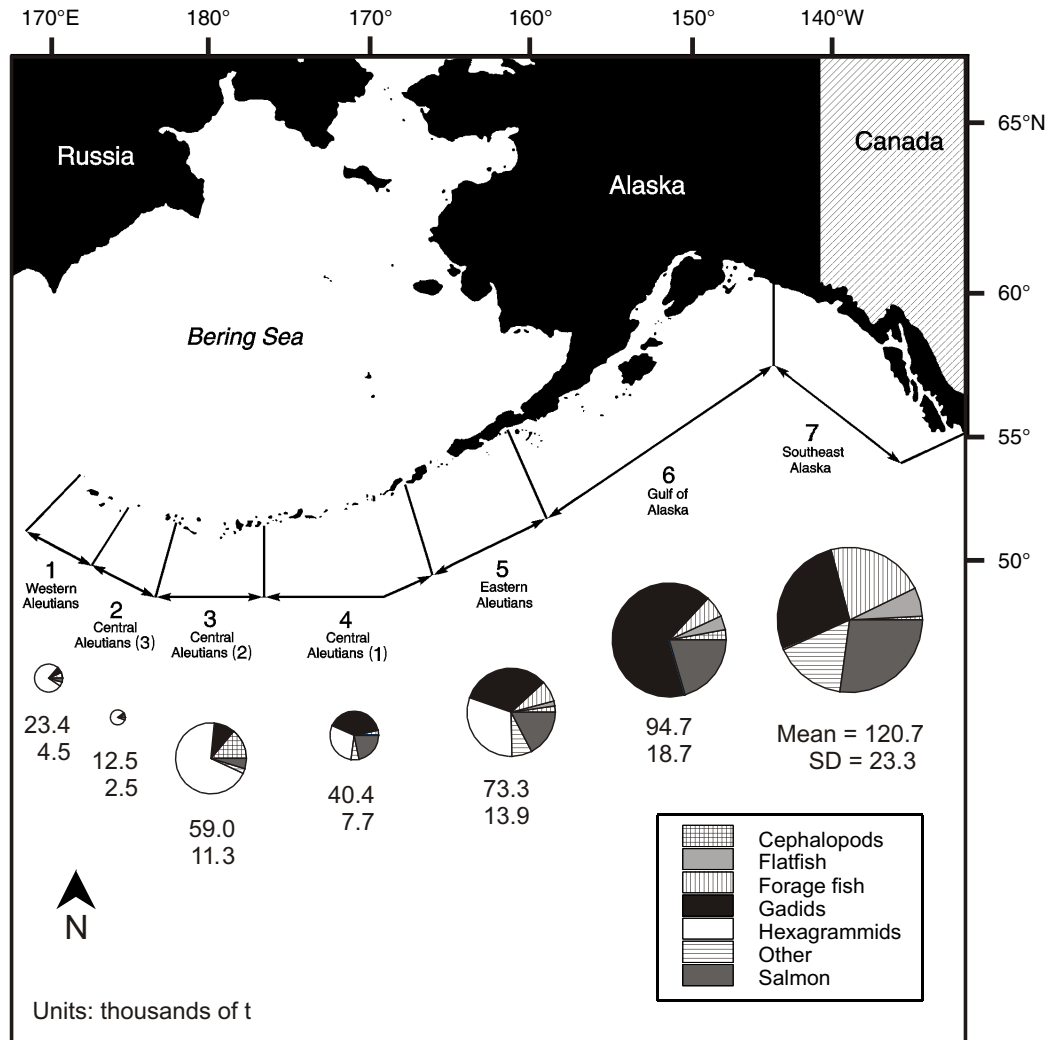
Figure 1

Estimated annual food biomass requirements (thousands of t) for Steller sea lions in 1998 in seven study areas of Alaska assuming that the summer diets were consumed all year long. SDs were obtained by using Monte Carlo simulations (1000 runs). Pie charts represent the proportions of diet biomass that each prey species category represents (defined in text). Diameters of the pie charts are proportional to their respective mean food requirement estimates. The map and study areas were adapted from Merrick et al. (1997) and Sease and Loughlin (1999). Numbers in parentheses in the central Aleutians (areas 2–4) are subarea numbers.

heat increment of feeding or the efficiency of using metabolizable energy). Metabolizable energy requirements of individuals were assumed to be the same in all regions of Alaska. Gross energy requirements of individuals were expected to vary among regions of Alaska because digestive efficiency and the heat increment of feeding are dependent upon the energy density of the diet, which varied among regions. Next, population size and composition were calculated by using pup count data from 1998, and a life table for Steller sea lions in Alaska. Population size varied by region of Alaska, but we assumed that population composition (i.e. sex and age structure) was the same for all regions. Finally, food requirements were

calculated by assuming a given diet composition (percent contribution of each prey category to diet biomass) and by using information on the energy density of prey. Diet composition varied by region of Alaska, but we assumed the energy density of individual prey categories did not.

The model incorporated a Monte Carlo random sampling routine which allowed us to estimate the error in the model predictions based on the assumed uncertainty in each parameter value. Three types of parameter sampling distributions were used: uniform (defined by upper and lower limits; e.g. 0.1–0.3), triangular (defined by a median, an upper limit and a lower limit; e.g. 0.2, 0.1–0.3), and normal (defined by a mean and SD; e.g. 0.2 ±0.05).

It is important to note that the model estimates of daily food requirements are not estimates of daily food consumption (Winship et al., 2002). Steller sea lions do not necessarily feed on a daily basis and breeding adults fast for periods during the breeding season. For example, the food required by a breeding male during the breeding season fast (to meet its energy requirement) would have been consumed before or after the breeding season (i.e. outside the breeding season). On an annual basis, however, the model estimates of food requirements are equal to food consumption if animals are consuming enough food to meet their energy requirements. We assumed that the amount of food consumed by the Steller sea lion population in Alaska in 1998 equaled the food requirement of the population.

Bioenergetic parameters

We used sampling distributions for bioenergetic parameters that were identical to those used by Winship et al. (2002) with the exception of fecal digestive efficiency and the heat increment of feeding for maintenance (for nonpups). Winship et al. (2002) defined fecal digestive efficiency as 1 minus the proportion of gross energy lost in feces, and assumed that its value ranged from 0.90–0.96 for Steller sea lions (i.e. fecal digestive efficiency was sampled from a uniform distribution). However, several studies have shown that the digestive efficiency of pinnipeds is positively correlated with the energy density of their prey (Keiver et al., 1984; Mårtensson et al., 1994; Lawson et al., 1997). In contrast, two other studies found that the digestive efficiencies of pinnipeds did not differ significantly among diets of different energy densities, although in both studies the average digestive efficiency was highest for the diet with the highest energy density (Fisher et al., 1992; Fadely et al.[1]). Rosen and Trites (2000a) found that the fecal digestive efficiency of captive Steller sea lions fed herring, pollock, salmon, and squid was positively correlated with the energy density of their diet. We therefore fitted a logistic equation to the data in Rosen and Trites (2000a; their Tables 1 and 2) using nonlinear least-squares regression (Nonlin; SYSTAT, Inc., 1992) and used this fitted equation ($n=20$, $r^2=0.75$) to calculate fecal digestive efficiency as a function of the energy density of prey:

$$DE_i = \frac{A}{1 + e^{-k(ED_i - ED_0)}},$$

where DE_i = fecal digestive efficiency for prey category i;

A = 0.951 (±0.0039 SE);

k = 1.86 (±0.016);

ED_i = energy density of prey category i (kJ/g wet mass); and

ED_0 = 2.10 (±0.089).

The fitted parameters (A, k, and ED_0) were randomly sampled from normal distributions with the previously described means and SEs (in each run of the model).

Winship et al. (2002) defined the heat increment of feeding for maintenance as the proportion of metabolizable energy used for maintenance that is lost due to the metabolic cost of digesting and processing food energy, and used a uniform sampling distribution of 0.10–0.15. However, there is evidence that the heat increment of feeding in Steller sea lions, like fecal digestive efficiency, varies with the energy density of prey (Rosen and Trites, 1997; 1999; 2000b). We fitted a linear equation to the data from Rosen and Trites (1997; their Table 1, including data for both meal sizes) and the raw data (Rosen[2]) from Rosen and Trites (1999) and Rosen and Trites (2000b) using linear least-squares regression and used this equation ($n=22$, $P<0.0001$, $r^2=0.60$) to calculate heat increment of feeding as a function of the energy density of prey:

$$HIF_i = a \times ED_i + b,$$

where HIF_i = heat increment of feeding for prey category i (as proportion of gross energy);

a = –0.013 (±0.0023 SE); and

b = 0.229 (±0.0173).

The fitted parameters (a and b) were randomly sampled from normal distributions with the previously described means and SEs (in each run of the model). HIF was then divided by fecal and urinary digestive efficiency to obtain the heat increment of feeding as a proportion of metabolizable energy (Winship et al., 2002).

Population parameters

We used the same sampling distributions for population composition parameters (survival, maturity, and reproductive rates) as outlined in Winship et al. (2002). The sampling distributions for population composition parameters used by Winship et al. (2002) were based on life tables developed for Steller sea lions (York, 1994, Trites and Larkin[3]) that were based on collections done in the 1970s in Alaska (Calkins and Pitcher, 1982). Those life tables were developed on the assumption of a stable population size. However, since the 1970s the sizes of Steller sea lion populations in some regions of Alaska

---

[1] Fadely, B. S., J. A. Zeligs, and D. P. Costa. 1994. Assimilation efficiencies and maintenance requirements of California sea lions (*Zalophus californianus*) fed walleye pollock (*Theragra chalcogramma*) and herring (*Clupea harengus*). Final report to the National Marine Mammal Laboratory (NMML), 28 p. NMML, NOAA, 7600 Sand Point Way N. E., Seattle, WA 98115.

[2] Rosen, D. A. S. 2001. Personal commun. Marine Mammal Research Unit, Fisheries Center, University of British Columbia. Room 18, Hut B-3, 6248 Biological Sciences Road, Vancouver, B.C., Canada, V6T 1Z4.

[3] Trites, A. W., and P. A. Larkin. 1992. The status of Steller sea lion populations and the development of fisheries in the Gulf of Alaska and Aleutian Islands. Unpubl. rep., 134 p. Marine Mammal Research Unit, Fisheries Center, University of British Columbia, Room 18, Hut B-3, 6248 Biological Sciences Road, Vancouver, B.C., Canada, V6T 1Z4.

Table 1

Number of Steller sea lion pups counted on rookeries in Alaska in 1998 (Sease and Loughlin, 1999) and minimum total breeding season population size estimates (including pups), assuming pups represent 20.5% of the population (Winship et al., 2002). Areas are defined in Figure 1.

Area	Number of rookeries	Geographic range	Pup count	Population size
Southeast Alaska	3	Forrester–White Sisters	4234	20,669
Gulf of Alaska	9	Seal Rocks–Chernabura	2971	14,503
Eastern Aleutian Islands	6	Pinnacle Rock–Akutan	2340	11,423
Central Aleutian Islands (subarea 1)	8	Bogoslof–Kasatochi	1297	6332
Central Aleutian Islands (subarea 2)	8	Adak–Ayugadak	1729	8440
Central Aleutian Islands (subarea 3)	3	Kiska–Buldir	355	1733
Western Aleutian Islands	3	Agattu–Attu	681	3324
All	40	Forrester–Attu	13,607	66,425

have declined dramatically (Loughlin et al., 1992; Trites and Larkin, 1996). Thus, it is unlikely that population structure was the same in the 1990s as it was in the 1970s and that population structure was the same in all regions of Alaska. Unfortunately, there are very few data available with which to determine the relationship between the structure and the rate of change in size of a population of Steller sea lions. To account for this uncertainty Winship et al. (2002) used sampling distributions for survival, maturity, and reproductive rates that approximated the uncertainty in population structure (ranges of sampling distributions were about 10–20%).

The population size during the breeding season in each region of Alaska was estimated by using pup count data from the U.S. National Marine Fisheries Service and Alaska Department of Fish and Game surveys done in June and July 1998 (Table 1; Sease and Loughlin, 1999). We assumed that the actual number of pups born could have been as much as 20% greater than the number counted because of pups that were hidden during the surveys, pup mortality before the survey dates, and births after the survey dates (Trites and Larkin, 1996). The number of pups in each region was therefore assumed to range from the values in Table 1 to $1.2 \times$ these values (uniform sampling distributions). Total population size was estimated by dividing the number of pups by the proportion of the total population size that they represented as described by Winship et al. (2002).

Diet parameters

Prey species were grouped into seven prey categories as defined by Merrick et al. (1997): 1) cephalopods: squid and octopus; 2) flatfish: Pleuronectidae; 3) forage fish: Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), eulachon (*Thaleichthys pacificus*), and capelin (*Mallotus villosus*); 4) gadids: walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and other Gadidae, 5) hexagrammids: Atka mackerel (*Pleurogrammus monopterygius*) and other Hexagrammidae; 6) salmon: Pacific salmon (*Oncorhynchus* spp.); and 7) other:

rockfish (*Sebastes* spp.), sculpins (Cottidae), pricklebacks (Stichaeidae), skates (*Raja* spp.), lamprey (*Lampetra* spp.), sharks, and other demersal fish.

The diet composition of Steller sea lions in southeast Alaska was estimated from data reported by Trites and Calkins[4] for scat collected in the 1990s on rookeries during the summer breeding season and on nonbreeding haulouts (in inside waters) during the rest of the year (Table 2). Split-sample frequencies of occurrence (Olesiuk et al., 1990) of prey categories were used as the median percent contributions of each prey category to diet biomass. Four seasonal diet compositions were used: a "winter" diet commencing on 1 December, a "spring" diet commencing on 1 March, a "summer" diet commencing on 1 June, and an "autumn" diet commencing on 1 September. In order to make the modeled transitions between seasonal diets more gradual, the season dates were sampled from uniform distributions with upper and lower limits equal to ±1 week. It was assumed that all ages and both sexes had the same diet composition.

Diet compositions for Steller sea lions in all other regions of Alaska (Gulf of Alaska–western Aleutian Islands) were estimated from data reported by Merrick et al. (1997) for scats collected mainly on breeding rookeries during the summers of the early 1990s (Table 2). As with southeast Alaska, split-sample frequencies of occurrence were used as the median percent contributions of each prey category to diet biomass. We assumed the same diet composition for all ages and both sexes year-round in these regions. The only area not covered by Trites and Calkins[4] and Merrick et al. (1997) was the eastern Gulf of Alaska. We assumed that the diet composition of Steller sea lions in the eastern Gulf of Alaska was the same as the diet of Steller sea lions in the Gulf of Alaska region from Merrick et al. (1997).

We randomly sampled the diet from triangular distributions to incorporate uncertainty in the diet composition

Table 2

Diet composition (median percent biomass contribution of each prey species category in the diet) of Steller sea lions in Alaska. Values for southeast Alaska are based on split-sample frequency of occurrence data from Trites and Calkins,[4] and values for the Gulf of Alaska through the western Aleutian Islands are based on split-sample frequency of occurrence data from Merrick et al. (1997). Prey categories are defined in the text and areas are defined in Figure 1.

Area	Prey category						
	Cephalopods	Flatfish	Forage fish	Gadids	Hexagrammids	Other	Salmon
Southeast Alaska							
Winter (Dec–Feb)	8.1	7.6	13.5	49.1	0.0	20.4	1.2
Spring (Mar–May)	5.0	7.6	21.0	52.5	0.0	12.5	1.4
Summer (Jun–Aug)	0.8	6.4	21.9	27.3	0.4	16.0	27.3
Autumn (Sep–Nov)	7.0	6.2	12.5	62.2	0.1	8.8	3.3
Gulf of Alaska	2.9	3.9	6.1	66.5	0.3	0.0	20.3
Eastern Aleutian Islands	2.3	1.8	7.7	32.9	30.7	7.3	17.3
Central Aleutian Islands (subarea 1)	0.0	0.0	3.3	40.2	29.4	5.4	21.8
Central Aleutian Islands (subarea 2)	13.7	0.0	0.0	9.7	69.7	2.2	4.7
Central Aleutian Islands (subarea 3)	7.1	0.0	0.0	3.2	84.2	4.9	0.5
Western Aleutian Islands	6.7	0.0	0.0	6.9	77.3	4.6	4.6

(percentage of biomass that each prey category represented in the diet). These distributions had medians from Table 2 and upper and lower limits equal to ±45% of medians ≥10%, or ±98% of medians <10%. These percentages were then standardized so that all prey categories were summed to 100% for a given diet. The ranges of the assumed errors in diet composition were determined by using estimates of the minimum and maximum split-sample frequencies of occurrence of prey categories (Olesiuk et al., 1990; Olesiuk, 1993; see "Discussion" section).

The energy density of fish is a function of their chemical composition, especially their lipid content (Stansby, 1976; Hartman and Brandt, 1995). Thus, the energy density of fish can vary with age (older fish tend to store more lipid; Brett, 1983; Harris et al., 1986; Paul et al., 1998a), season (lipid content can vary with foraging conditions; Paul et al., 1993; Paul et al., 1998a; Robards et al., 1999), reproductive status (lipid content of spawning fish can be different from nonspawning fish; Dygert, 1990; Smith et al., 1990; Hendry and Berg, 1999), and geographic location (feeding conditions can vary with location; Paul and Willette, 1997; Lawson et al., 1998; Paul et al., 1998b). The quantity and resolution of data on the energy density of prey of Steller sea lions varied depending on the prey species (Appendix I). When detailed season-specific energy-density data were available for prey species, we generally incorporated seasonal changes in energy density. Unfortunately, no detailed geographic-specific energy density data were available for any prey species; therefore we assumed that the energy density of prey did not vary among regions of Alaska. We used relatively wide ranges of possible energy-density values for all prey in order to incorporate the uncertainty in how energy density varies with season and geographic location.

Many data were available on the energy density of forage fish (Appendix I). The energy densities of forage fish species are relatively high, but vary seasonally in relation to spawning periods, the over-winter fast, and spring and autumn phytoplankton blooms (Anthony et al., 2000). For example, eulachon had a very high energy density (7.5–11.1 kJ/g wet mass) and its energy density was slightly higher in the summer than in late winter (Payne et al., 1999). The energy density of capelin was lower, ranging from 3.5 to 7.0 kJ/g wet mass. In the Gulf of Alaska, the energy density of capelin was high in June (start of spawning) after the spring phytoplankton bloom and decreased through the summer with advancing reproductive stage (Anthony et al., 2000). The energy density of capelin increases again in the fall and early winter as the fish feed on the autumn phytoplankton bloom (Lawson et al., 1998; Payne et al., 1999; Anthony et al., 2000).

Pacific herring and Pacific sandlance were the two main forage fish species consumed by Steller sea lions in Alaska in the 1990s (Merrick et al., 1997, Trites and Calkins[4]). The energy density of Pacific herring increased with age, and the energy density of adults (age >0) ranged from 4.4–11.7 kJ/g wet mass (Appendix I). In the Gulf of Alaska, Pacific herring were highest in energy content in the autumn and lowest in energy content in the spring (after the overwinter fast; Paul et al., 1998a), but the exact timing of these seasonal changes varied depending on the region of Alaska (Perez, 1994). Pacific sandlance (age >0) ranged in energy density from about 3.2 to 6.1 kJ/g wet mass. Pacific sandlance from the Gulf of Alaska was highest in energy content in June (after the spring bloom), and its energy content decreased through autumn (spawn mid-autumn) and remained low throughout the winter fasting period (Robards et al., 1999; Anthony et al., 2000). We assumed

the energy density of the forage fish prey category was 4.9–11.7 kJ/g in the summer and autumn, and 3.2–6.3 kJ/g in the winter and spring.

Gadids consumed by Steller sea lions in Alaska in the 1990s were primarily walleye pollock, but Pacific cod was also an important prey species (Merrick et al., 1997, Trites and Calkins[4]). The energy density of walleye pollock increases with age, and the energy density of pollock in the size range primarily consumed by Steller sea lions (age>0, range 5–65 cm; Pitcher, 1981, Calkins 1998, Calkins and Goodwin[5]) ranged from about 3.2 to 5.9 kJ/g (Appendix I). The data in Appendix I do not suggest that walleye pollock undergo marked seasonal changes in energy density in Alaska. Pacific cod (age>0) was similar in energy density to walleye pollock and ranged from about 3.3 to 4.5 kJ/g (Appendix I). However, Smith et al. (1990) found that adult Pacific cod had a relatively high energy density in early spring (ripe, prespawning), declined to a low energy density in the summer (postspawning), and then increased to a high energy density again by early winter. Because the energy density of Pacific cod throughout the year was within the range of the energy density of walleye pollock, we assumed that the energy density of the gadid prey category was constant year-round and equal to 3.2–5.9 kJ/g.

Flatfish species from the northeast Pacific Ocean had energy densities ranging from approximately 2.9 to 6.0 kJ/g (Appendix I). Two species, English sole (*Parophrys vetulus*) and yellowfin sole (*Pleuronectes asper*), exhibited seasonal changes in energy density. The energy density of adult female English sole increased from spring through mid-autumn (feeding and energy storage period) and decreased thereafter (Dygert, 1990). Juvenile and adult yellowfin sole increased rapidly in energy density at the beginning of summer (June, spawning period), and energy density then decreased through the following spring (Paul et al., 1993). Dygert (1990) and Paul et al. (1993) have suggested that these seasonal patterns of energy density are common for most northern flatfish species. We assumed the energy density of the flatfish prey category was 4.0–6.0 kJ/g in the summer and autumn and 2.9–4.9 kJ/g in the winter and spring.

The primary factors affecting the energy density of Pacific salmon are size and age (Appendix I). The data in Appendix I do not indicate substantial seasonal variability in the energy density of Pacific salmon. Energy density increases with size until salmon return to freshwater and spawn—at which point energy density drops drastically (Brett, 1983; Hendry and Berg, 1999). Steller sea lions in Alaska consumed salmon approximately 25–60 cm in length (Trites and Calkins[4]), which we assumed corresponded to a range in mass of approximately 0.3–3 kg, and an energy density ranging from about 6.1 to 8.7 kJ/g.

Hexagrammids were a major component of the diet of Steller sea lions in the western regions of Alaska during the 1990s (Table 2). The main hexagrammid species consumed was Atka mackerel (Merrick et al., 1997). Unfortunately, very few data are available on the energy density of Atka mackerel. Juvenile hexagrammids (≤12 cm), including Atka mackerel, have energy densities ranging from about 3.5 to 4.7 kJ/g (Appendix I). However, Steller sea lions likely consume fish longer than 12 cm, which may have higher energy densities. We therefore assumed the energy density of the hexagrammid prey category was 3.5–6.0.

Detailed seasonal and size-specific data on the energy density of cephalopods and other fish species were not available. We assumed (from the data in Appendix I) that the energy densities of the cephalopod and "other" prey categories were 3.8–6.5 kJ/g and 3.1–6.9 kJ/g, respectively.
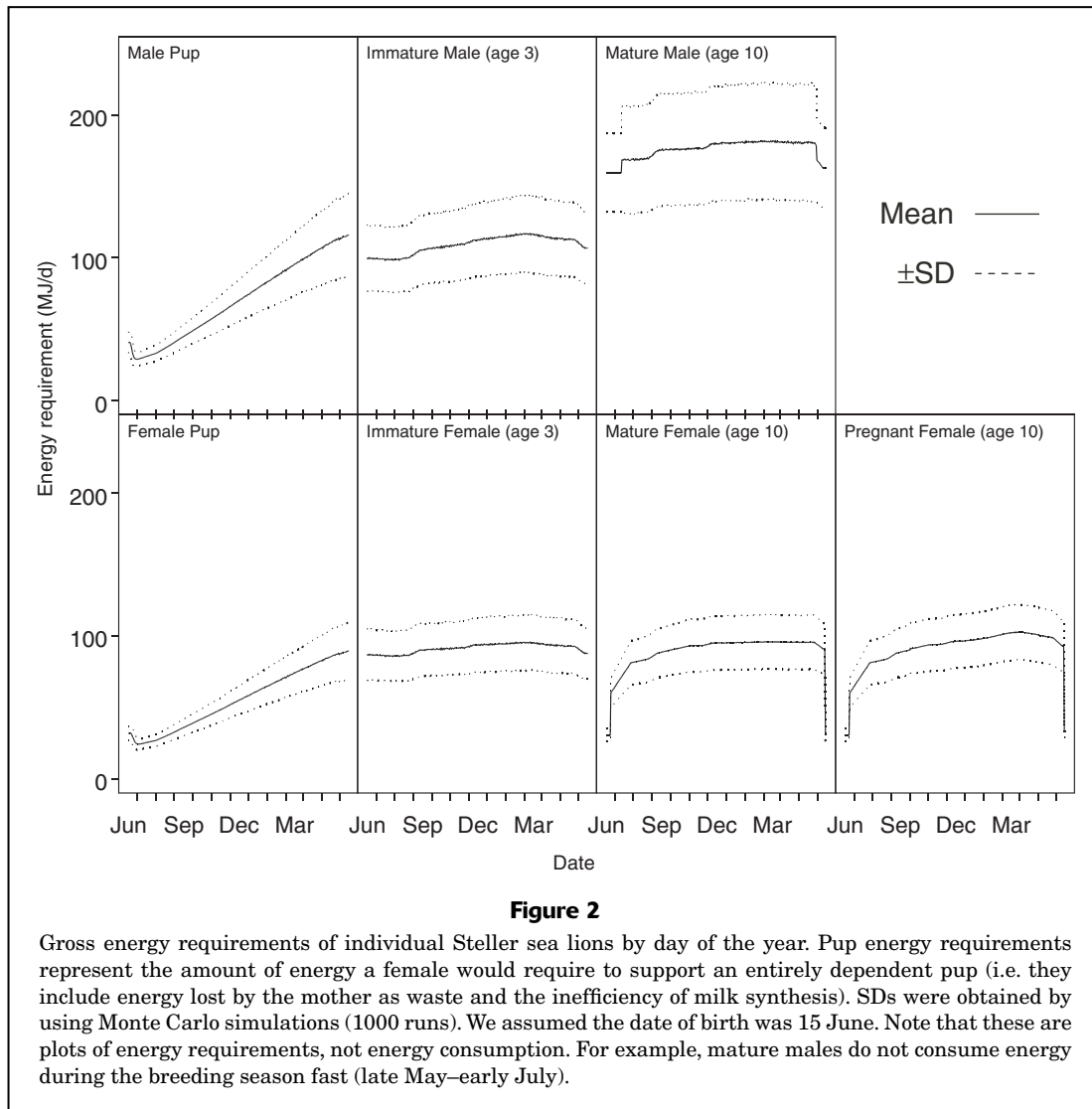
Results

Seasonal food requirements (southeast Alaska)

Predicted seasonal changes in gross energy requirements of Steller sea lions in southeast Alaska (per individual) were largely driven by changes in activity budgets (Fig. 2; Winship et al., 2002). Immature animals and mature males were assumed to have relatively constant activity budgets and therefore had relatively constant daily energy requirements. The exception was a drop in the energy requirements of mature males during the breeding season. Energy requirements of mature females were also lowest during the breeding season and generally increased from summer through the following spring, especially if females were pregnant. The energy required to nurse a pup increased steadily throughout the pup's first year of life.

A small part of the seasonal change in gross energy requirements of all animals other than pups can be attributed to variation in the energy density of prey and associated differences in digestive efficiency and the heat increment of feeding. The summer diet had the largest proportions of prey species with high energy densities (forage fish and salmon), and therefore had a higher overall energy density than the autumn, winter, and spring diets (Table 2). Thus, digestive efficiency was highest and the heat increment of feeding was lowest in the summer. The winter and spring diets in southeast Alaska had a lower energy density due to the higher proportions of species with low energy densities and because flatfish and forage fish were assumed to have a lower energy density during winter and spring. As a result, digestive efficiency was lower and the heat increment of feeding was higher during the winter and spring than during the summer. The energy density of the autumn diet (and digestive efficiency and the heat increment of feeding) was intermediate between the energy densities of the summer diet and the winter and spring diets. These seasonal changes in efficiency resulted in up to 4% increases in gross energy requirements during the autumn, winter, and spring in

[5] Calkins, D. G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpubl. rep., 76 p. Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Road, Anchorage, AK 99518-1599.

Figure 2
Gross energy requirements of individual Steller sea lions by day of the year. Pup energy requirements represent the amount of energy a female would require to support an entirely dependent pup (i.e. they include energy lost by the mother as waste and the inefficiency of milk synthesis). SDs were obtained by using Monte Carlo simulations (1000 runs). We assumed the date of birth was 15 June. Note that these are plots of energy requirements, not energy consumption. For example, mature males do not consume energy during the breeding season fast (late May–early July).

relation to summer (independent of seasonal changes in metabolizable energy requirements).

Estimated seasonal changes in food requirements in southeast Alaska during the 1990s (Fig. 3) were more pronounced than seasonal changes in energy requirements (Fig. 2) because seasonal changes in the energy density of the diet resulted in large seasonal changes in the amount of food biomass required per unit of gross energy. In general, food requirements were highest in the winter and spring when the energy density of the diet was lowest. Food requirements were lowest in the summer when the energy density of the diet was highest, and food requirements in the autumn were intermediate between those of summer and winter–spring. The maximum daily food requirements in southeast Alaska occurred in March when immature 3-year-old males and females required 25 (±6.9 SD) kg and 21 (±5.2) kg respectively, and mature 10-year-old males and nonpregnant females required 39 (±10.4) kg and 21 (±5.0) kg, respectively. The maximum daily

food requirement for a pregnant 10-year-old female nursing a pup averaged 40–46 kg (mid-May). In comparison, daily food requirements in summer, just after the breeding season (1 August), were only 62–69% of these maximum food requirements (immature 3-year-old male: 16 [±4.0] kg, immature 3-year-old female: 14 [±3.1] kg, mature 10-year-old male: 27 [±6.7] kg, mature nonpregnant 10-year-old female: 13 [±2.8] kg). A mature female nursing a pup required only an average of 17–18 kg of food per day at this time of year (39–43% of her maximum daily food requirement).

Regional food requirements

Total annual population food requirements in 1998 varied among regions, as expected because of differences in diet and population size (Fig. 1). When annual food requirements were estimated with diet information from summer only, the model predicted that the southeast Alaska popu-
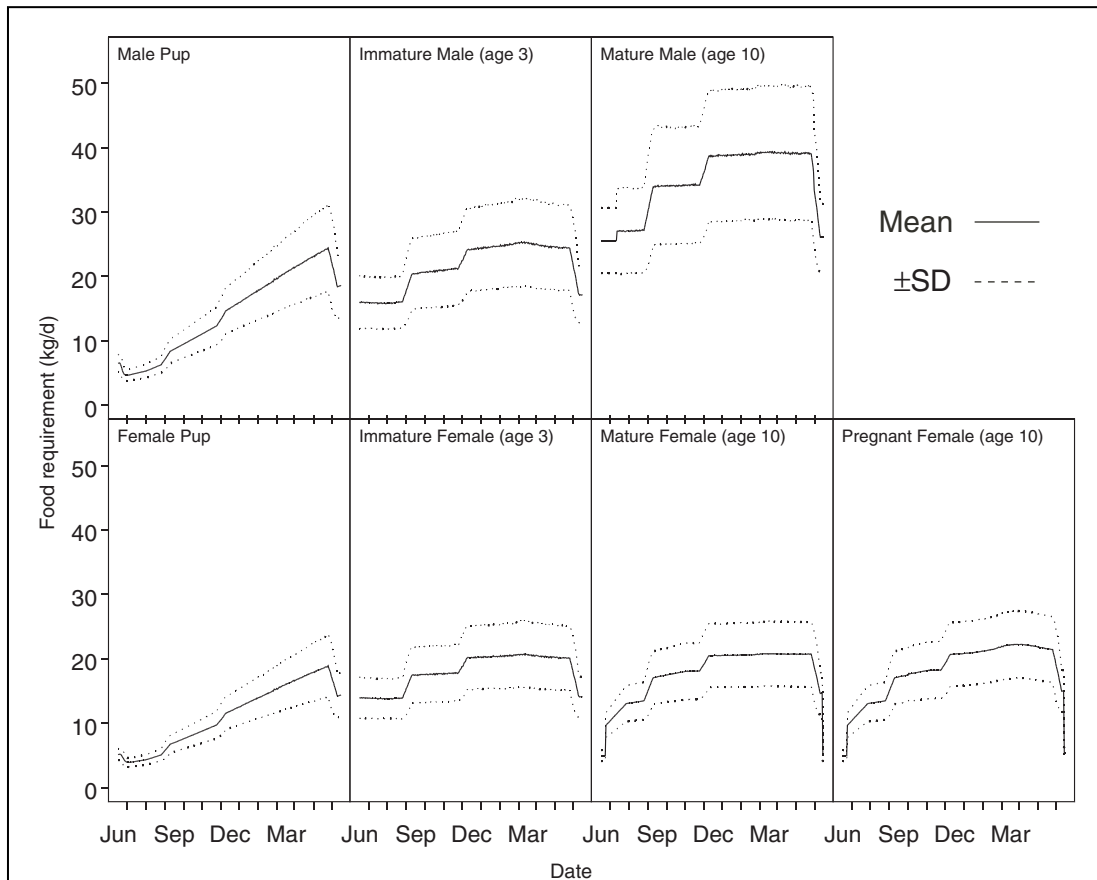
Figure 3

Food biomass requirements for individual Steller sea lions in southeast Alaska by day of the year. Pup food requirements represent the amount of food a female would require to support an entirely dependent pup. SDs were obtained by using Monte Carlo simulations (1000 runs). We assumed the date of birth was 15 June. Note that these are plots of food requirements, not food consumption. For example, mature males do not consume food during the breeding season fast (late May–early July).
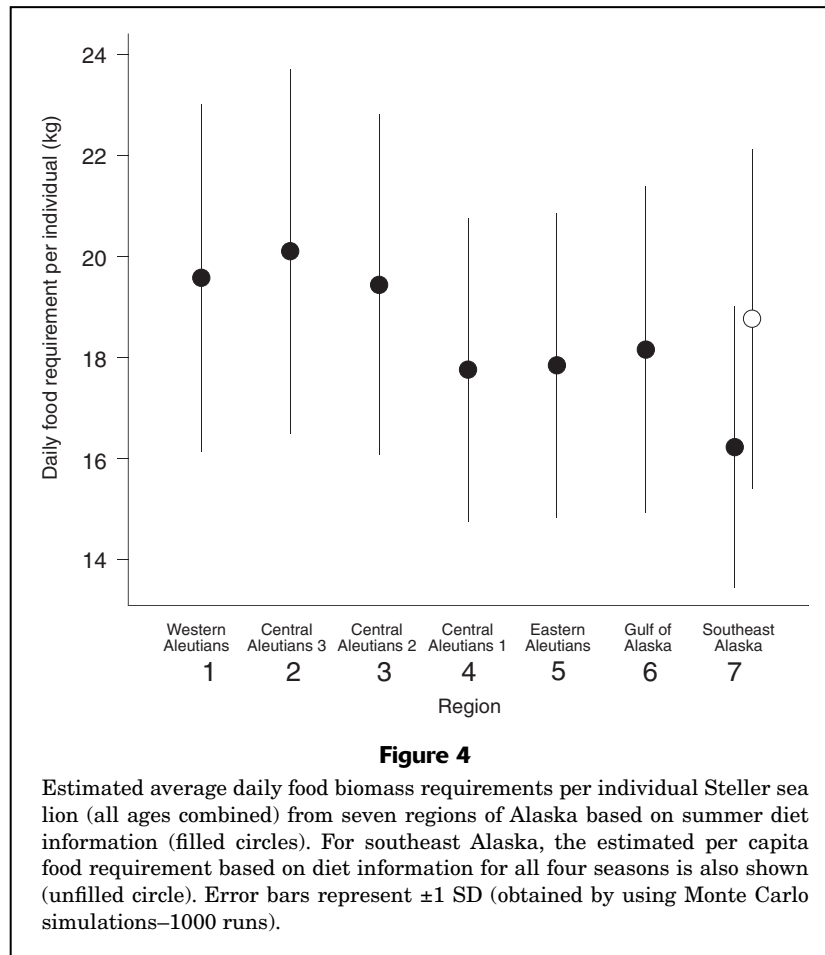
lation consumed the most prey biomass on an annual basis (121,000 [±23,300] t) and the central Aleutian Islands 3 population consumed the least (12,500 [±2470] t). The large difference in total consumption primarily reflects the large difference in population size between regions. For southeast Alaska, the only region where diet information was available for all four seasons, the estimated prey biomass consumed on an annual basis increased from 121,000 (±23,300) t (assuming a summer diet all year) to 140,000 (±27,800) t (when diet changed seasonally) because of higher proportions of low–energy-density prey in the diet (and therefore lower energy density of the diet) in autumn, winter, and spring (Table 2). The CVs of total annual population food biomass consumption were 19–20%.

Based on summer diets, the predicted average daily food requirement per individual (all ages) ranged from 16 (±2.8) kg (southeast Alaska) to 20 (±3.6) kg (central Aleutian Islands [subarea 3])—a 24% difference (Fig. 4). The average daily per capita food requirement for southeast

Alaska increased by 3 kg (to 19 [±3.4] kg) when the diets for all four seasons were considered. In general, per capita food requirements were lowest in regions where Steller sea lions consumed high proportions of high–energy-density prey (forage fish and salmon), as in the eastern Aleutian Islands and central Aleutian Islands (subarea 1), and were highest in regions where the diet contained larger proportions of low–energy-density prey (gadids and hexagrammids), as in the western Aleutian Islands and central Aleutian Islands (subareas 2 and 3).

The greatest estimated consumption of a single prey species category in a region in 1998 was 68,600 (±14,400) t of gadids in southeast Alaska (using diet information for all seasons; Fig. 5). Gadids were consumed in a similar amount in the Gulf of Alaska (62,700 [±12,800] t). Alaska-wide, the top two prey categories in terms of biomass consumption were gadids and hexagrammids (gadids – 179,000 [±36,700] t, hexagrammids – 104,000 [±20,600] t). The Steller sea lion population in the central Aleutian Islands (subarea 2) (Fig. 1) consumed the most hexagram-

Figure 4

Estimated average daily food biomass requirements per individual Steller sea lion (all ages combined) from seven regions of Alaska based on summer diet information (filled circles). For southeast Alaska, the estimated per capita food requirement based on diet information for all four seasons is also shown (unfilled circle). Error bars represent ±1 SD (obtained by using Monte Carlo simulations–1000 runs).

mid biomass of any region (41,000 [±8070] t). CVs of individual prey category consumption ranged from 20 to 39%.

Discussion

Uncertainty in model predictions

An important aspect of our model is that it produces distributions of predicted food requirements rather than point estimates (Winship et al., 2002). This allowed us not only to estimate mean predicted food requirements but also to estimate the potential error in these mean predictions by using either SD or CV (SD as a percentage of the mean). We found that the CVs of mean predicted food requirements at the population level (both total biomass and individual prey categories) were approximately 20–40%. The ranges of food requirements predicted by the model were of course much wider than ±1 CV. For instance, 5% of the predicted values lie beyond ±1.96 CV if the normal distribution is used to approximate the distribution of model predictions. The minimum and maximum food requirement estimates predicted by the model were generally <40% of the mean and >160% of the mean, respectively, if the CV of the mean predicted food requirement was 30%. Thus, the ranges of

predictions produced by our model reflect considerable uncertainty in the food requirements of Steller sea lions because of the assumed errors that we attributed to certain bioenergetic parameters (e.g. metabolic rate at sea), population parameters (e.g. age- and sex-specific survival rates), and diet parameters (e.g. diet composition). Future research on key parameters in our model will help to refine the predictions of this model and improve the accuracy of estimates of the food requirements of this species.
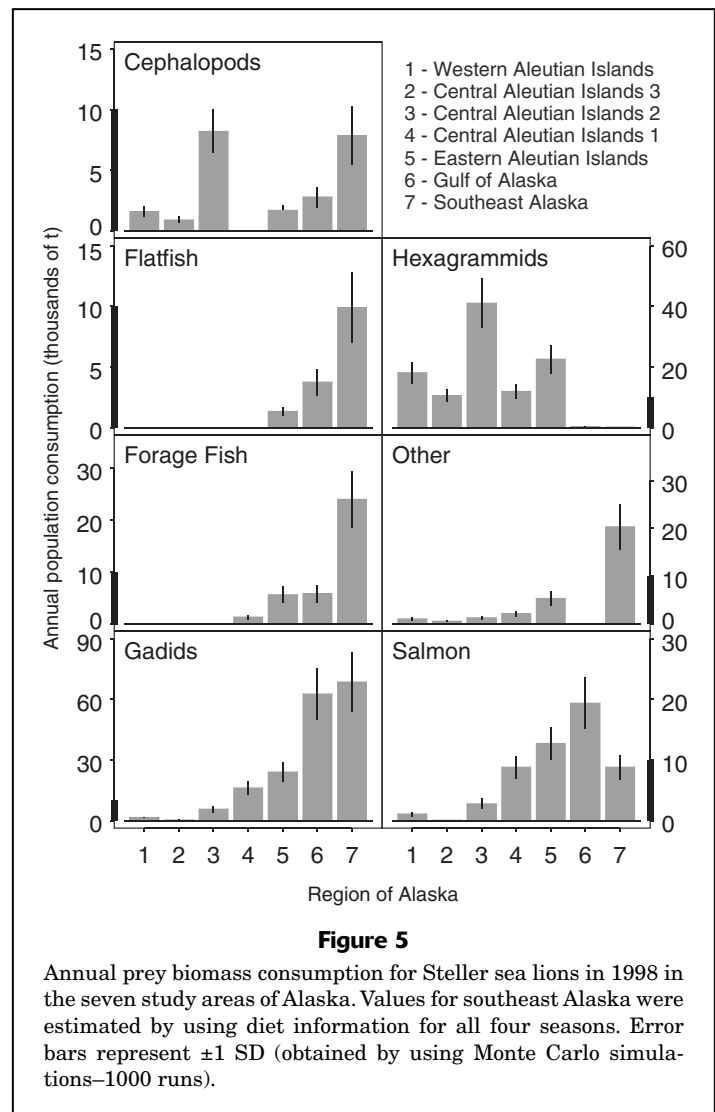
Biases in diet composition

The diet compositions that we used were estimated from the hard parts of prey found in scats collected on haul-outs and rookeries and were limited by incomplete sampling coverage by time of the year and by sex- and age-class. Diet data from the western Aleutian Islands through the Gulf of Alaska came mainly from mature females on breeding rookeries during late June, early July, and early August in the early 1990s (Merrick et al., 1997). Thus, these data reflect a specific segment of the population during a short period of the year.

We applied the diets reported by Merrick et al. (1997) to all age- and sex-classes of Steller sea lions in 1998 and assumed that those diets did not change seasonally. Data

reported by Sinclair and Zeppelin (2002) suggest that the dominant prey in more recently collected samples from the Gulf of Alaska and Aleutian Islands in summer (breeding females on rookeries) and winter (juvenile and adult males and females on nonbreeding haul-outs) were similar to those reported by Merrick et al. (1997). Sinclair and Zeppelin (2002) found walleye pollock more frequently than any other prey species in Steller sea lion scats from the Gulf of Alaska and eastern Aleutian Islands during the summer and winter, whereas Atka mackerel was the second most frequently occurring prey species in the eastern Aleutian Islands, and the most frequently occurring prey species in the central and western Aleutian Islands during summer and winter. However, Sinclair and Zeppelin (2002) did find significant seasonal changes in the frequency of certain prey species in the diets of Steller sea lions at specific sites in Alaska. For example, Pacific cod occurred more frequently in scats collected on haul-outs during the winter than in scats collected on rookeries during the summer in all regions (Gulf of Alaska through western Aleutian Islands). Pacific salmon occurred more frequently in the summer than in the winter in the Gulf of Alaska and the eastern Aleutian Islands, while this seasonal difference was reversed in the central and western Aleutian Islands. A seasonal change in the proportion of the diet comprising high-energy prey species like salmon can have a substantial effect on the total and per capita amount of food biomass required by Steller sea lions (e.g. our results for southeast Alaska). Nevertheless, given the similarities between the two summer and winter data sets (from Sinclair and Zeppelin, 2002, and Merrick et al., 1997), and given the level of uncertainty that we incorporated in our diet compositions, we feel that the diet compositions that we assumed for Steller sea lions in the western Aleutian Islands through Gulf of Alaska regions in 1998 were reasonable approximations.

The scat data we used to estimate the diet of Steller sea lions in southeast Alaska had better temporal and demographic coverage. Trites and Calkins[4] reported data from scats collected in every month except September. Although the scat data from the summer months were again from breeding females on rookeries, the scat data from the rest of the year were from nonbreeding animals on haul-outs. Animals using these haul-outs included adult and juvenile males and females. Thus, those scats were more representative of the average diet of the population than scats collected on rookeries during the breeding season. There is evidence that the diet of mature females on rookeries differs from the diet of nonbreeding animals on haul-outs during the summer (Trites and Calkins[4]), but it is difficult to translate this difference into sex- or age-specific dietary differences.

In addition to sampling limitations, there are at least two other potential biases associated with using scat data to assess diet composition. The first potential bias is the possibility that some of the consumed prey species

Figure 5

Annual prey biomass consumption for Steller sea lions in 1998 in the seven study areas of Alaska. Values for southeast Alaska were estimated by using diet information for all four seasons. Error bars represent ±1 SD (obtained by using Monte Carlo simulations–1000 runs).

were not represented in the scat samples (Bowen, 2000). Although the identification of prey hard parts other than otoliths in scats increases the probability of detection of prey species, cartilaginous fish or fish with small or fragile bony structures may be completely digested and not evident in scat (Olesiuk et al., 1990). For example, in captive Steller sea lion feeding trials, the average number of hard parts recovered in scat was 31.2 per pollock, but only 7.9 per herring (Cottrell and Trites, 2002). Thus, there was a greater chance of an individual herring being missed compared to an individual pollock. However, small fish are likely consumed in larger numbers, which would increase the likelihood of detecting their presence in scat.

The second potential source of dietary bias arises from using the "split-sample frequency of occurrence" technique to estimate the percentage of biomass that different prey represent in the diet. This technique assumes that the prey identified in a scat sample represent all the prey consumed in a meal, and that all prey species of a meal are consumed in equal biomasses (Olesiuk et al., 1990). This

method may overestimate the contribution of small prey and underestimate the contribution of large prey to diet biomass. However, as previously mentioned, such a bias would be reduced if small prey are consumed in greater numbers than large prey in a given meal. A potentially better technique than split-sample frequency of occurrence is volumetric or biomass reconstruction analysis (i.e. the estimation of the actual size of each prey in a scat from the size of otoliths or other hard parts), but otoliths are usually not available from Steller sea lion scat (Merrick et al., 1997) and digestion correction factors (Tollit et al., 1997) and regressions of hard-part size on body size are currently not available for prey of Steller sea lions.

Olesiuk et al. (1990) and Olesiuk (1993) estimated the error associated with a key assumption of the split-sample frequency of occurrence technique (all prey categories in a scat are consumed in equal quantities) by calculating the minimum and maximum split-sample frequencies of occurrence of prey. For example, the minimum split-sample frequency of occurrence of a prey category was calculated by assuming that when the prey category was found in a scat with another prey category, it represented a negligible proportion of the biomass of the meal represented by that scat. We considered their estimates of the minimum and maximum split-sample frequencies of occurrence of prey to approximate the total potential errors in the diet compositions we used. Thus, the assumed errors in diet were based only on the potential error in estimating diet from scats and not on the potential error due to sampling limitations.

Our assumed errors in diet composition were relatively large. For example, if a prey category was assumed to comprise a median of 50% of the diet, the proportion of the diet represented by that prey category in any one run of the model ranged from 27.5% to 72.5% (before the diet was standardized to 100%). Nevertheless there is still the possibility of sampling biases in the diet compositions that we assumed for Steller sea lions in Alaska. Future studies of the diet of Steller sea lions will allow us to obtain better estimates of the regional, seasonal, and intrapopulation variability in diet. Also, studies of captive Steller sea lions will assist in determining the biases and variability associated with the estimation of diet from scats (Cottrell and Trites, 2002).

## Effect of diet on food requirements

We found that changes in the energy density of the diet can have large effects on the amount of food that Steller sea lions need to consume. In southeast Alaska, seasonal changes in the energy density of the diet resulted in large seasonal changes in daily food requirements, even when daily energy requirements were relatively constant. Immature and mature animals (excluding lactating females) required approximately 45–60% more food per day in early spring than in late summer (Fig. 3). Regional differences in the energy density of the diet resulted in smaller, but still substantial differences in food requirements among Steller sea lions in different regions of Alaska (up to a 24% difference based on summer diets).

The effect of diet on food requirements, can be further illustrated by considering two diets: one of entirely gadids (walleye pollock, Pacific cod) and one of entirely small schooling fish (herring, sandlance). Based on caloric differences between prey types and differences in digestive efficiency and the heat increment of feeding, a 10-year-old male would require an average of 30 (±7.7) kg of small schooling fish per day (5% of body mass), but would require 41 (±9.7) kg of gadids (6% of body mass): a 37% increase in prey biomass requirements. A 10-year-old female's (pregnant, no pup) average daily food requirement would increase by a similar percentage with a diet shift from small schooling fish to gadids (15 [±3.7] kg to 21 [±4.7] kg or 6% to 8% of body mass).

A large animal may be able to compensate for changes in prey biomass requirements, but immature or recently weaned animals may be more susceptible to changes in prey biomass requirements because they need to consume more food per unit body mass than adult animals (Winship et al., 2002). A 1-year-old male would require an average of 16 (±4.2) kg of small schooling fish per day (12% of body mass), but would require an average of 22 ±5.4 kg of gadids (16% of body mass). Similarly, a 1-year-old female would need 14 (±3.2) kg of small schooling fish (13% of body mass) or 18 (±4.1) kg of gadids (17% of body mass). The difference in energy density between the gadid and forage fish categories was greater in the summer and autumn than in the winter and spring; thus the difference between the daily food requirement of a sea lion consuming only gadids and the food requirement of a sea lion consuming only forage fish was greatest in the summer and autumn. Although animals prey on more than one species category in nature, which would buffer the effects of changes in diet composition, differences in the energy density and digestibility of prey can have large effects on prey biomass requirements, especially for young animals.

Merrick et al. (1997) found a significant relationship between the diversities of Steller sea lion diets and the rates of change in the numbers of adult and juvenile Steller sea lions counted on rookeries between 1990 and 1994 in different regions of Alaska (Gulf of Alaska through the western Aleutian Islands). Sea lions in regions with high rates of population decline had low dietary diversity. Plotting the rates of population decline against the amount of prey required in each region (using summer diets), we found a significant (α=0.05) relationship (Spearman rank correlation coefficient r_s=−0.929, P=0.02; Fig. 6), indicating that sea lions in areas with high rates of decline had higher per capita food requirements. This finding suggests that the energy density of the diet may have had a role in the population decline in some regions of Alaska during the early 1990s.

The correlation we report between food requirements and population change (Fig. 6) is based on summer diets and limited data on the energy density of sea lion prey categories such as hexagrammids. When seasonal diet information for southeast Alaska was considered, our model predicted a substantially greater per capita food requirement in that region (Fig. 4). Seasonal data are required from all regions of Alaska to describe diet composition
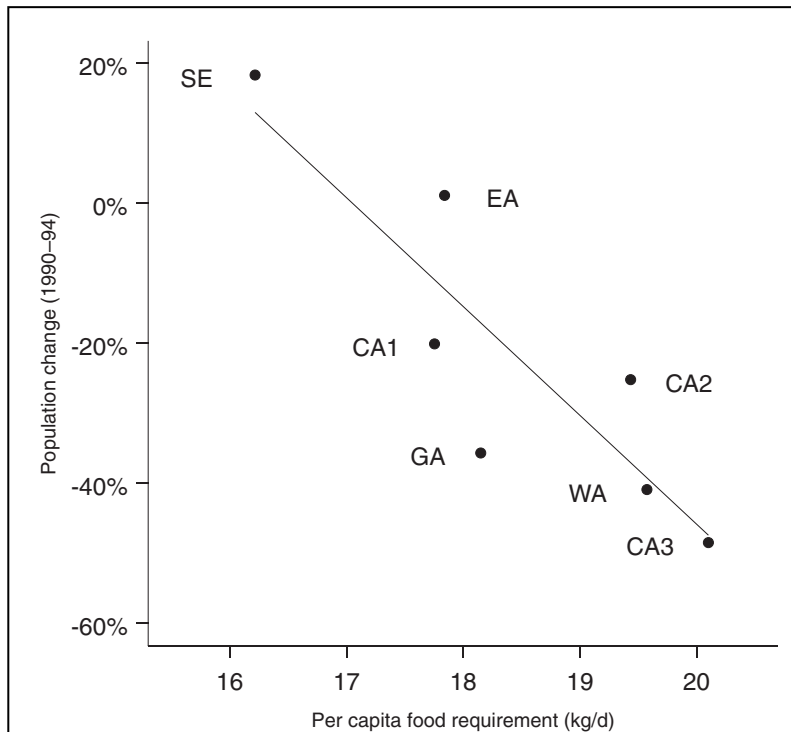
Figure 6

Per capita daily food biomass requirement predicted by our model (based on summer diets) versus rate of change in the number of adult and juvenile Steller sea lions counted on rookeries between 1990 and 1994 by region of Alaska (SE=Southeast Alaska, GA=Gulf of Alaska, EA=Eastern Aleutians, CA=Central Aleutians, WA=Western Aleutians). The Spearman rank correlation coefficient (r_s) for the data is –0.929 (P=0.02). The line represents a linear least-squares regression (r^2=0.77). Data on population change are from Merrick et al. (1997), except the value for southeast Alaska (18.3%) which we calculated from data reported by Strick et al. (1997) for three rookeries (Forrester, Hazy, and White Sisters islands).

and energy density, so that the potential relationship between rates of population change and per capita food requirements can be fully explored. Nevertheless, the data that are currently available are intriguing and suggest a possible mechanism for the original relationship reported by Merrick et al. (1997) between diet diversity and population decline.

Steller sea lions may use a couple of strategies to respond to increases in food requirements. The first and obvious strategy is to increase the rate of food intake. Many studies have found that animals increase their food intake on low-energy diets (Hammond and Wunder, 1991; Veloso and Bozinovic, 1993; Brekke and Gabrielsen, 1994; Weber and Thompson, 1998). Fadely et al.[1] found that the intake rates of captive California sea lions (*Zalophus californianus*) eating walleye pollock were approximately 1.4 times greater than when consuming herring. In order to increase their rate of food intake, Steller sea lions would likely have to increase the amount of time spent foraging or their activity level while foraging (or would have to do both). An increase in foraging time would likely result in

increased pup mortality because mothers would be absent from haul-outs for longer periods of time (Trillmich and Dellinger, 1991; Boyd et al., 1994) or in increased susceptibility of these mothers to predation by killer whales (*Orcinus orca*) or sharks. An increase in foraging intensity may result in an increase in the energy cost of foraging, and therefore additional increases in food requirements (Costa and Gentry, 1986).

A second strategy Steller sea lions may employ to respond to decreases in the energy content of their diet is to reduce energy expenditures and thereby prevent an increase in food biomass requirements. For example, Veloso and Bozinovic (1993) found that degus (*Octodon degus*) eating low-quality forage, had lower basal metabolic rates than degus eating high-quality forage. A similar metabolic depression was observed in captive Steller sea lions eating low-energy squid and walleye pollock (Rosen and Trites, 1999; Rosen and Trites, 2000b). Steller sea lions may also reduce energy expenditures by decreasing their activity levels. Studies of the rifleman (*Acanthisitta chloris*; Lill, 1991) and white-footed sportive lemur (*Lepilemur leuco-*

pus; Nash, 1998) found that animals conserved energy by reducing the time they spent active and by increasing the time they spent resting when energy requirements for thermoregulation increased during cold periods. Mature female Steller sea lions may also have an additional option of reducing energy investment in reproduction by aborting fetuses to conserve energy during periods of nutritional stress (Pitcher et al., 1998).

Steller sea lions consuming very low–energy-density diets may be unable to consume enough food biomass to meet even reduced energy requirements. This situation could result from prey handling and digestion-time constraints or from an inability to capture enough prey. Juvenile animals would likely be the most susceptible to both situations. As discussed, juvenile animals have much higher mass-specific food requirements, and young animals may not be able to process 16–17% of their body weight in food per day (mean daily food requirements of 1-year-olds on a strictly gadid diet). Juvenile animals may also experience diving constraints (e.g. dive depth; Merrick and Loughlin, 1997) that adults do not, and may have more difficulty capturing sufficient quantities of low-energy prey.

An important consideration regarding the effect of diet composition on food requirements is the energetic cost of foraging on different prey species. Differences in the size and behavior of individual prey items may reduce differences in food biomass requirements resulting from differences in the energy density of prey. For example, consider a situation where a Steller sea lion can consume either small herring of high energy density or large pollock of low energy density. To obtain a given amount of prey biomass the sea lion can consume either several small herring or one large pollock. Based on the energy density of the prey, the sea lion would acquire a greater absolute amount of energy from the herring than from the pollock. However, if the energetic cost of pursuing and capturing several herring was greater than the cost of pursuing and capturing one pollock, then the net amount of energy obtained (energy consumed minus energy spent) per unit of prey biomass may not differ between the herring and the pollock diets. In other words, the sea lion's food requirement would be similar whether it was foraging on the small herring or the large pollock.

We did not incorporate differential costs associated with foraging on different prey categories in our model. We also did not consider the size of individual prey items consumed by Steller sea lions. Data on foraging costs for Steller sea lions in relation to prey species and prey size are currently limited and should be incorporated into bioenergetic models as they become available, in the form of functional relationships between diet composition and the energetic cost of foraging.

Prey consumption by Steller sea lions in Alaska in 1998

Regional variation in the amount of prey consumed by Steller sea lions in Alaska in 1998 (Figs. 1 and 5) was mainly due to differences in population size, as well as differences in diet composition (previous section). Gadids and

hexagrammids were the top two prey categories in terms of biomass consumed. Gadids dominated the diet in the eastern areas (Gulf of Alaska), whereas hexagrammids dominated the diet in the western areas (central Aleutians 2 to western Aleutians). Gadids also dominated the diet in southeast Alaska when considered on an annual basis.

The mean model estimate of gadid consumption by Steller sea lions in all study regions of Alaska in 1998 was 179,000 (±36,700) t per year. This represents about 7% of the total estimated walleye pollock biomass, 20% of the total estimated Pacific cod biomass, or 5% of combined pollock and cod biomass dying naturally in 1998 in the Gulf of Alaska, Aleutian Islands, Bogoslof area, and eastern Bering Sea (Table 3). Steller sea lion consumption of gadids also represents 12% of the total gadid biomass removed in 1998 by commercial fisheries. Thus, estimated total gadid biomass consumption by Steller sea lions in Alaska is less than that taken by the fishery, and is small in relation to total gadid natural mortality. Livingston (1993) also estimated that the pollock biomass taken by sea lions in the eastern Bering sea in 1985 was small in relation to that taken by the fishery and remarked that cannibalism of adults on juveniles was the greatest source of mortality for walleye pollock.

We estimated that Steller sea lions in all areas of Alaska consumed a total of 104,000 (±20,600) t of hexagrammid biomass in 1998 (75% of estimated exploitable Atka mackerel biomass dying naturally in the Aleutian Islands, and 181% of fishery catches in the Aleutian Islands and the Gulf of Alaska in 1998; Table 3). Thus, Steller sea lions removed more Atka mackerel biomass than the fishery in 1998, and Steller sea lion predation accounted for a large proportion of natural Atka mackerel mortality. However, this proportion would be lower if Steller sea lions also prey on juvenile Atka mackerel. As with gadids, other fish species (e.g. Pacific cod) are also important predators on Atka mackerel (Yang, 1997).

Inferences about prey availability and competition for prey between fisheries and Steller sea lions should be made with caution given that we did not explicitly consider the size of prey in our study. For example, Steller sea lions have been shown to generally prey on juvenile pollock and not consume pollock longer than about 60 cm (Pitcher, 1981; Calkins, 1998; Calkins and Goodwin[5]). Thus, with respect to prey availability it may be more appropriate to compare our estimate of the gadid biomass consumed by Steller sea lions to the biomass of juvenile gadids dying naturally rather than to the total gadid biomass dying naturally. Our estimate of the biomass of gadids consumed by Steller sea lions in Alaska in 1998 represented 18% of the natural mortality of juvenile pollock and cod combined (23% of juvenile pollock alone or 80% of juvenile cod alone), which was more than triple the value (5%) when total pollock and cod biomass was considered (Table 3). The impact of Steller sea lions on specific segments of their prey populations (e.g. juvenile Pacific cod) may then be much greater than the impact that is suggested when only total biomass is considered. With respect to competition with fisheries, the pollock and cod fisheries generally target fish ≥3 years old. Thus,

Table 3

Biomass (t), natural mortality, fishery catches (t), and predicted Steller sea lion consumption of gadids (walleye pollock and Pacific cod) and hexagrammids (Atka mackerel) in Alaska in 1998.

	Walleye pollock	Pacific cod	Gadid (pollock+cod)	Hexagrammid (Atka mackerel)
Adult (age 3+)				
biomass [1]	7,362,000	2,125,000	9,487,000	536,000
M	0.30[2]	0.37[3]		0.30[4]
biomass dying naturally[5]	1,908,096	657,190	2,565,286	138,921
Juveniles				
biomass	1,616,049[6]	466,463[6]	2,082,512	no data
M	0.65[7]	0.65[7]		no data
biomass dying naturally	772,397	222,948	995,345	no data
Total				
biomass	8,978,049	2,591,463	11,569,512	
biomass dying naturally	2,680,493	880,138	3,560,631	
fishery catches[8]	1,250,594	267,968	1,518,562	57,493
Steller sea lion population consumption			179,000 ±36,700	104,000 ±20,600
% total biomass dying naturally	6.7	20.3	5.0	
% adult biomass dying naturally	9.4	27.2	7.0	74.9
% juvenile biomass dying naturally	23.2	80.3	18.0	
% fishery catches	14.3	66.8	11.8	180.9

[1] Sum of estimated exploitable biomass from Gulf of Alaska (pollock and cod only) (Plan Team for the Groundfish Fisheries of the Gulf of Alaska. 1999. Summary. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 1–31. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510), Aleutian Islands, Bogoslof (pollock only), and eastern Bering Sea (pollock and cod only) regions (Plan Team for the Groundfish Fisheries of the Bering Sea and Aleutian Islands. 1999. Summary. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 1–36. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510). Estimate of exploitable biomass of Atka mackerel in the Gulf of Alaska not available, but the population was much smaller than the Aleutian Islands population.

[2] Dorn, M. W., A. B. Hollowed, E. Brown, B. Megrey, C. Wilson, and J. Blackburn. 1999. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 33–104. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510

[3] Thompson, G. G., H. H. Zenger, and M. W. Dorn. 1999. Assessment of the Pacific cod stock in the Gulf of Alaska. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 105–184. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[4] Lowe, S. A., and L. W. Fritz. 1999. Assessment of Bering Sea/Aleutian Islands Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 569–638. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[5] Annual mortality rate = $1 - e^{-M}$.

[6] Assumed to be 18% of total biomass based on value used by Trites et al. (1999) for pollock.

[7] Assumed to be the median M reported by Wespestad and Terry (1984) for 1- and 2-year-old pollock (range=0.45–0.85).

[8] Sum of catches from Gulf of Alaska (Plan Team for the Groundfish Fisheries of the Gulf of Alaska, see Footnote 1 above), Aleutian Islands, Bogoslof (pollock only), and eastern Bering Sea (pollock and cod only) regions (Plan Team for the Groundfish Fisheries of the Bering Sea and Aleutian Islands, see Footnote 1 above).

there may only be minor overlap between the fish taken by humans and the fish taken by Steller sea lions even though our estimate of the gadid biomass consumed by Steller sea lions in Alaska in 1998 was 12% of the combined pollock and cod catch (Table 3).

Caution should also be used when making inferences about competition and prey availability even when estimates of prey biomass and catch are size-specific. Spatial and temporal distributions of prey (and fishing) at the local scale determine the availability of food resources for Steller sea lions. Estimates of total prey abundance are not enough to make inferences about the food that is available to Steller sea lions. For example, if estimates

of the amount of food that Steller sea lions require were less than the estimated available prey biomass (minus the prey taken by fisheries), it would not necessarily mean that Steller sea lions had enough to eat. Sea lions may not have access to all of the prey due to local differences between their foraging space and time and the spatial and temporal distribution of the fish. Local prey densities encountered by Steller sea lions are more relevant than absolute abundance when assessing prey availability.

Our study provides the first estimates of the biomass of prey consumed by Steller sea lions in different regions of Alaska. However, our estimates of prey consumption are neither species-specific nor size-specific and have con-

siderable uncertainty associated with them. Thus, the management applications of our findings are limited by the quality of data currently available for Steller sea lions. Nevertheless, our estimates of consumption shed light on the trophic relationships between Steller sea lions and their prey and provide insights into possible relationships between food consumption and differential rates of population decline in different regions of Alaska. As more detailed diet information becomes available for Steller sea lions in Alaska, our model can be used to provide more refined estimates of prey consumption that can be incorporated in prey stock assessments and management decisions (e.g. Hollowed et al., 2000).

Acknowledgments

Literature cited

Alverson, D. L.
   1992.   A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena.   Rev. Aquat. Sci. 6:203–256.
Anthony, J. A., D. D. Roby, and K. R. Turco.
   2000.   Lipid content and energy density of forage fishes from the northern Gulf of Alaska.   J. Exp. Mar. Biol. Ecol. 248: 53–78.
Bowen, W. D.
   2000.   Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks.   Can. J. Fish. Aquat. Sci. 57:898–905.
Boyd, I. L., J. P. Y. Arnould, T. Barton, and J. P. Croxall.
   1994.   Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance.   J. Anim. Ecol. 63: 703–713.
Brekke, B., and G. W. Gabrielsen.
   1994.   Assimilation efficiency of adult Kittiwakes and Brünnich's Guillemots fed Capelin and Arctic Cod.   Polar Biol. 14:279–284.
Brett, J. R.
   1983.   Life energetics of sockeye salmon, *Oncorhynchus nerka*.   *In* Behavioral energetics: the cost of survival in vertebrates (W. P. Aspey and S. I. Lustick, eds.), p. 29–63. Ohio State Univ. Press, Columbus, OH.

Calkins, D. G.
   1998.   Prey of Steller sea lions in the Bering Sea.   Biosphere Conserv. 1:33–44.
Calkins, D. G., and K. W. Pitcher.
   1982.   Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska.   *In* Environmental assessment of the Alaskan continental shelf: final reports of principal investigators, vol. 19, p. 445–546. U.S. Dep. Commer., N.O.A.A., Juneau, AK.
Costa, D. P., and R. L. Gentry.
   1986.   Free-ranging energetics of northern fur seals.   *In* Fur seals: maternal strategies on land and at sea (R. L. Gentry and G. L. Kooyman, eds.), p. 79–101.   Princeton Univ. Press, Princeton, NJ.
Cottrell, P. E., and A. W. Trites.
   2002.   Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*).   Mar. Mamm. Sci. 18:525–539.
Dygert, P. H.
   1990.   Seasonal changes in energy content and proximate composition associated with somatic growth and reproduction in a representative age-class of female English sole. Trans. Am. Fish. Soc. 119:791–801.
Fisher, K. I., R. E. A. Stewart, R. A. Kastelein, and L. D. Campbell.
   1992.   Apparent digestive efficiency in walruses (*Odobenus rosmarus*) fed herring (*Clupea harengus*) and clams (*Spisula* sp.).   Can. J. Zool. 70:30–36.
Hammond, K. A., and B. A. Wunder.
   1991.   The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. Physiol. Zool. 64:541–567.
Harris, R. K., T. Nishiyama, and A. J. Paul.
   1986.   Carbon, nitrogen and caloric content of eggs, larvae, and juveniles of the walleye pollock, *Theragra chalcogramma*.   J. Fish Biol. 29:87–98.
Hartman, K. J., and S. B. Brandt.
   1995.   Estimating energy density of fish.   Trans. Am. Fish. Soc. 124:347–355.
Hendry, A. P., and O. K. Berg.
   1999.   Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon.   Can. J. Zool. 77:1663–1675.
Hollowed, A. B., J. N. Ianelli, and P. A. Livingston.
   2000.   Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock.   ICES J. Mar. Sci. 57:279–273.
Keiver, K. M., K. Ronald, and F. W. H. Beamish.
   1984.   Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (*Phoca groenlandica*).   Can. J. Zool. 62:769–776.
Lawson, J. W., A. M. Magalhães, and E. H. Miller.
   1998.   Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density.   Mar. Ecol. Prog. Ser. 164:13–20.
Lawson, J. W., E. H. Miller, and E. Noseworthy.
   1997.   Variation in assimilation efficiency and digestive efficiency of captive harp seals (*Phoca groenlandica*) on different diets.   Can. J. Zool. 75:1285–1291.
Lill, A.
   1991.   Behavioural energetics of overwintering in the rifleman, *Acanthisitta chloris*.   Aust. J. Zool. 39:643–654.
Livingston, P. A.
   1993.   Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi* in the eastern Bering Sea.   Mar. Ecol. Prog. Ser. 102:205–215.

Loughlin, T. R., A. S. Perlov, and V. A. Vladimirov.
  1992.   Range-wide survey and estimation of total number of
    Steller sea lions in 1989.   Mar. Mamm. Sci. 8:220–239.
Mårtensson, P.-E., E. S. Nordøy, and A. S. Blix.
  1994.   Digestibility of crustaceans and capelin in harp seals
    (*Phoca groenlandica*).   Mar. Mamm. Sci. 10:325–331.
Merrick, R. L., M. K. Chumbley, and G. V. Byrd.
  1997.   Diet diversity of Steller sea lions (*Eumetopias juba-
    tus*) and their population decline in Alaska: a potential
    relationship.   Can. J. Fish. Aquat. Sci. 54:1342–1348.
Merrick, R. L., and T. R. Loughlin.
  1997.   Foraging behavior of adult female and young-of-the-
    year Steller sea lions in Alaskan waters.   Can. J. Zool. 75:
    776–786.
Nash, L. T.
  1998.   Vertical clingers and sleepers: seasonal influences on
    the activities and substrate use of *Lepilemur leucopus* at
    Beza Mahafaly Special Reserve, Madagascar.   Folia Pri-
    matol. 69 (suppl. 1):204–217.
Olesiuk, P. F.
  1993.   Annual prey consumption by harbor seals (*Phoca vit-
    ulina*) in the Strait of Georgia, British Columbia.   Fish.
    Bull. 91:491–515.
Olesiuk, P. F., M. A. Bigg, G. M. Ellis, S. J. Crockford, and
  R. J. Wigen.
  1990.   An assessment of the feeding habits of harbour seals
    (*Phoca vitulina*) in the Strait of Georgia, British Colum-
    bia, based on scat analysis.   Department of Fisheries and
    Oceans, Fisheries Research Branch, Pacific Biological Sta-
    tion, Nanaimo, B.C., Canada, Can. Tech. Rep. Fish. Aquat.
    Sci. 1730.
Paul, A. J., and J. M. Paul.
  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, A. J., J. M. Paul, and E. D. Brown.
  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, A. J., J. M. Paul, and R. L. Smith.
  1993.   The seasonal changes somatic energy content of Gulf
    of Alaska yellowfin sole, *Pleuronectes asper*.   J. Fish Biol.
    43:131–138.
  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.
Paul, A. J., and M. Willette.
  1997.   Geographical variation in somatic energy content of
    migrating pink salmon fry from Prince William Sound: a
    tool to measure nutritional status.   *In* Forage fishes in
    marine ecosystems, p. 707–720.   Univ. Alaska Sea Grant
    College Program Report 97-01, Fairbanks, AK.
Payne, S. A., B. A. Johnson, and R. S. Otto.
  1999.   Proximate composition of some north-eastern Pacific
    forage fish species.   Fish. Oceanogr. 8:159–177.
Perez, M. A.
  1994.   Calorimetry measurements of energy value of some
    Alaskan fishes and squids.   U.S. Dep. Commer., N.O.A.A.
    Tech. Memo. NMFS-AFSC-32, 32 p.
Pitcher, K. W.
  1981.   Prey of the Steller sea lion, *Eumetopias jubatus*, in
    the Gulf of Alaska.   Fish. Bull. 79:467–472.
Pitcher, K. W., D. G. Calkins, and G. W. Pendleton.
  1998.   Reproductive performance of female Steller sea lions:

an energetics based reproductive strategy?   Can. J. Zool.
    76:2075–2083.
Robards, M. D., J. A. Anthony, G. A. Rose, and J. F. Piatt.
  1999.   Changes in proximate composition and somatic energy
    content for Pacific sand lance (*Ammodytes hexapterus*) from
    Kachemak Bay, Alaska relative to maturity and season.   J.
    Exp. Mar. Biol. Ecol. 242:245–258.
Rosen, D. A. S., and A. W. Trites.
  1997.   Heat increment of feeding in Steller sea lions, *Eume-
    topias jubatus*.   Comp. Biochem. Physiol. A118:877–881.
  1999.   Metabolic effects of low-energy diet on Steller sea lions,
    Eumetopias jubatus.   Physiol. Biochem. Zool. 72:723–731.
  2000a.   Digestive efficiency and dry matter digestibility of
    Steller sea lions fed herring, pollock, squid, and salmon.
    Can. J. Zool. 78:1–6.
  2000b.   Pollock and the decline of Steller sea lions: testing
    the junk-food hypothesis.   Can. J. Zool. 78:1243–1250.
Sease, J. L., and T. R. Loughlin.
  1999.   Aerial and land-based surveys of Steller sea lions
    (*Eumetopias jubatus*) in Alaska, June and July 1997 and
    1998.   U.S. Dep. Commer., NOAA Tech. Memo. NMFS-
    AFSC-100, 61 p.
Sinclair, E. H., and T. K. Zeppelin.
  2002.   Seasonal and spatial differences in diet in the west-
    ern stock of Steller sea lions (*Eumetopias jubatus*).   J.
    Mammal. 83:973–990.
Smith, R. L., A. J. Paul, and J. M. Paul.
  1988.   Aspects of energetics of adult walleye pollock, *Ther-
    agra chalcogramma* (Pallas), from Alaska.   J. Fish Biol.
    33:445–454.
  1990.   Seasonal changes in energy and the energy cost of
    spawning in Gulf of Alaska Pacific cod.   J. Fish Biol. 36:
    307–316.
Stansby, M. E.
  1976.   Chemical characteristics of fish caught in the north-
    east Pacific Ocean.   Mar. Fish. Rev. 38:1–11.
Stewart, D. J., and M. Ibarra.
  1991.   Predation and production by salmonine fishes in Lake
    Michigan, 1978–88.   Can. J. Fish. Aquat. Sci. 48:909–922.
Strick, M., L. Fritz, J. P. Lewis, and D. C. McAllister.
  1997.   Aerial and ship-based surveys of Steller sea lions
    (*Eumetopias jubatus*) in Southeast Alaska, the Gulf of
    Alaska, and Aleutian Islands during June and July 1994.
    U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-71,
    55 p.
SYSTAT, Inc.
  1992.   SYSTAT for Windows: Statistics, version 5, 750 p.
    SYSTAT, Inc., Evanston, IL.
Tollit, D. J., M. J. Steward, P. M. Thompson, G. J. Pierce,
  M. B. Santos, and S. Hughes.
  1997.   Species and size differences in the digestion of oto-
    liths and beaks: implications for estimates of pinniped diet
    composition.   Can. J. Fish. Aquat. Sci. 54:105–119.
Trillmich, F., and T. Dellinger.
  1991.   The effects of El Niño on Galapagos pinnipeds.   *In*
    Pinnipeds and El Niño: responses to environmental stress
    (F. Trillmich and K. A. Ono, eds.), p. 66–74.   Springer-
    Verlag, Berlin, Germany.
Trites, A. W., and P. A. Larkin.
  1996.   Changes in the abundance of Steller sea lions (*Eume-
    topias jubatus*) in Alaska from 1956 to 1992: how many
    were there?   Aquat. Mamm. 22:153–166.
Trites, A. W., P. A. Livingston, M. C. Vasconcellos, S. Mackinson,
  A. M. Springer, and D. Pauly.
  1999.   Ecosystem change and the decline of marine mam-

mals in the Eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. Fisheries Centre Research Reports, vol. 7(1), 106 p.   Univ. British Columbia, Vancouver, B.C., Canada.

Van Pelt, T. I., J. F. Piatt, B. K. Lance, and D. D. Roby.
    1997.   Proximate composition and energy density of some North Pacific forage fishes.   Comp. Biochem. Physiol. A118: 1393–1398.

Veloso, C., and F. Bozinovic.
    1993.   Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent.   Ecology 74: 2003–2010.

Weber, M. L., and J. M. Thompson.
    1998.   Seasonal patterns in food intake, live mass, and body composition of mature female fallow deer (*Dama dama*).   Can. J. Zool. 76:1141–1152.

Wespestad, V. G., and J. M. Terry.
    1984.   Biological and economic yields for eastern Bering Sea walleye pollock under differing fishing regimes.   N. Am. J. Fish. Manage. 4:204–215.

Winship, A. J., A. W. Trites, and D. A. S. Rosen.
    2002.   A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA.   Mar. Ecol. Prog. Ser. 229:291–312.

Yang, M.-S.
    1997.   Trophic role of Atka Mackerel (*Pleurogrammus monopterygius*) in the Aleutian Islands.   *In* Forage fishes in marine ecosystems, p. 277–279.   Univ. Alaska Sea Grant College Program Report 97-01, Fairbanks, AK.

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

Appendix I

Energy density of prey of Steller sea lions in Alaska. Length and energy-density data are ranges, means, or ranges of means depending BC=bomb calorimetry).

Species	Location	Time of year
Cephalopods		
squid	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
squid (5 spp.)	Gulf of Alaska, Bering Sea, north Pacific Ocean	Feb, Jun, Jul
Flatfish		
arrowtooth flounder	Gulf of Alaska, Bering Sea	Feb, Jul, Aug
English sole	Washington	Jan–Mar, Jun, Jul, Sep–Dec
Pleuronectidae (≥2 spp.)	Gulf of Alaska	May–Sep
yellowfin sole	Gulf of Alaska	Jan–Nov
Forage fish		
capelin	Gulf of Alaska, Bering Sea	Jul, Aug
	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Bering Sea	
	Gulf of Alaska	May–Sep
	Gulf of Alaska, Bering Sea	Feb, Jun–Sep
eulachon	Gulf of Alaska	Mar, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska, Bering Sea	Feb, Mar, Jun–Sep
Pacific herring	Gulf of Alaska, Bering Sea	Jul, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska	Aug
	Gulf of Alaska	spring, fall
	Gulf of Alaska	Mar, Dec
	Gulf of Alaska, Southeast Alaska, British Columbia	
Pacific sandlance	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska, Bering Sea	Apr–Sep, Nov

Appendix I

on the data that were available. Method is the technique used to obtain the energy density value (PC=proximate composition analysis,

Age or length (or both)	Energy density (kJ/g wet mass)	Method	Source
7–13 cm	3.81	PC	Van Pelt et al. (1997)
	3.85–6.53	BC	Perez (1994)
	5.15	BC	Perez (1994)
adult, 39–40 cm	4.90 (Mar)	BC	Dygert (1990)
	5.95 (Oct)		
7–15 cm	2.86–3.95	PC	Anthony et al. (2000)
juvenile, 18–21 cm	3.3–3.5 (May)	BC	Paul et al. (1993)
adult, 24–29 cm	4.4 (Jun)		
	7.03	BC	Perez (1994)
age 1, 8–9 cm	4.84 (age 1)	PC	Van Pelt et al. (1997)
age 2, 10–12 cm	3.54–4.67 (age 2)		
	5.50	BC	Miller[1]
age 1, 5–8 cm	4.17 (age 1)	PC	Anthony et al. (2000)
age >1, 8–13 cm	6.7 (age >1, Jun)		
	3.7 (age >1, Sep)		
8–13 cm (Gulf)	5.26 (Gulf)	PC	Payne et al. (1999)
13–15 cm (BS)	6.48 (BS)		
	11.05 (August)	BC	Perez (1994)
	10.96 (March)		
age >0, 14–20 cm	7.49	PC	Anthony et al. (2000)
10–23 cm	10.10 (Feb–Mar)	PC	Payne et al. (1999)
	10.62–10.86 (Jun–Sep)		
	5.44 (BS)	BC	Perez (1994)
	11.72 (Gulf)		
age 0, <10 cm	3.69 (age 0)	PC	Anthony et al. (2000)
age >0, 10–19 cm	5.84 (age >0)		
6 cm	3.43	PC	Payne et al. (1999)
ages 0–7	5.7 (age 0, fall)	BC	Paul et al. (1998a)
	8.0 (age 1, fall)		
	9.4–10.2 (age 2, fall)		
	4.4 (age 0–1, spring)		
	5.2–6.3 (ages ≥2, spring)		
age 0, 8–9 cm	5.2 (Dec)	BC	Paul and Paul (1998)
	3.4–3.8 (Mar)		
	7.95	PC[2]	Stansby (1976)
age 0, 8–9 cm	4.95 (age 1)	PC	Van Pelt et al. (1997)
age 1, 11–13 cm	3.18 (age 0)		
age ≥2, 15–19 cm	5.67 (age ≥2)		
age 0, 7–10 cm	6.5 (age 0, Jun)	PC	Anthony et al. (2000)
age >0, 10–19 cm	4.8 (age 0, Jul)		
	5.3 (age 0, Aug)		
	5.6 (age >0, Jun)		
	4.9 (age >0, Sep)		
7–15 cm	5.20 (Gulf)	PC	Payne et al. (1999)
	6.11 (BS)		

Appendix I (continued)

Species	Location	Time of year
Pacific sandlance (cont.)	Gulf of Alaska	Feb, Jun–Nov
Gadids		
Pacific cod	Gulf of Alaska, Bering Sea	Jul, Aug
	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Gulf of Alaska	May–Sep
	Gulf of Alaska	Mar–May, Jul, Oct–Dec
walleye pollock	Gulf of Alaska, Bering Sea	Mar, Jul, Aug
	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Bering Sea	
	Gulf of Alaska	May–Sep
	Gulf of Alaska	Aug
	Gulf of Alaska	Mar, May, Jun, Aug, Oct
	Gulf of Alaska	Mar–Apr
	Gulf of Alaska	
Hexagrammids		
Atka mackerel	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
	Gulf of Alaska	Aug
greenling	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
lingcod	Gulf of Alaska	May–Sep
Salmon		
chinook		
coho		
pink	Gulf of Alaska	May–Sep
	Gulf of Alaska	May–Jun
sockeye	Gulf of Alaska	May–Sep
	northeast Pacific Ocean	entire life cycle
	southeast Bering Sea	Jul (prior to river entry)
Other		
pricklebacks	Gulf of Alaska	Jun, Aug
pricklebacks (6 spp.)	Gulf of Alaska	May–Sep
rockfish (*Sebastes* spp.)	Gulf of Alaska, Eastern Aleutian Islands	Jul, Aug
rockfish (≥3 *Sebastes* spp.)	Gulf of Alaska, Bering Sea	Feb, Jul, Aug
sculpins (4 spp.)	Gulf of Alaska, Bering Sea	Feb, Jul, Aug
sculpins (12 spp.)	Gulf of Alaska	May–Sep

[1] Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Rep. MMC-75/08, 27 p. U.S. Marine Mammal Commission, Washington, D.C.
[2] We assumed lipid = 39.3 kJ/g and protein = 17.8 kJ/g (Anthony et al. 2000).

Appendix I (continued)

Age or length (or both)	Energy density (kJ/g wet mass)	Method	Source
age 0, 6–9 cm	3.40–3.55 (age 0, 6 cm)	PC	Robards et al. (1999)
age 1 12–14 cm	4.62–4.86 (age 0, 9 cm)		
	3.22–3.32 (age ≥1, Nov)		
	3.23–3.25 (age ≥1, Feb)		
	5.46–5.75 (age ≥1, Jun–Jul)		
	3.93	BC	Perez (1994)
7–10 cm	2.94	PC	Van Pelt et al. (1997)
age 0, 6–9 cm	3.65 (age 0)	PC	Anthony et al. (2000)
age >0, 11–14 cm	3.54 (age >0)		
56–74 cm	4.00–4.30 (Mar)	BC	Smith et al. (1990)
	3.33–3.38 (Jul)		
	4.13–4.49 (Dec)		
43–53 cm	4.64	BC	Perez (1994)
age 0, 5–9 cm	2.73	PC	Van Pelt et al. (1997)
	5.89	BC	Miller[1]
age 0, 5–6 cm	3.47 (age 0)	PC	Anthony et al. (2000)
age >0, 12–18 cm	3.24 (age >0)		
7–8 cm	3.93	PC	Payne et al. (1999)
3–11 cm	2.7 (Jun)	BC	Paul et al. (1998b)
	3.4 (Aug)		
	3.6 (Oct)		
	3.4–4.0 (Mar)		
	4.0 (May)		
adult	3.68–4.03 (ripe)	BC	Smith et al. (1988)
	3.26–3.41 (spent)		
juvenile, <34 cm	5.45	BC	Harris et al. (1986)
7 cm	4.02	PC	Van Pelt et al. (1997)
12 cm	4.66	PC	Payne et al. (1999)
6–7 cm	3.45	PC	Van Pelt et al. (1997)
7–9 cm	3.98	PC	Anthony et al. (2000)
equation relating energy	6.06 (300 g)		Stewart and Ibarra (1991)
density to weight	8.72 (3 kg)		
equation relating energy	6.06 (300 g)		Stewart and Ibarra (1991)
density to weight	8.72 (3 kg)		
age 0, 6–10 cm	3.41 (age 0)	PC	Anthony et al. (2000)
age >0, 10–14 cm	3.73 (age >0)		
fry, 3–6 cm	3.2–4.4	BC	Paul and Willette (1997)
age 0, 7–8 cm	4.35	PC	Anthony et al. (2000)
entire life cycle	6.68 (300 g)		Brett (1983)
	7.77 (2.1 kg)		
adult, 49 cm	6.89–7.69	PC	Hendry and Berg (1999)
9–24 cm	5.40	PC	Payne et al. (1999)
8–30 cm	4.11–4.90	PC	Anthony et al. (2000)
4–6 cm	2.97	PC	Van Pelt et al. (1997)
	5.77–6.23	BC	Perez (1994)
	5.56 (northern rockfish, BS, Jul)		
	6.85 (northern rockfish, Gulf, Feb)		
	3.51–5.19	BC	Perez (1994)
4–22 cm	3.05–5.26	PC	Anthony et al. (2000)