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ORIGINAL PAPER

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Body mass and composition responses to short-term low energy intake are seasonally dependent in Steller sea lions (*Eumetopias jubatus*)

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Abstract Steller sea lions (*Eumetopias jubatus*) were fed restricted iso-caloric amounts of Pacific herring (*Clupea pallasi*) or walleye pollock (*Theragra chalcogramma*) for 8–9 days, four times over the course of a year to investigate effects of season and prey composition on sea lion physiology. At these levels, the sea lions lost body mass at a significantly higher rate during winter (1.6 ± 0.14 kg day^{-1}), and at a lower rate during summer (1.2 ± 0.32 kg day^{-1}). Decreases in body fat mass and standard metabolic rates during the trials were similar throughout the seasons and for both diet types. The majority of the body mass that was lost when eating pollock derived from decreases in lipid mass, while a greater proportion of the mass lost when eating herring derived from decreases in lean tissue, except in the summer when the pattern was reversed. Metabolic depression was not observed during all trials despite the constant loss of body mass. Our study supports the hypothesis that restricted energy intake may be more critical to Steller sea lions in the winter months, and that the type of prey consumed (e.g., herring or pollock) may have seasonally specific effects on body mass and composition.

Keywords Steller sea lion · Nutritional stress · Low energy diet · Season · Pollock

Introduction

A possible change in the abundance or type of available prey may underlie the decline of Steller sea lions (*Eumetopias jubatus*) in western Alaska (Alverson 1992; Merrick et al. 1997; Rosen and Trites 2000b; Trites and Porter 2002). As the sea lion population declined in the 1980s, females (pregnant and nonpregnant) exhibited decreased body size (Calkins et al. 1998), while estimated birth rates, and juvenile and adult survival rates appeared to have been negatively impacted (Holmes and York 2003; Winship and Trites 2006). Such changes could be a direct result of reductions in the quality, quantity, or availability of prey—commonly known as the 'Nutritional Stress' hypothesis (Alverson 1992; Merrick et al. 1997; Trites and Donnelly 2003).

Health consequences related to gadid-dominated diets have been speculated upon in a number of studies (e.g., Geraci 1975; Thompson et al. 1997; Rosen and Trites 2000b). Captive feeding experiments have revealed that young Steller sea lions may not be able to consume sufficient quantities of low-fat prey (squid and walleye pollock) to maintain body mass (Rosen and Trites 2000b), despite partial compensation by decreasing their resting metabolic rates (i.e., metabolic depression, Rea et al. 1999; Rosen and Trites 2004). It has therefore been proposed that diets high in gadid and other low-energy species are nutritionally inadequate for young Steller sea lions, and may have contributed to the observed population decline (Trites and Donnelly 2003).

The potential effects of periods of inadequate nutrition on sea lion populations are likely further complicated by the seasonal nature of their energy budgets. In other words, the potential impact of nutritional stress may be seasonally dependent. Low juvenile survival rates (York 1994; Pitcher et al. 1998; Holmes and York 2003) might be a direct result of low energy intake at times of year when food intake requirements for immature (< age 3) female Steller sea lions in Southeast Alaska are high, such as from March to May (Winship et al. 2002). Adequate food intake is crucial to young animals, who allocate the bulk of their energy towards growth and development. Nutritionally stressed sea lions may have a smaller body size, lower fat deposition and/or compromised immune systems and, as a result

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may not survive severe (abiotic or biotic) environmental conditions. Such nutritional effects might be magnified during times of the year when required energy expenditures are greatest.

Food consumption by wild Steller sea lions likely fluctuates seasonally in response to changes in energy requirements (Winship et al. 2002) associated with such activities as breeding from late May to early July (Pitcher and Calkins 1981), periods of growth (lean tissues and energy reserves) and molting from mid-June to early November (Lager et al. 1994; Daniel 2003). Sea lions spend proportionally more time feeding at sea during winter and spring compared to summer (Merrick and Loughlin 1997; Trites and Porter 2002). Foraging time for lactating females is also longer in winter than in summer, suggesting a greater effort is required to obtain sufficient food in winter due to dispersed fish distribution and/or increased energy needs (Merrick and Loughlin 1997; Trites and Porter 2002).

Seasonal changes in energy budgets of sea lions may include shifts in body mass and body condition (relative lipid reserves) due to changes in energy expenditures (including basal metabolism), and may occur independent of changes in food/energy intake. Experiments with iso-caloric diets comprised of high- or low-fat prey demonstrated that changes in body lipids of juvenile Steller sea lions was affected more by season and gender than by the amount of lipid consumed by the animals (Rosen and Trites 2005). Experimentally fasted juvenile Steller sea lions lost more body mass during the non-breeding season than during the breeding season (Rea et al. 1999). However, these studies were not specifically designed to examine how animals that undergo natural seasonal changes in their energy budget respond to unpredicted decreases in energy intake at different times of the year.

The differential seasonal effect of restricted food on sea lion physiology has important implications for Steller sea lion conservation. Measures of health that might be used to assess the status of individual animals can be confounded by seasonal differences in physiology and behavior. For example, absolute or relative body lipid stores may undergo natural changes that do not reflect changes in animal health per se. Similarly, animals may differentially defend their energy (lipid) reserves from the effects of decreased energy intake at different times of the year. Therefore, the potential effect of changes in prey availability (due to either anthropogenic or natural factors) must be viewed on a seasonal rather than overall basis. Thus, controlled feeding experiments are required to ensure that physiological data obtained from wild animals are properly interpreted in light of potentially critical periods of the year when decreased energy intake might disproportionately affect sea lion health.

The following feeding study on young captive Steller sea lions was designed to investigate the impact of season on the effects of reduced energy intake and prey composition on sea lion body mass, lipid reserves, body condition (% total body fat), and metabolic rate. The results of these experiments have significant bearing on understanding the importance of seasonal changes in the availability and quality of prey on Steller sea lion physiology.

Materials and methods

Experimental design

All procedures and protocols involving animals were conducted under the authority of the University of British Columbia Animal Care Permit No. A98-0095.

Seven female Steller sea lions—five juveniles, 2.5–3.0 years old; and two sub-adults, 5.5–6.0 years old—participated in the study. The animals were held in an outdoor facility at the Vancouver Aquarium Marine Science Centre and had previously participated in other research projects since captured as pups. All of the study animals typically ate a daily ration of thawed Pacific herring (*Clupea pallasi*), equivalent to approximately 5–6% of their body mass supplemented with vitamin tablets (1 tablet per 3 kg food; 5 M26 Vita-zu tablets, Purina Test Diets, Richmond, IN, USA). Food intake (kg day^{-1}) and body mass (± 0.1 kg) were recorded daily. Proximate nutrient composition analyses of representative fish samples (the same batches of herring and pollock were used throughout the trials) were conducted by Norwest Labs (Surrey, BC, Canada). Gross energy content was calculated from composition analyses by appropriate conversions of lipid (39.3 kJ g^{-1}) and protein (18.0 kJ g^{-1}) content (Schmidt-Nielsen 1997).

The seven sea lions were divided into two experimental groups (Table 1): the first had four animals (one sub-adult and three juveniles) and the second had three animals (one sub-adult and two juveniles). The diet of each group was alternated between Pacific herring and walleye pollock (*Theragra chalcogramma*), except for one juvenile from the first group who refused the pollock diet and was therefore fed herring exclusively. As a result, one group of animals consumed herring during the winter and summer season and pollock during spring and fall, while the second group consumed the opposite diet. When consuming herring (mean wet weight 88.9 ± 5.4 g; fork length 19.5 ± 0.3 cm), the sea lions were fed amounts equivalent to 1% of their initial (day 1) body mass throughout each trial. Pollock consumption was set at 1.6–2.6% of their initial body mass (mean wet weight 29.9 ± 6.6 g; fork length 15.0 ± 1.1 cm). These diets were calculated to be energetically equivalent (i.e., iso-caloric; with 1% of an animal's body mass of herring equal to 1.6% pollock in the winter trials and 2.6% during the rest of the year). The sea lions were maintained on each diet for up to 9 days per experimental trial. Previous studies (Rosen and Trites 2002) indicated the animals would lose approximately 2.3 kg day^{-1} for 9–14 days if completely fasting. Therefore, a 9-day period was chosen based on the

Table 1 Pre- (initial) and post-experimental (final) body mass (kg), total body fat (% of total mass) and metabolic rate (MR; MJ day^{-1}) of Steller sea lions

Animal	Age class		Winter		Spring		Summer		Fall	
			Initial	Final	Initial	Final	Initial	Final	Initial	Final
F03BO	Juvenile	Diet	Herring		Pollock		Herring		Pollock	
		Body mass (kg)	92.6	78.2	106.5	98.0	107.3	100.1	106.3	98.0
		Body fat (%)	11.3	8.7	22.2	17.1	19.1	5.6	16.6	12.2
		MR (MJ day^{-1})	38.9	38.3	39.4	37.4	15.4	21.8	49.7	46.4
F03ED	Juvenile	Diet	Herring		Herring		Herring		Herring	
		Body mass (kg)	101.4	84.4	114.8	101.2	120.4	110.0	110.4	95.1
		Body fat (%)	13.1	1.3	20.0	15.8	14.7	12.2	10.3	5.2
		MR (MJ day^{-1})	48.4	44.0	40.5	51.8	39.4	34.3	58.2	54.8
F00NU	Juvenile	Diet	Pollock		Herring		Pollock		Herring	
		Body mass (kg)	121.0	107.4	125.5	113.8	113.2	97.8	128.6	112.0
		Body fat (%)	15.3	11.3	18.4	16.0	7.2	3.0	11.3	6.8
		MR (MJ day^{-1})	39.4	41.4	35.9	37.5	32.5	40.4	66.3	44.8
F00TS	Juvenile	Diet	Pollock		Herring		Pollock		Herring	
		Body mass (kg)	119.8	102.6	137.8	124.4	135.4	125.1	136.0	121.3
		Body fat (%)	11.2	5.5	21.9	18.8	11.8	11.3	9.3	12.7
		MR (MJ day^{-1})	40.3	40.6	45.5	41.0	33.5	33.1	63.6	48.5
F00YA	Juvenile	Diet	Herring		Pollock		Herring		Pollock	
		Body mass (kg)	117.6	103.1	124.5	110.6	116.2	106.3	129.9	118.2
		Body fat (%)	13.7	12.0	19.4	15.6	12.5	7.7	11.7	7.3
		MR (MJ day^{-1})	45.3	37.8	50.1	43.1	34.7	29.4	60.3	60.9
F97SI	Sub-adult	Diet	Herring		Pollock		Herring		Pollock	
		Body mass (kg)	178.0	161.7	166.5	151.0	174.6	163.2	179.7	168.4
		Body fat (%)	15.9	14.7	19.2	10.4	17.7	10.9	14.6	10.6
		MR (MJ day^{-1})	46.3	37.3	40.1	30.5	32.5	24.9	45.3	45.8
F97HA	Sub-adult	Diet	Pollock		Herring		Pollock		Herring	
		Body mass (kg)	154.1	136.5	145.9	131.6	132.5	117.7	149.7	136.4
		Body fat (%)	17.1	15.3	16.3	13.9	8.8	5.7	14.1	12.5
		MR (MJ day^{-1})	–	–	55.1	58.3	38.6	48.7	77.2	77.1

expectation that the sea lions would lose 10–15% of their body mass under a restricted energy intake regime. Self-imposed Animal Care Protocols limited body mass loss to 15%, and consequently the trial for one animal ended after 8 days in the summer. Two additional (herring-fed) animals in the summer and two (herring-fed) animals in the fall also had their trials concluded after 8 days due to logistical difficulties (staff availability, etc.), although the animals had not lost 15% of their body mass.

To examine seasonal variation in response to undernutrition, the experimental protocol was repeated four times during the year: winter (November–December 2002), spring (February–March 2003), summer (May–June 2003), and fall (August–September 2003).

Data collection

Hydrogen isotope dilution (Reilly and Fedak 1990) was used to determine body fat content in the morning of the first and last (9th or 10th) day of each feeding trial. The dilution procedure was conducted before the first feed of the day (i.e., > 16 h after the last meal), and gas anesthesia (isoflurane) was used under veterinarian supervision to minimize stress during blood draws. A baseline serum sample (1 ml blood) was obtained before an appropriate dose (0.10–0.15 g kg^{-1} body mass) of heavy water (D_2O) was administered intramuscularly. After a (previously validated; D. Rosen unpublished data) 2.0–2.5 h equilibration period, a second serum sample was collected. Sera were separated using standard techniques (including running a centrifuge at 3,500 rpm for 5 min) and stored at −70°C. Sera and dose samples were analyzed by Metabolic Solutions (Nashua, NH, USA) for isotope concentrations. Total body water was converted to lean tissue mass (which include all nonlipid sources including protein, water, and bones) using formulae from Reilly and Fedak (1990), corrected for an assumed 4% underestimation of injectate. Although a conversion formula specific to Steller sea lions does not exist, use of the Reilly and Fedak (1990) equation will yield internally consistent results that are comparable to those obtained in other studies of Steller sea lions. Nor are the results significantly different than those derived from using equations in Arnould et al. (1996). Lipid mass was calculated as the remainder of lean mass from total body mass. Body composition was also calculated as percentage total body fat (where TBF% = lipid mass/total mass × 100).

Standard metabolic rate (SMR) was measured by open circuit respirometry. Measurements were obtained 1 or 2 days prior to the start of each trial, and towards the end of the trial (7th or 8th day). The animals entered and remained calm in a sealed opaque dry metabolic chamber (~1,050 l). Two animals (F97SI and F00BO) in the summer and fall were placed inside a transport cage, which was then wheeled into a metabolic tent. Measurements were made under SMR conditions for non-mature animals—postabsorptive, quiescent but awake, nonpregnant, and within their assumed thermal neutral zone (Kleiber 1975). Air was drawn at a constant rate (150–200 l min^{-1}) sufficient to prevent extreme change in gas concentrations (O_2 > 19.0%, CO_2 < 1.9%). Air circulation was ensured by a small fan in the chamber and tent. Sea lion behavior was monitored via a video camera.

Oxygen and carbon dioxide concentrations within a desiccated subsample of expired air were determined by a S-3A/I Solid Oxide (stabilized zirconia) Cell Analyzer (Ametek Inc., Pittsburgh, PA, USA) and an AR−60 Infrared Gas Analyzer (Anarad Inc., Santa Barbara, CA, USA), respectively, for winter and spring trials. Expired airflow temperature was monitored by a La Crosse Technology Wireless Thermometer, and barometric pressure, humidity and environmental temperature were monitored by a Temperature Station WS-7014U (Springfield Instrument Canada, Mississauga, ON, Canada). These measures were used to correct airflow to standard temperature and pressure, dry (STPD). A different system was used in the summer and fall trials, consisting of a FC-1B Oxygen Analyzer, a CA-1B Carbon Dioxide Analyzer, and a 500H Flow Generator & Controller (all Sable Systems Henderson, NV, USA). For both setups the expired air current was continuously sub-sampled, and a Sable Data Acquisition System (Sable Systems, Salt Lake City, UT, USA) took an average concentration from 100 sub-samples every second.

The sea lions were trained to remain calm in the chamber for 1–2 h after a minimum 15-min acclimation period. Oxygen consumption was converted to energy utilization using the equation: 1 l O_2 = 20.0 kJ.

For comparative purposes we also chose to calculate mass-corrected standard metabolic rate as $\mathrm{SMRc} = \mathrm{SMR}\ \mathrm{M}^{-0.67}$ (Rosen and Trites 2002). This differs slightly from Kleiber's (1975) inter-specific predictive equation for adult mammals (where $\mathrm{SMR} = 70\mathrm{M}^{0.75}$), but is a conversion often used in mammalian energetic studies.

The dates and patterns of new hair growth during the molt were recorded for each Steller sea lion as a routine weekly observation by research staff. The mean duration of molting was calculated from the first date of signs of new hair and the date of termination of new hair growth (Daniel 2003).

Data analyses

All results were calculated as mean ± standard deviation (SD). Seasonal variations in pre-experimental (initial) values were determined using one-way repeated measure ANOVAs (SAS, version 8.2, SAS Institute, Cary, NC, USA). Two-way repeated measures ANOVA was used to evaluate the effect of changes from the initial values in diet and season. We selected the most parsimonious model and calculated post hoc tests of specific differences (when main effects were significant). Correlations were determined using multiple linear regressions (Splus 6.1, Insightful Inc., Seattle, WA, USA). Differences were considered significant at $P < 0.05$.

Results

Food intake

Steller sea lions consumed an average of 1.3 ± 0.25 kg day^{-1} (mean ± SD) of herring and 3.1 ± 0.85 kg day^{-1} of pollock throughout the trial. Their daily gross energy intakes (GEI) were 10.4 ± 2.0 MJ day^{-1} on the reduced herring diet and 9.4 ± 2.5 MJ day^{-1} on the reduced pollock diet, which were not statistically different ($t_{2,26} = 1.18$, $P = 0.25$). Protein contents were similar between the herring (16.3 ± 0.02% wet weight) and pollock (14.7 ± 0.77%), but lipid content was higher in the herring (13.3 ± 0.09%) than in the pollock (0.95 ± 0.37%) diet. Although the sea lions consumed equal calories from the herring and pollock diets, differences of composition in food intake resulted in the sea lions ingesting 2.3 times more protein from the pollock diet but only 20% of the fat compared to when they were eating herring.

Body mass and condition

Average pre-experimental (initial) body mass of all seven Steller sea lions was 130.2 ± 23.5 kg (Table 1). There were no significant fluctuations throughout the year ($F_{3,18} = 1.72$, $P = 0.19$; Fig. 1). There were significant differences in the initial percent body fat (as % total body mass) between seasons ($F_{3,18} = 9.01$, $P < 0.001$). The percentage of initial body fat increased from winter (14.0 ± 2.3%) to spring (19.6 ± 2.0%), decreased from spring to summer (13.1 ± 4.4%) and stayed constant from summer to fall (12.6 ± 2.6%; Table 1; Fig. 1).

While daily loss of body mass (which accounts for differences in trial lengths) was seasonally dependent ($F_{3,14} = 4.26$, $P = 0.025$; winter, 1.6 ± 0.14 kg day^{-1}; spring, 1.3 ± 0.22 kg day^{-1}; summer, 1.2 ± 0.32 kg day^{-1}; and fall, 1.4 ± 0.33 kg day^{-1}), there was a significant interaction between season and diet ($F_{3,14} = 5.07$, $P = 0.014$; Table 2). Significant effects of diet were found in summer and fall, whereby the pollock-fed group lost body mass at a higher rate (1.4 ± 0.35 kg day^{-1}) than the herring-fed group (0.97 ± 0.18 kg day^{-1}) in the summer trial, while the rate was higher in the herring-fed group (1.6 ± 0.17 kg day^{-1}) than the pollock-fed group (1.0 ± 0.19 kg day^{-1}) in the fall trial (Table 2).

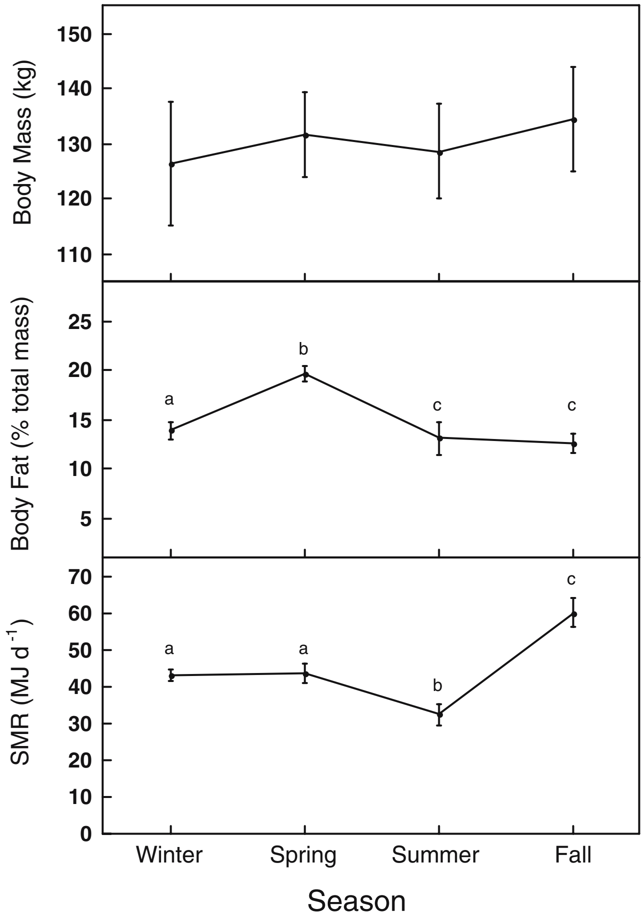

Fig. 1 Seasonal variation in initial body mass, total body fat, and standard metabolic rate (SMR). Data are shown as mean ± SE; $n = 7$ for each season. There were significant seasonal differences in percent body fat (as % total body mass) and SMR, as denoted by different letters

On average (across all diets and seasons), Steller sea lions lost 0.69 ± 0.52 kg day^{-1} of lean mass and 0.66 ± 0.38 kg day^{-1} of total body fat mass. Daily rates of lean mass loss were greater than rates of body fat mass loss in almost all trial groups, except for the spring and fall pollock-fed groups and the summer herring-fed group (Table 2, Fig. 2). There was no effect of either season or diet on both daily rates of lean mass loss (season, $F_{3,14} = 2.49$, $P = 0.10$; diet, $F_{1,5} = 0.31$, $P = 0.60$; Table 2) and body fat mass loss (season, $F_{3,14} = 0.62$, $P = 0.61$; diet, $F_{1,5} = 0.14$, $P = 0.73$; Table 2). However, there was a significant interaction of season and diet on daily rate of lean mass loss ($F_{3,4} = 8.32$, $P = 0.002$, Table 2). In the spring and fall trials, mean daily rates of lean mass loss were higher in the herring-fed group than in the pollock fed group, however, the trend was reversed in the summer trial (Table 2, Fig. 2).

On average, 54% of the total body mass loss derived from decreases in body fat (53.6 ± 49.4% on the reduced herring diet; and 53.7 ± 24.7% on the reduced pollock diet; $F_{1,5} = 0.6$, $P = 0.98$). Pooling the data from both diet groups showed that changes in lipid mass comprised the smallest portion of total body mass lost in winter (39.3 ± 16.8%) and the greatest in summer (73.2 ± 67.2%), although there was no significant overall seasonal effect ($F_{3,14} = 1.07$, $P = 0.39$; Table 3). However, there was a significant interaction between the effects of season and diet on the percent of total body mass loss due to changes in body fat ($F_{3,14} = 4.71$, $P = 0.017$) (Fig. 2). In most trials the pollock-fed group lost a greater portion of their mass from body fat compared to the herring-fed group across each season. The only exception was the herring-fed group in summer that lost body mass exclusively from body fat (106.8 ± 74.0%), while only 28.5 ± 8.5% of the body mass loss was derived from lipid in the pollock-fed group ($F_{1,14} = 3.06$, $P = 0.008$; Table 3). Within the herring-fed group, the amount of total body mass loss attributable to fat loss also differed between summer (106.8 ± 74.0%) and the other seasons: winter (37.7 ± 22.6%; $F_{1,14} = 2.89$, $P = 0.012$), spring (45.7 ± 26.4 %; $F_{1,14} = -2.58$, $P = 0.022$), and fall (24.1 ± 14.4%; $F_{1,14} = 3.48$, $P = 0.0037$).

Standard metabolic rate

The pre-experimental SMRs varied throughout the year ($F_{3,17} = 27.0$, $P < 0.001$). Although no changes were noted from winter (43.1 ± 4.1 MJ day^{-1}) to spring

Table 2 Mean daily rate of body mass (BM) loss, total body fat (TBF) loss and lean mass (LM) loss

	Winter		Spring		Summer		Fall	
	Herring	Pollock	Herring	Pollock	Herring	Pollock	Herring	Pollock
BM (kg day^{-1})								
Mean	1.6^{p}	1.6^{p}	1.3^{pq}	1.3^{pq}	0.97^{q}	1.4^{pr}	1.6^{p}	1.0^{qr}
SD	0.13	0.22	0.11	0.37	0.18	0.35	0.17	0.19
TBF (kg day^{-1})								
Mean	0.60^{x}	0.66^{x}	0.61^{x}	1.0^{x}	0.97^{x}	0.42^{x}	0.38^{x}	0.69^{x}
SD	0.41	0.11	0.10	0.54	0.52	0.20	0.48	0.14
LM (kg day^{-1})								
Mean	0.95^{ae}	0.95^{ae}	0.72^{ac}	0.26^{bc}	0.01^{b}	0.99^{ad}	1.2^{a}	0.35^{bcde}
SD	0.32	0.24	0.11	0.40	0.62	0.15	0.49	0.14

Different letters within row indicate values are significantly ($P < 0.05$) different

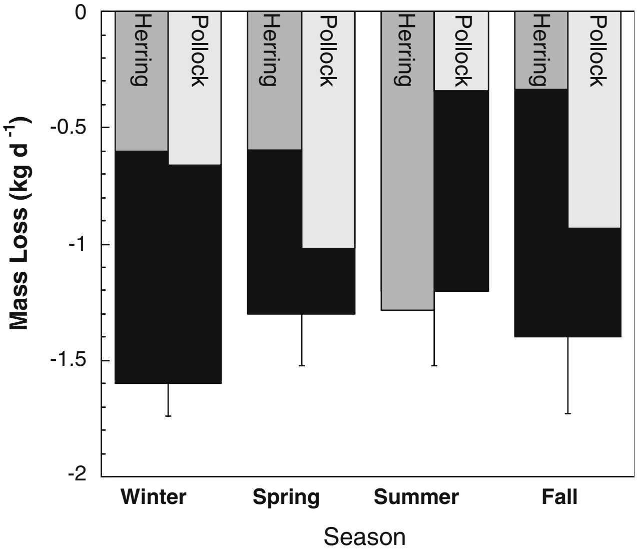

Fig. 2 Mean ± SD of rate of total body mass loss (*black bars*) during feeding of herring or pollock ($n = 7$ for each season). Mass loss was significantly greater in the winter trials ($P = 0.012$). The contribution of lipid loss to total mass loss is also shown separately for herring (*medium bars*) and pollock (*light bars*) diets. There was a significant season × diet interaction—more of the mass loss derived from lipid stores while consuming pollock than when consuming herring, except in the summer when the pattern was reversed. The $>$ 100% lipid loss in the herring group in the summer suggests they were gaining lean body mass while losing overall body mass

(43.8 ± 6.8 MJ day^{-1}), metabolism decreased from spring to summer (32.4 ± 8.0 MJ day^{-1}), and increased from summer to fall (60.1 ± 10.6 MJ day^{-1}; Table 1; Fig. 1). Average SMR was 4.1 times higher than that predicted by Kleiber's calculation for adult, terrestrial mammals. Neither pre- nor post-experimental SMR correlated with body mass ($P > 0.05$).

We obtained both initial and final SMRs from only two animals fed pollock during the winter trial, because one animal did not remain calm in the chamber for the entire period of oxygen consumption measurement. Absolute changes between standard metabolism at the start and end of the feeding trials differed significantly between the herring-fed groups and the pollock-fed groups ($F_{1,5} = 7.84$, $P = 0.038$; interaction season × diet, $F_{3,13} = 6.44$, $P = 0.006$). Excluding the animal that only consumed herring, average decrease in SMR when eating herring was 5.0 ± 7.9 MJ day^{-1}, and only 0.1 ± 5.4 MJ day^{-1} when consuming pollock. However, statistical significance was lost when the data were transformed into percent changes.

Table 3 Body fat mass loss measured as percentage of total body mass loss

Diet (%)	Season			
	Winter	Spring	Summer	Fall
All				
Mean	39.3	59.8	73.2	42.3
SD	16.8	24.1	67.2	31.1
Herring				
Mean	37.7 ^{a}	45.7 ^{a}	106.8 ^{b}	24.1^{a}
SD	22.6	26.4	74.0	14.4
Pollock				
Mean	41.4 ^{a}	78.5 ^{ab}	28.5 ^{a}	66.6 ^{ab}
SD	8.6	6.2	8.5	32.5

Different letters within herring and pollock indicate values are significantly ($P < 0.05$) different

Molting observations

Six of the seven animals showed signs of new hair growth in late July, and one animal showed evidence in late August. The end date of molting ranged from September 30th to November 4th (five out of the seven animals completed molting in October). Mean duration of molting was 80.6 ± 14.6 days.

Discussion

Seasonal fluctuations of initial values

The sea lions in our study had initial body lipid stores ranging from 7.2 to 22.2% of their body mass, which were comparable with the total body fat stores of shot animals from the wild population (Pitcher et al. 2000). As predicted, our sea lions showed seasonal fluctuations in their pre-experimental body fat mass (Fig. 1), as commonly seen in other mammals that have pronounced seasonal life histories (Young 1984; Korhonen 1988; Ryg et al. 1990; Lager et al. 1994; Campbell and MacArthur 1998; Pulawa and Florant 2000).

The simplest explanation of the seasonal changes we observed in mass is that animals accumulated lipid reserves by consuming greater amounts of food, leading to increased total body mass and increased body condition (which is often used as a simple field indicator of relative health). However, in our sea lions, seasonal changes in lipid mass did not correspond with seasonal changes in body mass, or result in significant changes in body condition (Fig. 1). This was likely due to concurrent changes in lean tissue mass, particularly given the importance of somatic growth in young animals. Additionally, these seasonal increases in the blubber layer were not merely a product of increasing energy intake, given that an increase in blubber during the winter–spring interval was not accompanied by an increase in energy intake (unpublished data). Rather, the lack of correlation between (pre-experimental) energy intake and lipid stores indicates underlying seasonal changes in energy expenditures. In all likelihood, these energy expenditures in our captive animals were associated with the molting period, and/or were reflected by changes in SMR. This disassociation between seasonal changes in body mass or condition and food intake is commonly seen in a variety of mammals, including pinnipeds (e.g., Holand 1992; Renouf et al. 1993; Rosen and Renouf 1998; Lehmer and Van Horne 2001).

The higher level of total body fat we observed in spring (prior to the new hair growth; Fig. 1) was similar to the pattern seen in phocid seals (although usually associated with an increase in food intake, Lager et al. 1994; Boily 1996). It is unclear whether increases in fat stores occur in preparation for the expenses associated with the breeding or molting period, given that poor condition can delay both processes (Stewart and Macdonald 1997). The primary need for increased energy reserves during molting in pinnipeds is often assumed to be related to associated periods of fasting or decreased food intake (e.g., Worthy et al. 1992; Lager et al. 1994; Boily 1996). Steller sea lions in our study did not fast during their molt (unpublished data), nor are they known to fast in the wild (Merrick et al. 1997; Sinclair and Zeppelin 2002; Daniel 2003). Data from other captive Steller sea lions suggests that voluntary food intake is generally lower during warmer months and higher during colder months (Kastelein et al. 1990; Nitto et al. 1998).

The SMRs of the sea lions in our study showed seasonal variations (Fig. 1), as has been shown for other mammalian species (Bailey 1965; Armitage and Shulenberger 1972; Ward and Armitage 1981; Campbell and MacArthur 1998). In our study, SMR was lowest in the summer and highest in the fall. Rosen and Renouf (1998) suggested that seasonal changes in resting metabolism were more related to the total amount of energy used (food plus tissue catabolism), rather than just the energy ingested. Similarly, changes in standard metabolism in our sea lions were clearly not the sole source of changes in energy expenditures. For example, the percentage of body fat increased between winter and spring, despite no significant change occurring in metabolism (and an apparent decrease in food intake). Lower metabolic rates were recorded in winter, as has been observed in other species such as the woodchuck (*Marmota monax*, Bailey 1965), reindeer (*Rangifer tarandus*, Nilssen et al. 1984), and harbour seal (Hedd et al. 1997; Rosen and Renouf 1998). Lowering metabolism during winter possibly serves to decrease the catabolism of fat reserves and preserves a minimum blubber layer for thermoregulation. However, resting metabolic rates of gray seals (*Halichoerus grypus*) were highest in winter (Boily and Lavigne 1997), as were those of other phocid species including harbour seals and spotted seals (*Phoca largha*) (Ashwell-Erickson et al. 1986).

Molting is often described as an energetically 'expensive' activity due to an increased metabolism associated with increased growth (of the hair and dermis) or thermoregulatory costs (Worthy et al. 1992; Lager et al. 1994; Boily 1996). However, quantitative evidence is equivocal (Ashwell-Erickson et al. 1986; Boily 1996; Boily and Lavigne 1997; Rosen and Renouf 1998). Metabolic studies on otariids have shown that pups have elevated metabolic rates during molt (Donohue et al. 2000; Beauplet et al. 2003), but no such studies have been conducted on molting juveniles or adults. Comparing our animals prior to the new hair growth (summer) and at the end of new hair growth (fall) showed elevated body mass and SMR, but no changes in total body fat. The lack of change observed in fat mass and the increase in lean tissue mass suggest an energetic shift from thermoregulation to somatic growth expenditures.

Seasonal effects of short-term low energy intake

The natural seasonal fluctuations we observed in body condition and metabolic rates might lead to the prediction that sea lions would suffer disproportionately from unexpected food restriction during periods of lower body fat reserves, such as summer or fall. Alternately, it might be argued that decreased food intake would have a greater impact on Steller sea lions in the (presumably) high-energy requirement seasons such as summer (reproduction), or in the thermally demanding winter period.

The most apparent impacts of food restriction are decreases in body mass. However, the source of that mass loss is also important. General fasting theories suggest that lipid from the hypodermal blubber layer is the primary internal energy source for pinnipeds while lean body mass is generally conserved (except for the demands of gluconeogenesis) as prolonged protein catabolism eventually leads to death (Øritsland 1990). However, a minimal blubber layer is required for thermoregulation, and otariids possess a much thinner blubber layer than phocid seals (Bryden and Molyneux 1978). Therefore, a sea lion in a negative energy state must balance its catabolism of internal tissues by taking into account their energy density (yield), the physiological consequences of depletion, and the extent of the energy deficit. These considerations likely result in disparate priorities for tissue use at different times of the year.

The results of our study illustrate that Steller sea lions respond differently to short-term, low energy intake at different times of the year. Differences in body mass loss attributable to diet type (herring or pollock) observed in some seasons also suggest that diet composition has an additional impact on Steller sea lion health at certain times of the year.

The rate of mass loss was highest in winter and lowest in summer. There are several reasons why Steller sea lions may be more susceptible to food restriction in the winter than in the summer. Differences in rates of body mass loss may relate to higher thermoregulatory demands during the winter. Standard metabolism (which would include any inadvertent costs due to thermoregulation) was higher in the winter than the summer, although it was highest in the fall. There were no significant seasonal differences in rates of lipid catabolism that might be expected if the blubber layer were being conserved for thermoregulatory purposes during colder periods. The higher relative rates of lipid loss of the herring-fed group during the summer and lower rates during other months may have been the product of lower absolute changes in body mass and/or greater relative use of lean tissue rather than conservation of lipid stores per se.

Alternatively, Steller sea lions may be most susceptible to food deprivation during periods when very high energy intake levels are part of their normal life history. Winter months are characterized by high somatic growth and acquisition of lipid reserves, probably supported by high rates of food intake (Winship et al. 2001). Voluntary food intake of Steller sea lions in captivity is generally lower in warmer months and higher in colder months (Kastelein et al. 1990; Nitto et al. 1998). Therefore, it is possible that natural differences in energy state (and the related physiological states) predispose the sea lions to be more susceptible to unpredicted food restriction during the winter months and less during the summer.

It is interesting to note that the period when Steller sea lions appear to have the greatest ability to endure lower energy intake coincides with the period when the average energy density of their diet in the wild is the highest. This is partly due to changes in intra-specific composition, but mostly due to changes in prey items. For example, the diet of sea lions in southeast Alaska is characterized by an increase in high-energy density prey during the summer months. As a result of these seasonal changes in energy requirements and prey energy density, the predicted food requirements (kg day^{-1}) may be lowest in summer and highest in winter and spring particularly for the populations in southeast Alaska based on dietary information (Winship and Trites 2003). Therefore, our results might also suggest that Steller sea lions are more susceptible to restricted energy intake in cold periods when energy and food requirements are greatest, than in warm periods when energy and food requirements are lower. However, the significant differences in daily rates of body mass loss and lean tissue mass loss between the herring and pollock-fed groups in the summer trial may mean that sea lions are better able to conserve lean tissue in response to a reduced amount of food when consuming herring than pollock during this period, while the reverse relationship occurs in the fall.

The anatomical sources of the changes in body mass are noteworthy because decreases in body mass were not necessarily primarily derived from body fat. First, as noted by Rosen and Trites (2005), the fact that higher body mass loss does not always translate into higher total body fat mass loss, raises concerns over using percent lipid mass as a measure of sea lion health (often referred to as a ‘condition index’) among wild populations (Guinet et al. 1998; Pitcher et al. 2000; Luque and Aurioles-Gamboa 2001). For example, although the sea lions in our study lost an average of 11.2% of their initial body mass over a short period of time, body condition decreased by only 4.1%. Changes of this scale would be almost impossible to detect in cross-sectional sampling of wild populations given the individual and seasonal variation observed in the initial condition values in our small group of healthy sea lions. Second, the animals catabolized a large proportion of nonlipid tissues when losing body mass, contrary to our expectations and the general model for fasting pinnipeds (Cherel et al. 1992; Noren and Mangel 2004). This has important implications to the long-term physiological effect of periods of food restriction on animal health.

A previous study by Rosen and Trites (2005) suggested that submaintenance low-lipid diets resulted in a greater portion of mass loss deriving from lipid stores compared to similar mass loss while consuming high-lipid prey. The results of the current study suggest that while this may be true at certain times of the year, the effect was highly seasonally dependant. During most of the trials, the animals on the pollock diet lost more of their internal lipid reserves than those on the herring diet. However, the greatest loss in body fat occurred amongst the herring-fed group during summer, when over 100% of body mass loss came from body fat mass. The high proportion (> 100%) of mass loss from body fat means that animals actually increased lean mass tissues while they lost body fat. For example, one animal in summer lost a total of 11.4 kg of body mass over 9 days, a result of losing 13.2 kg of body fat mass while gaining 1.8 kg of lean mass (meaning body fat mass loss accounted for 116% of her total body mass loss). The reason for the high rate of lipid loss is not clear—the pollock-fed group lost only 28% of its body mass loss from total body fat during the same period. It is also unclear why the herring-fed group used such a high proportion of lipid while the pollock-fed group used such a high proportion of lean mass—or what caused the diet-related difference. The differences between these values are greater than inherent inaccuracies of the deuterium dilution technique.

Although Steller sea lions ingested the same energy from the herring and pollock diet, the energy source differed between them. When the sea lions ate pollock, they consumed 2.3 times more protein, but only 20% of the lipid that the herring group received. Although most studies of the effect of prey type on pinniped health have concentrated on energy and fat content, protein content may also prove a critical factor. Energy available for metabolism may have also differed between diets. Since digestive efficiency and dry matter digestibility are higher in herring (95.4 and 90.1%, respectively) than pollock (93.9 and 86.5%, respectively) during full-sized meals (Rosen and Trites 2000a), the sea lions in our study may have derived less net energy from the pollock than from the herring. It is interesting that significant differences in daily rates of body mass and lean tissue loss due to diet types were observed only in the warmer months (Table 2; summer and fall). This indicates that the effects of diet composition were more prominent in summer and fall, and diminished in winter and spring.

A reduction in metabolism (metabolic depression) is an option for animals to limit their energy expenditures and therefore body mass loss in response to reduced energy intake (Øritsland 1990). Metabolic depression has been shown to occur in fasting Steller sea lions (Rosen and Trites 1999) and harbour seals (Markussen et al. 1992). Alternatively, some Steller sea lions exhibited elevated metabolic rates in response to an energetically restricted diet (~50–70% of their normal intake for ~30 days, Rosen and Trites 2002). In our study, the animals exhibited neither consistent increases nor decreases in metabolic rate. Rosen and Trites (2002) suggested that the differential response exhibited between fasting (decreased metabolism) and food restricted (increased metabolism) sea lions was partly due to daily food intake rather than mass loss. Changes in metabolism were likely independent of GEI, as suggested by Rosen and Renouf (1998). Circulating hormones, such as leptin, may have played a more important role in energy metabolism (Reidy and Webber 2000).

Our study only reports the gross effects of seasonal food restriction on body mass, composition, and metabolism. Understanding the proximate mechanisms that regulate the differences observed between seasons is equally important. Specifically, it is important to investigate whether the observed physical differences are related to an interaction between circulating hormones, body condition and metabolic rate, particularly given the roles hormones serve to control a sea lion's energy budget. This likely means that the relationship between circulating hormones, body condition, and metabolic status also changes seasonally. Understanding this relationship will not only provide a clearer understanding of sea lion physiology, but may result in concentrations of hormones in the blood circulation being useful indicators of the relative energetic status of Steller sea lions in the wild.

Conclusion

Steller sea lions undergo natural seasonal fluctuations in body condition and metabolic rate. Our data suggest that sea lions gain mass from fall to spring, and maintain mass from spring to summer. When faced with short, intense periods of restricted food intake, the sea lions in our study lost body mass at higher rates during the colder seasons and at slower rates during the warmer seasons. These changes in mass coincide with the predicted food/energy requirements for the wild Steller sea lions, and suggest that Steller sea lions may be more susceptible to these types of intense nutritional stress during winter. The loss of body mass we observed was not solely due to changes in lipid mass, and could not be explained by parallel changes in metabolism. This suggests a variety of mechanisms influence changes in body mass, and that these mechanisms may be season specific. The type of fish consumed under conditions of severely restricted intake had no significant effect on changes in metabolism or body mass. However, prey composition had a significant effect on body condition (i.e., % body fat), although the nature of these changes was also season specific.

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