

Potential Effects of Short-Term Prey Changes on Sea Lion Physiology

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Abstract

Changes in the proximate composition of prey can result in a nutritional imbalance in individual animals, regardless of total energy intake. This mechanism has been hypothesized to have contributed to the decline of Steller sea lions (*Eumetopias jubatus*). Yet little is known about how otariids react physiologically to short-term changes in prey quality and availability. A series of studies with young captive Steller sea lions tested several potential links between prey quality and sea lion health. Body composition (fat to total mass ratio) of animals fed constant, maintenance-level, isocaloric diets of high- or low-lipid prey changed with season, but overall was not affected by prey composition. The sea lions appeared to prioritize maintaining core growth rates even when energy was limited, electing to deplete lipid reserves to fulfill energy deficits, resulting in changes in relative body condition. In contrast, sea lions subject to short-term, sub-maintenance diets of high- or low-lipid prey utilized a greater portion of their lipid reserves when losing body mass on low lipid prey. Experiments with different ad libitum feeding regimes indicated that sea lions are readily able to alter food intake levels to compensate for differences in prey energy content and, to a lesser degree, prey availability. However, the results also suggest that decreases in prey quality and/or foraging opportunities can readily combine to require food intake levels that are greater than the digestive capacity of the individual. This is particularly true for young animals that may already be living “on the edge” energetically.

Introduction

The population of Steller sea lions (*Eumetopias jubatus*) has declined more than 80% since the 1970s (Loughlin 1998), and continues to decrease within the western portion of their range. A prevalent hypothesis to explain this decline proposes that changes in the quality and/or availability of prey have resulted in an undefined nutritional inadequacy affecting sea lion health and, ultimately, has caused changes in key life history parameters (e.g., reproduction, survival) (Alverson 1992).

A number of studies have examined differences in gross morphology between populations of Steller sea lions from the western and eastern populations to test whether there are indications of nutritional stress among the former (Calkins and Goodwin 1988, Calkins et al. 1998, Pitcher et al. 2000). Interpretation of these data has relied upon comparisons to other mammalian species, as few studies have empirically examined the effect of changes in prey quality and intake on otariid physiology and morphology. This paper presents a series of experiments, using captive Steller sea lions, which attempted to empirically address the following questions:

1. Do differences in prey composition—without differences in energy intake—negatively affect sea lion health?
2. Do differences in prey quality magnify the effects of energetically inadequate food intake?
3. Do inherent digestive constraints contribute to inadequate prey intake?

The “nutritional stress” hypothesis proposes diet-induced changes in undefined aspects of sea lion “health.” The first two studies specifically investigated the effects of prey composition on body mass, lipid mass, and relative body composition. Other measures of sea lion physiology concurrently measured—metabolism, hematology and blood biochemistry—are not presented here. The first two experiments differ from others on captive pinnipeds in that they controlled for differences in energy intake between diets in an attempt to differentiate between the effects of food quality and energy intake. Our experiments utilized relatively short-term changes in prey type and intake levels (30-42 days) that mimicked hypothesized similar changes in prey availability of wild Steller sea lions.

The third experiment raises the question whether nutritional stress from lack of sufficient food intake is likely to occur in the wild. Foraging theory predicts that animals should proportionately increase their food intake to compensate for reduced nutritional quality and/or prey availability (Perry and Pianka 1997). However, the theoretical intake levels will—at some point—exceed the digestive capacity of the predator

(Weiner 1992). We tested the ability of young, captive Steller sea lions to compensate for short-term changes in prey energy density and availability, and quantified the maximum amount of food a young sea lion could consume.

Methods

General experimental design

The experiments were conducted with a group of Steller sea lions (7 female, 1 male) that had been captured as pups and raised at the Vancouver Aquarium Marine Science Centre (Vancouver, Canada). The normal diet of the sea lions was herring, supplemented with other fish and vitamins (5M26 Vitazu tablets, Purina Test Diets). Some of the sea lions took part in more than one of the three experiments in this study (Table 1).

Our study consisted of three separate experiments (detailed below). In all three experiments, body mass and food intake was measured daily. At the start and end of each trial of experiments 1 and 2, body composition was determined using deuterium dilution (Reilly and Fedak 1990).

Experiment 1: maintenance pollock vs. herring

The experimental design has been previously described in Rosen and Trites (2005). Briefly, three juvenile sea lions were alternately fed controlled amounts of either pollock (6.3-7.4% lipid, 5.36-5.81 kJ g⁻¹ wet weight) or herring (13.8% lipid, 9.57 kJ g⁻¹) for 42 days. Food intake between the diets was balanced for gross energy content (i.e., isocaloric), as determined from sample composition analysis (Norwest Labs, Edmonton, Alberta), and kept constant for each sea lion for the entire experiment. Gross energy intake levels for mass maintenance for each sea lion were determined based on previous feeding levels. Food intake averaged 6.5 kg d⁻¹ for animals on the herring diet and 9.4 kg d⁻¹ when eating pollock, with overall average gross energy intake = 61.5 MJ d⁻¹. The trials were run consecutively from 26 January to 18 July 2000, when the sea lions were 2.5-3.0 years old. To minimize seasonal biases, diet type for each sea lion was alternated between experimental trials, and different sea lions were on different diets during the same trial (Table 1).

Experiment 2: sub-maintenance Atka mackerel vs. herring

The experimental design has been previously described in Rosen and Trites (2005). Briefly, the experiments were conducted on four female Steller sea lions (ages 4.3-5.5 years over the course of trials). They were alternated between isocaloric diets of Atka mackerel (4.9-6.7% lipid, 4.8-5.4 kJ g⁻¹ wet weight) and herring (10.3-13.4% lipid, 7.0-8.2 kJ g⁻¹) between October 2001 and January 2003. The level of food intake (~35.6 MJ d⁻¹) was set a priori at a level estimated to produce a 10-15% loss of initial body mass over the 30 day trials.

Table 1. Schedule summary for the two diet manipulation experiments by month (although not all in the same year). Experiment 1: maintenance level pollock (P) versus herring (H); experiment 2: sub-maintenance level Atka mackerel (A) versus herring. Also listed are the length of each trial in days and the individual sea lions used in each study. For experiment 2, A/H refers to a sea lion fed Atka mackerel the first year and herring the following year.

Experiment	N	D	J	F	M	A	M	J	J	No. days	Animal ID
1. Maintenance pollock versus herring				H		P		H		42	M97KO F97SI
				P		H		P		42	F97HA
2. Sub-maintenance Atka mackerel versus herring	A/H		H/A							29	F97HA
	H/A		A/H							29	F97SI
			H	A						29	F00NU
			A	H						29	F00YA

To control for seasonal and developmental effects, the trials were paired to ensure that individual sea lions were fed alternate species of prey during each period, and that trials were repeated with opposite diets during the same season in the following year (Table 1).

Experiment 3: satiation and compensation

The experimental design has been previously described in Rosen and Trites (2004). Briefly, five female Steller sea lions participated in the study (aged 1 year old at the start of the experiment). The experiment was designed to minimize the effects of training and research staff on the food intake patterns of the sea lions (Shettleworth 1989). The trials took place in dry animal holding runs containing feeding troughs with a continuous water inflow. A weighed amount of fish was added to their feeding troughs, and each sea lion had a full trough of fish for 7 continuous hours, usually starting at 0900 hr. Fish were refreshed and/or replaced as needed.

A crossover design was used with four treatment conditions consisting of a combination of prey type (either high energy density herring or low energy density capelin; *Mallotus villosus socialis*) and prey availability (food available either daily or on alternating days). The four treatments were alternated after 4 consecutive “feeding” days (i.e., 7 experimental days for alternate day treatments) for four of the animals both within and between each trial, so that no two animals repeated the same combination

within a trial or during the course of the experiment. Each trial lasted 20 days, and the experiment consisted of 4 trials over one year, denoted as Summer-01 (July-August 2001), Fall-01 (October-November 2001), Winter-02 (January-February 2002), and Fall-02 (October-November 2002). The herring in the study averaged 90.6 g and 21.9 cm (total length), and the capelin 24.0 g and 16.2 cm. Energy density was 8.05 kJ g⁻¹ and 4.41 kJ g⁻¹, respectively.

Food intake was averaged for each sea lion for each treatment combination, excluding the first day as an adjustment day. Food intake data were transformed into measures of gross energy intake to test whether the animals changed their food intake to maintain average gross energy intake across diet treatments. The theoretical intakes were calculated in relation to the "baseline" values of the daily herring (DH) treatment. Assigning this treatment a value of 100% of expected values meant that alternate herring (AH) treatments had an expected value of 200%. This is based on the prediction that the sea lions would compensate for fasting days by eating twice as much on the days food was available to them. Based on differences in gross energy content, the daily capelin (DC) intake should be 183% of the DH intake, and the alternate capelin (AC) intake should be 366% of DH intake.

Results

Experiment 1: maintenance pollock vs. herring

Body mass increased an average of 2.9±2.7 kg (mean±SE) over an entire herring trial and 0.2±2.6 kg over a pollock trial. Animals on both diets gained an average of 3.8±1.8 kg of lean tissue mass over a single trial. At the same time, they lost an average of 0.9±2.7 kg lipid mass while eating herring and 3.6±1.4 kg on the pollock diets. There was a good correlation between changes in total body mass and changes in lean tissue mass ($F_{1,10} = 9.84$, $P = 0.01$, $r^2 = 0.50$), largely driven by the strong relationship within the herring treatments ($P = 0.007$, $r^2 = 0.91$). There was no significant relationship between changes in total body mass and lipid mass ($F_{1,10} = 1.98$, $P = 0.20$), regardless of diet. Changes in body composition, measured as lipid mass as a percent of total body mass, declined marginally for both herring (-1.1%) and pollock (-2.1%) diets. The observed changes in relative body condition were related to changes in lipid mass ($F_{1,10} = 80.27$, $P < 0.0001$, $r^2 = 0.89$) rather than changes in lean tissue mass ($F_{1,10} = 4.30$, $P = 0.06$), regardless of diet type.

There was a significant effect of season on changes in body condition ($F_{1,8} = 5.35$, $P = 0.05$), with the rate of lipid mass loss increasing from January to July. Changes in lean tissue mass also differed during the year, and were highest in May (Fig. 1).

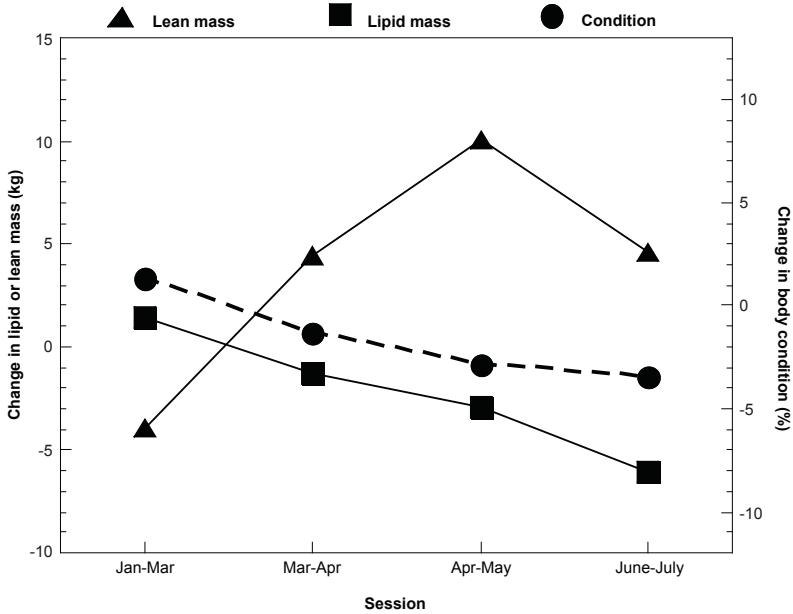


Figure 1. Mean changes in lipid mass (kg), lean tissue mass (kg), and relative body condition (%) during the maintenance level diet manipulations (experiment 1). Data are mean values for all animals eating pollock or herring. Body condition was calculated as: lipid mass/body mass \times 100. Figure modified from Rosen and Trites (2005).

Experiment 2: sub-maintenance Atka mackerel vs. herring

Since all of the trials were purposely balanced for season (each animal completed an Atka mackerel and herring trial for each season), we decided to analyze the data using paired *t*-tests with each pair of data corresponding to the two prey types matched for season for each animal.

As predicted for isocaloric diets, there was no difference in absolute or relative body mass loss attributable to diet (Atka mackerel 14.93 ± 1.1 kg, $10.1 \pm 0.5\%$; herring 15.50 ± 1.6 kg, $10.6 \pm 1.0\%$) ($t_5 = 0.453$, $P = 0.67$).

More of the total mass loss was derived from decreases in lipid stores when the animals were consuming Atka mackerel than herring ($63.64 \pm 15.94\%$ vs. $40.29 \pm 9.41\%$) ($t_5 = -2.82$, $P = 0.037$). On average, sea lions lost more lipid mass (9.16 ± 1.80 kg) while consuming Atka mackerel than herring (6.52 ± 1.65 kg) ($t_5 = -2.98$, $P = 0.031$) (Fig. 2). Although the sea lions lost less lean body mass (5.78 ± 2.77 kg) while consuming Atka mackerel than herring (8.98 ± 1.43 kg), this difference was not significant ($P = 0.18$). A closer examination of the changes in lean body mass indicated

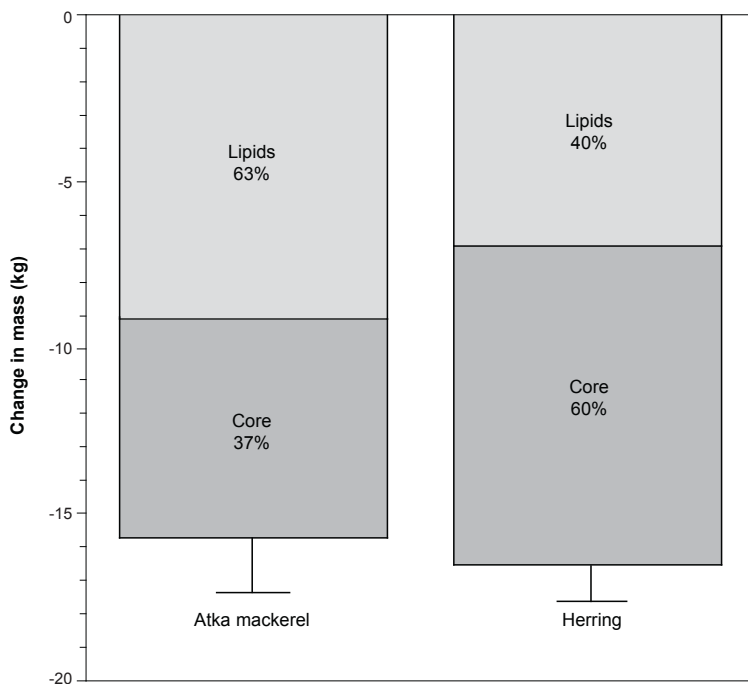


Figure 2. Average change in lipid and lean tissue mass during 30 day sub-maintenance diets of Atka mackerel and herring. There was a significant difference between diets in the amount of lipids lost, but not in the amount of lean tissues lost. Complete data are available in Rosen and Trites (2005).

that, on average, the sea lions lost a total of 1.80 ± 0.38 kg protein while eating Atka mackerel, compared to 2.18 ± 0.32 kg while eating herring. This meant that a large proportion of total mass loss could be attributed to protein catabolism when consuming either herring ($14.31 \pm 1.5\%$) or Atka mackerel ($11.69 \pm 2.3\%$).

Since relative body condition (lipid mass as % total mass) is a product of changes in both lipid and lean tissues, there were no significant diet-related differences in changes in relative body condition ($P = 0.066$). Relative body condition averaged $16.0 \pm 1.5\%$ at the start of the trials, and decreased $5.33 \pm 1.67\%$ while sea lions were eating Atka mackerel and $2.04 \pm 1.03\%$ while they were consuming herring.

Overall, there was a strong relationship between changes in body condition and changes in lipid mass ($r^2 = 0.92$, $P < 0.0001$). There was also a slightly weaker relationship between changes in relative condition and

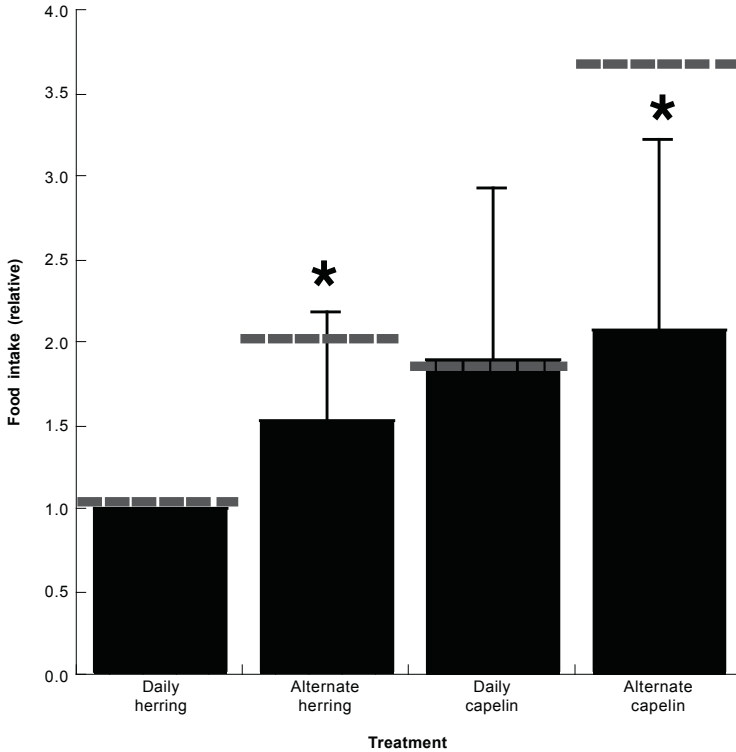


Figure 3. Average daily food intake (\pm SD) relative to the “baseline” amount of fish consumed during the daily herring phase of the study. Dotted lines represent “expected” values required to maintain an equivalent gross energy intake based on relative energy content of herring and capelin and daily or alternate day prey availability. An asterisk indicates significant differences between observed and expected consumption levels. Modified from Rosen and Trites (2004).

changes in lean body mass ($P = 0.0002$, $r^2 = 0.76$). There was no apparent effect of diet type on either relationship.

Experiment #3: satiation and compensation

There were significant differences in food intake related to type of prey and frequency of feeding ($F_{3,45} = 14.23$, $P < 0.0001$). Specifically, average food intake during DH treatments (8.31 ± 2.8 kg) was significantly less than during AH treatments (11.54 ± 3.0 kg). Intake during both herring treatments was significantly lower than both the DC (14.04 ± 3.6 kg) and

AC (15.16 ± 5.4 kg) treatments, which did not differ significantly from each other. Although there was no significant difference in the mean intake between the DC and AC treatments, the variation was greater in the latter due to some animals eating extraordinary amounts on individual days. The greatest consumption during a single day was 28.4 kg ingested by a ~ 100 kg animal during the winter phase.

Food intake during the AH treatment was 1.52 ± 0.67 times that of the DH treatment (Fig. 3), which was significantly lower than the 2.0 times predicted increase required to provide equivalent gross energy intake to the DH treatments. Similarly, the observed 2.07 ± 1.15 times increase in food intake during AC treatments relative to the DH treatments was significantly less than the predicted 3.66 times increase. However, the 1.89 ± 1.04 times increase in food intake during the DC relative to the DH levels was not significantly different from the 1.83 times increase predicted from gross energy contents of herring and capelin.

Discussion

The nutritional stress hypothesis proposes that changes in the diet (or dietary requirements) of Steller sea lions were a contributing factor to their population decline (Alverson 1992, Trites and Donnelly 2003). The implied nutritional imbalance has frequently been interpreted to be the result of decreased energy intake due to changes in prey type, abundance, or distribution.

Several studies have investigated the effects of prey quality on body mass and composition in pinnipeds. Studies with a variety of captive pinnipeds have shown that animals do not appear to alter food intake sufficiently to compensate for differences in prey energy density when switched between *ad libitum* diets of low-energy and high-energy prey. This results in decreased growth rates, body mass, and body condition (Kirsch et al. 2000, Rosen and Trites 2000, Stanberry 2003). However, two other studies (one that used the same animals as Stanberry 2003) failed to find an effect of prey quality on body mass or composition (Castellini 2002, Trumble et al. 2003).

It is difficult to determine from these former studies whether the potential effects of dietary differences were due to prey proximate composition or energy content. This is partly because energy content is closely linked to lipid content in fish (having negligible carbohydrate content), and partly because these studies were conducted using *ad libitum* feeding regimes. The experiments we describe used controlled, isocaloric diets to separate the potential effects of energy and lipid content of prey on sea lion physiology.

Effects on body composition

The combined results of our experiments with captive Steller sea lions indicate that lipid content of prey appears to have no significant effect on body mass or condition when the animals can physically consume sufficient prey to meet all of their energy needs. However, low-lipid prey results in greater losses of lipid reserves when energy intake is insufficient due to increased energy expenditures and/or restricted intake.

The animals on the maintenance-level diet retained the same lean tissue growth regardless of diet type, with greater variation in lipid mass during the year. These results suggest that lean tissue growth is a priority for energy partitioning, and that the “remainder” of the energy budget serves to increase (positive energy state) or decrease (negative energy state) internal lipid reserves. This hypothesis is supported by the evidence that (at maintenance energy intake levels) changes in total mass are driven by changes in lean tissue while changes in relative body condition are driven by changes in lipid stores (Fig. 1). In other words, lipid energy reserves will be proportionately depleted if energy intake is insufficient to support lean body mass growth, a process similarly demonstrated with captive juvenile harp seals (Kirsch et al. 2000). This trend was most evident during the spring season (April-May), when growth rates for total body mass (+7.2 kg) and core tissue (+10.1 kg) were highest, and substantial decreases occurred in lipid stores (−2.9 kg) (Fig. 1).

The differential effect of prey composition on body lipid reserves was most clearly demonstrated in the sub-maintenance, Atka mackerel vs. herring trials (experiment 2). The sea lions lost both lean body mass (and accompanying protein) and lipid stores, although a greater portion (64%) of total mass loss was attributable to changes in lipid stores when the animals consumed the low-lipid Atka mackerel, compared to when consuming herring (40%). As a result, the sea lions had lower relative lipid reserves (as a percent of body mass) when losing mass on the low-lipid diet.

Tissue catabolism

In our second experiment the Steller sea lions used a surprising amount of lean body mass (~48%) to meet their energy requirements during sub-maintenance intake conditions. The reason for the high rate of protein catabolism that we observed is unclear, but such levels of core tissue loss are normally considered a sign of severe nutritional stress (Øritsland 1990). During periods of mass loss, pinnipeds (like many vertebrates) are expected to primarily deplete lipid reserves (Cherel et al. 1992). The relative extent of lipid stores has often been used as a measure of body condition and general health (Pitcher et al. 2000). In these experiments, changes in relative condition were largely driven by changes in lipid mass (despite substantial changes in core tissues during experiment

2). This supports the general concept of using percent body lipids as a health indicator. However, the average decreases in relative condition during a 30 day period of definite nutritional stress was very small (4.2%) with substantial variation, suggesting that such changes would be very difficult to detect in samples of wild Steller sea lions. It is possible that our results were biased due to dehydration in the study animals. Dehydration while using deuterium dilution would result in greater apparent levels of protein catabolism. However, most hematological indicators of this condition were absent (e.g., changes in sodium or potassium levels, although hematocrit did increase). As a diagnostic tool, these physiological changes/differences in hydration state would also be shared by wild sea lions undergoing the same type of nutritional stress. Our results, combined with the large natural seasonal variation in lipid stores and the inherent errors associated with the deuterium dilution technique (Roberts 1989), question the efficacy of using percent lipid mass as a realistic measure of Steller sea lion health status. Other physiological indicators, such as changes in blood biochemistry, may prove to be more effective diagnostic tools (e.g., Rea et al. 1998, 2000).

Compensatory food intake

However, questions arise as to whether the restricted food intake used in these experiments represents a realistic condition. Specifically, would Steller sea lions in the wild not compensate for decreases in prey quality or availability simply by increasing food intake?

The results of our final study (experiment 3) demonstrate that young Steller sea lions appear to have the physiological ability to alter food intake levels to compensate for changes in energy density and, to a lesser degree, availability of prey. The sea lions in our study altered their intake when switched between the daily herring and the daily capelin to retain the same gross energy intake. They also increased their intake when switched between conditions when food was available daily and every other day, although total average intake levels were less in the latter trials.

However, the experiment also clearly demonstrates that this capacity for compensation is limited. It is elementary that there must come a point when the theoretical intake levels needed to compensate for decreasing nutritional value and/or availability of prey will surpass the actual digestive capacity of the predator (Weiner 1992). It is important, therefore, to establish the maximum digestive capacity of Steller sea lions to set realistic limits on foraging and bioenergetic models. As a rough estimate, the sea lions in our experiment seemed unable to consistently ingest food at levels greater than approximately 16-20% of their own body mass.

The results of these experiments support the hypothesis that the intersecting costs to a sea lion faced with decreasing prey availability and net energy value quickly combine to a point where the calculated

required food intake surpasses the digestive capacity of the individual sea lion. Such rough estimates of maximum food intake can be integrated with data on available foraging times and ranges of prey energy densities to estimate a variety of variables, including the minimum frequency and energy density of prey needed to sustain an animal (Rosen and Trites 2004). It can also be used to estimate minimum energy deficits that arise from scenarios where an animal is unable to ingest sufficient prey to meet its energy requirements. In general, bioenergetic models would suggest that Steller sea lions that have the highest relative energy demands (young animals and lactating females) may not be able to consume sufficient quantities of low-energy or dispersed prey in the wild to meet their energetic needs (Winship and Trites 2003).

Summary

The combined results of our experiments with captive Steller sea lions suggest that lipid content of prey does not appear to have a significant effect on body mass or condition when energy intake is sufficient to meet all needs. Sea lions appear able to ensure sufficient energy intake by increasing consumption of low-energy prey and, to a lesser degree, altering food intake to compensate for changes in prey availability. This ability is limited, however, by the digestive capacity of the animal. When energy intake is insufficient due to either restricted intake or increased expenditures (such as high growth rates), consumption of low-lipid prey results in greater decreases in lipid reserves. At maintenance levels, sea lions appeared to prioritize lean tissue growth, even at the expense of lipid stores. A surprisingly high rate of lean tissue catabolism was observed during periods of mass loss due to energy restriction. While changes in relative body condition were largely driven by changes in lipid mass, the resulting scope of changes in relative body condition was very small.

Acknowledgments

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