Metabolic Effects of Low-Energy Diet on Steller Sea Lions, *Eumetopias jubatus*

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ABSTRACT

Diets of six Steller sea lions (*Eumetopias jubatus*) were switched between a high (herring) and a low (squid) energy density food for 14 d to determine the effects on ingested prey mass, body mass, resting metabolic rate, and the heat increment of feeding. Body mass was measured daily, and resting metabolism was measured weekly by gas respirometry. Ingested food mass did not differ significantly between the squid diet and the control or the recovery herring diet periods. As a result of differences in energy density, gross energy intake was significantly lower during the squid diet phase than during either the control or recovery periods. As a result, sea lions lost an average of 1.1 kg/d, totaling 12.2% of their initial body mass by the end of the experimental period. The heat increment of feeding for a 4-kg squid meal was significantly lower than for a similarly sized meal of herring. Decreases in both absolute (24.0 to 18.0 MJ/d, −24%) and mass-corrected (903 to 697 kJ/d/kg$^{0.67}$, −20%) metabolism were observed by the end of the squid feedings. This study suggests that sea lions can depress their resting metabolism in response to decreases in energy intake or body mass, regardless of satiation level.

Introduction

Prey choice should be a function of the availability of and net energy (NE) derived from specific items. The latter is a product of the energy density (gross energy content) and digestibility of the prey item. A predator may partially compensate for lower energy density prey by increasing ingested mass, a strategy ultimately limited by prey availability and the physical and physiological constraints of capturing and consuming more prey.

Decreased energy intake may also result from decreased prey availability. Changes can be due to large-scale ecological shifts (e.g., El Niño, the North Pacific Regime Shift) or short-term, predictable changes (e.g., seasonal availability). Regardless of the ultimate cause of decreased energy intake, pinnipeds utilize a number of behavioral and physiological adaptations to minimize the effects of the deficit. Decreasing energy expenditures from activity, thermoregulation, and resting metabolic rate (RMR) are strategies that increase survival time by limiting the loss of body mass.

The decrease in RMR below normal levels is known as metabolic depression (Keys et al. 1950; Grande et al. 1958). Metabolic depression has been documented during periods of experimental fasting in both marine (Gallivan and Best 1986; Markussen et al. 1992; Boily and Lavigne 1995) and terrestrial mammals (Grande et al. 1958; Montemurro and Stevenson 1960; Cahill 1978; Harlow 1981), although its duration appears to be finite (McCance and Mount 1960; McCarter et al. 1985; McCargar et al. 1993). It also occurs in phocid seals during periods of natural fasting (Heath et al. 1977; Ashwell-Erickson and Elsner 1981; Nordøy et al. 1990; Rea and Costa 1992; Rosen and Renouf 1998). Metabolic depression occurs among terrestrial mammals during periods of experimental food restriction (Mitchell 1962; Forsum et al. 1981; Hill et al. 1985; Munch et al. 1993), but it is unclear whether a similar response occurs in pinnipeds (Markussen 1995).

Captive pinnipeds are often unable to maintain their body mass when switched to a lower energy density diet, despite being fed ad lib. (Mårtensson et al. 1994; D. Rosen and A. Trites, unpublished data). This has critical consequences for species whose prey base shifts over time. Such an ecological shift may have occurred in the Bering Sea (Kerr 1992; Francis and Hare 1994; Trites et al., in press), where a number of pinniped and seabird populations have experienced significant declines (Pitcher 1990; Trites 1992; Byrd and Dragoo 1997), including a 70% reduction in Steller sea lion numbers since 1970 (National Marine Fisheries Service 1992; Trites and Larkin 1996).

The following study investigates the physical and physiological consequences of shifting the diet of captive Steller sea lions from high to low energy density items (i.e., herring to squid). We examined changes in body mass, resting metabolism, and gross energy intake (GEI) to determine which mechanisms were utilized to compensate for the lower energy density prey. We

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also measured the heat increment of feeding (HIF) to better estimate the NE sea lions derive from eating squid.

Material and Methods

The study group consisted of six juvenile Steller sea lions (three males and three females). All had been introduced to captivity as pups and ranged from 1.6 to 3.5 yr old when tested (December 1995–July 1996). Sea lions were held in an outdoor compound at the Vancouver Aquarium (British Columbia, Canada) with access to filtered (ambient temperature) seawater and haul-out space. Their normal diet consisted of thawed herring (*Clupea harengus*) fed ad lib. twice per day and small quantities of other fish species (including squid). Diets (both normal and experimental) were supplemented with vitamin tablets (5M26 Vita-zu tablets, Purina Test Diets, Richmond, Ind.).

Sea lions were fed exclusively herring during a 2-wk control period. They were then fed squid (*Loligo opalescens*) over a 13–18-d experimental period, after which their diet was switched back to herring for a 14-d recovery period. The sea lions were fed on an ad lib. basis during all phases. Body mass was monitored daily throughout the study by having the animals hold position on a platform scale (± 0.05 kg).

Herring and squid composition analyses were performed at the Department of Fisheries and Oceans, West Vancouver Science Lab. Energy density was determined through oxygen-bomb calorimetry of representative samples. Samples of each species were also analyzed to determine lipid (modified Bligh-Dyer technique; Bligh and Dyer 1959), protein (Kjeldahl nitrogen extraction), ash, and water content. Gross energy intake was calculated by multiplying ingested food mass (IFM) by energy density. As the composition of herring changed depending on the lot used, GEI was calculated specifically for the lot that was being consumed at the time.

Resting metabolic rate was measured five times on each sea lion during the study. The first measure was made within 7 d before the switch in diet from herring to squid. Subsequent measurements were made 1 and 2 wk into the experimental period and 1 and 2 wk after switching back to herring (recovery period).

Metabolism was measured using open-circuit (gas) respirometry under accepted RMR conditions for nonmature animals (postabsorptive, quiescent but awake, nonpregnant, within their presumed thermoneutral zone [testing temperatures = 6°–19°C]; Kleiber 1975). Measurements were made in a ~1,050-L dry metabolic chamber, equipped with a fan to circulate air, a water-cooling system, and a video camera and fluorescent light to monitor the sea lion's activity. The sea lions were trained to remain calm within the chamber since they were pups. Metabolism was monitored over a 45–110-min period after a minimum 15-min acclimation period. Measurements of resting metabolism were obtained from extended (minimum 15 min) periods of low, constant oxygen consumption associated with periods of inactivity.

Air was drawn through the chamber at a constant rate (150–170 L/min, measured between the chamber and the pump) sufficient to prevent extreme changes in gas concentrations (specifically, $O_2 > 19.5\%$; $CO_2 < 1.0\%$). Oxygen and carbon dioxide concentrations ($\pm$ 0.01%) within a desiccated subsample of the excurrent airstream were determined by an S-3A/I solid oxide (stabilized zirconia) cell analyzer (Ametek, Pittsburgh, Pa.) and an AR-60 infrared gas analyzer (Anarad, Santa Barbara, Calif.), respectively. Barometric pressure and expired air temperature at the flowmeter were recorded for flow-rate corrections to STPD (Airguide Instruments, Chicago). The excurrent airstream was continuously subsampled, and a Sable data acquisition system (Sable Systems, Henderson, Nev.) calculated an average gas concentration (from 200 subsamples) every second. Changes in gas concentration were converted to oxygen consumption rates (using eq. 3[b], Withers 1977) and then to energy utilization using the equation 1 L $O_2 = 20.1$ kJ. Gas concentration readings were baselined against ambient air concentrations every 2 h during the HIF trials, and the entire system was recalibrated through the course of the experiments using gases of known concentrations and a standard nitrogen dilution technique (Fedak et al. 1981).

Metabolism is partially a function of body mass, both on an inter- and an intraspecific basis. Therefore, it is possible that observed changes in resting metabolism are merely a function of concurrent changes in body mass. Unfortunately, there is little consensus on how (or whether) to correct estimates of metabolism for changes in body mass. Most short-term changes in body mass for pinnipeds derive from changes in the hypodermal blubber layer. If this layer is presumed to be relatively metabolically inert, then the animal's metabolic mass remains largely unaltered, and changes in resting metabolism can be viewed solely in terms of the relatively minor changes in lean body mass (Cunningham 1991; Rea and Costa 1992). However, this may not be the case (Lavigne et al. 1986; Ferraro and Ravussin 1992; McNab 1997). As a conservative measure (i.e., least likely to reject the null hypothesis), a mass-corrected measure of resting metabolism of $\mathrm{RMR_{corr}} = \mathrm{kJ/d/kg^{0.67}}$ was used.

The HIF for a squid meal was measured for five of the six sea lions at the end of the experimental (squid diet) period. A baseline (control) measure of RMR was taken at the start of each test. Each animal was then fed a squid meal of known size (approximately 4 kg, their normal meal size). Metabolism was monitored through its postprandial rise until it returned to the prefeeding baseline level. The HIF was calculated as the total postfeeding energy expenditure above baseline levels, expressed as a proportion of GEI (see Rosen and Trites 1997 for details).

Results

The sea lions consumed an average of 6.9 ± 0.3 kg/d (mean ± SEM) and 7.9 ± 0.6 kg/d of herring during the control and recovery periods, respectively, and 6.9 ± 0.9 kg/d of squid during the experimental period (Fig. 1). Differences in the mean IFM between phases were not statistically significant (repeated measures ANOVA, $F_{2,10} = 2.39$, $P = 0.14$).

Energy density of herring ranged from 7.28 to 9.86 kJ/g (range of lot averages), while average energy density of squid was 3.69 kJ/g (Table 1). Due to the lower energy density of the squid, GEI during the experimental period (25,492 ± 3,410 kJ/d) was significantly lower than during the control (51,502 ± 3,360 kJ/d) and recovery (64,910 ± 5,259 kJ/d) periods (repeated measures ANOVA, $F_{2,10} = 91.10$, $P < 0.001$; treatment mean differences compared using the Scheffé test; Fig. 1).

The GEI was sufficient to maintain moderate growth (<0.4 kg/d) during the control phase. The sea lions lost an average 12.2% of initial body mass over the 2-wk experimental period when they were fed the lower-energy squid (Table 2). There was no significant difference in the rate of body mass loss during the first (1.22 ± 0.09 kg/d) and second weeks (1.03 ± 0.15) of the squid diet (paired $t_5 = 0.93$, $P = 0.39$). The sea lions began to recover body mass shortly after they were switched back to the herring diet and showed a significantly greater rate of mass gain during the first recovery week (0.83 ± 0.05 kg/d) compared to the second week (0.33 ± 0.13 kg/d; paired $t_5 = 4.21$, $P = 0.008$). Overall, the rate of mass gain during the recovery period was lower than the rate of mass loss during the squid diet, so that the sea lions reached 94% of their initial mass after the 2-wk recovery period.

The sea lions had been tested in the metabolic chamber since they were pups and usually remained quiescent for the duration of the measurements (including the extended period necessary to measure HIF). However, female 3 would not remain quiescent long enough to get an accurate RMR measurement or an estimate of HIF. Similar factors prevented obtaining an RMR measurement for female 2 during the second week of the experimental (squid) phase.

Resting metabolic rate averaged 24.0 ± 2.0 MJ/d during the control period (for comparative purposes, this translated into an average of 6.07 mL O_2/min/kg). It was 10.1% ± 5.1% ($N = 5$) lower than control levels after the first week of squid feeding and a total of 24.2% ± 3.4% ($N = 4$) lower by the end of the experimental period (Fig. 2; Table 3). Mass-

Table 1: Mean composition of prey items (per g wet weight) derived from analysis of representative samples

Species	Energy (kJ/g)	Water (%)	Protein (%)	Lipid (%)
Squid	3.69	82.5	12.8	2.4
Herring:				
Lot 1	7.58	73.0	18.3	8.4
Lot 2	7.28	72.6	16.3	9.4
Lot 3	9.86	71.5	17.1	9.5

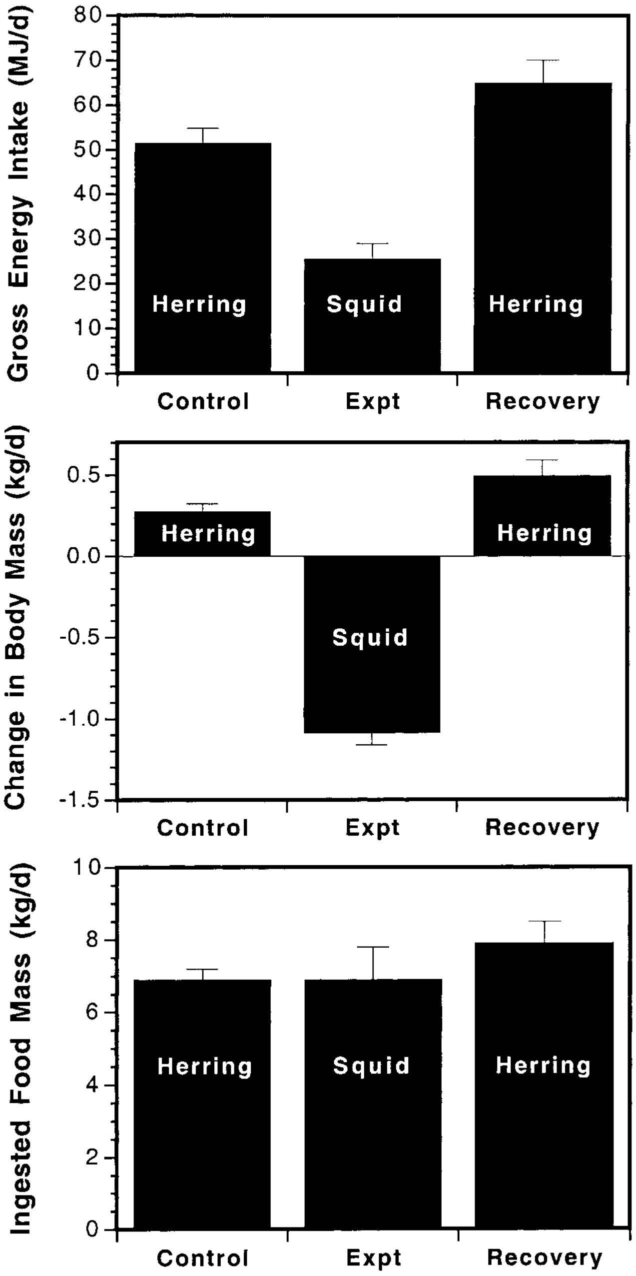

Figure 1. Average gross energy intake (*top*), changes in body mass (*middle*), and ingested food mass (*bottom*) during the control (herring diet), experimental (squid diet), and recovery (herring diet) periods. Column height represents the mean from six sea lions; error bars denote 1 SE.

corrected resting metabolism decreased 7.0% ± 5.3% from control levels of 903 ± 77 kJ/d/kg$^{0.67}$ after the first week of squid feeding and 19.6% ± 4.1% after the second. Metabolism increased after the first week of the recovery (herring diet) period, reaching control levels for two sea lions, but remained depressed for the other three sea lions. Overall, RMR and RMR$_{corr}$ were at 10.6% ± 4.9% and 5.9% ± 4.6% below control levels, respectively, during the first recovery week. Metabolism returned to within 10% of initial levels during the second recovery week for all sea lions except male 3 (overall RMR = $-9.7\% \pm 2.6\%$; RMR$_{corr}$ = $-7.1\% \pm 2.0\%$).

The HIF due to the ingested 4-kg squid meal lasted 8.2 ± 1.4 h and averaged 19.4% ± 1.8% of GEI (Fig. 3). This value was significantly higher than the 12.4% ± 0.9% previously measured (Rosen and Trites 1997) for 4-kg herring meals for the same animals (arcsine transformed data, paired $t_4 = 5.66$, $P = 0.005$). While HIF is defined as the energy needed to digest and assimilate a meal, in our study it also included the cost of raising the temperature of the prey items to body temperature (e.g., Wilson and Culik 1991). The methods and food items used in this study necessitated this added thermal cost and, therefore, provide a more ecologically relevant value.

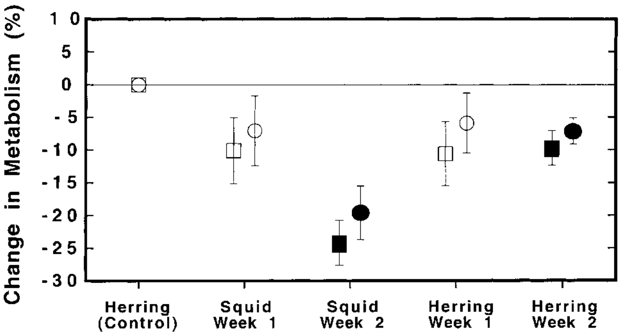

Figure 2. Changes in resting metabolism (kJ/d; *squares*) and mass-corrected metabolism (kJ/d/kg$^{0.67}$; *circles*) during the 2 wk of squid diet and 2 wk of herring diet. Percentage changes (mean ± SEM) are calculated in reference to changes from control (herring diet) values. Significant differences from control values denoted by closed symbols. Points are staggered for clarity.

Discussion

The most unforeseen result of this experiment was that the sea lions did not ingest more food in response to the lower energy density of the squid. We had initially predicted that once body mass/condition began to decrease, the sea lions would increase the amount of food they ingested to maintain a level of energy intake similar to that of their herring diet. Instead, IFM remained relatively constant, resulting in decreased energy intake and substantial decreases in body mass. For comparison, the rate of body mass loss while the sea lions were consuming squid ad lib. was about half of that exhibited by the same animals during an experimental fast (Rosen and Trites 1998).

Table 2: Changes in body mass (kg/d) during the experiment

Subject	Initial Mass (kg)	Experimental Period		Recovery Period	
		Week 1	Week 2	Week 1	Week 2
Male:					
1	161.6	−1.29	−1.55	+.69	−.30
2	144.5	−1.04	−.96	+.74	+.53
3	158.9	−.89	−1.11	+1.03	+.43
Female:					
1	124.7	−1.34	−1.20	+.91	+.36
2	110.3	−1.54	−.44	+.81	+.50
3	107.3	−1.21	−.92	+.78	+.48

Note. Mass changes at day 7 and day 14 of the experimental period are calculated in reference to initial body mass at the start of the experimental (squid diet) period. Mass changes at day 7 and day 14 of the recovery (herring diet) period are calculated in relation to body mass at the end of the experimental period. Female 1 and male 1 were only on the squid diet for 13 d due to high rates of mass loss. Mass loss for week 2 of the experimental period was therefore only calculated over 6 d for those animals. Mass changes during the recovery period were calculated in reference to body mass at the end of the squid trials, as with the other subjects.

Physical satiation may explain why the sea lions did not increase their food intake, although the role of palatability cannot be discounted. We do not know how long the sea lions could have tolerated this rate of body mass loss, although one reasonable prediction is that changes in their energy expenditures and GEI would have eventually reached some equilibrium, where body mass would stabilize at some decreased level.

Changes in Metabolic Rate

Regardless of the reasons for the lack of increase in IFM, the immediate result was a dramatic loss in body mass. These circumstances triggered at least one compensatory mechanism—metabolic depression. This controlled reduction in resting metabolic rate is a physiological response associated with periods of fasting or hypophagia in a wide range of vertebrates. Metabolic depression is presumed to be an adaptive mechanism designed to moderate the impact of lower levels of energy intake on other parameters of an animal's energy budget. More specifically, the decreases in metabolism help to minimize body mass loss during times of low-energy intake and, ultimately, delay death by starvation.

In our study, the metabolism of the Steller sea lions dropped dramatically over the course of the squid trials. The 16%–26% decrease we observed in absolute resting metabolism after 2 wk of a low-energy diet was comparable to that observed in other marine mammals during periods of experimental fasting, in-

Table 3: Changes in absolute and mass-corrected resting metabolic rates during the feeding experiment

		Experimental Period		Recovery Period	
Subject	Control	Week 1	Week 2	Week 1	Week 2
Absolute metabolism (kJ/d):					
Male:					
1	18,075	15,007 (−17.0)	13,988 (−22.6)	18,103 (+.2)	16,872 (−6.7)
2	23,095	18,622 (−19.4)	15,604 (−32.4)	20,208 (−12.5)	21,540 (−6.7)
3	30,628	32,125 (+4.9)	22,681 (−25.9)	24,652 (−19.5)	24,433 (−20.2)
Female:					
1	23,511	23,342 (−.7)	19,764 (−15.9)	23,795 (+1.2)	21,901 (−6.8)
2	24,618	20,125 (−18.3)	...	19,120 (−22.3)	22,632 (−8.1)
Mass-corrected metabolism (kJ/d/kg$^{0.67}$):					
Male:					
1	625.6	521.0 (−16.7)	505.9 (−19.1)	643.2 (+2.8)	591.6 (−5.4)
2	858.3	698.0 (−18.7)	606.4 (−29.3)	775.2 (−9.7)	806.6 (−6.0)
3	1,034.0	1,104.4 (+6.8)	821.0 (−20.6)	880.3 (−14.9)	879.6 (−14.9)
Female:					
1	941.9	983.8 (+4.4)	854.2 (−9.3)	1,009.1 (+7.1)	887.9 (−5.7)
2	1,053.3	936.6 (−11.1)	...	897.7 (−14.8)	1,019.8 (−3.2)

Note. Metabolism was measured before the switch from herring to squid diet (control), at 1 wk and 2 wk into the experimental (squid diet) period, and at 1 wk and 2 wk into the recovery (herring diet) phase. Metabolism is expressed as absolute measured resting metabolic rate (RMR in kJ/d; upper portion) and as a mass-corrected measure (RMR_{corr} in kJ/d/kg$^{0.67}$; lower portion). Values in parentheses represent the percent change relative to the control value.

cluding harbour seals (20%, Markussen et al. 1992) and manatees (22.5%, Gallivan and Best 1986). It was also within the range of seasonal metabolic depression associated with hypophagia in harp seals (Renouf and Gales 1994), and harbour seals (Rosen and Renouf 1998) although it was less than the 56% decrease exhibited in grey seal pups during the postweaning fast (Nordøy et al. 1990).

It is important to emphasize that the decreases in resting metabolism we observed during the experimental period were not simply the result of concurrent changes in body mass, as suggested by some species that undergo predictable fasts as part of their life cycle. Neither manatees (Gallivan and Best 1986) nor badgers (Harlow 1981) displayed any change in mass-specific metabolism after a 2-wk (experimental) fast, although the latter did exhibit mass-specific depression at 30 d. As noted by Harlow (1981), a reduction in metabolism due to changes in body mass cannot be considered adaptive. There is much debate about how to calculate mass-corrected metabolism in a biologically relevant manner. The results of the conservative measure we have chosen are consistent with the mass-specific decreases in metabolism during undernutrition reported in humans (Keys et al. 1950; Grande et al. 1958) and other terrestrial mammals (McCance and Mount 1960; Hill et al. 1985; Munch et al. 1993). Such metabolic depression is hypothesized to be a consequence of changes in either overall cellular metabolism (Grande et al. 1958) or a selective loss or partial shutdown of tissues with a particularly high metabolic rate (Kleiber 1975).

Heat Increment of Feeding

During the period of squid feeding, the GEI of the sea lions was only 50% of control (herring diet) levels. However, decreases in energy intake levels are more accurately calculated as NE. For this value, it is necessary to estimate losses from urinary energy, fecal energy, and HIF.

Interpretation of HIF values can be difficult because, while

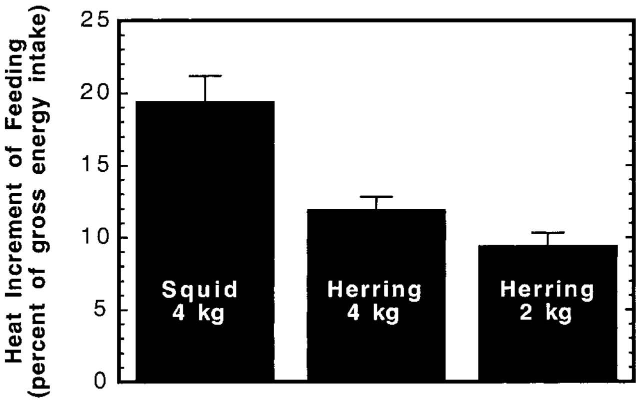

Figure 3. Comparison of the costs of the heat increment of feeding (mean ± SEM) for meals of squid or herring. The HIF was calculated from the postprandial rise in metabolism expressed as a percent of gross energy intake (kJ/kJ × 100). Data for the herring meals from Rosen and Trites (1997).

the parameter is usually expressed as a proportion of the GEI of the meal, it can also be expressed in absolute energetic terms. In our study, HIF made up a greater proportion of the squid meal (19.4%) than the herring meal (12.4%), although the absolute cost was less for the squid meal (716 J/g) than the herring meal (1,167 J/g).

The increase in heat production associated with meal ingestion (HIF) is believed to be the combined result of the mechanical and biochemical processes of food breakdown and the cost of protein synthesis and somatic growth. The extent of the HIF is at least partially dictated by the size and composition of the meal (Kriss et al. 1934; Hoch 1971; Blaxter 1989). In our study, the decreased energy intake resulting from the lower energy density of squid (3.69 kJ/g) versus herring (9.41 kJ/g) was amplified by the higher HIF for squid. The apparent effect of caloric density has been similarly demonstrated in other marine mammal species, including sea otters (Costa and Kooyman 1984) and harbour seals (Markussen et al. 1994), although it was not seen with northern elephant seals (Barbour 1993) (Table 4).

More specifically, several studies have demonstrated a relationship between protein (Buttery and Annison 1973; Krieger 1978; Jobling 1983; Brown and Cameron 1991) or lipid (Beamish and Trippel 1990) content of food and the extent of the HIF effect in domestic species. As HIF is greater for protein than lipid (Hoch 1971; Blaxter 1989), this cost of digestion should be proportional to the protein : lipid ratio in the diet (Beamish and Trippel 1990). In our study, HIF was proportionally greater for the squid (protein : lipid = 5.3; Table 1) than the herring meal (protein : lipid = 2.0).

A curvilinear increase in HIF with total ingested energy (Blaxter and Boyne 1978; Webster 1981) means that proportionally more energy is lost through HIF with larger meal sizes. This effect has been reported in northern elephant seals (Barbour 1993) and Steller sea lions (Rosen and Trites 1997). This suggests that sea lions would have difficulty compensating for the decreased energy density of squid versus herring, due to the additional HIF cost of squid and the additional cost of increasing IFM.

This prediction assumes that HIF is an energetic waste product. However, heat generated through HIF might be utilized to stave off hypothermy when animals are below their thermoneutral zone, thereby reducing the increment in energy expenditure needed to maintain homeothermy (Masman et al. 1988; Meienberger and Dauberschmidt 1992; however, see Klassen et al. 1989; MacArthur and Campbell 1994). Therefore, caution should be taken when interpreting these results in terms of their overall impact on the sea lion's energy budget.

Scale of Metabolic Changes

The observed differences in IFM translated into an average decrease in GEI of approximately 26,000 kJ/d. This represents an average decrease in net energy intake of 20,074 kJ/d for each animal, after incorporating the HIF for 4-kg meals of herring and squid, as well as estimates for urinary (5.5% GE, Miller 1978; Ashwell-Erickson and Elsner 1981) and fecal (10.0% GE, Fadely et al. 1990; D. Rosen and A. Trites, unpublished data) energy loss. This estimate of the decrease in net energy intake is probably a minimum value, since studies with other marine mammals indicate that digestive efficiency decreases with decreasing prey energy density (Fisher et al. 1992; Nordøy et al. 1993; Mårtensson et al. 1994; Lawson et al. 1997).

There are a number of ways that an animal's energy budget adjusts to changes in energy intake. Metabolic depression is presumed to be one such compensatory mechanism. Although

Table 4: Summary of studies investigating the effect of various prey items on heat increment of feeding (HIF) in marine mammals

Species/Prey	Energy Density (kJ/g)	HIF (%)	Source
Steller sea lion			This study; Rosen and Trites 1997
Squid	3.7	19.4	
Herring	9.4	12.4	
Sea otter			Costa and Kooyman 1984
Squid	3.6	13.2	
Clams	5.0	10.0	
Harbour seal			Markussen et al. 1994
Herring	6.6–8.7	5.1	
Herring	10.1–12.6	9.0	
Northern elephant seal			Barbour 1993
Capelin	4.8	12.3	
Herring	6.6	10.3	

Note. HIF expressed as a proportion of GEI. The apparent difference recorded for northern elephant seals was not statistically different.

the observed decrease in RMR was dramatic, it needs to be put into a broader context. The substantial (24%) decrease in RMR observed in the Steller sea lions after 2 wk of a low-energy diet translated into a decrease in energy expenditure (directly through this parameter) of 5,354 kJ/d (range: 3,747–7,947 kJ/d). However, the decreased energy expenditure due to changes in RMR was equivalent to only 27% of the decrease in net energy intake.

Bioenergetic Cofactors

As calculated above, the direct energetic savings from metabolic depression were relatively minor compared to the decreases in net energy intake. This raises questions of why the scope of metabolic depression was not greater and why resting metabolism is not depressed more often.

Clearly, there is a limit to how far resting metabolism can be lowered. This level is partially defined by the minimal energetic requirements of basic cellular and physiological processes. There are also potential costs associated with metabolic depression, such as a reduction in somatic growth (see sec 8.8 in Blaxter 1989) and a need for metabolic water (Thouzeau et al. 1999).

More often, animals will utilize a number of energy-sparing strategies during periods of prolonged or predictable low food intake or availability, such as decreases in activity, lowered growth rates, and even hypothermia. Decreased activity in response to decreases in energy intake has been documented in several marine mammals, including manatees (Gallivan and Best 1986), sea otters (Costa and Kooyman 1984), and harbour seals (Renouf and Noseworthy 1991; Rosen 1996). Physiological adjustments that keep animals inappetent during predictable periods of fasting will avoid the increase in activity associated with foraging in hungry animals (Mrosovsky and Sherry 1980; Steffens and Strubbe 1987; Mrosovsky 1990). While this strategy of decreased energy expenditure (including decreased RMR) is beneficial under specific conditions, it is clearly not a viable long-term arrangement.

In a broader ecological context, the inability of the Steller sea lions to maintain body mass while consuming low-energy, low-fat prey in the laboratory may be indicative of similar problems in the wild. Steller sea lions from the western (declining) population subsist primarily on another low-energy prey item, walleye pollack (*Theragra chalcogramma*; Merrick et al. 1997). The sea lions in this population are smaller now than during the 1950s (Calkins et al. 1998), when they consumed a diet of fattier, more high-energy prey items. The impact of decreased energy intake would be most devastating on juvenile animals due to their higher energy demands, relatively smaller stomachs, and limited foraging experience. Coincidentally, this is the segment of the population that has been modeled to be most responsible for the overall population decline (York 1994).

Conclusion

Steller sea lions were unable to maintain their body mass when eating squid, despite being fed ad lib. They derived less NE due to the combined effects of lower energy density and higher HIF. This resulted in the sea lions consuming ~20,000 kJ/d less NE. The results of our study suggest that Steller sea lions responded to such an energy deficit by depressing their metabolism (regardless of satiation level), which has been observed in terrestrial mammals. The shifts we observed in resting metabolism were greater than could be accounted for solely by decreases in body mass. Depression of resting metabolism translated into relatively minor direct energy savings (~5,300 kJ/d). Other bioenergetic reactions to decreased energy intake may provide greater energetic savings. These results suggest that juvenile Steller sea lions may have limited options when faced with changes in prey type in the wild.

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