Pollock and the decline of Steller sea lions: testing the junk-food hypothesis

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Abstract: The decline of Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska and the Aleutian Islands may be the result of them eating too much pollock (a gadid fish) instead of a more balanced and diverse diet containing fattier fishes, such as herring or sandlance. We sought to test this junk-food hypothesis by feeding six captive Steller sea lions (ages 0.9–4.5 years) only pollock or herring. All sea lions gained mass while eating herring. However, eating only pollock for short periods (11–23 d) caused the study animals to lose an average of 6.5% of their initial body mass (0.6 kg/d) over an average feeding trial of 16 d (initial mass averaged 125 kg). The animals were allowed to eat as much pollock as they wanted but did not increase their food intake to compensate for the low energy they were receiving. The sea lions showed progressive metabolic depression while losing body mass on a pollock-only diet. The loss of body mass while eating pollock was due to the lower gross energy content of pollock versus herring, the higher cost of digesting pollock, and the increased energy loss from digesting the larger quantity of fish needed to compensate for the lower energy content of pollock. Thus, our sea lions would have had to eat 35–80% more pollock than herring to maintain similar net energy intakes. Results from our captive-feeding studies are consistent with the junk-food hypothesis and have serious implications for Steller sea lions that have been eating primarily pollock in the Gulf of Alaska and the Aleutian Islands.

Résumé : Le déclin des Otaries de Steller (*Eumetopias jubatus*) dans le golfe d'Alaska et les îles Aléoutiennes est peut-être attribuable à la consommation excessive de goberge (un gadidé) au lieu d'un régime équilibré et diversifié contenant des poissons plus gras tels le hareng et le lançon. Nous avons tenté d'éprouver cette hypothèse du régime de mauvaise qualité (junk-food hypothesis) en nourrissant six Otaries de Steller en captivité (âgées de 0,9 à 4,5 ans) uniquement de goberge ou uniquement de hareng. Toutes les otaries ont subi des augmentations de masse à la consommation de hareng. Cependant, la consommation de goberge pour de courtes périodes (11–23 jours) a entraîné des pertes moyennes de 6,5 % de la masse initiale (0,6 kg par jour) au cours d'une période alimentaire d'essai de 16 jours (masse initiale moyenne de 125 kg). Les animaux pouvaient manger autant de goberge qu'ils voulaient, mais ils n'ont pas augmenté leur consommation totale pour compenser la perte d'énergie encourue. Les otaries ont subi une dépression métabolique progressive par perte de masse lorsqu'ils ont adopté le régime constitué uniquement de goberge. La perte de masse au régime de goberge est attribuable au contenu énergétique brut réduit des goberges comparativement à celui des harengs, au coût énergétique supérieur de digestion de la goberge, et à la perte énergétique plus grande encourue lors de la digestion dune quantité de poisson plus grande nécessaire pour compenser le contenu énergétique plus faible de la goberge. Donc, nos otaries auraient dû consommer 35–80 % plus de goberge que de hareng pour parvenir à consommer la même quantité d'énergie. Nos résultats sur l'alimentation en captivité confirment l'hypothèse du régime de mauvaise qualité et reflètent les troubles graves encourus par les Otaries de Steller qui ont fait une consommation excessive de goberge dans le golfe d'Alaska et les îles Aléoutiennes.

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Introduction

Steller sea lions (*Eumetopias jubatus*) range from California to Alaska, across the Aleutian Islands to Russia, and south to northern Japan. The western portion of the population has been declining since the mid-1970s, and in 1997 the

species was given endangered status in the region between Prince William Sound and the far Aleutian Islands (Trites and Larkin 1996; Loughlin 1998). The decline of this portion of the population is in sharp contrast with the growth of Steller sea lion populations along the coasts of southeast Alaska, British Columbia, and Oregon.

Most researchers believe that changes in the available-prey base is the most likely cause of the decline of the western population of Steller sea lions (Alaska Sea Grant 1993). In the Gulf of Alaska and the Aleutians, there is mounting evidence that the population declines might be related to the quality and diversity of prey available to sea lions in the wild (Alverson 1992; Merrick et al. 1997). The nutritional-stress hypothesis is based on the concern that the diets of sea lions in the area of population decline may be "nutritionally inadequate." Poor nutrition caused by a lack of quantity,

quality, or availability of prey can stunt growth, reduce birth rates, and increase mortality through disease, predation, and starvation.

Stomach contents and fecal analysis show that Steller sea lions eat a wide range of species, including walleye pollock, Pacific cod, octopus, squid, salmon, Pacific herring, Pacific sandlance, capelin, flatfish, rockfish, and Atka mackerel (National Marine Fisheries Service 1992). However, two significant regional and temporal dietary differences have been noted since the 1950s that have bearing on the population declines. The first was an apparent switch in the diet of Steller sea lions in the Gulf of Alaska from mostly small schooling fatty fishes (such as herring, sandlance, capelin, and smelt) in the 1950s and 1960s to mostly gadid species (such as pollock) in the 1980s and 1990s (Alverson 1992; Merrick et al. 1997). The second difference is that the sharpest declines in Steller sea lion populations have occurred in areas with the lowest diversity of diet (Merrick et al. 1997), and typically where pollock has dominated the diet.

Some researchers have suggested that Steller sea lion populations are declining because they eat too much pollock, which contain fewer calories, and not enough of the fattier high energy fishes (Alverson 1992). This has been referred to as the junk-food hypothesis. While the junk-food hypothesis has gathered increasing popularity, there have been no empirical data on the whole-animal response to different types of prey. Instead, researchers have attempted to document the secondary effects of (assumed) nutritional stress, such as changes in body size, blood chemistry, and behavioural and life-history patterns (Calkins et al. 1998; Pitcher et al. 1998; Rea et al. 1998; Milette 1999). We wanted to document the primary effects of nutrition on the whole animal by conducting feeding experiments using pollock and herring.

We sought to test the junk-food hypothesis by switching the diet of captive Steller sea lions between pollock and herring. We kept six sea lions on single-species diets for 2–3 weeks and allowed them to consume as much food as they wanted during the experiment. We measured changes in the amount of food they ingested (ingested food mass, IFM), their gross energy intake (GEI), the heat increment of feeding (HIF), resting metabolic rate (RMR), and body mass. Results from these junk-food experiments reveal physiological responses to different prey types and provide significant insights into the role that diversity and quality of diet may be playing in the decline of Steller sea lions in Alaska.

Materials and methods

Subjects

The study group consisted of six juvenile Steller sea lions (three males and three females). All had been captured as pups and were held in an outdoor compound at the Vancouver Aquarium Marine Science Centre (British Columbia, Canada) with access to filtered (ambient temperature) seawater and haul-out space. The sea lions were 0.9–4.5 years old during the experiments. Body mass was monitored daily throughout the study by having the animals hold position on a platform scale (±0.05 kg). All experimental protocols were in accordance with the guidelines of the Canadian Council on Animal Care and The University of British Columbia Animal Care Committee.

Diet manipulation

The normal diet of the Steller sea lions consisted of thawed herring (*Clupea harengus*) and small quantities of other fish species fed ad libitum 2–3 times a day. Each day, including during the experimental periods, the diet was supplemented with vitamin tablets (1 tablet/3 kg food; 5M26 Vita-zu tablets, Purina Test Diets, Richmond, Ind.). As part of a series of experiments, the sea lions initially underwent 1–2 diet switches. During each 2-week control period, the sea lions were fed their regular ad libitum diet composed mostly of herring (other species made up <10% of the control or recovery diets and included squid, Atka mackerel, and pollock). The sea lions were then switched to an ad libitum pollock diet for a 11- to 24-d experimental period, after which their diet was switched back to herring for a 14-d recovery period. During each feeding, the sea lions were allowed to eat as much fish as they wanted; feeding was stopped when the animals began to play with their fish or showed a general disinterest in eating more.

A second set of more detailed trials (during which RMR and HIF were measured, see below) were performed following the initial set of 10 trials. These final trials differed only in that the Steller sea lions were fed herring exclusively during the 2-week control and recovery periods, and the experimental period was set at a uniform 2 weeks. Full trials were completed with five of the six sea lions because female 3 began to refuse pollock after 7 d (partial data are presented for female 3 for comparative purposes but were not used in any of the analyses).

IFM was recorded daily. Fish-composition analyses were performed at the Department of Fisheries and Oceans, West Vancouver Science Laboratory, Vancouver, B.C. Samples of each species were also analyzed to determine lipid (Bligh and Dyer 1959), protein (Kjeldahl nitrogen extraction), ash, and water content. Energy density was determined through oxygen bomb calorimetry of representative samples. GEI was calculated by multiplying ingested mass by energy density.

Metabolism

RMR was measured 4–5 times on five of the Steller sea lions during the last set of trials. We were not able to obtain accurate metabolic readings for female 3. The first measure was made within 7 d prior to switching the diet from herring to pollock (control). Measurements were also made 6–7 d (experimental week 1) and 13–14 d (experimental week 2) into the experimental period. We attempted to measure RMR 6–7 and 13–14 d (recovery weeks 1 and 2, respectively) after switching the diet back to herring but were usually only able to obtain reasonable measurements for one of these periods (see Results).

We measured metabolism using open-circuit (gas) respirometry in a dry metabolic chamber under standard RMR conditions for non-mature animals (Kleiber 1975). Details of the method and equipment are given in Rosen and Trites (1997). Briefly, the animals were trained to remain calm within the chamber for 60- to 90-min periods. Air was drawn through the chamber at a constant rate and a subsample of the excurrent air stream was sampled for O_2 and CO_2 concentrations. Changes in gas concentrations were corrected for STPD (standard temperature and pressure, dry) and converted to energy used, given the relationship that 1 L O_2 = 20.1 kJ. Resting metabolism was calculated from extended (minimum 15 min) periods of low constant O_2 consumption associated with periods of inactivity.

Observed changes in resting metabolism may merely be a function of concurrent changes in body mass, given that metabolism is partially a factor of body size. There is no consensus as to how (or whether) to correct measurements of metabolism for changes in body mass. If short-term changes in body mass are derived primarily from the (possibly metabolically inert) hypodermal blubber layer, then changes in resting metabolism can be viewed independently of changes in body mass or 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). Thus, for this study we also calculated mass-corrected metabolism, RMR_c ($kJ \cdot d^{-1} \cdot kg^{-0.67}$), which is a conservative measure (i.e., least likely to reject the null hypothesis) of relative resting metabolism.

Heat increment of feeding

HIF for a pollock meal was measured for five of the six Steller sea lions at the end of the experimental (pollock diet) period, using the same methods as those detailed in Rosen and Trites (1997). A baseline (control) measure of RMR was taken at the start of each test. Each animal was then fed a pollock 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. HIF was calculated as the total postfeeding energy expenditure above baseline levels, expressed as a proportion of GEI.

Statistical analysis

Differences in weekly rates of body mass loss, IFM, and GEI were tested using either a two repeated-factor ANOVA (all trials) or a single repeated-factor ANOVA (last set of trials only). Values for HIF from the 4 kg pollock meal were compared with values obtained from the same individuals for a 4 kg herring meal, using a repeated-measures ANOVA. Treatment-mean differences for all significant ANOVAs were tested using a post hoc Scheffé comparison at $\alpha = 0.05$. Tests for differences in metabolism (RMR and RMR_c) and body mass from control levels were performed by calculating the percent change from control values for each week for each sea lion. A small-sample t test was then used to test for population differences from zero change (Campbell 1989).
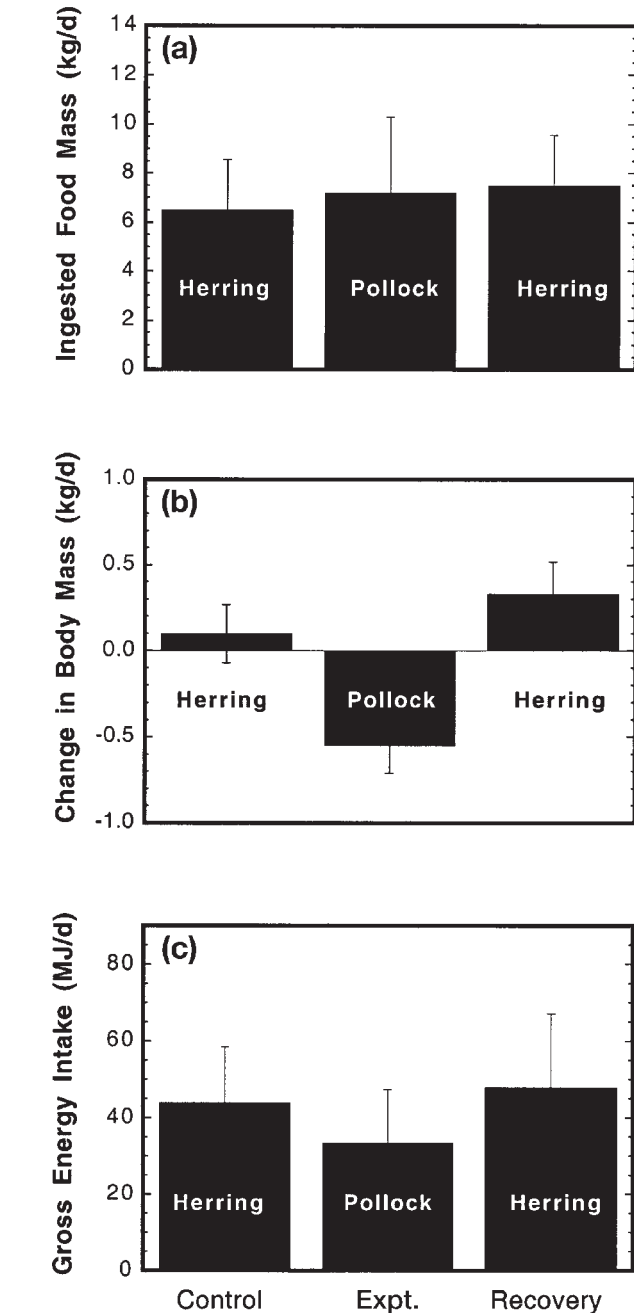
Results

Food intake

Using data from all 16 trials, the IFM of pollock during the experimental period (mean $\pm$ SD = 7.2 $\pm$ 3.1 kg/d) did not differ significantly from that of primarily herring during the control (6.5 $\pm$ 2.1 kg/d) or recovery (7.5 $\pm$ 2.1 kg/d) periods ($F_{[2,10]} = 0.73$, $p = 0.49$; Fig. 1). Restricting the comparison to the last set of five uniform trials, when the diet was exclusively herring (and omitting the partial trial from female 3), yields the same conclusion. Average IFM did not differ significantly during the experimental (pollock) phase (10.3 $\pm$ 1.5 kg/d) compared with the control (8.8 $\pm$ 2.0 kg/d) or recovery (herring) (9.7 $\pm$ 2.4 kg/d) periods ($F_{[2,8]} = 1.90$, $p = 0.21$).

Across all trials, GEI was significantly lower during the experimental (pollock) period (33.39 $\pm$ 9.2 MJ/d) than during either the control (42.11 $\pm$ 17.63 MJ/d) or recovery (47.94 $\pm$ 19.20 MJ/d) periods ($F_{[2,10]} = 3.309$, $p = 0.045$; Fig. 1). Similarly, for the final set of five trials, GEI was significantly lower during the experimental period (46.79 $\pm$ 6.65 MJ/d) than during either the control (60.23 $\pm$ 15.11 MJ/d) or recovery (66.17 $\pm$ 18.56 MJ/d) periods ($F_{[2,8]} = 5.53$, $p = 0.03$).

Body mass changes

The initial body mass of the Steller sea lions averaged 127.1 $\pm$ 34.9 kg (average mass of the five sea lions in the final set of trials was 166.6 $\pm$ 31.8 kg) (Table 1). Rates of change in body mass during the experimental phase (–0.6 $\pm$ 0.2 kg/d) were significantly different from those during

Fig. 1. Ingested food mass (*a*), changes in body mass (*b*), and gross energy intake (*c*) during the control (herring diet), experimental (pollock diet), and recovery (herring diet) phases of the feeding experiment. Data (mean $\pm$ SD) are from all trials and all animals (*n* = 6 Steller sea lions, *N* = 15 trials in total), except the last partial trial from female 3. There were no significant differences in ingested food mass between the phases. Gross energy intake and changes in body mass were significantly lower during the pollock diet phase than during the herring diet phases.

either control (0.1 $\pm$ 0.2 kg/d) or recovery (0.3 $\pm$ 0.2 kg/d) periods across all trials ($F_{[2,10]} = 8.36$, $p = 0.009$; Fig. 1). Similarly, for the five sea lions in the final set of trials, mass change was significantly greater during the experimental period (–0.6 $\pm$ 0.3 kg/d) than during either the control (0.1 $\pm$ 0.3 kg/d) or recovery (0.4 $\pm$ 0.2 kg/d) periods ($F_{[2,8]} = 11.81$, $p = 0.004$).

Table 1. Details of the experimental feeding trials, including Steller sea lion age, length of pollock feeding (experimental) phase, and control values for body mass, resting metabolism (RMR), and mass-corrected metabolism (RMR_c).

	Age (years)	Length of trial (d)	Body mass (kg)	RMR (MJ/d)	RMR_c (MJ·d^{-1}·kg$^{-0.67}$)
Male					
1	2.0	11	119.0		
	2.0	14	110.9		
	3.9	14	183.5	20.37	0.62
2	2.0	11	109.0		
	2.0	14	104.0		
	3.9	14	153.5	28.83	1.02
3	1.6	19	109.0		
	1.8	24	131.8		
	4.4	14	214.0	35.02	0.96
Female					
1	1.6	18	95.4		
	1.8	22	113.1		
	4.5	13	145.6	38.35	1.36
2	1.9	19	98.2		
	4.5	13	136.6	37.39	1.39
3	0.9	22	74.8		
	2.8	7	135.4		

Note: Data from the last incomplete trial for female 3 were not used in the final analysis.

Over the course of the experimental period, body mass decreased $6.5 \pm 3.7\%$ from initial values, when the data from all trials were pooled. However, although the rates of body mass change were similar among all trials, the animals lost a greater proportion of their starting mass during the earlier trials, owing to their smaller initial mass. In the first two sets of trials, the Steller sea lions lost $7.9 \pm 3.6\%$ (range 3.6–16.4%) of their initial body mass during the experimental period compared with $4.5 \pm 3.0\%$ (range 1.4–8.9%) during the experimental period in the final set of trials.

Resting metabolic rate

RMR was only measured during the final trials, on five of the six Steller sea lions. RMR averaged 32.0 MJ/d during the control periods (Table 2). It dropped to 30.5 MJ/d (–3.2% mean change from control levels, calculated from individual changes) after the first experimental week and to 27.2 MJ/d (–14.7%) by the end of the experimental period. RMR was 31.9 MJ/d (–6.1%) after the first recovery week and 31.0 MJ/d (–0.2%) at the end of the second (Fig. 2). The average RMR was significantly lower than control levels after the second week of the experimental period ($t_4 = 9.41$, $p = 0.006$) and after the first week of the recovery period ($t_3 = 2.78$, $p = 0.05$).

Correcting for body mass yields an average RMR_c of 1.07 ± 0.3 MJ·d^{-1}·kg$^{-0.67}$ during the control period (Table 2). This is approximately 2.45 times the rate predicted by Kleiber (1975) for adult mammals and is typical for young growing animals. RMR_c dropped slightly to 1.02 ± 0.2 MJ·d^{-1}·kg$^{-0.67}$ after the first experimental week (–3.1% change from control levels) and was 0.93 ± 0.3 MJ·d^{-1}·kg$^{-0.67}$ (–12.9%) at the end of the second week. RMR_c increased to 1.06 ± 0.2 MJ·d^{-1}·kg$^{-0.67}$ (–4.9%) after the first week of the recovery phase and was 1.10 ± 0.3 MJ·d^{-1}·kg$^{-0.67}$ (+0.8%) at the

end of the second week (Fig. 2). As with RMR, RMR_c was significantly lower than control levels after the second week of the experimental period ($t_4 = 11.4$, $p = 0.003$) and after the first week of the recovery period ($t_3 = 2.8$, $p = 0.05$).

Heat increment of feeding

The HIF averaged $15.7 \pm 0.8\%$ of GEI for a 4 kg meal of pollock. This was significantly higher than the $11.9 \pm 0.9\%$ reported from the same animals (at approximately the same age) for a 4 kg meal of herring (Rosen and Trites 1997). It was also significantly lower than the $19.4 \pm 1.8\%$ estimated for a similarly sized meal of squid ($F_{[2,8]} = 23.55$, $p < 0.001$; Rosen and Trites 1999) (Fig. 3).

Discussion

The rising dominance of pollock and the significant declines in fatty fishes observed in the diets of Steller sea lions in the areas of population decline over the past three decades corresponds to changes in the relative abundance of these species in the North Pacific (Alverson 1992). These changes also correspond to the timing of the Steller sea lion decline. Regardless of the reason for the changes in fish stocks (Alverson 1992; Kerr 1992; Francis et al. 1998; Springer 1998), the current dominance of pollock in the ecosystem (Trites et al. 1999) and in the diet of Steller sea lions (Merrick et al. 1997) makes pollock an obvious suspect in resolving why Steller sea lion populations have declined. However, there has been minimal direct testing of whether pollock deserves the junk-food label it has acquired, as a result of the hypothesis put forward by Alverson (1992) in the early 1990s.

Bioenergetic results from our study are consistent with the predictions of the junk-food hypothesis. Although the Steller sea lions ate the same amount of pollock as herring, they

Fig. 2. Changes in resting metabolism (RMR; MJ/d) and mass-corrected metabolism (RMR$_c$; MJ·d^{-1}·kg$^{-0.67}$) during the 2-week pollock diet and 2-week herring diet. Changes (mean ± SD) are calculated as percent change from control (herring diet) values.
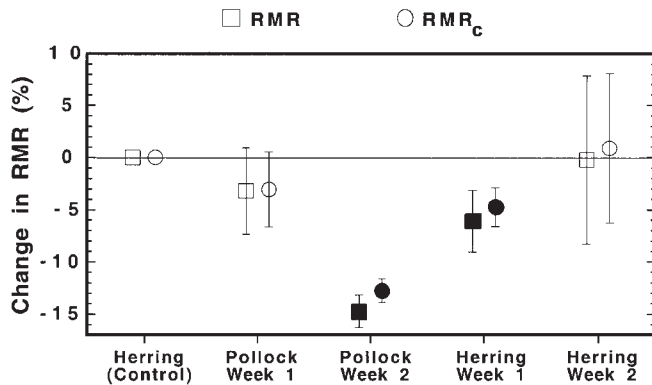
Fig. 3. Heat increment of feeding (mean ± SD) for a 4 kg meal of pollock (this study), a 4 kg meal of squid (Rosen and Trites 1999), and 2 and 4 kg meals of herring (Rosen and Trites 1997). All estimates are significantly different from each other.
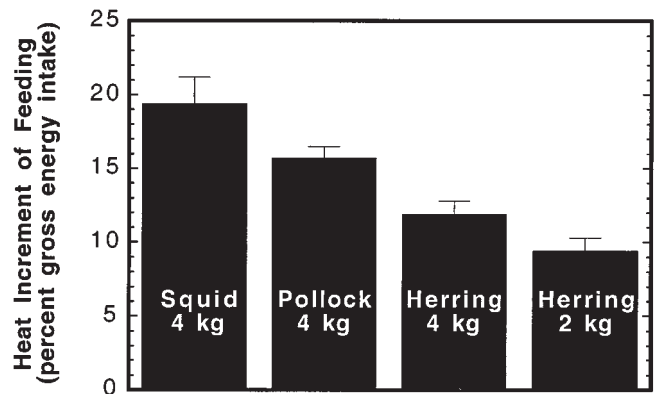
Table 2. Change in mass-corrected metabolism (RMR$_c$) and resting metabolism (RMR) of Steller sea lions during the experimental (pollock diet) and recovery (herring diet) periods, calculated as percent change from the control (herring diet) value.

	RMR$_c$					RMR				
		Experimental week		Recovery week			Experimental week		Recovery week	
	Control value (MJ·d^{-1}·kg$^{-0.67}$)	1	2	1	2	Control value (MJ/d)	1	2	1	2
Male										
1	0.62	6.8	−11.6	—	15.2	20.37	6.4	−12.8	—	15.9
2	1.02	1.8	−13.9	−3.5	—	28.83	3.6	−13.8	−3.5	—
3	0.96	−1.0	−13.9	−2.4	—	35.02	−0.1	−13.9	−2.8	—
Female										
1	1.36	−12.5	−16.0	−8.8	−5.2	38.35	−14.7	−20.9	−12.0	−8.0
2	1.39	−10.4	−9.4	—	−7.7	37.39	−11.2	−12.4	—	−8.5

lost substantial body mass while consuming pollock. They exhibited decreases in resting metabolism that are usually associated with fasting or decreased prey availability. However, these metabolic adjustments were not sufficient to arrest the loss of body mass and lead us to two central questions. Why did the sea lions lose mass on the pollock diet and what are the possible ecological implications of these results?

Cost of eating pollock

A prominent distinction between pollock and herring is the large difference in gross energy density (a result of differences in lipid content). Values for the pollock we fed our Steller sea lions ranged from 4.54 to 4.72 kJ/g compared with values of 6.40–7.58 kJ/g for the herring. This difference in energy content suggests that a sea lion would have to consume ~35–65% more pollock than herring to achieve the same GEI.

To calculate the net energy (i.e., "biologically useful" energy) available from these two prey items, estimates of digestive efficiency, urinary energy, and HIF must also be incorporated. Combining estimates of gross energy density, digestive efficiency (93.9% for pollock, 95.4% for herring; Rosen and Trites 2000), HIF (15.7 vs. 11.9%; this study; Rosen and Trites 1997), and urinary energy loss (5%;

Ashwell-Erickson and Elsner 1981) indicates that Steller sea lions would have to consume an average of ~56% (range 35–80%) more pollock than herring to maintain a comparable net energy intake. The considerable range in this estimate reflects the high variability in gross energy density of pollock and herring (see below).

The relative amount of pollock needed to yield the same net energy as herring may be even more substantial than the above calculations suggest. The energetic difference between prey species is compounded by the additional HIF cost associated with larger meal sizes (Blaxter and Boyne 1978; Webster 1981; Rosen and Trites 1997). This becomes important for animals that attempt to maintain net energy by increasing the quantity of the lower energy density prey that they consume.

The Steller sea lions in our study lost substantial body mass while on a pollock diet, primarily because they failed to increase IFM sufficiently to compensate for decreased energy intake. This is troubling, considering that foraging theory suggests that animals should increase their food intake (via greater foraging effort) when faced with decreased energy intake. However, it also highlights the complex relationship between short-term and long-term regulation of food intake and body mass. While it is unknown exactly why the sea lions failed to increase their food intake, it

appears that physical satiation prevailed over any parallel stimuli resulting from decreased energy intake (see Steffens and Strubbe 1987). At the same time, certain physiological responses to decreased energy intake, specifically metabolic depression (see below), were observed.

Ecological implications

The possible implications of our findings are particularly critical for younger individuals in the population for several reasons. First, younger animals have higher mass-specific energy needs than older animals (Kleiber 1975). This implies that younger animals are less able to alter their level of energy intake without severely impacting their overall energy budget. Second, younger animals have relatively smaller stomachs than larger, older animals (Calder 1984). This means that younger animals are physically less able to increase their food intake to compensate for increased energetic demands or decreased prey energy density. Finally, absolute differences in body mass loss (e.g., 0.6 kg/d) resulting from energy deficits have a greater absolute impact on body mass and condition in smaller animals (e.g., total mass loss was 7.9% of initial mass during the first trials and 4.9% over the last trials, when the animals were older and larger). Thus, young animals, which are the portion of the population thought to be driving the Steller sea lion population decline in Alaska (York 1994), may not be able to compensate for a diet dominated by pollock.

Some captive pinniped studies have shown that older otariids can maintain body mass on a pollock diet, at least over extremely short periods (~5 d) (Miller 1978; Fadely et al. 1994), although the amount needed for maintenance was greater than predicted from energetic estimates. When grey seals were switched from a diet of herring and capelin to one of pollock, it was difficult to get them to ingest sufficient pollock to maintain their body mass (S. Iverson, personal communication). When body mass did stabilize, it was found that body condition had decreased significantly.

Instead of increasing their level of food intake in response to the lower energy density of pollock, our Steller sea lions appeared to implement an alternate strategy of metabolic depression to compensate for their decreased energy intake. During predictable or prolonged periods of decreased energy intake, animals should theoretically limit their energy expenditure to minimize their energy debt. Minimizing the energy debt conserves body mass (particularly core-protein components) and ultimately delays starvation. Our sea lions showed progressive metabolic depression during the pollock diet phase, when they had decreased energy intake. This response is similar to that exhibited by Steller sea lions eating squid or undergoing complete fasts (Rosen and Trites 1999). While this metabolic adjustment may have served to limit the loss of body mass, this clearly would not be a beneficial long-term strategy for a wild sea lion.

Great care must be taken in extrapolating the results of a short-term captive feeding experiment to animals foraging in the wild. However, our study is the first to directly examine the effects of a pollock diet on the individual animal as a means of evaluating the nutritional-stress hypothesis. These initial results are consistent with the hypothesis that a heavy reliance on eating pollock may present difficulties for sea lion survival. This is not to say that Steller sea lions should not eat pollock because it is clearly part of a balanced diet, as shown by the range of species, including pollock, that are consumed by the increasing population of Steller sea lions in southeast Alaska (A. Trites and D. Calkins, unpublished data). However, heavy reliance on pollock may have detrimental effects on the health of Steller sea lions, either owing to its low energy, low fat, or some other intrinsic factor (see below).

Further research

A great deal of further research needs to be completed before the nutritional-stress hypothesis can be fully evaluated. Future studies are needed to clarify the long-term effects of eating primarily pollock. For example, what are the long-term effects of a decreased energy diet on body mass and condition? Does sea lion mass remain depressed or does food intake eventually increase to maintain sufficient net energy intake? Future studies are also needed to better understand the feeding ecology of sea lions. For example, how does access to prey affect total food intake? Would a more "natural" uneven feeding schedule or more frequent feedings offered throughout the day affect satiation levels and, therefore, food intake totals of our captive animals?

The feasibility of pollock as an adequate nutritional source includes aspects other than energetic considerations. For example, mink that consumed only gadids suffered pelage depigmentation, anaemia, poor reproductive rates, and high mortalities (Stout et al. 1960), which have been attributed to the iron-binding properties of trimethylamine oxide byproducts (Rouvinen et al. 1997). Similar blood chemistry abnormalities may occur in harbour seals that consume gadids (Thompson et al. 1997). Low-fat diets are also known to result in vitamin E deficiency in pinnipeds (Geraci 1975). Thus, the specific composition of pollock (e.g., amino acids, vitamins, minerals) may lead to health problems independent of energy density.

To properly evaluate the physiological interactions between Steller sea lions and their prey, it is also important to conduct research on their ecological interactions. Further research is needed into the composition of prey species in and around Steller sea lion foraging sites. As foraging regimes and locations may vary seasonally, critical Steller sea lion foraging habitat must be identified and appropriate fisheries surveys carried out to determine not just species composition but also fish condition. As demonstrated in our study, the size and energy density of prey can have a tremendous impact on a sea lion's overall energy budget. The pollock we used in our study (42.6 ± 4.8 cm) were at the larger end of the spectrum of what is normally eaten by Steller sea lions in the wild (23.5–40.9 cm), although larger fish constituted the major part of the food intake in the wild (Merrick and Calkins 1996). Unfortunately, little is known about the changes in the energy density of pollock with size, age, or season (see Harris et al. 1986; Anthony and Roby 1997).

Conclusions

In summary, it is clear that the Steller sea lions in our study lost body mass, owing to the lower net energy of pollock compared with herring. Our experiments showed

that this energy deficit was not solely the result of differences in gross energy content but was also due to the additional costs of digestion. The effects of the decreased energy intake were sufficient to trigger metabolic adaptations normally associated with fasting animals. However, these metabolic responses were insufficient to halt body mass loss over the time frame of our experiment.

Our study is just a single step in defining the potential impacts of diet changes on Steller sea lions. However, it is clear that the large differences in energetic parameters associated with pollock and fattier fishes, such as herring, would make it that much more difficult for Steller sea lions to thrive on a diet consisting primarily of pollock. Thus, our data are consistent with the junk-food hypothesis, and suggest that there may be serious consequences for young Steller sea lions that rely heavily on pollock.

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