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Examining the potential for nutritional stress in young Steller sea lions: physiological effects of prey composition

Abstract The effects of high- and low-lipid prey on the body mass, body condition, and metabolic rates of young captive Steller sea lions (*Eumetopias jubatus*) were examined to better understand how changes in prey composition might impact the physiology and health of wild sea lions and contribute to their population decline. Results of three feeding experiments suggest that prey lipid content did not significantly affect body mass or relative body condition (lipid mass as a percent of total mass) when sea lions could consume sufficient prey to meet their energy needs. However, when energy intake was insufficient to meet daily requirements, sea lions lost more lipid mass (9.16 ± 1.80 kg $\pm$ SE) consuming low-lipid prey compared with eating high-lipid prey (6.52 ± 1.65 kg). Similarly, the sea lions lost 2.7 ± 0.9 kg of lipid mass while consuming oil-supplemented pollock at maintenance energy levels but gained 5.2 ± 2.7 kg lipid mass while consuming identical energetic levels of herring. Contrary to expectations, there was a $9.7 \pm 1.8\%$ increase in metabolism during mass loss on submaintenance diets. Relative body condition decreased only $3.7 \pm 3.8\%$ during periods of imposed nutritional stress, despite a $10.4 \pm 4.8\%$ decrease in body mass. These findings raise questions regarding the efficacy of measures of relative body condition to detect such changes in nutritional status among wild animals. The results of these three experiments suggest that prey composition can have additional effects on sea lion energy stores beyond the direct effects of insufficient energy intake.

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Introduction

A prevalent hypothesis to explain the > 80% decline of Steller sea lions (*Eumetopias jubatus*) in western Alaska is that changes in the quality and/or availability of prey caused changes in key life history parameters (e.g., reproduction, survival) through an indeterminate nutritional inadequacy (see Trites and Donnelly 2003). A simple explanation of the underlying mechanisms for the population decline is that the sea lions could not obtain sufficient prey to meet their energetic needs (Alverson 1992). This hypothesis is supported by observations that the diet of animals from declining regions switched from high- to low-energy density prey (Merrick et al. 1997), while the summer diet of stable or increasing populations in southeast Alaska and British Columbia had greater proportions of small forage fish such as sandlance (*Ammodytes hexapterus*) and herring (*Clupea harengus pallasi*) (Winship and Trites 2003). The low energy density of the dominant prey in the western population (Winship and Trites 2003) suggests that certain portions of the population (e.g., yearlings or lactating females with their high relative energy demands) may not have been able to obtain or consume sufficient prey at certain times of the year (Rosen and Trites 2004).

However, the high abundance of dominant prey species consumed by sea lions in the Gulf of Alaska (walleye pollock, *Theragra chalcogramma*, a gadid) and Aleutian Islands (Atka mackerel; *Pleurogrammus monopterygius*, a hexagrammid) during the 1990s suggests other causes for the observed decline in Steller sea lions (Merrick and Calkins 1996; Wespestad et al. 2000; Sinclair and Zeppelin 2002). An alternate hypothesis is that the animals obtained sufficient energy, but the chemical composition of the prey differentially affected sea lion

physiology. Unfortunately, the observed correlations between diet characteristics and rates of population change (e.g., Merrick et al. 1997; Winship and Trites 2003) cannot differentiate which characteristic of the prey is driving the relationship. The most apparent difference between the principal dietary species of Steller sea lions is that Atka mackerel and walleye pollock have relatively low energy densities compared with herring (although there can be considerable ranges within species due to body size and season) (Payne et al. 1999; Anthony et al. 2000). However, differences in energy content are primarily the product of variation in lipid content, suggesting that differences in proximate composition may be more important than energy content per se. Additionally, since the type of lipid present (e.g., fatty acid profile) also differs among species, the importance of differences in lipid biochemistry on sea lion health cannot be discounted (Donnelly et al. 2003). This makes it difficult to attribute potential negative health effects on consumers to energy content versus a specific chemical characteristic.

Few controlled experiments have tested the impact of prey quality on sea lion physiology. Animals can adapt to changes in food quality and availability in a number of ways. Changes in food intake, metabolism, activity levels, and digestive efficiency are all mechanisms that might be employed to maintain critical body mass and body condition. Therefore, the responses of animals to changes in diet are difficult to determine a priori. The goal of our study was to determine the differential effect of low-lipid versus high-lipid prey on the physiology of young sea lions (i.e., body mass and composition changes, and metabolism) by manipulating the diets of captive Steller sea lions and controlling for differences in prey energy content. We explored two potential ecological scenarios: (1) when prey is adequate for maintenance energy needs; and (2) when food intake is limited (submaintenance). We also tested the hypothesis that lipid composition would have an effect on sea lion physiology irrespective of lipid density, by manipulating the lipid content of pollock.

Methods

General experimental design

Our study consisted of three separate experiments designed to explore different scenarios under which food quality might affect sea lion physiology.

Experiment 1 alternately placed animals on maintenance level, isocaloric diets of either pollock or herring, with a balanced or unbalanced daily feeding schedule. This was designed to reveal whether the proximate composition of prey (high- or low-lipid) had different physiological effects when the sea lions were provided with a controlled, 'adequate' food intake. A changing feeding schedule (detailed below) was implemented to determine whether short-term consistency of food availability was an important factor in any measured physiological responses.

Experiment 2 tested whether food quality differentially affected sea lion physiology when prey availability/intake was limited. The sea lions in these trials were maintained on submaintenance isocaloric diets of either high-lipid herring or low-lipid Atka mackerel.

In experiment 3 animals were fed isocaloric diets of either herring or pollock augmented with pollock oil to increase the lipid content to that of herring. The goal was to differentiate the potential effects of lipid concentration in pollock from those of the composition of the lipid component itself.

In all three experiments the sea lions were usually fed twice a day, similar to their training protocol before and between experiments. Body mass was measured daily, and body composition was determined at the start and end of each trial (see below). Resting metabolic rates were measured at the start and end of experiments 1 and 2.

Study animals

The experiments were conducted with a group of Steller sea lions that had been captured as pups and raised at the Vancouver Aquarium Marine Science Centre (Vancouver, Canada). The usual 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 (Table 1) .

Experiment 1: maintenance pollock vs herring

Three juvenile sea lions, one male (M97KO) and two females (F97HA, F97SI), were alternately fed a controlled amount of either pollock or herring for 42 days. Food intake between the diets was balanced for gross energy content, as determined from proximate analysis (Norwest Labs, Edmonton, AB, Canada). Gross energy intakes for mass maintenance for each sea lion were determined from previous feeding levels and by the calculated maximum food intake imposed by the uneven feeding schedule of the experimental design (see below).

During each trial the animals were fed either an equal amount every day ("even food" trials) or 15 20% of the daily average food was fed one day and 180 185% was fed the next ("bulk food"). This meant that each sea lion was subject to four 45-d experimental trials, each with a different combination of food type and feeding schedule. The trials were run consecutively from 26 January to 18 July 2000, when the sea lions were 2.5 3.0 year old. To minimize seasonal bias, trials were designed so that no sea lions were on the same food type/feeding schedule combination at the same time.

Table 1 Schedule summary for the three experiments by month (although not all in the same year): experiment#1: maintenance level pollock (P) versus herring (H); experiment#2: submaintenance level Atka mackerel (A) versus herring; experiment#3: fat-supplemented pollock (FP) versus herring

Experiment	S	O	N	D	J	F	M	A	M	J	J	A	#Days	Animal ID
1. Maintenance pollock						H	P	H	P				42	M97KO F97SI
						P		H	P		H		42	F97HA
2. Sub-maintenance Atka mackerel			A/H		H/A								29	F97HA
			H/A		A/H								29	F97SI
					H	A							29	F00NU
					A	H							29	F00YA
3. Fat-supplemented pollock									FP				34	F00YA F00NU F97HA
									H				34	F00TS F00ED F97SI F00BO

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 2: submaintenance Atka mackerel vs. herring

Two female sea lions (F97HA, F97SI) from experiment 1 were fed isocaloric diets of Atka mackerel and herring for 29 days between October 2001 and January 2003 (ages 4.3 5.5 year over the course of trials). These two animals each completed four trials, two with each prey species. Unlike experiment 1, the trials were not conducted successively, but separate trials were conducted in October/November and January/February of each year (Table 1). 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. Food intake was set a priori at a level estimated to produce a 10 15% loss of initial body mass over the trials. Two additional female sea lions (3.5 4.5 year; F00NU, F00YA) were used to repeat the trials in a similarly balanced design in February of 2003 and 2004.

Experiment 3: fatty pollock vs. herring

Seven female juvenile Steller sea lions were used in this study (an eighth began the study but was removed for unrelated health reasons). Two of the females (F97HA and F97SI) were 6 year old at the start of the trials, and five (F00BO, F00ED, F00NU, F00TS, F00YA) were 3 year old. The sea lions were fed diets of either herring or walleye pollock supplemented with additional pollock oil ("fatty pollock") for 34 days.

The food intakes for each diet were calorically equivalent, based on proximate composition of fish and oil samples. The herring had a gross energy concentration of 8.12 kJ g^{-1}, with a lipid content of 13.2% (wet mass). The pollock had a 'natural' composition of 4.49 kJ g^{-1} and 4.3% lipid. Gel caps were filled with pollock oil and inserted into each fed fish in quantities sufficient to bring the gross energy and lipid content to 8.52 kJ g^{-1} and 13.2%, respectively. The gross energy intake for each animal was calculated to be equivalent to a maintenance level diet based on previous food intakes. Three sea lions were assigned to the 'fatty pollock' group, and four to the herring treatment, with one of the older females assigned to each group and the average mass of the younger animals approximately equal in the two groups.

Body condition

Body composition was determined using deuterium dilution. After drawing a background serum sample, deuterium oxide was injected at a dose of 0.10 0.15 mL kg^{-1} . A second serum sample was obtained 120 140 min after injection (timing validated through previous experiments). Deuterated serum and dosage samples were analysed by Metabolic Solutions Inc. (Nashua, NH, USA). Total body water was converted to total body protein/lipid using calculations based on Reilly and Fedak (1990). While the precision of this technique has been previously examined (Bowen and Iverson 1998; Speakman et al. 2001), its most apparent weakness is that the mathematical model used to convert water content to body composition was originally developed for phocid species. However, we chose this model over other options (e.g., Arnould et al. 1996; Bowen and Iverson 1998) to facilitate comparisons with other Steller sea lion researchers. The different equations did not yield significantly different results.

Resting metabolism

Resting metabolic rate was determined at the start and end of experiments 1 and 2 from indirect calorimetry (gas respirometry). The procedures are detailed previously (Rosen and Trites 1997, 1999). Briefly, the animals were trained to enter a dry metabolic chamber. Air was drawn through the chamber at a constant rate sufficient to prevent substantial depletion of O_2 ($<18.5\%$), and a desiccated subsample was analyzed for oxygen and carbon dioxide concentrations. Output from the gas

analyzers was recorded using a Sable Data Acquisition System (Sable Systems, Henderson, NV).

Oxygen and carbon dioxide concentrations were analyzed by a S-3A/I solid oxide (stabilized zirconia) cell analyzer (Ametek Inc.) and an AR-60 infrared gas analyzer (Anarad Inc.), respectively. Air flow through the chamber was regulated by a King flow meter, and flow was corrected to STPD using ambient measures. In later trials, oxygen and carbon dioxide were measured using Sable System FC-1B and CA-1B analyzers, respectively, coupled to a 500H Flow Generator and Controller.

Resting metabolism was measured at the start and end of each trial. The sea lions were tested in the morning, approximately 18 h after their last meal. Only those measurements where the sea lions were sufficiently quiescent to obtain a constant (>15 min) reading of oxygen consumption, were used in the analyses. Rates of oxygen consumption were converted to metabolic (energy consumption) rates assuming 1 L $O_2 = 20.1$ kJ.

Statistical analyses

Statistics were calculated using SAS 8.2 for mixed ANOVAs, and Statview 5.0.1 (SAS Institute, Cary, NC, USA) for all other statistics. Zar (1996) was used for statistical consultation. For experiment 1, a series of mixed type model ANOVAs were used to test for differences in changes in body mass, body fat, or body condition that could be attributed to prey type, feeding regime, or season.

For experiment 2, randomized incomplete block ANOVAs could have been used to test for treatment effects. However, this approach would have decreased the degrees of freedom in order to test for effects that the experiment was designed to eliminate (i.e., season). Since all 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. Although this ignores the assumed independence among samples, it yields clearer, more relevant results. Diet-related changes in body mass as a function of initial mass were tested using an ANCOVA, with initial mass as the covariate.

Results

### Experiment 1: maintenance pollock vs. herring

Food intake averaged 6.5 kg day^{-1} for animals on the herring diet and 9.4 kg day^{-1} on pollock. Two different lots of pollock were used, with the majority of the food averaging 5.81 kJ g^{-1} gross energy (all values wet mass basis) and supplementary lots averaging 5.36 kJ g^{-1}, with lipid contents between 6.3 and 7.4%. The herring averaged 9.57 kJ g^{-1} (13.8% lipid). This translated into average gross energy intakes of 62.1 MJ day^{-1} on herring and 61.0 MJ day^{-1} on pollock.

Body mass of the two female sea lions at the start of the experiment were 102.0 and 135.2 kg, while the male weighed 187.4 kg. Body mass increased an average of 2.9 ± 2.7 kg (mean $\pm$ 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 protein mass over a single trial. At the same time, they lost an average of 0.9 ± 2.7 kg lipid mass on herring and 3.6 ± 1.4 kg on the pollock diet (Fig. 1). There was a strong correlation between changes in total body mass and changes in lean tissue mass ($F_{1,10} = 9.84$, $P = 0.01$, $r^2 = 0.50$) (Fig. 2), 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 were no differences in changes in body mass, body fat, or body condition that could be attributed to prey type or feeding regime. There was no effect of season on changes in either body mass or body fat, but there was a significant effect of season on changes in body condition ($F_{1,8} = 5.35$, $P = 0.05$). Relative body condition decreased during the course of the experiments as a result of continual lipid mass loss from January to July (Fig. 3), combined with changes in lean tissue mass (Fig. 4). Unfortunately, it was not possible to differentiate between seasonal and practice effects.

Average resting metabolic rate differed between study animals, at least partly due to differences in mean body mass. Oxygen consumption for the male sea lion averaged 109.2 L O_2 h^{-1}, which approximates to 52.6 MJ day^{-1} or 279 kJ kg^{-1} day^{-1}. Oxygen consumption for F97SI averaged 68.6 L O_2 h^{-1} (33.1 MJ day^{-1}, 253 kJ kg^{-1} day^{-1}) and 58.5 L O_2 h^{-1} (28.2 MJ day^{-1}, 257 kJ kg^{-1} day^{-1}) for F97HA. These values are approximately 2.8 times that estimated by Kleiber (1975) for adult terrestrial mammals, as would be expected for young, growing animals. There was no relationship between metabolic rate and either lean or total body mass within each sea lion, possibly because the trials did not involve large changes in body mass (1.6 ± 1.8 kg). However, there were consistent increases in metabolic rate during periods of high growth and decreases during periods of mass loss. Overall, changes in metabolic rate (-7.4 to $+16.5$ L O_2 h^{-1}) were more strongly correlated to changes in total body mass ($F_{1,10} = 136.18$, $r^2 = 0.93$, $P < 0.001$) than to changes in lean mass ($F_{1,10} = 7.33$, $r^2 = 0.42$, $P = 0.02$), suggesting that the increases in metabolic rate might have been a direct product of the cost of growth.
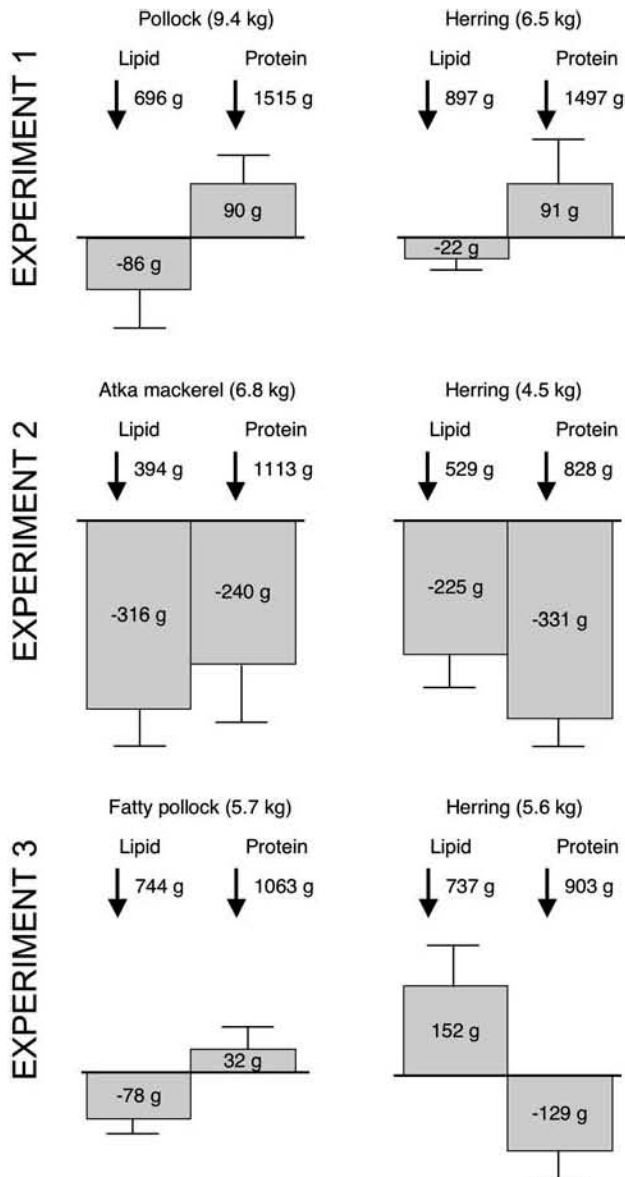
Fig. 1 Calculated daily dietary intake of lipid and protein and corresponding changes in body lipid stores and lean tissue during each of the three experiments (mean ± SE). The average daily food intakes (wet mass) for each of the experimental diets are also listed next to the species names

Experiment 2: submaintenance Atka mackerel vs. herring

The average lipid content (percent wet mass) of the Atka mackerel used ranged from 4.9% to 6.7%, and contained 4.8–5.4 kJ gross energy g^{-1}. The herring ranged from 10.3 to 13.4% lipids and 7.0 to 8.2 kJ g^{-1}. The sea lions were fed an average of 6.79 kg Atka mackerel and 4.46 kg herring per day (equivalent to approximately 4.6% and 3.1% of their initial body mass, respectively). Gross energy intake averaged 35.5 MJ day^{-1} for Atka mackerel and 35.7 MJ day^{-1} for herring. This gave an average, mass-specific energy intake of 240 kJ kg^{-1} day^{-1} for both diets.
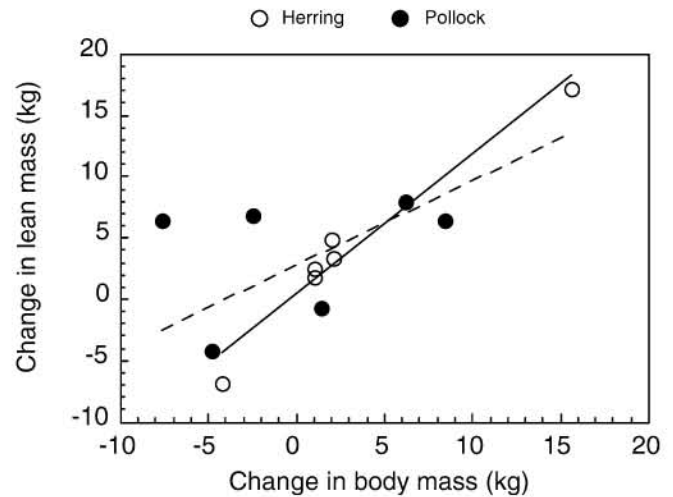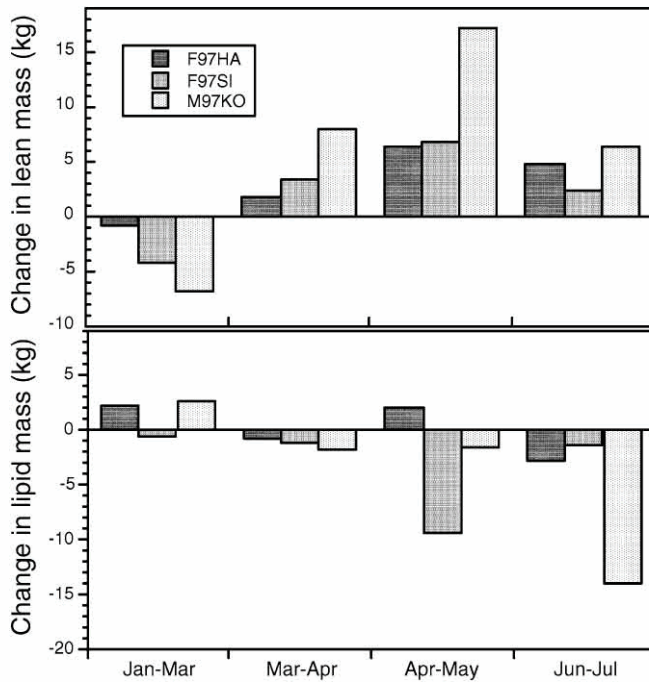

Fig. 2 Relationship between changes in total body mass and changes in lean tissue mass when Steller sea lions were fed isocaloric 'maintenance' levels of either pollock or herring (experiment 1). Changes in overall body mass were largely attributable to changes within lean tissues on the herring diets. The *solid regression line* is for data from the herring diets only ($r^2 = 0.91$), and the *broken line* is for both diets combined ($r^2 = 0.50$)

Initial body mass did not differ between treatments, with the mass of the two older females ranging from 130.0 kg to 151.8 kg, and that of the younger females from 119.7 kg to 144.0 kg. As predicted for isocaloric diets, there was no difference in body mass loss between trials for sea lions that consumed either Atka mackerel (14.93 ± 1.1 kg) or herring (15.50 ± 1.6 kg) ($t_5 = 0.453$, $P = 0.67$). Similarly, there was no difference in mass loss expressed as a percentage of initial body mass (Atka $= 10.1 \pm 0.5\%$, herring $= 10.6 \pm 1.0\%$; $F_{1,8} = 0.005$, $P = 0.95$).
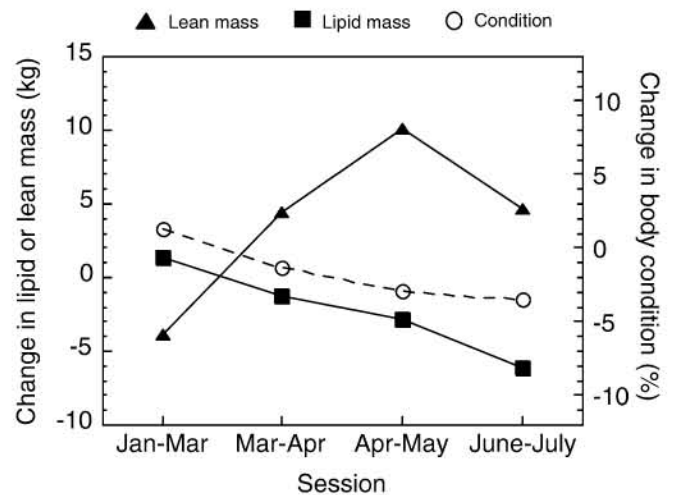
Fig. 3 Mean changes in lipid mass (kg), lean tissue mass (kg), and relative body condition (%) during the maintenance level diet manipulations (experiment 1). Data are mean values for all animals eating pollock or herring. Body condition was calculated as: lipid mass/body mass × 100

Fig. 5 Change in relative body condition (lipid mass/total mass × 100) in relation to changes in lipid stores during submaintenance feeding with Atka mackerel (*closed circles*) and herring (*open circles*) (experiment 2). *Regression line* is for data from both treatments combined
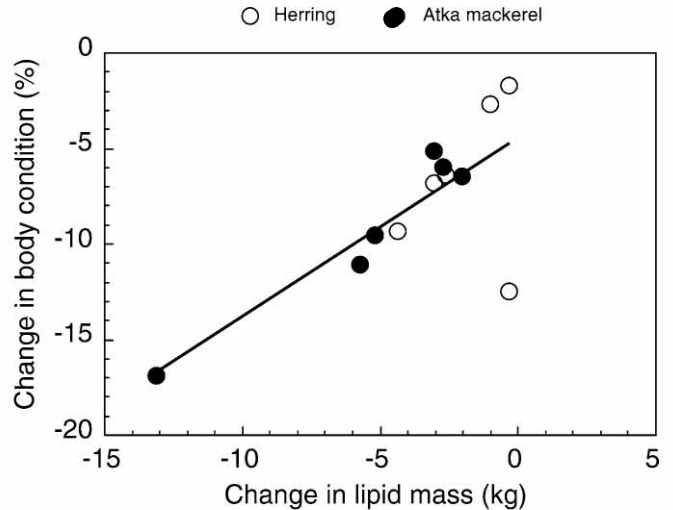
Fig. 4 Changes in lean tissue mass (kg; *top*) and lipid tissue mass (kg; *bottom*) during the maintenance level diet manipulations (experiment 1). Data are presented individually for the male (M97KO) and two female (F97SI, F97HA) sea lions during each season

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. $40.29 \pm 9.41\%$) (paired $t_5 = -2.82$, $P = 0.037$) (Fig. 1). On average, sea lions lost more lipid mass (9.16 ± 1.80 kg) while consuming Atka mackerel than herring (6.52 ± 1.65 kg) (paired $t_5 = -2.98$, $P = 0.031$), but not lean mass (5.78 ± 2.77 kg vs. 8.98 ± 1.43 kg, respectively). Similarly, diet-related differences in changes in relative body condition (lipid mass as % total mass), which is a product of changes in both lipid and lean tissues, were not statistically significant ($P = 0.066$). Relative body condition averaged $16.0 \pm 1.5\%$ at the start of the trials, and decreased by $5.3 \pm 1.7\%$ on Atka mackerel and by $2.0 \pm 1.0\%$ on herring.

Overall, there was a strong positive relationship between change in body condition and change in lipid mass ($r^2 = 0.92$, $P < 0.0001$) (Fig. 5). There was also a slightly weaker relationship between change in body condition and change in lean tissues ($P = 0.0002$, $r^2 = 0.76$). There was no significant effect of diet type on either relationship.

Initial rates of oxygen consumption ranged from 49.2 to 56.5 L O_2 h^{-1}. Rates of oxygen consumption were more closely related to body mass than age, and were equivalent to 191 kJ kg^{-1} day^{-1} or 2.2 times Kleibers (1975) estimate for adult mammals. Overall, there was a $9.7 \pm 1.8\%$ increase in metabolic rate over the course of the feeding trials. However, there was no significant relationship between change in metabolic rate and the extent of mass loss (either in absolute or relative terms), partially because the experimental design sought to limit variation in mass loss across trials. The average increase in metabolism during the Atka mackerel feedings (11.5%) was higher than during the herring feedings (7.9%), but the difference was not statistically significant ($P = 0.06$).

Experiment 3: fatty pollock vs. herring

The herring averaged 13.2% lipid and 8.1 kJ gross energy g^{-1}, and the unaltered pollock ranged between 1.5% and 4.3% lipid (depending on individual lot) and 3.4 to 4.5 kJ g^{-1}. Adding pollock oil increased the lipid content to 13.1 13.2% and gross energy to 8.5 8.6 kJ g^{-1}. The sea lions were fed an average of 5.6 kg day^{-1} herring and 5.7 kg day^{-1} fatty pollock, yielding isocaloric gross energy intakes of 45.4 and 48.2 MJ day^{-1} respectively ($F_{1,5} = 0.42$, $P = 0.55$). The small differences in gross energy intake were a product of differences in average body mass between groups.

As expected for isocaloric diets, there were no significant differences in changes in total body mass between trials when the sea lions consumed herring (0.8 ± 1.7 kg) or fatty pollock (-0.8 ± 1.1 kg) ($F_{1,5} = 0.41$, $P = 0.55$). However, there were significant differences in changes in body composition during the trials. The sea lions lost 2.7 ± 0.9 kg lipid while consuming fatty pollock, but gained 5.2 ± 2.7 kg lipid while consuming herring ($F_{1,5} = 6.35$, $P = 0.05$) (Fig. 1). This translated into a significant difference in changes in relative lipid mass, with body composition decreasing ($-2.2 \pm 0.7\%$) on fatty pollock diets, and increasing on herring diets ($3.5 \pm 1.5\%$) ($F_{1,5} = 10.17$, $P = 0.02$).

Discussion

A central question arising from the Nutritional Stress Hypothesis is whether prey composition adversely affects the health of Steller sea lions (Alverson 1992; Trites and Donnelly 2003). While this proposed physiological mechanism might appear to be simple to test, our experiments with captive sea lions illustrate the inherent underlying complexity.

In the first experiment, there were no significant effects of prey type on body mass, body condition or absolute lipid stores when sea lions were on maintenance diets. This result is similar to those from another study with Steller sea lions (Castellini 2002), although experiments with phocid seals have yielded less consistent results (Kirsch et al. 2000; Stanberry 2003; Trumble et al. 2003).

The lack of statistical effect of prey type observed in our study occurred despite the fact that, while the animals gained the same amount of lean tissues on both 'maintenance' diets they concurrently lost 3.6 kg of lipid reserves on pollock but only 0.9 kg of lipids on herring. The statistical results may partly be the result of small sample size, but they are also due to the tremendous effect of season on changes in body composition. Body composition changed significantly during the course of the experiment, with the greatest changes apparent in the male sea lion during the latter phases (Fig. 4). In the spring and summer trials the preference for lean tissue growth—even at the expense of lipid reserves—was demonstrated by the male gaining an average of 11.8 kg lean tissue, while losing 7.8 kg lipid. The females also gained an average of 5.2 kg lean tissue while losing 2.9 kg lipid during these latter two phases.

These results suggest that lean tissue growth is a priority for energy partitioning at certain times of the year, and that the 'remainder' of the energy budget serves to increase (positive energy state) or decrease (negative energy state) internal lipid reserves. This is likely particularly true for young Steller sea lions, as in our studies. In general, younger animals are more inclined to conserve growth rates during suboptimal energetic conditions, possibly since their capacity for later compensatory growth is limited (Wilson and Osbourn 1960). This hypothesis is supported by the evidence that (at maintenance energy intakes) changes in total mass were driven by changes in lean tissue (Fig. 2) while changes in relative body condition were driven by changes in lipid stores (Fig. 3). In other words, lipid energy reserves were proportionately depleted when energy intake was insufficient to support lean tissue growth (Fig. 4). Curiously, the opposite trade-off was observed during the spring "fatty pollock" trials, when lipid acquisition appeared to be a priority for the herring-fed group (Fig. 1). During these periods of high growth, the 'maintenance' level diets were (almost by definition) insufficient to meet these increased energy requirements for growth. Under such conditions, the composition of prey items might be predicted to have an additional effect on sea lion body condition.

The second experiment specifically tested the hypothesis that low prey quality magnifies the effect of insufficient energy intake. The experimental design eliminated some of the variables that may have limited the statistical power of the first experiment. Only female sea lions were used (gender effects), the trials were non-consecutive (practice effects), each animal performed a diet trial on the opposite prey type (herring or Atka mackerel) during the same season in the following year (seasonal effects), and the diets were set at a level that ensured a substantial decrease in body mass (10 15%) over each 29-day trial. Similar to the first experiment, these trials also used young sea lions (the portion of the population thought to be most at risk, York 1994), and the results must be viewed within this context.

As predicted, animals consuming the lower-lipid Atka mackerel lost more lipid reserves than when they ate high-lipid herring. This change in absolute lipid reserves was closely correlated to changes in relative body composition, but overall the diet-related differences in lipid loss did not translate into differences in relative body condition. This is partly due to the fact that relative body condition is a ratio and that a large portion of the total mass loss derived from loss of lean tissues. This pattern of simultaneous lipid and lean tissue catabolism resulted in very small changes in body condition (a ratio of these two measures) during the trials, regardless of diet. On average, the relative body condition of an animal losing $> 10\%$ of its body mass decreased by just 4%, which is well within the operational error associated with deuterium dilution techniques (Speakman et al. 2001). Our results, combined with the observation that periods of lean tissue growth in sea lions are usually not accompanied by corresponding increases in lipid stores, 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; Kitaysky et al. 1999; Rosen et al. 2004).

While the sea lions lost more lipid mass on the low-lipid prey, the use of lipid reserves as a measure of general 'health' is also problematic. Lipid reserves in sea lions fulfill the (sometimes contrary) dual roles of insulation and energy reserve. According to general fasting physiology theory, a pinniped should primarily utilize lipid stores to fulfill additional energy requirements, except for a small amount of protein catabolism required for gluconeogenesis for the central nervous system (Cherel et al. 1992). Only when lipid stores are depleted should substantial protein utilization occur (since protein degradation is the proximate mechanism for death). Therefore, the extent of subcutaneous lipid stores has traditionally been assumed to be an indication of a pinniped's energy state or health status.

However, our second experiment demonstrated that Steller sea lions use a surprising amount of protein (48%

on average) to meet their energy requirements during acute periods of submaintenance energy intake. The reason for this high rate of protein catabolism is unclear, although the expectation that pinnipeds will primarily utilize lipids is largely based upon research with phocid seals that have substantially greater relative lipid reserves than otariids. Otariids may employ a different strategy of tissue catabolism. Usually such high levels of lean tissue loss are considered a sign of severe nutritional stress (Rea et al. 2000). Paradoxically, while the sea lions in our study lost more lipid reserves on Atka mackerel, they lost a greater amount of lean tissues on herring. More information is required to understand the physiological consequences of lean and lipid tissue catabolism before either can be used as definitive measures of sea lion health.

Changes in body mass during the first and second experiments were also related to changes in resting metabolic rate, although not always in a consistent or predicted manner. When animals were fed a maintenance diet in the first experiment, changes in metabolic rate were positively related to changes in body mass.

In the second experiment, when the sea lions were losing substantial body mass on a submaintenance diet, we expected to see metabolic depression. Metabolic depression is often exhibited when animals are confronted with both predictable (e.g., hibernation, post-weaning fasts) and unexpected food shortages, and serves to limit body mass loss due to energy deficits (Øritsland 1990). Metabolic rates actually increased during the submaintenance diet trials, despite substantial decreases in body mass. These data agree with the results of previous experiments where food restriction led to a 'foraging response' rather than a 'fasting response' (Rosen and Trites 2002). If this metabolic increase were to occur in the wild, decreases in food availability (due to changes in either food distribution or abundance) might produce a greater net energy deficit than first suspected. However, our results must be viewed in the context of laboratory animals whose 'hunger response' may have been triggered by anthropogenic or training parameters (Shettleworth 1989).

Understanding the impact of prey lipid content on Steller sea lion physiology is complicated by additional factors. Fat digestion is likely to be optimized under different digestive conditions (including mixed diets), particularly given their need for emulsification and hydrolysis prior to absorption (Zurovchak et al. 1999; Trumble et al. 2003). Also, the observed differences in lipid utilization attributable to prey quality in the second experiment may have been due to the chemical composition of those lipids and not solely to the amount of lipids in the prey. In the third experiment, the animals consuming the fat-supplemented pollock lost lipid reserves compared to those consuming iso-lipid and iso-caloric herring, resulting in decreases in relative body composition. This suggests that pollock lipids may not confer the same nutritional benefit as herring lipids with regard to maintaining lipid reserves in the sea lion. While care was taken to supplement the pollock with

natural pollock oil, it is not possible to completely rule out that the results were partly due to some unknown modification of the oil. Donnelly et al. (2003) reported a decline in the reproductive parameters of rats fed pollock-oil supplemented diets compared with iso-caloric herring-based or unaltered pollock diets.

The restricted scope of animal-based laboratory studies can only document changes in individual physiology and not on parameters that can affect changes at the population level (e.g., reproductive success and survival). There is evidence from studies of wild seabirds that both long- and short-term natural changes in the quality of available prey can affect a variety of health and reproductive parameters (Ainley et al. 1995; Barrett 1996; Litzow et al. 2002; although see Bryant et al. 1999). Unfortunately, comparable data on the population-level effects of natural variation in prey quality among marine mammals (outside of dramatic events such as El Niño) are scarce. However, continued research on both captive and wild Steller sea lions will contribute to a better understanding of both the physiological and life-history consequences of such ecological changes.

The combined results of our three 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. However, consumption of low-lipid prey results in greater decreases in lipid reserves when energy intake is insufficient due to either increased expenditures or restricted intake. The chemical composition of lipid sources also appears to affect body lipid reserves. At maintenance levels, sea lions appeared to prioritize lean tissue growth rates, 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 were either very small or non-existent. This raises questions regarding the efficacy of using body condition as an indicator of energy state among wild Steller sea lions.

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