

Changes in Metabolism in Response to Varying Energy Intake in a Marine Mammal, the Steller Sea Lion

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Introduction

When faced with decreases in energy intake, an animal has two disparate options. Under most conditions, hunger stimulates increased foraging activity, a strategy of short-term increased energy expenditure off-set by a reasonable expectation of foraging success. However, when faced with periods of predictable or prolonged shortages of energy intake (although not necessarily energy availability), the animal should limit energy expenditures.

The most common response to experimental undernutrition or fasting in homeotherms is metabolic depression. Invoking such physiologic responses that limit energy expenditures limits tissue loss and delays death by starvation. Some species of marine mammals have exhibited metabolic depression, although its occurrence, scope, and triggers are still unclear.

This study was designed to document the extent of metabolic depression in Steller sea lions. It investigated the role of energy and food intake on metabolic depression, and the relationship between changes in body mass and the scope of metabolic depression.

Methods

The study group consisted of five juvenile Steller sea lions (*Eumetopias jubatus*) held in an outdoor compound at the Vancouver Aquarium (British Columbia, Canada). The animals had been introduced into captivity as pups, and were 2 to 4.5-yr-old at the time of the study.

The sea lions normally ate thawed herring (*Clupea harengus*), supplemented with vitamin tablets, and small quantities of other fish species. However, they sometimes ate exclusive diets of alternate species, including pollock and squid, as part of other experiments.

During our experiment, the sea lions were maintained on an ad libitum herring diet for a minimum 2-wk "control" period. They were then subject to four "experimental" conditions, after which they

were returned to a normal herring diet for a minimum one (usually two) week "recovery" period. The experimental conditions were:

- 1) Fasting: a 9 to 14-day period of complete fasting, during which the sea lions were given access to water, and ice was used as a training reinforcement.
- 2) Food restriction: the sea lions were given -50% of their normal herring intake for 27 to 28 days, thereby reducing both ingested food mass (IFM) and gross energy intake (GEI).
- 3 & 4) Pollock and squid diets: the sea lions were fed an ad libitum diet of pollock or squid for 12 to 14 days, resulting in greater decreases in GEI than IFM.

Body mass was measured daily (± 0.2 kg), and IFM was recorded daily (when applicable). GEI was calculated from data of the energy density of the specific prey items (determined by bomb calorimetry of samples).

As part of a larger research project, measurements of the sea lions' resting metabolic rate (RMR) were routinely taken since the time they were pups using flow-through gas respirometry (for details see Rosen and Trites, 1997) Metabolism was measured within a dry metabolic chamber under accepted conditions of RMR (Kleiber, 1975).

RMR was measured weekly, starting prior to the diet manipulation (control period), through the experimental period, and continuing 2 wk after the switch back to herring (recovery period).

Results

GEI during the experimental phases of the treatment conditions averaged 46.8 MJ/day for the pollock diet, 32.7 MJ/day for the food restriction, and 25.5 MJ/day for the squid diet. GEI was significantly lower during the experimental than the control or recovery phases for all treatment conditions. IFM during the experimental phase was lower only during the fasting and food restriction conditions.

Mass loss varied with gross energy intake: pollock diet = 0.55 kg/day, squid diet = 1.09 kg/day, food restriction = 0.35 kg/day, and fasting trials = 2.32 kg/day.

Metabolic depression was observed during the fasting trials, as well as the two GEI limitation trials (Figure 1). Resting metabolic rate was $30.7 \pm 4.2\%$ (mean \pm SE) lower by the end of the experimental fasting period compared to control levels. During the squid trials, RMR was $24.2 \pm 3.4\%$ lower by the end of the second week, and $14.7 \pm 1.6\%$ lower by the end of the second week of the pollock trials. In contrast, RMR remained unchanged during the experimental period of the food restriction trials, except for week 2 when there was a significant increase (Figure 2). Mean RMR increased during the recovery periods, although high individual variation reduced its statistical significance.

Metabolism is at least partially a factor of body mass. To determine whether the observed changes in RMR were the direct consequence of concurrent changes in body mass, a conservative measure of mass-corrected metabolism based on interspecific allometry. (Kleiber, 1975) was calculated ($RMRc = RMR/mass^{0.75}$).

RMRc showed the same pattern as RMR:RMRc decreased $21.7 \pm 4.2\%$ by the end of the fasting period, and was $19.0 \pm 4.2\%$ and $12.7 \pm 1.1\%$ lower by the end of the second week of the squid and pollock trials, respectively.

D i s c u s s i o n

While metabolic depression has been demonstrated as a response to both experimental and natural decreases in energy intake in terrestrial mammals, the triggers and extent of metabolic depression among marine mammals is still inconclusive.

It is unclear why the sea lions seemed to exhibit a "hunger response" only during the food restriction, nor is it evident why they did not increase IFM during the pollock and squid diet trials to maintain GEI levels. However, the sea lions did clearly show a decrease in metabolism (independent of changes in body mass) during all but the food restriction experimental conditions consistent with the theory of metabolic depression.

A rapid, pronounced onset of metabolic depression in response to experimental fasting has been reported for both harbour (Markussen, 1995) and grey seals (Boily and Lavigne, 1997). Gallivan and Best (1986), however, suggested that the apparent metabolic depression exhibited by manatees could be attributed solely to changes in body mass and the cost of digestion.

We found a strong relationship between the proportion of initial body mass loss and the degree of metabolic depression in Steller sea lions. This relationship is similar to the one proposed by Oritsland and Markussen (1990) (Figure 3). The scope of changes in metabolism exhibited during the restriction and fasting trials also agree with estimates of seasonal changes in RMR exhibited by harp (Renouf and Gales, 1994), grey (Boily and Lavigne, 1997), and harbour (Rosen and Renouf, 1995) seals.

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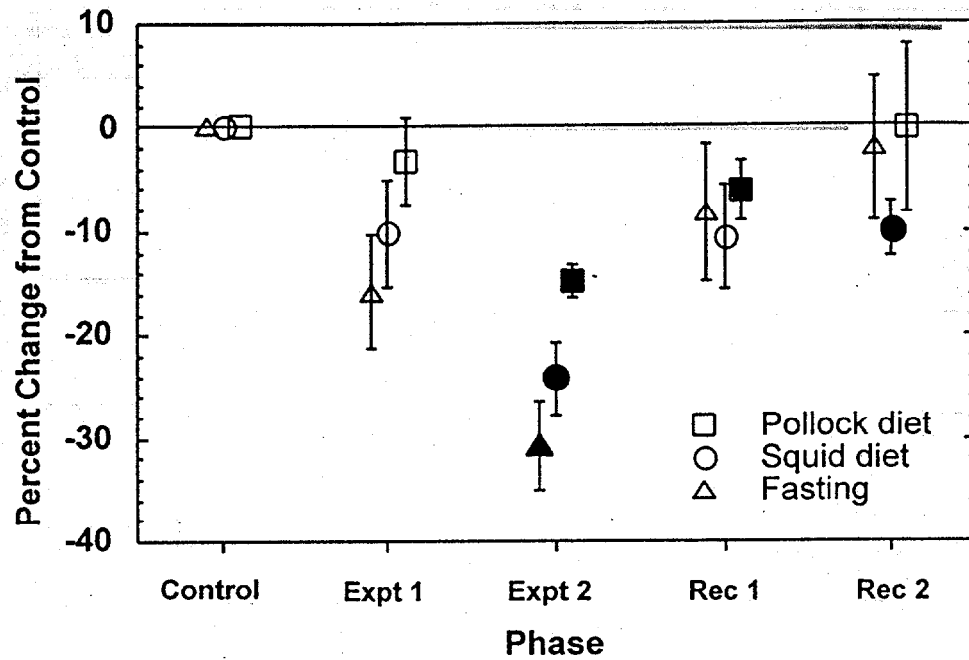


Figure 1. Weekly changes in RMR in relation to control levels during experimental (Expt 1 and Expt 2) and recovery (Rec 1 and Rec 2) phases of the fasting, pollock diet, and squid diet conditions. Closed symbols (mean \pm SE) are significantly different from control levels, while open symbols are not. Data points represent ~7-day intervals (-S-day for the fasting trials), and are staggered for clarity.

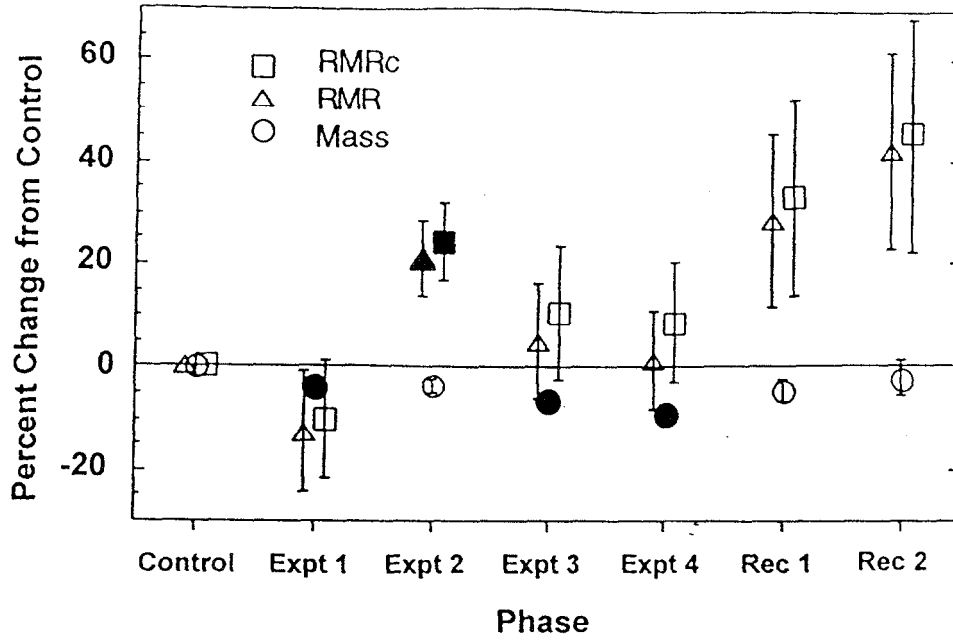


Figure 2. Weekly changes in RMR, RMRc and body mass in relation to control levels during experimental (Expt) and recovery (Rec) phases of the food restriction conditions. Closed symbols (mean \pm SE) are significantly different from control levels, while open symbols are not. Data points are staggered for clarity.

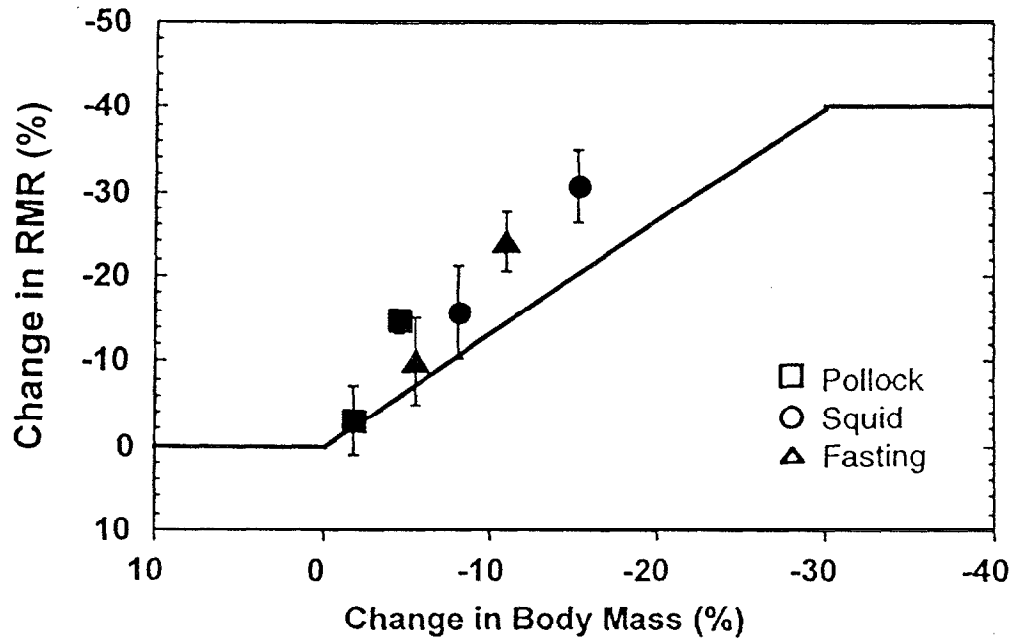


Figure 3. Changes (from control levels) in resting metabolism in comparison to changes in body mass during the experimental phases of the fasting, squid diet, and pollock diet conditions. For reference, the solid line represents the relationship proposed by Oritsland and Markussen (1990).