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# Changes in metabolism in response to fasting and food restriction in the Steller sea lion (*Eumetopias jubatus*)

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## Abstract

Many animals lower their resting metabolism (metabolic depression) when fasting or consuming inadequate food. We sought to document this response by subjecting five Steller sea lions to periods of: (1) complete fasting; or (2) restricting them to 50% of their normal herring diet. The sea lions lost an average of 1.5% of their initial body mass per day (2.30 kg/d) during the 9–14-day fast, and their resting metabolic rates decreased 31%, which is typical of a ‘fasting response’. However, metabolic depression did not occur during the 28-day food restriction trials, despite the loss of 0.30% of body mass per day (0.42 kg/d). This difference in response suggests that undernutrition caused by reduced food intake may stimulate a ‘hunger response’, which in turn might lead to increased foraging effort. The progressive changes in metabolism we observed during the fasts were related to, but were not directly caused by, changes in body mass from control levels. Combining these results with data collected from experiments when Steller sea lions were losing mass on low energy squid and pollock diets reveals a strong relationship between relative changes in body mass and relative changes in resting metabolism across experimental conditions. While metabolic depression caused by fasting or consuming large amounts of low energy food reduced the direct costs from resting metabolism, it was insufficient to completely overcome the incurred energy deficit. © 2002 Elsevier Science Inc. All rights reserved.

**Keywords:** Bioenergetics; Fasting; Metabolic depression; Steller sea lions

## 1. Introduction

Steller sea lions (*Eumetopias jubatus*) are the largest of the *Otariidae*, and have experienced dramatic population declines that may be related to changes in the abundance or quality of prey available to them (Alverson, 1992; Loughlin, 1998). Bioenergetic models have been developed to understand the relationship between food availability and various parameters of the animal’s energy budget (Winship et al., 2002), but a key missing variable is the fundamental response of

sea lions to unpredictable changes in food availability.

An animal faced with decreases in food availability has two disparate sets of physiological and behavioural options—it can increase foraging effort or it can limit energy expenditures. Increasing foraging activity (‘hunger response’) is a strategy of short-term increases in energy expenditure off-set by a reasonable expectation of foraging success (Cornish and Mrosovsky, 1965; Collier, 1969). Limiting energy expenditures (‘fasting response’) is a longer-term strategy often employed by animals faced with periods of predictable or prolonged shortages in energy intake (although not necessarily energy availability)

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(Westerterp, 1977). It is unclear under what conditions animals might favour one response over another.

The fasting response includes a suite of energy conservation adaptations that animals can employ to limit tissue loss and, ultimately, delay death by starvation. They can include decreased locomotion, increased sleep and decreases in thermal and metabolic set-points. Keys et al. (1950) noted that lowering metabolism (metabolic depression) was the most common response to experimental undernutrition or fasting in homeotherms. Metabolic depression is usually measured as decreases in basal or resting metabolism, and has been demonstrated as a response to environmental stress in all vertebrate classes and in almost all major invertebrate phyla (Guppy et al., 1994). However, evidence that metabolic depression occurs in response to decreased food availability among marine mammals is equivocal, even though most species are subject to regular episodes of fasting or severe food restriction as part of their life history.

Previous studies have documented metabolic depression in captive Steller sea lions in response to experimental diet manipulations. In these studies, the animals lost body mass when switched from a high energy herring diet to an ad libitum diet of low energy squid or pollock (Rosen and Trites, 1999, 2000). However, it is unclear from these experiments what the relative role changes in body mass, food intake, or energy intake played in triggering decreases in metabolism.

We sought to determine the physiological responses of Steller sea lions to unpredicted changes in food and energy intake by documenting the extent of metabolic depression in these animals. We measured the resting metabolism of captive Steller sea lions subjected to periods of fasting and experimentally restricted food intake. We also examined the relationship between changes in body mass and the scope of metabolic depression.

## 2. Materials and methods

### 2.1. Study animals

The study group consisted of five juvenile Steller sea lions. The animals were captured as pups, and were 2.5–4.5 years old at the time of the study. The sea lions were held in an outdoor compound at the Vancouver Aquarium Marine

Science Centre (British Columbia, Canada) with access to ambient seawater and haul out space. The sea lions normally ate thawed herring (*Clupea harengus*), supplemented with vitamin tablets (also added during all experimental diets), and small quantities of other fish species, including pollock and squid.

### 2.2. Experimental conditions

The experiments began with a minimum 2-week control period during which the sea lions were maintained on an ad libitum diet of herring. The animals were then subject to one of the experimental conditions, after which they were returned to a normal herring diet for a 2-week recovery period. All five sea lions were subject to both of the experimental treatments. The experimental conditions were:

- i. Fasting: a 9–14-day period of complete fasting, during which the sea lions had access to water and received ice as a training reinforcement. Fasting ended at 14 days or when the animals lost 15% of their initial body mass, whichever came first.
- ii. Food restriction: the sea lions were given ~50–75% of their normal herring intake for 27–28 days. Individual food levels were controlled to attain a consistent, moderate rate of body mass loss (0.4–0.5 kg/d). This condition reduced both ingested food mass (IFM) and gross energy intake (GEI).

### 2.3. Variables measured

Body mass was measured daily by having the animals hold position on a platform scale ( $\pm 0.1$  kg). Ingested food mass was also recorded each day ( $\pm 25$  g). Gross energy intake was calculated using the energy density of the specific prey items, determined by proximate composition analysis and bomb calorimetry of representative samples (Dept. of Fisheries and Oceans Science Branch Laboratory, West Vancouver and the Animal Science Lab, University of British Columbia) (Table 1).

Resting metabolic rate (RMR) was measured using flow-through gas respirometry. Details of the apparatus and procedures have been previously described (Rosen and Trites, 1997). Briefly, the sea lions were trained to voluntarily enter and remain calm within a dry metabolic chamber. Air was drawn through at a constant rate and a

Table 1

Average initial (control) values (mean  $\pm$  S.E.M.) of body mass (kg), gross energy intake (MJ/d), resting metabolic rate (RMR; MJ/d) and mass-corrected metabolism (RMR<sub>c</sub>; RMR/Mass<sup>0.67</sup>) for each of the experimental trials

Treatment	Body mass	Energy intake	RMR	RMR <sub>c</sub>
Fast	150.2 $\pm$ 5.3	50.1 $\pm$ 7.7	27.16 $\pm$ 2.86	2.17 $\pm$ 0.23
Food restriction	141.7 $\pm$ 11.1	50.9 $\pm$ 4.2	20.43 $\pm$ 2.00	1.73 $\pm$ 0.18

desiccated subsample of expired air was continuously analysed for oxygen and carbon dioxide concentrations, and digitised with a Sable Data Acquisition system. Gas concentration readings were baselined against ambient air concentrations before and after each trial, 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 was measured under accepted conditions of RMR for immature animals (Kleiber, 1975) and only measurements where the sea lions were sufficiently quiet were used in the analysis. RMR was measured as mean oxygen consumption (Withers, 1977) from a minimum 15 min period of low, stable readings corresponding with appropriate resting behaviour. Oxygen consumption rates were converted to energy utilisation using the equation: 1 l O<sub>2</sub> = 20.0 kJ.

RMR was measured several times for each animal during each experimental condition. Metabolism was measured once prior to the food restriction manipulation (control value), and weekly during the experimental and recovery periods. During the fasting trials RMR measurements were made at approximately 5 and 10 days into the experimental phase, and weekly during the recovery period.

Metabolism is at least partially a factor of body mass. However, the contribution of changes in adipose tissue to changes in metabolism, particularly during periods of rapid weight loss, is still open to debate (Ferraro and Ravussin, 1992; Rea and Costa, 1992). To ensure that the observed changes in RMR were not the direct consequence of concurrent changes in body mass, a conservative measure of mass-corrected metabolism was calculated such that RMR<sub>c</sub> = RMR/mass<sup>0.67</sup>.

All percentage data were normalised (arc-sine transformation) prior to statistical tests. Repeated measure ANOVAs were used to test for differences in GEI and IFM between phases within each treatment. Mean treatment differences were tested

with a Scheffé post hoc analysis. Changes in metabolism and body mass for each week for each treatment were tested against zero change (control levels) using a small-sample *t*-test.

### 3. Results

#### 3.1. Food intake

By design, ingested food mass was lower during the experimental phase of both the fasting and food restriction conditions than during their respective control or recovery phases (restriction:  $F_{2,8} = 9.03$ ,  $P < 0.01$ ), as was gross energy intake (Fig. 1b). During the experimental phases of the food restriction trials, gross energy intake averaged 26.6  $\pm$  3.9 MJ/d (mean  $\pm$  S.E.M.), a 49.6% decrease from control levels. The slight increases in food intake exhibited during the recovery phase of both the fasting and restriction trials (relative to control levels) were not statistically significant.

#### 3.2. Body mass

Body mass was constant or moderately increased during the control phases of all the treatments. Rates of body mass loss during the experimental phases were: 0.42  $\pm$  0.05 kg/d (food restriction) and 2.30  $\pm$  0.28 kg/d (fasting trials) (Fig. 1c). Mean initial body mass was not the same between experimental trials (Table 1). However, rates of changes in body mass expressed as a percentage change per day from initial body mass followed a similar pattern as absolute mass changes: -0.30% (food restriction) and -1.53% (fasting trials).

#### 3.3. Metabolic rate

A decrease in RMR was observed during the fasting trials (Fig. 2), but not during the food restriction treatment (Fig. 3). Given the considerable variation in metabolism related to differences in body mass and development between and within

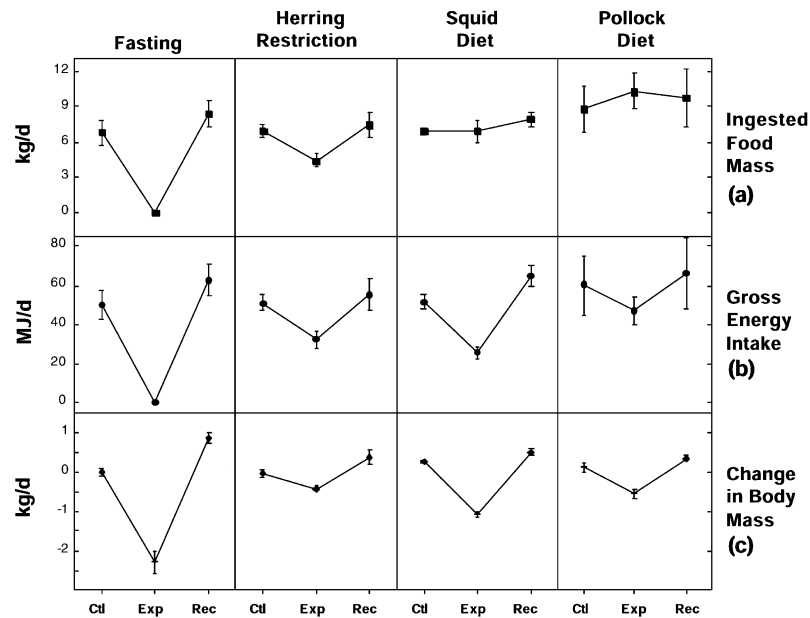


Fig. 1. Ingested food mass (a); gross energy intake (b); and changes in body mass (c); during the control, experimental and recovery periods for the fasting and food restriction trials. For comparison, data are included from experiments where the sea lions were switched from a herring diet to one of either squid (Rosen and Trites, 1999) or pollock (Rosen and Trites, 2000). Data represent mean  $\pm$  S.E.M. values. All experimental values were significantly different from control values, except for ingested food mass for the squid and pollock diet experiments.

treatments, mean changes in metabolism are most accurately described in relation to each animal's control level (Fig. 2). RMR averaged  $27.16 \pm 2.86$  MJ/d during the control phase of the fasting trials. After the first week of fasting, average RMR was

$23.18 \pm 3.19$  MJ/d (a  $-15.8\%$  change from control levels,  $t_4 = 2.87$ ,  $P < 0.03$ ). We were unable to obtain an accurate measure of RMR for one of the sea lions at the end of the experimental fasting period. The average RMR for the other four

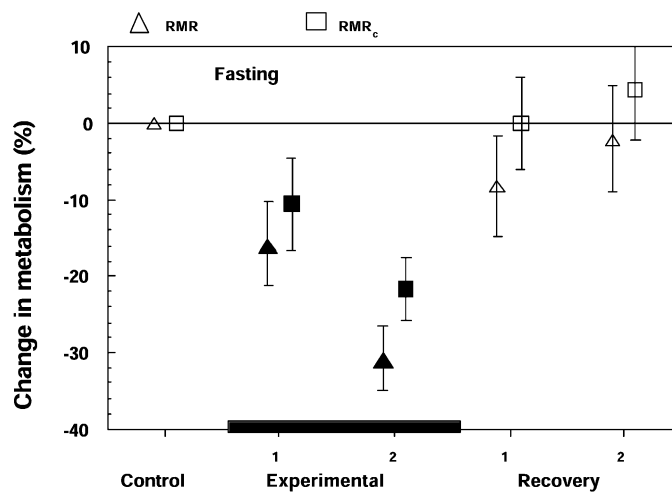


Fig. 2. Weekly changes in resting metabolic rate (RMR), mass-corrected metabolic rate (RMR<sub>c</sub>) calculated as percent change from control levels during experimental and recovery phases of the fasting trials. Closed symbols (mean  $\pm$  S.E.M.) are significantly different from control levels, while open symbols are not. Data points represent  $\sim 5$ -day intervals, and are staggered for clarity.

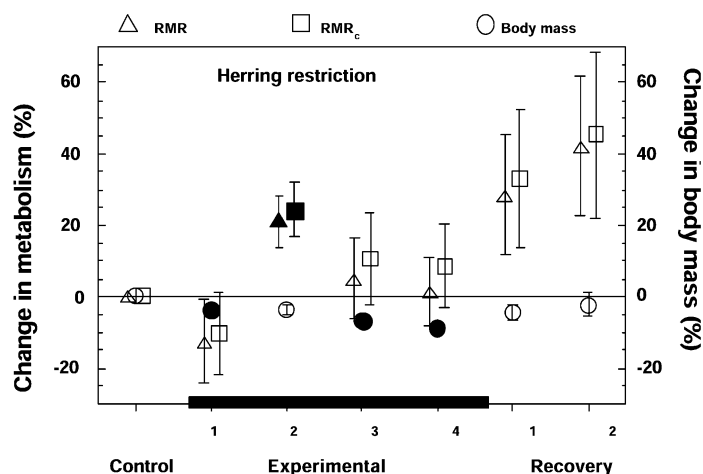


Fig. 3. Weekly changes in resting metabolic rate (RMR), mass-corrected metabolic rate (RMR<sub>c</sub>) and body mass calculated as percent change from control levels during experimental and recovery phases of the food restriction conditions. Closed symbols (mean  $\pm$  S.E.M.) are significantly different from control levels, while open symbols are not. Data points are staggered for clarity.

animals was  $17.58 \pm 2.07$  MJ/d, which was a  $-30.7\%$  change from their respective control levels ( $t_3 = 7.26$ ,  $P < 0.01$ ). RMR increased during the recovery period, reaching control levels by the end of the second week.

In contrast, RMR during the experimental period of the food restriction trials was not significantly different from the initial (control) mean value of  $20.43 \pm 2.00$  MJ/d, except during week 2 when metabolism was significantly greater than control levels ( $24.80 \pm 3.07$  MJ/d,  $+21.1\%$ ,  $t_4 = 2.92$ ,  $P = 0.05$ ) (Fig. 3). Mean resting metabolism increased during the recovery periods, reaching  $26.85 \pm 3.87$  MJ/d ( $+42.1\%$ ) by the end of the second week but, due to a high level of variance, this increase was not statistically different from control levels.

Changes in mass-corrected resting metabolic rate (RMR<sub>c</sub> = RMR/mass<sup>0.67</sup>) showed the same pattern as those in resting metabolism (Figs. 2 and 3). RMR<sub>c</sub> decreased from a control value of  $0.95 \pm 0.10$  MJ/d/kg<sup>0.67</sup> to  $0.86 \pm 0.12$  MJ/d/kg<sup>0.67</sup> after  $\sim 5$  days ( $-11.2\%$ ,  $t_4 = 3.95$ ,  $P = 0.02$ ) to  $0.68 \pm 0.07$  MJ/d/kg<sup>0.67</sup> for the four animals tested ( $-22.7\%$ ,  $t_3 = 5.11$ ,  $P = 0.02$ ) by the end of the fasting period. During the food restriction condition, RMR<sub>c</sub> was significantly higher from control levels ( $0.75 \pm 0.08$  MJ/d/kg<sup>0.67</sup>) only during the second week of the experimental phase ( $0.93 \pm 0.11$  MJ/d/kg<sup>0.67</sup>,  $+24.0\%$ ,  $t_4 = 3.2$ ,  $P = 0.04$ ).

## 4. Discussion

### 4.1. Metabolic depression

The 30% decrease in RMR exhibited by the Steller sea lions when fasted exceeded the large changes in metabolism recorded when the animals were maintained on low energy density diets. In these latter experiments, the sea lions were switched from an ad libitum, high energy density herring diet to an ad libitum, low energy diet of squid or pollock (Rosen and Trites, 1999, 2000). Despite the ad libitum feeding regime, the animals lost on average 12% and 7% of their body mass, respectively, and exhibited significant decreases in both absolute RMR (squid =  $-24.2 \pm 3.4\%$ , pollock =  $-14.7 \pm 1.6\%$  from control levels after 2 weeks) and RMR<sub>c</sub> (squid =  $-19.0 \pm 4.2\%$ , pollock =  $-12.7 \pm 1.1\%$ ) (Fig. 2). As the changes in metabolism in all three experiments could not be attributed to concurrent changes in body mass, it is legitimate to state that metabolic depression occurred.

Metabolic depression in response to decreased food or energy intake has been observed in a wide range of animals. It is a common response to periods of experimental fasting among rats and humans (Grande et al., 1958; Montemurro and Stevenson, 1960; Cahill, 1978; Munch et al., 1993; Munch, 1995), although the evidence is not unanimous (Webber and MacDonald, 1994). The sea

lions in our study exhibited strong metabolic depression in three of the four experimental conditions with decreased food and/or energy intake (i.e. fasting, pollock diet and squid diet, but not restricted food intake).

Evidence from other marine mammals of metabolic depression from unpredictable changes in food availability is equivocal. Gallivan and Best (1986) suggested that the change in metabolism seen in an experimentally fasted manatee could be attributed to changes in body mass. In contrast, Markussen (1995) reported a rapid (within 24 h) 20% decrease in mass-specific metabolism in experimentally fasted harbour seals.

#### 4.2. Response to undernutrition

Metabolic depression is also a common response to various levels of experimental undernutrition in humans (Grande et al., 1958) and rats (Hill et al., 1985; Munch et al., 1993; Munch, 1995). However, there is no evidence for this response among pinnipeds. Sea lions fed 50% of their normal diet (our study) and harbour seals fed 10% of their normal diet (Markussen, 1995) both exhibited metabolic rates equal to or greater than control levels.

It is interesting that metabolism increased or remained constant in these studies when the amount of food was restricted versus the metabolic depression exhibited under other experimental conditions. Although the rate of daily mass loss during the period of food restriction in our study was lower than during either the fasting or low energy trials, total mass loss during the latter weeks of food restriction surpassed levels associated with metabolic depression under other experimental conditions. Similarly, while harbour seals lost body mass at similar rates during fasting and food restriction trials, metabolic depression was exhibited in the former not the latter (Markussen, 1995).

The contrary metabolic responses may be related to the different levels of physiological regulation of food intake. An increase in metabolism associated with decreases in energy intake are characteristic of the increased foraging effort seen in the 'hunger response' (Webber and MacDonald, 1994). Although the 'hunger response' is largely mediated by biochemical feedback via the hypothalamus (including changes in hormonal balance), short-term chemical (e.g. gut and pancreatic hormones) and physical satiation (e.g. stomach dis-

tension) also play a role (Steffens and Strubbe, 1987).

In the fasting experiments, the lack of both physical and biochemical satiation resulted in a typical metabolic slowdown. In the food restriction trials, however, the low level of food intake did not satisfy the animal's energy demands, as evidenced by the loss of body mass. The hunger response our study animals exhibited suggests that the biochemical or mechanical cues from partial meals were insufficient to induce satiation, yet precluded a fasting response. The potential effect of the behavioural expectation of further feeding should not be discounted.

The pollock and squid diet experiments represent conditions where the sea lion may be receiving conflicting cues regarding its energetic state. The sea lions were consuming a 'full meal' in regard to ingested food mass, a state when physical cues such as stomach distension would normally signal physical satiation (Read et al., 1994). A number of studies have demonstrated that food mass is a stronger cue for satiation than energy intake (see review in Rolls and Bell, 1999). However, the longer lasting biochemical cues resulting from the deficit in gross energy intake (due to decreased energy density of the prey), and subsequent loss of body mass, apparently overrode the short-term physical cues of satiation (Read et al., 1994). The result was a 'fasting response' from an animal that was, in one respect (ingested food mass), consuming their normal food intake.

#### 4.3. Degree of metabolic depression

Metabolic depression can occur as a very rapid response to decreased levels of energy intake, and is most clearly demonstrated by animals that undergo periods of torpor (Hudson, 1973; Mrosovsky and Sherry, 1980; Merkt and Taylor, 1994). Biochemically, the onset of metabolic depression may be triggered by the shift from glycogenolysis to gluconeogenesis which occurs after the first 1–3 days (Phase 1) of fasting (Cahill, 1978; Cherel et al., 1992). In harbour seals, fasting metabolism was attained within 24 h (Markussen, 1995), and a similarly rapid response was suggested by Boily and Lavigne (1995) for grey seals. Although onset time was not measured in the current study, we have recorded a metabolic depression of 20–25% in a group of younger Steller sea lions (age 6–14 weeks) after only 36–72 h of fasting (Rosen and

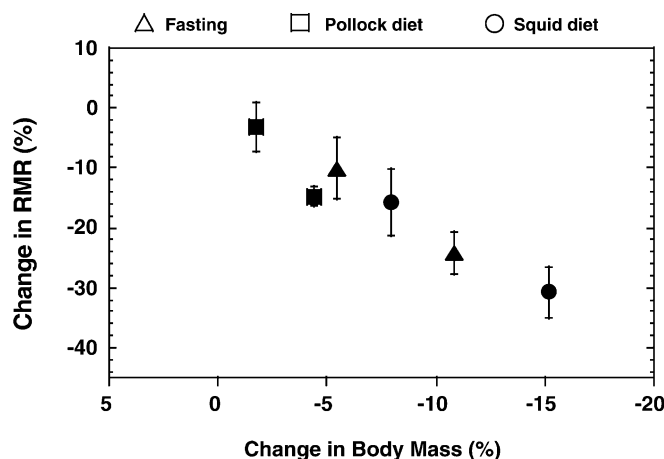


Fig. 4. Weekly percent changes (from control levels) in resting metabolic rate (RMR) in comparison to changes in body mass during the experimental phases of the fasting (this study), squid diet (Rosen and Trites, 1999) and pollock diet (Rosen and Trites, 2000) experiments.

Trites, unpubl. data), corresponding to equally rapid biochemical responses (Rea et al., 2000).

Metabolic depression is usually expressed as a graduated rather than discrete response, the result of a resetting of some physiological 'set point' (Lyman, 1982). While it may be triggered by changes in fuel homeostasis, its magnitude may be related to relative body mass loss. Øritsland (1990) suggested that the 'metabolic depression factor' changed as body mass differed from some 'optimal' level. In our studies with Steller sea lions, there is a strong relationship between relative changes in body mass and metabolism during fasting, and squid and pollock diet conditions (Fig. 4). Similar relationships have been reported for terrestrial mammals (Munch et al., 1993).

#### 4.4. Recovery period

In contrast to the experimental period, metabolism of the sea lions during the recovery period did not appear to be related to relative total body mass loss. Across species, the relationship between metabolism, mass loss, and growth rates immediately following an episode of reduced food intake is inconsistent, and probably reflective of different general recovery strategies.

Animals may attempt to regain their set point body mass as quickly as possible after a period of undernutrition. Rats, for example, appear to employ a set of strategies to maximise post-deprivation growth rates, including increased food

intake, an increased digestive efficiency during the early stages of refeeding and a prolonged metabolic depression (Boyle et al., 1981; Munch et al., 1993). However, not all studies support the hypothesis of 'maximised recovery'. Adolph (1947) and Hamilton (1969) both reported post-fasting anorexia in rats, while Merkt and Taylor (1994) reported an immediate return of metabolism to pre-experimental levels after food restriction in desert mice.

Among pinnipeds, the response to refeeding may be related to the predictability of the fluctuation in energy intake (see Section 4.6). In food restriction and fasting experiments, Markussen (1995) found that metabolism in harbour seals was still depressed for at least a week after refeeding commenced. In our study, resting metabolism was still below control levels after the first week of refeeding, although high variability during the fasting trials meant that this difference was only statistically significant for the pollock and squid diet trials. In contrast, Worthy (1987) reported an immediate increase in metabolism in harp and grey seal pups after the onset of feeding following the natural postweaning fast.

The usefulness of sustained metabolic depression during post-fasting recovery to promote recovery of body mass may seem self evident, but it is unclear how this might function or be accurately measured. Apart from any physiological limitations of uncoupling resting and growth metabolic expenditures, measurements of resting metabolism will

automatically include the bioenergetic expenditure related to growth, resulting in an apparent increase in measured RMR (as opposed to a measure of true basal metabolism).

#### 4.5. *Consequences of metabolic depression*

While decreases in metabolism may be related to the degree of relative body mass loss, metabolic depression is limited in both duration and magnitude (McCarter and McGee, 1989). Since metabolic depression is hypothesised to be a consequence of changes in either overall cellular metabolism (Grande et al., 1958; Guppy et al., 1994) or a selective loss or partial shutdown of tissues with a particularly high metabolic rate (Kleiber, 1975), there must be a physiological limit to how far these factors can be reduced. Additionally, decreases in metabolism may be precluded by potential conflicts with thermoregulatory abilities and water balance (Aschoff and Pohl, 1970; Fuglei and Øritsland, 1999). On a biochemical level, metabolic depression may cease when the animal enters into Phase III fasting, when body lipid reserves reach a critical point, and protein utilisation predominates. At this stage, animals resort to critical survival measures, including an increase in locomotor activity associated with increased foraging effort (independent of food availability) (Cahill, 1978; Cherel et al., 1992).

The hypothesised function of metabolic depression is to limit tissue catabolism by limiting energy expenditures and, ultimately, stave off starvation (Keys et al., 1950). But to what degree do changes in RMR directly contribute to energy savings? Unlike the sea lions in our studies, desert mice can switch down their metabolism sufficiently to maintain body mass indefinitely on 50% food restriction (Merkt and Taylor, 1994). The greatest degree of metabolic depression exhibited by the sea lions in our studies was the impressive 30% decrease in RMR seen during the fasting trials. This decrease in RMR translated into a theoretical reduction in total energy expenditure of 8.3 MJ/d. However, using some rough estimates, this value represents catabolism of tissue in the order of 0.30 kg/d (at 75% blubber and 25% lean tissues), a relatively small amount compared to the observed daily mass loss of 2.3 kg/d.

Perhaps not all of the savings due to metabolic depression can be directly calculated from changes in RMR. Metabolic depression may be a byproduct

or facilitator of other bioenergetic adaptations. For example, metabolic depression is associated with decreases in activity even in animals which do not undergo torpor or hibernation (Westerterp, 1977; Harlow, 1981), and increased activity will moderate the level of metabolic depression (Ballor et al., 1990). Decreased activity is a viable strategy during periods when the expectation of foraging success is low.

However, a strategy of overall decreased energy expenditure during periods of low food intake is not always possible. During the breeding season, food intake (but not food availability) is limited for many species of pinnipeds (including Steller sea lions) that must remain on land to either maintain breeding opportunities or care for young. For males, activity levels may remain high when defending reproductive assets (females or territory), and females must incur the high cost of lactation. There is evidence that lactating female grey seals utilise metabolic depression to help maintain energy balance while simultaneously fasting and nursing a pup (Mellish et al., 2000). Clearly, the bioenergetic response of an animal will partially depend on the cause and timing of the decreased low food intake.

#### 4.6. *Effect of predictability*

There are several factors that can affect the degree of metabolic depression in response to low food availability exhibited by animals: whether periods of food restriction are part of their natural history, the timing of the restriction, and the source of the restriction.

The magnitude and duration of metabolic depression appears to be partially dependent on the natural pattern of food restriction normally experienced by the animal. Not all mammals exhibit metabolic depression in response to experimental fasting, a characteristic that has been interpreted to indicate that food deprivation has not been a critical factor in their recent history (e.g. Weber and O'Connor, 2000). In contrast to the prolonged metabolic depression exhibited by various pinnipeds, humans exhibit a rise in resting metabolism after the first 72 h of fasting. This difference may be related to the fact that seals undergo fasts as part of their natural life history (Bonner, 1984), and their physiology may be more predisposed or able to utilise metabolic depression



during periodic fasting episodes, even if those events are unpredictable.

In general, the occurrence and manifestation of metabolic depression has been shown to differ according to the source and type of undernutrition. Mrosovsky (1990) categorised these controlled (rheostatic) changes in metabolism as either predictive or reactive rheostasis, depending on whether it is a response to future or immediate conditions.

While the evidence for reactive metabolic depression among pinnipeds is mixed, there is stronger evidence for predictive metabolic depression among pinnipeds. This can take the form of seasonal variation in metabolism related to specific life history events (Ashwell-Erickson et al., 1986; Rosen and Renouf, 1998). Metabolic depression may also be associated with the natural disruption of the food supply experienced by young pinnipeds (particularly phocid seals) during the postweaning fast (Nordøy et al., 1990; Rea and Costa, 1992, although see Nordøy and Blix, 1985; Worthly and Lavigne, 1987).

It is unclear whether the metabolic response of mammals to experimental or unpredicted changes in food availability is greater at times of the year when they are more likely to naturally experience decreased energy intake. Fuglei and Øritsland (1999) found no effect of season on the degree of metabolic depression in response to experimental food restriction in arctic foxes. In a series of experiments with captive Steller sea lions, Rea et al. (1999) suggested that the biochemical response (changes in blood urea nitrogen and ketone bodies) to food deprivation depended on whether the episodes occurred within the breeding season or not. Although our study was not designed to address this issue, there does not appear to be any difference in the metabolic response due to the time of the year.

#### 4.7. Conclusions

Metabolic depression appears to be a strategy that Steller sea lions employ in response to periods of fasting and decreased energy intake. This was experimentally demonstrated during unpredictable periods of fasting, as well as when ingested food mass remained constant but gross energy intake was decreased. However, metabolic depression did not occur during periods of undernutrition brought about by decreases in both gross energy intake and

ingested food mass. Rather, these conditions appeared to stimulate a typical hunger response that might lead to increased foraging activity in wild animals.

These results have important implications in the bioenergetics of wild Steller sea lions. Animals forced to switch to less energetically desirable prey types exhibit physiological responses similar to those during fasting bouts. Although the decreases in resting metabolism are designed to conserve body mass, they are insufficient to compensate for the ensuing energy deficit, resulting in significant decreases in body mass. The results from these experiments can be incorporated into dynamic bioenergetic models to better elucidate the impact of changes in prey availability on Steller sea lions.

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