



Fasting affects the surface and diving metabolic rates of Steller sea lions *Eumetopias jubatus*

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ABSTRACT: Changes in metabolic rates were measured in 3 captive female Steller sea lions *Eumetopias jubatus* that experienced fasts during summer and winter. We measured metabolic rates (via O₂ consumption) before (MR_s, surface) and after (DMR, dive + surface interval) the sea lions dove to 10–50 m depths. Measurements were obtained prior to and immediately after 9 to 10 d fasts, and during a 14 d recovery period. The sea lions lost significantly more body mass (M_b) during the winter fast (10.6%), compared with the summer (9.5%). Mass-corrected dive metabolic rate ($cDMR = DMR \times M_b^{-0.714}$) was not affected by dive depth or duration, but increased significantly following the winter fasts ($13.5 \pm 8.1\%$), but did not change during summer ($-1.1 \pm 3.2\%$). However, mass-corrected surface metabolic rate (cMR_s) decreased significantly after both the summer ($-16.4 \pm 4.7\%$) and winter ($-8.0 \pm 9.0\%$) fasts. Consequently, the ratio between $cDMR$ and cMR_s was significantly higher in winter, suggestive of an increased thermal challenge and convective heat loss while diving. Increased cMR_s following the fast indicated that digestion began during foraging and was not deferred, implying that access to ingested energy was of higher priority than optimizing diving ability. $cDMR$ was elevated throughout the recovery period, independent of season, resulting in a 12% increase in foraging cost in winter and a 3% increase in summer. Our data suggest that Steller sea lions are more sensitive to changes in body condition due to food shortages in the winter compared with the summer.

KEY WORDS: Diving physiology · Body condition · Digestion

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INTRODUCTION

The rate at which marine mammals consume O₂ ultimately determines their aerobic dive duration and the efficiency with which they forage (Kooyman & Ponganis 1998, Costa & Sinervo 2004). Marine mammals have developed different physiological and behavioural strategies to conserve O₂ to maximize diving time and foraging efficiency. For example, seals may defer digestion until the end of a foraging bout (Sparling et al. 2007) and increase efficiency of diving by interspersing periods of active swimming with long episodes of passive gliding (Williams et al. 2000). Diving seals can also become hypothermic and suspend

shivering, which reduces metabolic rate and the O₂ consumption rate (Kvadsheim et al. 2005).

Diving efficiency and optimal use of O₂ may be negatively affected by substantial loss of insulative fat stores associated with reduced food intake (Webb et al. 1998, Watanabe et al. 2006). On the other hand, fasting-induced physiological changes include a reduction in metabolism as a means of reducing use of internal energy sources (Guppy & Withers 1999). While fasting, subcutaneous fat is used as a nutritional resource and metabolic depression can extend the time these resources will last (Castellini & Rea 1992). Most pinnipeds experience natural periods of fasting and respond with metabolic depression (Markussen &

Ryg 1992, Rea & Costa 1992). This has been documented in fasted and food-restricted Steller sea lions *Eumetopias jubatus* (Shreber, 1776) on land (Rosen & Trites 2002, Jeanniard du Dot et al. 2008). In most vertebrates, fasting-induced hypometabolism is the result of down-regulation of body functions such as protein synthesis, and thermoregulation to limit tissue catabolism (Øritsland 1990, Guppy et al. 1994). Consequently, hypometabolism that is fasting-induced may also increase the aerobic dive duration for marine mammals. Reduced insulative fat stores, on the other hand, may significantly increase heat loss and metabolic rate through increased thermoregulatory costs, thereby reducing aerobic dive duration.

Understanding how natural or unpredicted periods of fasting affect the metabolic cost of foraging is needed to predict the consequences of food shortages on the energy budget and foraging strategies of marine mammals (Williams et al. 2007). The aims of this study were: (1) to measure the metabolic rates of foraging Steller sea lions experiencing reduced food intake (i.e. acute fasting) to determine how fasting might affect the foraging costs of marine mammals, (2) to observe how quickly reductions in metabolic rates could be reversed when a fasted animal regained access to food, and (3) to investigate how fasting-induced changes in foraging costs vary with season to identify whether there are particular times of the year when Steller sea lions are more vulnerable to alterations in prey availability. Such information can be incorporated into future bioenergetic models to estimate total energy budgets and food requirements of wild Steller sea lions, and may help with population and fisheries management.

MATERIALS AND METHODS

Animals. All experiments were conducted under permits from Animal Care Committees of the University of British Columbia (UBC) and the Vancouver Aquarium, Canada. Experimental trials were conducted between May and November 2007. Three female Steller Sea lions were used in all trials; 2 sea lions were 9 years old (F97HA and F97SI) and the third was 6 years old (F00BO). The animals were housed and trained since pups at the Vancouver Aquarium and transferred to the UBC Open Water Research Station located in a coastal inlet in British Columbia in 2003 where the study took place. The animals were housed in a floating net pen (3.6 × 3.6 × 6.1 m) suspended in seawater with a haulout space.

The animals freely chose to cooperate and were never restrained or confined during the experimental trials. During each trial, the sea lion wore a body har-

ness with an attached VHF transmitter and depth data logger (Sensus ReefNet Ultra U-05272). The VHF transmitter allowed the sea lion to be tracked in case the animal left the trial area. Body mass (M_b , kg) was measured daily by having the animals hold position on a platform scale (± 0.5 kg). M_b was measured before each trial and opportunistically during fasting (depending on animal cooperation).

Experimental conditions. The experiment consisted of three 9 to 10 d fasting sessions (Fast 1, 2, and 3). Fasts 1 and 2 were both conducted in the summer (3 May to 3 July 2007) and Fast 3 in the winter (22 October to 13 November 2007). Each fasting session consisted of a series of pre-fast diving trials followed by a fasting period and a subsequent 2 wk recovery period during which 5 post-fast dive trials were conducted at pre-determined intervals (Table 1). All trials were performed in the morning, at least 16 h and up to 216 h postprandial. To ensure that the sea lions were not naïve to the required dive parameters during a trial, each animal was trained at each depth for 5 to 7 d prior to collecting any data (see 'Trial procedure' for details of experimental setup).

Fasts 1 and 3 included dives to a maximum depth of either 30 m (F97SI) or 50 m (F97HA and F00BO), depending on the willingness of the individual sea lion (Table 2). During Fast 1, F97HA and F00BO would not dive to 50 m for the Post 1 and Post 2 trials. We therefore reduced the dive depth to between 20 to 40 m to collect post-fasting data. Fast 2 utilized only shallow dives to 10 m for all 3 animals. We evaluated how dive depth affected the metabolic rate of a dive event (DMR, dive + surface interval) by comparing the results of Fasts 1 and 2, and assessed seasonal changes by comparing Fasts 1–2 with Fast 3.

The sea lions' normal diet consisted of previously frozen herring (*Clupea pallasii*) and small quantities of squid, supplemented with vitamins. On the first day of fasting, the animals were fed 30% of their normal base amount in the morning, and were thereafter fasted for

Table 1. *Eumetopias jubatus*. Diving trial schedule for 3 female Steller sea lions during the recovery period after a 9 to 10 d fast. Pre-fast trials were control trials and were conducted before the onset of fasting. All days are relative to the last d of fast (Post 1), represented by Day 0

Trial	Days since end of fast
Pre-fast	-11 to -24
Fast	-9 to -10
Post 1	0
Post 2	1 to 2
Post 3	4 to 5
Post 4	7 to 8
Post 5	12 to 13

Table 2. *Eumetopias jubatus*. Dive depths (m) for 3 female Steller sea lions (F00BO, F97SI and F97HA) during 3 fasting sessions; summer (Fast 1, 2) and winter (Fast 3). nd: no data. Parentheses: no. of dives

Fast	Animal	Pre-fast	Post 1	Post 2	Post 3–5
1	F00BO	50 (7)	30 (8)	50 (4)	50 (4)
	F97SI	30 (6)	30 (6)	30 (5)	30 (4–5)
	F97HA	50 (6)	20–40 (6)	30–50 (4)	50 (4)
2	F00BO	10 (6)	10 (6)	10 (3)	–
	F97SI	10 (6)	10 (7)	10 (4)	10 (4)
	F97HA	10 (6)	10 (6)	10 (4)	10 (5)
3	F00BO	50 (6)	50 (7)	50 (4)	50 (4)
	F97SI	30 (6)	30 (6)	30 (4)	30 (4)
	F97HA	50 (6)	50 (6)	50 (4)	50 (4)

9 to 10 d. The fasting period was designed to result in a total mass loss ~10% of the initial M_b , but not exceeding 15% (as per Animal Care protocols). During Fast 1, one sea lion (F97HA) would not dive during the Post 1 trial. She was therefore fasted for one more day, resulting in a total fasting period of 10 d. During preparation for trials, transportation to the trial area, and during the Post 1 trial attempt, she received ~7% of her normal daily food intake (~0.5kg). A minimal amount of food (<100 g) was given to the animals before each trial to facilitate separation from other animals in the pen area. Separate experiments not reported in this study were conducted to ensure that this amount of food did not affect the metabolic rate.

Average daily mass of the food intake (i.e. food base) was predetermined by the trainers and differed between animals depending on individual and seasonal M_b . The sea lions received a significantly higher food base in the winter compared with the summer, both for the pre-fast period ($16.2 \pm 4.4\%$; $p = 0.0002$, average of the last 5 d prior to fasting) and the recovery period ($12.1 \pm 7.2\%$; $p = 0.0103$, avg. of the first 5 d after fasting). Mass-specific gross energy intake during the pre-fast period ranged from 215 to 474 $\text{kJ kg}^{-1} \text{d}^{-1}$ in the summer (Fasts 1 and 2) and between 296 to 505 $\text{kJ kg}^{-1} \text{d}^{-1}$ in the winter (Fast 3). During recovery, the aim was to increase M_b to pre-fast levels by the end of the 14 d period. Therefore, seasonal variation in mass-specific gross intake was also observed during the recovery period and ranged between 222 to 512 $\text{kJ kg}^{-1} \text{d}^{-1}$ in the summer and from 356 to 566 $\text{kJ kg}^{-1} \text{d}^{-1}$ in the winter. The higher food base in the winter was given to minimize differences in pre-fast weights between fasting sessions and to ensure that each sea lion had recovered and returned to the same pre-fast M_b before each fasting session. This increase in food base requirements during winter was comparable with previous studies ($18.7 \pm 3.6\%$ increase in the winter) (Jeanniard du Dot et al. 2008). The amount of food

given during each trial varied on a daily basis, with sea lions receiving more food during trial days to secure animal motivation. Two sea lions showed signs of stomach discomfort during the recovery period of Fast 2 (F00BO from Post 2, F97HA from Post 4) and these animals were excluded from the study for the remainder of this recovery phase.

The trial area for Fast 1 and Fast 3 was situated in a fjord located ~7 km from the location of the research station. The water depth at this location enabled dives up to 50 m. The trial area for Fast 2 was near the research station, allowing dives up to 10 m. The sea lions were transported to the trial area (Fast 1 and 3) by a specially designed 22 ft (6.70 m) transport boat. Another 22 ft (6.70 m) research boat carried the research equipment and towed a floating barge (containing the respirometry dome) to the trial area.

Experimental set up and variables measured. Variables are defined in (Table 3). Metabolic rates (MR) were estimated using flow-through respirometry to measure the O_2 consumption rate (\dot{V}_{O_2} ; $\text{l O}_2 \text{min}^{-1}$). The floating experimental barge had a rectangular hole into which a cage ($152 \times 152 \times 250 \text{ cm}$) was placed. The cage extended into the water and was equipped with a submerged opening at the bottom and was manually closed to keep the animal in the cage after entering. It also had an open top into which a floating transparent Plexiglas respirometry dome (100 l internal volume) was placed where the animal could breathe.

A mass flow meter (Flow Kit Model 500H, Sable System Int.) pulled air through the dome at a flow rate of 475 l min^{-1} . The mass flow meter automatically corrected flow rate to standard temperature and pressure (STP) despite variation in temperature and barometric pressure. The O_2 and the CO_2 levels in the expired air were determined by extracting a subsample of the air passing through a canister of anhydrous CaSO_4 (W. A. Hammond Drierite) to a paramagnetic O_2 (FC-1B O_2 , Sable Systems Int.) and an infrared CO_2 analyzer (CA-1B, Sable Systems Int.). Data were sampled at 2 Hz and

Table 3. *Eumetopias jubatus*. List of symbols and abbreviations

Variable	Definition
d_f (min)	foraging time (excludes ascent and descent time)
d_t (min)	total dive time
DMR ($\text{l O}_2 \text{min}^{-1}$)	diving metabolic rate
c DMR ($\text{ml O}_2 \text{min}^{-1} \text{kg}^{-0.714}$)	mass-corrected diving metabolic rate
M_b (kg)	body mass
MR ($\text{l O}_2 \text{min}^{-1}$)	metabolic rate
MR _s ($\text{l O}_2 \text{min}^{-1}$)	surface metabolic rate
c MR _s ($\text{l O}_2 \text{min}^{-1}$)	mass-corrected surface metabolic rate
RMR ($\text{l O}_2 \text{min}^{-1}$)	resting metabolic rate
\dot{V}_{O_2} ($\text{l O}_2 \text{min}^{-1}$)	rate of O_2 consumption

saved to a laptop. Temperature (°C) and humidity (%) of the excurrent gas were measured using a commercial sensor (Springfield Precise Temp. Springfield Precision Instrument). Measurement of humidity of the excurrent air made it possible to correct flow to STP dry (STPD). The effective volume of the system, including the volume of the respirometer and the plastic hose connected to the analyzer was 120 l. A flow rate of 475 l min⁻¹ gave a time constant of 15 s and the time required to reach a 95% fractional transformation to a new steady state was 3.2× the time constant or 48 s (Fahlman et al. 2005).

The O₂ and CO₂ analyzers were calibrated before and after each trial using ambient air (20.94% O₂, ~0.05% CO₂) and a commercial mixture of 1.0% CO₂ in N₂ (Praxair). Simultaneous N₂ and CO₂ dilution tests (Fahlman et al. 2005) were used to determine the accuracy of the respirometry system. These tests were repeated regularly between trials and showed that the difference between the observed and expected values were within 4%. Addition of CO₂ confirmed that negligible amounts of CO₂ were lost by dissolving in the seawater.

A PVC tube was extended to depth and attached to a pump system located on the corner of the barge (bilge pump [Rule] submerged, 14 to 400 l h⁻¹) and a bladex valve with a plunger. The tube and pump system allowed fish (previously frozen herring, cut into ~25 g pieces) to be delivered to a predetermined depth at a constant rate of 10 fish pieces min⁻¹. Two underwater cameras, 1 at the bottom of the cage (surface camera [650 Sea-Drop, Sea-Viewer Underwater Video System]) and the other at the end of the feeding tube (depth camera [Scout XL, AquaVu Underwater Viewing System]), were connected to a monitor (AquaVu Underwater Viewing System, Scout XL), making it possible to observe the sea lion at depth and when inside the dome. The output from the cameras was fed to a DVD recorder allowing each dive trial to be recorded.

Water temperatures at the surface and at the end of the feeding tube were monitored during each trial using remote temperature loggers (Onset Computer Corp.). Temperature at depth was 10.5 ± 2.0°C in summer and 10.8 ± 0.6°C in winter, and at the surface 14.4 ± 2.6°C in the summer and 10.0 ± 1.5°C in the winter.

Trial procedure. Each sea lion was instructed by a trainer to swim into the dome. The trial started once the animal surfaced inside the dome. The animal was kept in the dome for approximately 6 min to measure the surface metabolic rate (MR_s), but the time was extended if steady values of O₂ and CO₂ were not recorded during the last 2 min. Previous unpublished trials at our facility of resting metabolism measured up to 30 min have shown that this shorter duration is sufficient to accurately measure the surface metabolic

rate and short enough to avoid stress. Following the measurement of MR_s, the animal was instructed to dive to a pre-determined depth (10, 30, or 50 m) where pieces of herring were delivered until the sea lion decided to return to the dome. While submerged, the animal did not receive any instructions from the trainer and the duration of the dive was determined by the sea lion. After re-surfacing, the sea lion was kept in the dome via behavioural control until the \dot{V}_{O_2} had returned to pre-dive levels (approx. 5–7 min). Each trial included 3–6 repeated dives (1 trial d⁻¹) for each animal. Dives shorter than 20 s and those where the sea lion accidentally surfaced outside the dome were excluded from the analyses.

Definitions and calculation of MR_s and DMR. Activity level varied when the sea lions were breathing in the respirometry dome within the cage. The animals did not always remain resting at the water surface but alternated resting periods at the surface with periods lying at the bottom of the cage. Hence, the obtained metabolic values during prolonged periods in the respiratory dome were defined as MR_s rather than as resting metabolic rate. \dot{V}_{O_2} was calculated by integrating the instantaneous O₂ consumption rate (Bartholomew et al. 1981) over periods when the sea lion was breathing in the dome. MR_s was computed as the total O₂ consumed during a period of stable O₂ values (usually between 2 to 3 min) and divided by the duration of stable O₂ values. DMR was estimated by dividing the total O₂ consumed during the entire post-dive surface interval by the duration of the dive and post-dive surface interval (Sparling & Fedak 2004). Consequently, this is not a true measure of diving metabolic rate, but rather an estimate of the cost of each dive event (Fahlman et al. 2008c).

As metabolic rate is related to M_b with mass-exponent estimates ranging between 0.66 to 0.75, depending on whether one subscribes to the geometric or quarter-power scaling exponent (West et al. 2002, White 2003), fasting-induced hypometabolism would be detected as a deviation away from this universal constant (Fahlman et al. 2005). Therefore, mass-corrected DMR (${}_c\text{DMR} = \text{DMR} \times M_b^{-0.714}$; ml O₂ min⁻¹ kg^{-0.714}) and MR_s (${}_c\text{MR}_s = \text{MR}_s M_b^{-0.714}$) were calculated using an intra-specific mass-exponent reported for marine mammals (Hunter 2005). Using this mass-exponent ensured that observed changes in DMR and MR_s were independent of concurrent changes in M_b .

Calculation of foraging duration (d_f). The total decrease in foraging time was estimated by calculating the effect of the increase in ${}_c\text{DMR}$ on available foraging duration (d_f, this excludes ascent and descent duration). The fractional change in ${}_c\text{DMR}$ ($\Delta_c\text{DMR}$, %) during the recovery changed the total dive duration (d_t) by:

$$\Delta d_t = \Delta_c\text{DMR} \times d_t \quad (1)$$

where Δd_t is the change in total dive duration (min). In the present, the mean dive duration for a dive to 50 m was 3.7 min with an available foraging time of 1.2 min (Fahlman et al. 2008a). The change in available foraging time (Δd_f , %) was thereafter estimated as

$$(\Delta d_f = \Delta d_t d_f^{-1}) \quad (2)$$

Statistical analysis. Our objective was to assess how mass-corrected surface and diving metabolic rate changed after fasting and over the recovery period. We did this by comparing cMR_s and $cDMR$ separately for the following: (1) the direct effect of fasting (Pre-fast vs. Post 1 metabolic rates), (2) the nature of recovery from a fast (Post 1 vs. Post 2, Post 3, Post 4 and Post 5), and (3) the overall effect of fasting, including the direct effect of fasting and the recovery period (Pre-fast to Post 5 metabolic rates).

Statistical analyses were performed using the software RGui (R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, v.2.5.1, 2007). The effect of fasting on cMR_s , $cDMR$ and M_b (dependent variables) was determined using linear mixed-effects (lme) models (nlme library from Pinheiro et al. 2006). Fasting session (Fast 1, 2 or 3), fasting state (Pre-fast to Post 5), dive duration, dive number (the number of the dive during the diving trial) and dive depth were tested as independent fixed covariates. Animal was included as a random effect. This approach considered individual variation relative to the population mean by accounting for the correlation between repeated measurements on the same animal. Forward and backward stepwise techniques were used to search for the best model. Selection of the model best explaining the data was based on Akaike Information Criterion (AIC).

Statistical significance for each variable in the mixed effect model was set at $\alpha \leq 0.05$. In this study p-values ≤ 0.05 were considered as significant whereas $0.05 < p \leq 0.1$ were considered a trend. Data are presented as mean values \pm SD unless otherwise stated.

RESULTS

Effects of fasting on body mass and food intake

Mean M_b before the fast was similar between the 3 fasting sessions, and was 144.2 ± 0.7 , 219.6 ± 0.4 and 168.5 ± 1.6 kg respectively for F00BO, F97SI and F97HA ($p > 0.1$). Details of changes in M_b during the fasting and recovery periods are summarized in Table 4.

Total M_b loss was higher in the winter compared with the summer ($p = 0.044$). The daily M_b loss (%) decreased linearly in relation to pre-fast values during the fast ($p < 0.01$) and the decrease was significantly

Table 4. *Eumetopias jubatus*. Body mass M_b (kg) and change in M_b (kg and %) during a 9 to 10 d fasting and a 2 to 14 d recovery period for 3 female Steller sea lions in summer and winter

	Summer	Winter
M_b before fast (kg)	177.5 ± 38.7	177.3 ± 37.8
M_b after fast (kg)	161.4 ± 36.1	158.7 ± 34.8
Total M_b loss during fast (%)	-9.5 ± 0.3	-10.6 ± 0.8
M_b loss d^{-1} during fast (%)	-1.06 ± 0.10	-1.24 ± 0.12
Total gain in M_b during recovery (%)	6.5 ± 1.2	6.3 ± 1.2
Gain in M_b d^{-1} during recovery (%)	0.54 ± 0.10	0.50 ± 0.11

higher in the winter ($p = 0.016$) compared with the summer. The average daily gain in M_b during the 14 d recovery period was $0.52 \pm 0.03\% d^{-1}$ and did not differ between seasons ($p > 0.1$; Fig. 1A).

The daily mass-specific rate of loss in M_b ($g kg^{-1} d^{-1}$) remained steady throughout the fasting period ($p > 0.1$) and was higher during the winter fast ($13.4 g kg^{-1} d^{-1}$) compared with the summer fast ($11.0 g kg^{-1} d^{-1}$; $p = 0.039$; Fig. 1B). The daily mass-specific rate of gain in M_b during recovery was similar between seasons ($p > 0.1$), but decreased asymptotically toward zero with days of recovery.

Effect of fasting on metabolic rate

There was a significant correlation between \log_{10} -transformed surface metabolic rate ($\log MR_s$) and body mass ($\log M_b$, $p < 0.01$). For pre-fast $\log MR_s$ the mass-exponent was 1.44, while the exponent for the entire fasting session (Pre-fast to Post 5) was 1.12. A similar analysis for dive metabolic rate (DMR) gave a mass-exponent of 0.72 for the pre-fast value ($p < 0.01$), and 0.76 when including all values (Pre-fast to Post 5).

Surface metabolic rates (Pre-fast to Post 5) ranged between 0.71 to $2.09 l O_2 min^{-1}$, and cMR_s ranged between 20 to $48 ml O_2 min^{-1} kg^{-0.714}$. Mean $cDMR$ was $12.4 \pm 12.8\%$ higher than cMR_s for the 3 fasting sessions (Pre-fast to Post 5; $p < 0.05$), but mass-corrected surface metabolic rate did not differ between the 2 summer fasts, Fast 1 and 2 ($p > 0.1$). The data were therefore pooled to compare the summer fast with the winter fast (Fast 3). Overall, cMR_s was significantly higher in the winter compared with the summer, both before and after fasting ($p < 0.031$). Mass-corrected surface metabolic rate decreased in both seasons on the last day of fasting (Post 1), and dropped more in the summer ($-16.4 \pm 4.7\%$, $p < 0.0001$) than winter ($-8.0 \pm 9.0\%$, $p < 0.05$).

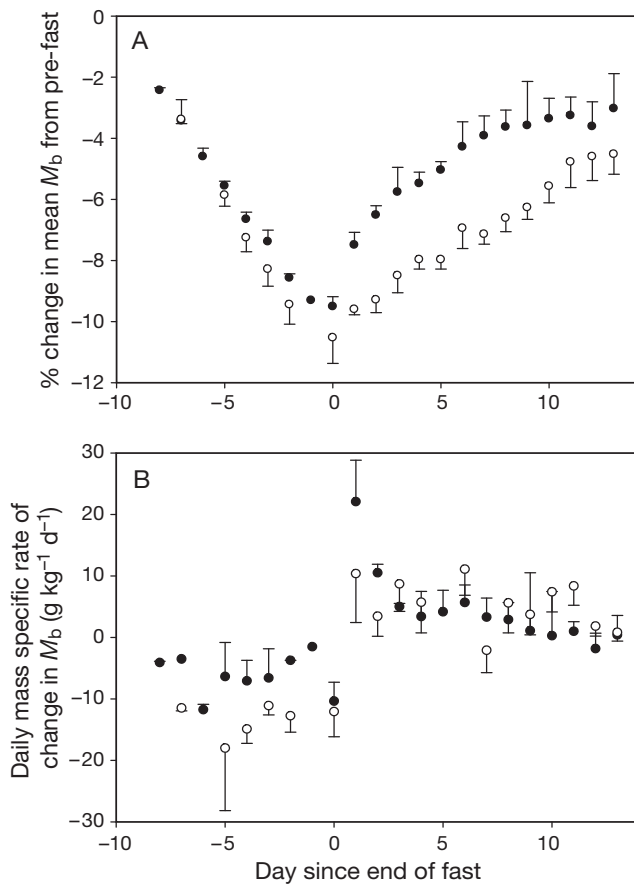


Fig. 1. *Eumetopias jubatus*. Change in mean body mass (\pm SD) of 3 female Steller sea lions during fasting (Days -10 to -1) and subsequent feeding (Days 0 to 13): (A) percent change in M_b relative to pre-fasting mass during summer (closed circles) and winter (open circles); (B) daily rate of mass loss relative to the previous day mass ($\text{g kg}^{-1} \text{d}^{-1}$) in summer (closed circles) and winter (open circles). Animals began receiving food on Day 0. Negative day-values = remaining number of fasting days. Positive values = number of recovery days since end of fasting

Independent of season, ${}_c\text{MR}_s$ was similar to pre-fast values on the second day of recovery, where it stabilized and remained throughout the recovery period (Fig. 2). An asymptotically increasing function showed that the intercept ($p = 0.0001$, Eqs. (3) & (4)) but not the slope ($p > 0.1$) differed between seasons during the 14 d recovery period. The best equations to describe mass-corrected metabolic rate ($\text{ml O}_2 \text{min}^{-1} \text{kg}^{-0.714}$) relative to days post-fast were:

$${}_c\text{MR}_{s \text{ summer}} = 2.57 \cdot 10^{-2} + 9.0 \cdot 10^{-3} \cdot (1 - e^{-d}) \quad (3)$$

$${}_c\text{MR}_{s \text{ winter}} = 3.25 \cdot 10^{-2} + 7.23 \cdot 10^{-3} \cdot (1 - e^{-d}) \quad (4)$$

Each dive trial consisted of 3 to 8 dives. Analysing the first post-fasting trial (Post 1) revealed that ${}_c\text{MR}_s$ increased significantly after the first dive in the trial ($p < 0.01$), compared to pre-dive values, and remained elevated until the end of the trial. For the pre-fasting

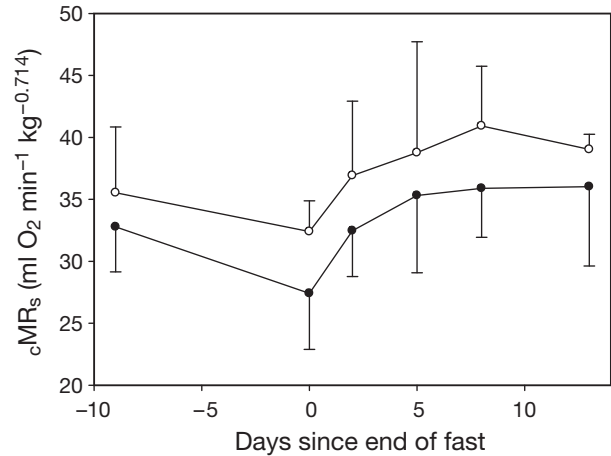


Fig. 2. *Eumetopias jubatus*. Mean (\pm SD) mass-corrected surface metabolic rates (${}_c\text{MR}_s$; $\text{l O}_2 \text{min}^{-1} \text{kg}^{-0.714}$) for 3 female Steller sea lions prior to fasting (Day -9) and during the 14 d recovery period (Days 0 to 13) that followed the 9 d fast in summer (closed circles) and winter (open circles). Animals began receiving food on Day 0. Negative day-values = remaining number of fasting days; positive values = number of recovery days since end of fasting

trial and the remaining post-fasting trials (Post 2 to Post 5), ${}_c\text{MR}_s$ remained constant throughout the trial and did not differ from the pre-dive value ($p > 0.3$). This was true for both the summer (Fig. 3A) and the winter fasts (Fig. 3B).

The overall mean dive duration was 3.4 ± 1.5 min (range 0.4 to 7.0 min). Dive duration increased with depth ($p > 0.0001$) from 2.9 ± 1.2 min at 10 m (summer Fast 2), to 3.7 ± 1.6 min at 20 m to 50 m (summer, Fast 1), and 3.6 ± 1.5 min at 30 m to 50 m during winter (Fast 3).

DMR ranged between 0.97 to 2.30 $\text{l O}_2 \text{min}^{-1}$ and ${}_c\text{DMR}$ between 30 to 53 $\text{ml O}_2 \text{min}^{-1} \text{kg}^{-0.714}$. Neither dive depth, dive sequence number, nor dive duration significantly affected mass-corrected diving metabolic rate ($p > 0.1$). As ${}_c\text{DMR}$ did not differ between the 2 summer fasts ($p > 0.1$), the data were pooled for the summer fasts and compared with the winter fast.

Mass-corrected diving metabolic rate differed between seasons and was significantly higher in the winter compared with the summer, both before and after the fast ($p < 0.0001$). Immediately following the fast (Post 1), ${}_c\text{DMR}$ increased in the winter ($13.5 \pm 8.1\%$, $p < 0.0001$) but did not change in the summer ($-1.1 \pm 3.2\%$; $p > 0.05$).

During the recovery period in both seasons, ${}_c\text{DMR}$ initially increased and then decreased towards the pre-fast value (Fig. 4). The shape of the recovery curve for mass-corrected diving metabolic rate was best described by a polynomial equation ($p < 0.05$), and showed a significant difference in intercepts ($p < 0.0001$) and a trend towards a difference in shape of the re-

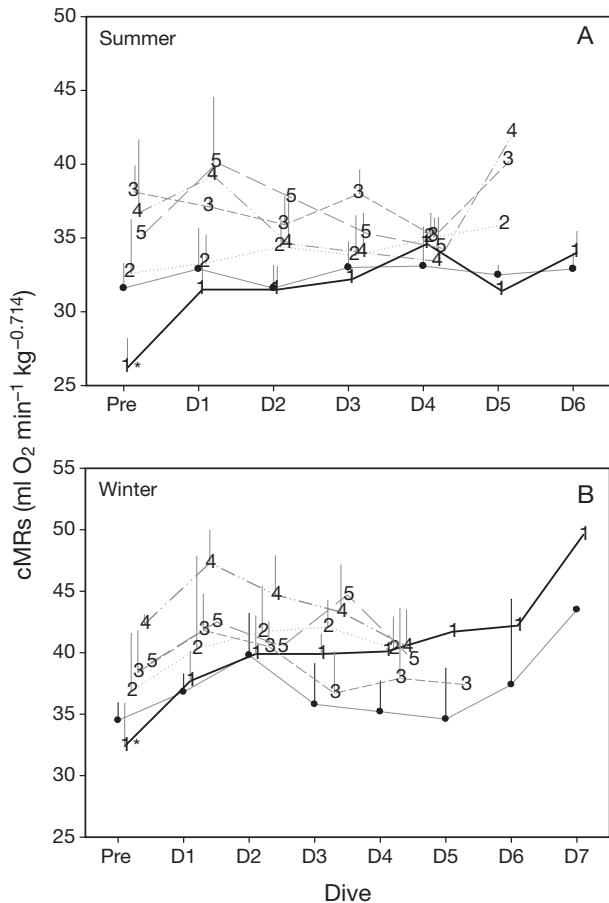


Fig. 3. *Eumetopias jubatus*. Mean (\pm SD) mass-corrected surface metabolic rates (cMR_s ; $l\ O_2\ min^{-1}\ kg^{-0.714}$) associated with individual dives made by 3 female Steller sea lions before (\bullet) and following fasting (1–5) during (A) summer and (B) winter. The numeric symbols (1–5) indicate the pre-defined post-fasting days when metabolism was measured following the fast. Metabolism was measured prior to diving (Pre) and following each of up to 7 consecutive dives (D1–D7). Stars show significant values in relation to the rest of the dives in the trial

covery curve between seasons ($p < 0.1$). The best equations to describe mass-corrected metabolic rate ($ml\ O_2\ min^{-1}\ kg^{-0.714}$) relative to days post-fast were:

$$cDMR_{summer} = 3.63 \cdot 10^{-2} + 8.81 \cdot 10^{-4} \cdot d + -6.70 \cdot 10^{-5} \cdot d^2 \quad (5)$$

$$cDMR_{winter} = 4.46 \cdot 10^{-2} - 1.20 \cdot 10^{-4} \cdot d + 1.10 \cdot 10^{-5} \cdot d^2 \quad (6)$$

The total increase in $cDMR$ during the 14 d recovery period that followed fasting was predicted by integrating the predicted mass-corrected diving metabolic rate recovery curves (Eqs. 5 and 6), after correcting for seasonal differences (difference in pre-fast $cDMR$ in the summer and the winter fast). The increase in mass-corrected diving metabolic rate during the entire recovery period was 12% in the winter and 3% in the summer.

As transit time to and from the prey patch was not affected by fasting, the 12% post-fasting increase in

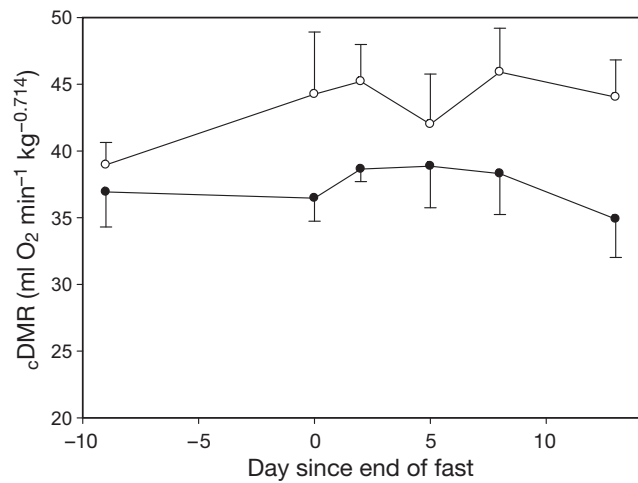


Fig. 4. *Eumetopias jubatus*. Mean (\pm SD) mass-corrected dive metabolic rate ($cDMR$; dive + surface interval; $l\ O_2\ min^{-1}\ kg^{-0.714}$) for 3 female Steller sea lions before and after a 9 to 10 d fast and during a 14 d recovery period in summer (\bullet) and winter (\circ). Animals began receiving food on Day 0. Negative day-values = remaining number of fasting days; positive values = number of recovery days since end of fasting

$cDMR$ in winter and 3% increase in summer resulted in an estimated 18% decrease in foraging duration in the winter and 5% decrease in the summer during the 14 d recovery period.

DISCUSSION

Previous studies with sea lions indicated changes in energy demand during the breeding season (Williams et al. 2007, Jeanniard du Dot et al. 2008). Our data complement those results and also show that prolonged fasting affects the metabolic cost of foraging in a large, freely-diving marine mammal. Our data revealed that sea lions significantly decreased their cMR_s after fasting in summer (-16.4%) and winter (-8.0%), and indicates a fasting-induced metabolic depression that is beyond what can be attributable solely to normal allometric changes in M_b . Fasting did not affect $cDMR$ in the summer but caused a 13.5% increase in $cDMR$ during winter immediately following the fast.

One of the most striking results of our study is the divergent seasonal response in $cDMR$ compared with the decrease in cMR_s during both seasons. This divergent metabolic response can potentially be explained by an increase in thermoregulatory cost while diving after the fast. Such an increased heat loss is assumed to result from a decrease in the insulative fat stores which was particularly noticeable in the winter trial with greater weight loss. While cMR_s returned to pre-fast values on the second day of recovery, $cDMR$ was elevated

throughout the recovery period (while M_b was lower), supporting the suggestion that the sea lions experienced a fasting-induced thermoregulatory challenge while diving during the recovery period. In addition, our data also indicate that digestion was occurring while diving following the fast, as shown by an increase in mass-corrected surface metabolic rate while diving. As a result, calculated available foraging time decreased by 5% in the summer and as much as 18% in the winter during the recovery period. Such a decrease in foraging ability following fasting would make Steller sea lions more vulnerable to changes in prey availability during the recovery period, especially in the winter.

Change in M_b after fasting

Body tissue is used as a nutritional resource when mammals fast. In our study, both total M_b loss and the daily M_b loss from pre-fast values after a 9 to 10 d fast was higher in the winter (-10.6% in total, $-1.2\% \text{ d}^{-1}$) compared with the summer (-9.5% in total, $-1.1\% \text{ d}^{-1}$) (Fig. 1). The daily percent M_b loss from pre-fast values was generally lower than what has been previously reported in fasted subadult ($-1.2\% \text{ d}^{-1}$; 3.5–6.0 yr old) and juvenile ($-1.8\% \text{ d}^{-1}$; 1.8 to 2.5 yr old) Steller sea lions in either season ($-1.7\% \text{ d}^{-1}$ and $-1.5\% \text{ d}^{-1}$) (Rea et al. 2007). The percent M_b loss in our study was also lower than that reported in fasted juveniles ($-1.53\% \text{ d}^{-1}$, 2.5 to 4.5 yr old; Rosen & Trites 2002). This lower rate of mass loss was surprising since, in contrast to previous studies, our animals were housed in a floating pen exposed to ambient environmental extremes.

While we did not believe our sea lions acquired any food during their fast, we cannot rule out the remote possibility that they captured small fish that might have swum into their pen. Although we never noted any small fish in the pen, we are cognisant that our experimental results may not be reflective of a true fast, and could instead indicate metabolic changes occurring during extreme food restriction.

A more likely explanation for the noted lower M_b loss is that our animals were older (6 to 9 yr) than the sea lions in the previous studies. Younger animals have a higher mass-specific metabolic rate (Kleiber 1975) and would therefore lose relatively more body mass. Previous studies have shown that juvenile Steller sea lions lost proportionally more weight compared to subadults during the breeding season (Rea et al. 2007), and that M_b loss during a short fast in a 6-wk old pup was particularly high ($-2.5\% \text{ d}^{-1}$) (Rea et al. 2000). In addition, younger individuals have additional metabolic priorities for growth and might not be able to depress their metabolic rate sufficiently to conserve body reserves during fasting.

A higher M_b loss in the winter compared with the summer concurs with previous acute food restriction studies among juvenile and subadult Steller sea lions (Kumagai et al. 2006) and fasted subadults (Rea et al. 2007). Subcutaneous fat is the preferred tissue catabolised during fasting, since it provides greater energy per mass than protein (Schmidt-Nielsen 1997) and this preference has been observed among Steller sea lions when fed restricted amounts of food (Kumagai et al. 2006, Jeanniard du Dot et al. 2008). The increase in energy utilisation in the winter could be due to lower environmental temperatures. The average temperature at the surface was higher in the summer compared with the winter, but there was only a slight difference in the temperature at depth between seasons. Nevertheless, the mean temperature during a diving bout (surface + dive) was lower in the winter (see 'Materials and methods: Experimental set up and variables measured'). In a homeotherm, temperatures below the lower limit of the thermoneutral zone (TNZ) increase energy requirements by increased thermoregulatory costs. We suggest that, in our study, water temperatures reached below the sea lions' TNZ in the winter. This resulted in an increase in thermoregulatory costs and greater rates of body mass loss in the winter compared with the summer.

Change in metabolic rate after fasting

Fasting has important consequences on specific physiological mechanisms such as digestion and thermoregulation. A reduction in metabolism by down-regulation of body functions such as protein synthesis, thermoregulation, and digestion is a typical option for animals to limit energy expenditure and tissue catabolism in response to reduced energy intake (Øritsland 1990, Castellini & Rea 1992, Guppy et al. 1994).

The sea lions in our study increased both cMR_s and $cDMR$, before and after the fast, to compensate for the increased thermoregulatory challenge and higher M_b loss after the winter fast as compared with the summer fast. An increase in metabolic rate (in air) of Steller sea lions during periods of mass loss in winter was previously suggested to be evidence of a metabolic strategy that differed between winter and summer (Kumagai et al. 2006). However seasonal trends in metabolic strategies even under 'normal' feeding conditions diverge between species. While there is an overall trend in grey seals *Halichoerus grypus*, harbour seals *Phoca vitulina*, and harp seals *Phoca groenlandica* for seasonal decreases in resting metabolic rate (RMR) to be correlated with increases in M_b and body fat, the timing of these cycles differs between species (Hedd et al. 1997, Rosen & Renouf 1998, Sparling et al. 2006). The

pre-fast M_b in our study was similar between the summer and the winter fasts, suggesting similar levels of insulation. The higher MR in the winter likely reflects an increased thermoregulatory challenge associated with colder environmental conditions. The significantly higher food base in the winter during both the pre-fast and recovery period likely reflects changes in seasonal energy budgets, including these increased thermoregulatory costs, consistent with increased winter food requirements reported in other pinnipeds (Renouf and Noseworthy 1991, Rosen & Renouf 1998, Jeanniard du Dot et al. 2008) and from bioenergetic modelling (Winship et al. 2002).

A reduction in metabolism was observed in our study directly after fasting (Post 1), with a significant decrease in cMR_s by 16.4% in the summer and 8.0% in the winter. These are comparable to the absolute changes in metabolism following similar fasts in Steller sea lions (30% decrease while resting in air; Rosen & Trites 2002) and sub-adult harbour seals (*Phoca vitulina*; 20% reduction while resting in water; Markussen & Ryg 1992). Consequently our data support the suggestion that Steller sea lions respond to fasting by reducing energy requirements and consequently reducing surface metabolic rate, to save energy stores.

In contrast to cMR_s , the $cDMR$ did not change in the summer and increased by 13.5% in the winter immediately after fasting (Post 1). This indicates that food restriction may result in additional changes in metabolic costs and physiological trade-offs while diving, compared with resting. These changes have been poorly investigated in diving mammals and may significantly affect foraging efficiency. Food restriction might alter the metabolic cost of diving and foraging through (1) an increased emphasis on the onset of digestion while actively foraging, (2) decreasing buoyancy that alters the metabolic cost of descending or ascending to depth and (3) increasing thermoregulatory costs due to the decrease in insulative fat stores and subsequent increase in both heat conductivity and convection while diving.

Digestive processes increase the rate of O_2 consumption (Kriss et al. 1934). Some marine mammals, such as phocid seals, appear to defer digestion until the end of a foraging bout to maximize dive efficiency by decreasing metabolic overhead (Crocker et al. 1997, Sparling et al. 2007). However, the trade-off between prey acquisition and digestion has received limited attention (Rosen et al. 2007), especially in marine mammals under energetic pressure. Our study showed that cMR_s increased after the pre-dive period immediately after fasting (Post 1). This increase may indicate that sea lions begin to digest their food during foraging after a period of fasting, as opposed to their normal strategy of deferring digestion. This immediate onset of digestion after a period of diving was observed in

both seasons, but not during the pre-fast trials or during any other recovery trial. An instantaneous onset of digestion after fasting implies that access to ingested energy is of higher priority than aerobic diving capacity. Immediate digestion may also indirectly decrease thermoregulatory costs of diving (Wilson and Culik 1991), although such thermal substitution is questionable in marine mammals (Rosen & Trites 2003). Alternatively, the increase in mass-corrected surface metabolic rate after the pre-dive period might reflect cessation of metabolic depression upon exercise. However, this seems unlikely in our case since we compared periods of resting with periods of activity.

Alternately, changes in diving costs could have been due to changes in buoyancy via changes in body lipid content. Most buoyancy studies of marine mammals have focused on buoyancy related changes in dive behaviour (Webb et al. 1998, Skrovan et al. 1999, Sato et al. 2003, Watanabe et al. 2006), while few studies have investigated how changes in buoyancy affect the metabolic cost of diving (Fahlman et al. 2008b). One study investigating the effect of artificial changes in buoyancy on Steller sea lions (equivalent to ~12 to 26% subcutaneous fat) did not reveal any changes in DMR with changes in buoyancy for dives between 10 and 30 m (Fahlman et al. 2008b). Assuming that the fraction of subcutaneous fat to total body mass lost is similar to that previously measured in sea lions (winter 90 to 100%, summer 65 to 73%, Jeanniard du Dot et al. 2008), the amount of subcutaneous fat lost by sea lions in our study was similar to that found by Fahlman et al. (2008b). This suggests that the changes we observed were not caused by changes in buoyancy, perhaps because the experimental dive depths were too shallow to reveal any metabolic changes caused by alteration in buoyancy (Fahlman et al. 2008b). On the other hand, it is possible that the Steller sea adjusted to changes in buoyancy by adjusting their inhaled air volume to counteract changes in buoyancy as suggested by Kooyman (1973) and similar to what has been seen in king penguins (Sato et al. 2002). Hence, fasting induced changes in diving metabolic rate are not likely to be caused by the effect of changes in body lipid stores on cost of swimming via changes in buoyancy.

It is more likely that fasting-induced changes in diving metabolic rate were caused by changes in thermal capacity. Water conducts heat 26 times better than air and the convective heat loss can be 1000 times greater. Although no clear information exists on the thermoneutral zone (TNZ) for Steller sea lions, studies on adult California sea lion *Zalophus californianus* and Antarctic fur seal *Arctocephalus gazella* pups and yearlings suggest their lower critical temperature is approx 14°C (Liao 1990, Rutishauser et al. 2004). Rosen & Trites (2003) estimated temperatures between 2 and

8°C to be partly below the TNZ of juvenile Steller sea lions. However, as body condition shows seasonal variation in many species of marine mammal the thermoneutral zone may also vary seasonally.

Steller sea lions and other otariids have a thin layer of insulative fat compared with phocids, and show less dramatic seasonal variation in total body lipid composition (e.g. Webb et al. 1998, Pitcher & Calkins 2000). However, catabolism of lipids for energy utilization will decrease the thickness of the hypodermal blubber layer. A theoretical model by Roscow (2001) has shown that the degree of heat loss in Steller sea lions under a variety of aquatic and terrestrial conditions increased when the insulative lipid layer decreased, resulting in a thermoregulatory challenge that increased the metabolic rate.

In our study, $\dot{V}O_2$ decreased significantly immediately after fasting in both seasons, but decreased more in the summer (–16.4%) compared with the winter (–8.0%). This indicates one of 2 possible responses: (1) metabolic depression was greater than the increased heat loss caused by the reduction in body fat, or (2) the peripheral temperature was reduced to minimize thermoregulatory cost similarly to that seen in fasted king penguins (Fahlman et al. 2005). It was suggested that an animal that employs peripheral vasoconstriction can decrease the proportion of the body maintained at deep body temperature in response to changes in environment or insulation, hence reduce metabolic expenditure (see Worthy 1991). Unfortunately, we cannot determine which or to what extent these strategies were used by the sea lions because we were unable to measure core and peripheral body temperatures during our study.

The ratio between $\dot{V}O_2$ and $\dot{V}O_{2s}$ increased after the fast in both seasons. Consequently, reduced insulation likely increased convective heat loss during active swimming, increasing the overall cost of foraging. During winter, this thermal challenge after the fast was great enough to increase mass-corrected diving metabolic rate above the pre-fasting value. If the sea lions had used a strategy of reduced body temperature to reduce mass-corrected surface metabolic rate, it is possible that the additional thermal challenge from swimming reached a lower critical threshold. Once this threshold was reached, further reduction in body temperature may not have been possible. The sea lions may therefore have been forced to increase heat production, resulting in a $\dot{V}O_2$ that was higher than the pre-fast value, despite a reduction in the resting $\dot{V}O_2$.

Recovery period

Independent of season, the decrease in $\dot{V}O_2$ measured directly after the fast returned to pre-fast values

within the second day of recovery, where it stabilised and remained throughout the recovery period (see Eqs. 3 and 4). $\dot{V}O_2$ showed a similar increase but increased to values that exceeded the pre-fast trials, in both summer and winter (see Eqs. 5 and 6). The increase in $\dot{V}O_2$ and $\dot{V}O_{2s}$ was most likely due to the up-regulation of body functions that were down-regulated during the fast. Similar rapid recoveries of RMR have been seen in fasted harp seal pups, grey seal pups (Worthy 1987) and Steller sea lions (Rosen & Trites 2002); although one study showed metabolic depression persisting at least one week after re-feeding in harbour seals (Markussen & Ryg 1992).

While resumption of normal body functions is rapid and may return mass-corrected surface metabolic rate to pre-fasting levels soon after re-feeding (Fahlman et al. 2005), mass-corrected diving metabolic rate during the recovery period remained elevated in the summer and to a higher degree in the winter. If a reduction in insulative body fat was partly responsible for the changes in foraging cost, DMR should have remained elevated during most of the recovery period while the sea lions were still restoring their fat reserves. This additional metabolic cost was particularly noticeable in the winter when fasting increased foraging cost by 12% during the 14 d recovery period compared to 3% in the summer. The elevated metabolic cost resulted in less O_2 available for diving and foraging, thereby reducing the foraging efficiency. This increase in metabolic cost may seem small, but can have a significant overall effect on foraging behaviour by decreasing the foraging duration by as much as 18% in the winter and by 5% in the summer, during a 3.7 min dive to 50 m. Available foraging time will further decrease with increasing dive depth (increased travel duration) or a decrease in swim speed. In addition, the higher metabolic rate also results in an increase in the total food requirement.

The particular vulnerability of Steller sea lions to food shortages in the winter agrees with the conclusions from other acute food restriction studies on Steller sea lions (Kumagai et al. 2006). In our study, the effect of fasting was also noticeable in the summer, the breeding season for this species. The foraging success of female Steller sea lions directly after the first week they spend on shore with their pups (the perinatal period) (Milette & Trites 2003) and the subsequent foraging cycles are critical for the survival of the pup. A 5% increase in foraging cost during that time could therefore have a considerable effect on the health of both the mother and her pup and their subsequent chance of survival. This increase in foraging cost would further be enhanced by diminishing prey and changes in food quality and diversity. Inadequate food intake resulting in nutritionally stressed animals

(Calkins et al. 1998) is one of the leading hypotheses to explain the drastic decline of the Western population of Steller sea lions in the Gulf of Alaska and Aleutian Islands (Trites & Donnelly 2003, Guénette et al. 2006).

In conclusion, we suggest that reduced subcutaneous fat associated with fasting caused ρ DMR of Steller sea lions to increase during winter and throughout a 14 d recovery period in winter and summer. This increase potentially decreased the sea lions' aerobic dive duration and foraging time, and occurred in spite of a drop in ρ MR_s. The increased ratio between the ρ DMR and ρ MR_s of fasted sea lions further suggests that convective heat loss during active swimming may pose an additional metabolic challenge in both seasons. Additional costs may also be incurred by fasted animals initiating digestion while diving rather than postponing digestion until foraging has ceased. These findings can be incorporated into bioenergetic models to estimate the food requirements of Steller sea lions and better evaluate the impact that seasonal changes in the availability of prey can have on their populations.

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