

A model to predict fasting capacities and utilization of body energy stores in weaned Steller sea lions (*Eumetopias jubatus*) during periods of reduced prey availability

D.P. Noren, L.D. Rea, and T.R. Loughlin

Abstract: The population decline of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) may be linked to a decline in juvenile survivorship. Limitations in prey availability may contribute to the decline, thus it is important to understand fasting capacities of Steller sea lions. For most mammals, fat catabolism is the preferred energetic pathway to ensure that protein is spared. However, marine mammals also have a conflicting requirement to conserve fat because the main site of fat storage is the blubber layer, which is also their primary thermal barrier when at sea. We developed a dynamic state variable model to demonstrate how protein and fat reserve utilization and maximum fasting duration are influenced by body condition and time spent foraging. This model was parameterized with respect to conditions faced by juvenile and subadult Steller sea lions foraging unsuccessfully during a period of reduced prey availability. The model accurately predicted changes in fat and protein mass of juvenile and subadult Steller sea lions fasting in captivity. Furthermore, the model demonstrated that body lipid content, body mass, and the proportion of time spent in water influence energy reserve catabolism and maximum fasting durations. Consequently, small, lean individuals are particularly susceptible to reductions in prey availability.

Résumé : Le déclin de la population de lions de mer de Steller (*Eumetopias jubatus* (Schreber, 1776)) peut être relié à la diminution de la survie des jeunes. Comme des restrictions dans la disponibilité des proies peuvent contribuer à ce déclin, il est important de comprendre les capacités de jeûne des lions de mer de Steller. Chez la plupart des mammifères, le catabolisme des graisses est la voie énergétique préférée pour assurer la préservation des protéines. Cependant, les mammifères marins ont un problème additionnel car ils ont besoin de conserver leurs graisses parce que le site principal d'entreposage des graisses est la couche de lard qui leur sert aussi de principale barrière thermique lorsqu'ils sont en mer. Nous avons mis au point un modèle variable en état dynamique pour démontrer comment l'utilisation des protéines et des réserves lipidiques et la durée maximale du jeûne sont influencées par la condition corporelle et le temps consacré à la recherche de nourriture. Les paramètres du modèle ont été ajustés pour tenir compte des conditions vécues par les lions de mer de Steller jeunes et subadultes qui recherchent vainement leur nourriture durant une période de disponibilité réduite des proies. Le modèle prédit avec justesse les changements de masse des lipides et des protéines chez des jeunes et des subadultes du lion de mer de Steller jeûnant en captivité. De plus, le modèle démontre que le contenu lipidique du corps, la masse corporelle et la proportion du temps passé dans l'eau influencent le catabolisme des réserves énergétiques et la durée maximale du jeûne. En conséquence, les individus petits et maigres sont particulièrement vulnérables aux réductions de disponibilité des proies.

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Introduction

Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) range throughout the North Pacific Ocean rim (Loughlin et al. 1992). These animals suffered a major decline in abundance throughout their western population since the 1960s (Kenyon and Rice 1961; Merrick et al. 1987). Limitations in prey availability may have contributed to this decline (Holmes et al. 2007). Furthermore, the population decline may partially be linked to reduced juvenile survivorship (York 1994; Holmes and York 2003; Winship and Trites 2006; Holmes et al. 2007). This is not surprising, as recently weaned juveniles may be more vulnerable to food limitation since they have limited foraging experience and dive capacities (Pitcher et al. 2005; Richmond et al. 2006). Thus, it is important to understand the fasting capabilities during periods of food limitation for this susceptible portion of the population.

The weaning process of Steller sea lion pups is not fully understood. Many Steller sea lion pups wean at approximately one year of age, but others are weaned after the age of two or three (Pitcher and Calkins 1981; Trites and Porter 2002; Pitcher et al. 2005; York et al. 2008). As juvenile Steller sea lions age, the proportion of each day spent in water increases (Loughlin et al. 2003). Thus, it is likely that juveniles that are greater than one year of age and spend the majority of each day in the water are weaned and foraging independently (Loughlin et al. 2003). However, because of their limited diving capacity (Richmond et al. 2006), inexperience, and relatively small home range, young animals may be limited in what food is available to them (Merrick and Loughlin 1997).

If young Steller sea lions are unsuccessful in finding and consuming prey, they must rely on their body energy stores to meet metabolic demands. The mammalian body catabolizes glycogen, fat, and protein for energy during a fast (Castellini and Rea 1992). Once glycogen stores are depleted early in the fasting period, animals typically oxidize fat for energy and partially spare protein (Castellini and Rea 1992). Terminal starvation occurs when 30 to 50% of body protein has been metabolized. At this point, lipid utilization falls and death can occur if fasting continues (Castellini and Rea 1992).

Generally, animals ought to avoid catabolizing prime protein sources, specifically cardiac muscle, which is depleted soon after other protein stores become limited in nonfasting adapted species (Goodman et al. 1984). However, for many species, large lipid reserves are also important for survival. For example, marine mammals store fat in a blubber layer, which serves as both the primary energy source during fasting and the primary thermal barrier in water. Blubber is also important for buoyancy and streamlining (Webb et al. 1998). Theoretically, a reduction in the blubber layer of sea lions that are unsuccessful in capturing prey could result in a thermal challenge as they attempt to forage in the ocean. This exemplifies the two conflicting functions of the blubber layer, an energy source to be utilized and a thermal barrier to be conserved (Nordøy and Blix 1985; Worthy and Lavigne 1987; Ryg et al. 1988). The balance of these functions may affect survivorship during the first independent foraging efforts.

If weaned Steller sea lions do not successfully capture prey, they are forced to fast while attempting to forage in cold northern Pacific Ocean and Bering Sea waters. While foraging unsuccessfully, the animals' body energy stores are needed to support basal metabolic needs, as well as the increased energetic costs of swimming and diving in the open ocean (Costello and Whittow 1975; Boyd et al. 1995; Rosen and Trites 2002; for review see Rosen et al. 2007). Body condition (Øritsland et al. 1985; Carlini et al. 2001; Noren 2002; Noren et al. 2003; Noren and Mangel 2004) and the proportion of time spent in water (Worthy and Lavigne 1987) influence the ratio of fat and protein catabolized during a fast and thus the maximum duration that recently weaned pinnipeds can sustain fasting (Carlini et al. 2001; Noren 2002; Noren et al. 2003; Noren and Mangel 2004). Consequently, patterns of utilization of fat and protein reserves and maximum fasting duration may vary among individual Steller sea lions with differing percent fat content of total body mass (%TBF), as well as with the amount of time spent each day foraging unsuccessfully in the ocean.

In this study we modeled how weaned juvenile and subadult Steller sea lions utilize their body energy stores when they are forced to fast for a 1-month period. To illustrate the role of individual variation in fasting metabolism, we developed a dynamic state variable model (Mangel and Clark 1988; Mangel and Ludwig 1992; Clark and Mangel 2000) that adaptively adjusts utilization of fat and protein stores during fasting according to anticipated effects on fitness (Noren 2002; Noren and Mangel 2004). Because Steller sea lions are weaned from 1 to 3 or more years after birth, we compared model predictions to body composition changes measured in both juvenile (1.75–2 years old) and subadult (3.5–6 years old) Steller sea lions fasting in captivity (Rea et al. 2007). We then made novel predictions for patterns of body energy store utilization and maximum fasting duration capabilities for fasting juvenile Steller sea lions representing a wide range of body mass and fat content and spending variable proportions of each day on land and in water.

Materials and methods

Study area and subjects

Juvenile Steller sea lions in Alaska are the primary focus of this model. Values of body mass and percent fat content of total body mass (%TBF) measured in wild juvenile (14–26 months old; age determined by methods of King et al. 2007) Steller sea lions from Alaska (Rea 2002) were used to construct the fitness curve used in the model (described below). Results from fasting trials on captive juvenile and subadult Steller sea lions (Table 1; Rea et al. 2007) were used to estimate the potential range for levels of fat and protein catabolism during fasting and to test the accuracy of the model.

Model theory

We constructed a model to predict how fat and protein stores are utilized by recently weaned Steller sea lions that are forced to fast for 4 weeks owing to a lack of prey. In addition, the model predicted the maximum fasting duration possible for sea lions that were not expected to survive a 4-

Table 1. Body mass (B), protein mass (P), fat mass (F), fat content (F/B), experimental fasting period, and calculated mean allocation (proportion of metabolic demands met by fat catabolism) for fasting subadult and juvenile Steller sea lions (*Eumetopias jubatus*).

Animal	Age class	Age (years)	B1 (kg)	P1 (kg)	F1 (kg)	F1/B1 (%)	Fasting period (days)	B2 (kg)	P2 (kg)	F2 (kg)	F2/B2 (%)	Calculated mean allocation
M1	SA	4	150.7	29.4	41.7	27.7	14	128.7	27.2	27.9	21.7	0.93
M2	SA	3.5	165.7	39.6	18.9	11.4	14	130.6	32.3	10.9	8.3	0.70
F1	SA	4	137.7	27.1	37.3	27.1	12	117.3	24.2	27.6	23.5	0.88
F1	SA	5.5	167.5	33.9	41.9	25.0	9	144.0	33.0	21.6	15.0	0.98
F2	SA	4.5	140.2	31.6	23.3	16.6	8	117.4	27.7	14.7	12.5	0.83
F2	SA	6	164.0	33.2	41.1	25.1	13	140.0	31.7	22.4	16.0	0.97
M3	JUV	2	150.0	33.8	24.8	16.5	5	138.0	31.0	18.4	13.3	0.84
M4	JUV	1.75	125.6	26.2	28.7	22.8	7	112.8	25.3	18.9	16.7	0.96
M4	JUV	2	145.4	34.1	19.0	13.1	7	126.0	31.4	9.8	7.8	0.88
F3	JUV	2	87.4	17.9	20.9	23.9	7	75.6	18.0	8.8	11.6	1.00
F4	JUV	1.75	104.2	20.9	26.8	25.7	7	94.2	20.2	19.4	20.6	0.96
F4	JUV	2	111.0	24.5	20.2	18.2	7	96.2	22.7	12.0	12.5	0.91

Note: M designates male, F designates female, SA designates subadult, and JUV designates juvenile. The parameters B1 and B2, P1 and P2, etc. designate measurements made at the beginning and end of the fasting trial, respectively. Some individuals were used in a second fasting experiment that was initiated at least 4–18 months after the first trial. Mass and body composition data are from Rea et al. (2007).

week period of food deprivation. The state of a sea lion can be characterized by its body mass $B(t)$, fat mass $F(t)$, and protein mass $P(t)$ measured in kilograms at time t ; any two of the three implies the third according to the following relationship (also see Table 2):

$$[1] \quad B(t) = F(t) + 3.7P(t)$$

where the constant 3.7 accounts for the hydration state of protein. In what follows, we used body mass and protein mass, with fat mass computed from the other two.

Metabolic demand as a function of body mass was derived from the Kleiber (1975) equation for basal metabolic rate (BMR):

$$[2] \quad M = 0.293B^{0.75}$$

where M is metabolic rate ($\text{MJ}\cdot\text{day}^{-1}$) and B is body mass (kg).

Multipliers of BMR were applied to account for increased metabolism in immature animals and metabolic costs of behaviours in air and water (Table 2). The resting metabolic rate (RMR) measured for one 2-year-old Steller sea lion in a metabolic chamber was 2.3 to 2.4 times Kleiber's predicted BMR (Rosen and Trites 1997), which is similar to RMRs measured for other juvenile and subadult otariids (Thompson et al. 1987; Rosen and Trites 1997; Donohue et al. 2000; Rutishauser et al. 2004) resting in air. We thus incorporated a basal metabolic multiplier of 2.5 into the model for periods when juvenile Steller sea lions are on land since activity levels on land are generally low and young pinnipeds are often resting or sleeping (Worthy 1987; Blackwell and Le Boeuf 1993). When sea lions fast on land only, metabolic demand is

$$[3] \quad M(t) = 2.5[0.293B(t)^{0.75}]$$

where $M(t)$ is metabolic rate in $\text{MJ}\cdot\text{day}^{-1}$ and $B(t)$ is body mass in kg at time t . Energy expenditure for juvenile Steller sea lions swimming at a speed of $3.4 \text{ m}\cdot\text{s}^{-1}$, the calculated optimal velocity and observed preferred swimming speed, is five times maintenance metabolism (Rosen and Trites 2002). Similarly, the daily energetic cost of juvenile California sea lions (*Zalophus californianus* (Lesson, 1828)) swim-

ming at 1.8 and $2.6 \text{ m}\cdot\text{s}^{-1}$ were 2.7 to 6.4 times Kleiber's predicted BMR (calculated from Feldkamp 1987 and Williams et al. 1991), and the average at sea field metabolic rate estimated via doubly-labelled water for lactating adult female California sea lions is approximately five times Kleiber's predicted BMR (calculated from Costa et al. 1991). Thus, a basal metabolic multiplier of five was used for periods when juvenile Steller sea lions are at sea. When sea lions fast on land and in water, metabolic demand is

$$[4] \quad M(t) = 2.5p[0.293B(t)^{0.75}] + 5(1-p)[0.293B(t)^{0.75}]$$

where $M(t)$ and $B(t)$ are as above (see eq. 3), p is the proportion of the day spent on land, and $1-p$ is the proportion of the day spent in water. This metabolic need can be met by catabolizing a mixture of fat and protein, in which energy gained from the oxidation of fat and protein are 39.3 and $18.0 \text{ MJ}\cdot\text{kg}^{-1}$, respectively (Schmidt-Nielsen 1997).

An allocation strategy consists of a sequence $\{a(t)\}$ representing the fraction of metabolic need on day t met by catabolizing fat. The values for $a(t)$ ranged from 0.7 to 1.0, which are similar to those measured in fasting juvenile and subadult Steller sea lions (Table 1; Rea et al. 2007). Given a body mass $B(t)$, protein mass $P(t)$, and fat mass $F(t)$ (eq. 1) on day t , if allocation $a(t)$ is used to meet metabolic demand computed from eq. 4, the dynamics of protein and fat are

$$[5] \quad \begin{aligned} P(t+1) &= P(t) - [1 - a(t)]M(t)/18.0 \\ F(t+1) &= F(t) - a(t)M(t)/39.3 \end{aligned}$$

Body mass $B(t+1)$ at time $t+1$ is computed from eq. 1.

Steller sea lion fasting model

This dynamic state variable model allows us to determine the optimal allocation of body reserves (fat and protein) to meet daily metabolic demands and maximize a measure of fitness. The fitness proxy of our model is survival, which is determined by minimum levels of fat necessary for insulation in the ocean and maximum levels of fat that would not hinder diving. Because the model predicts daily allocation levels, it has the additional feature of allowing for plasticity in allocation levels throughout the fasting duration.

Table 2. Parameters, interpretations, and values in the dynamic state variable model.

Parameter	Interpretation	Value
T	Length of fasting period (days)	(1) Captive experimental fasting periods; (2) Maximum fasting duration ($T_{\max} = 28$ days or when B_{crit} , P_{crit} , or C_{crit} is reached)
$B(t)$	Body mass (kg at time t)	
$P(t)$	Protein mass (kg at time t)	
$F(t)$	Lipid mass (kg at time t)	$B(t) - 3.7P(t)$
$M(t)$	Metabolic rate (MJ·day ⁻¹ at time t)	(1) Fast spent on land: $M(t) = 2.5[0.293B(t)^{0.75}]$; (2) fast spent on land and in water: $M(t) = 2.5p[0.293B(t)^{0.75}] + 5(1 - p)[0.293B(t)^{0.75}]$, where p is the proportion of day on land and $1 - p$ is the proportion of day in water
	Energy provided from fat mass lost (kg·MJ ⁻¹)	1/39.3
	Energy provided from protein mass lost (kg·MJ ⁻¹)	1/18.0
$C(t)$	Lipid content at time t	$F(t)/B(t)$

The allocation of body reserves to meet metabolic needs for each day was determined by taking into account the fitness of the juvenile Steller sea lions' present and future body conditions. We defined body condition C as the relative fat content of each juvenile:

$$[6] \quad C(t) = F(t)/B(t)$$

We modeled the fasting period of length T days, where $T_{\max} = 28$ days or when the level for B_{crit} , P_{crit} , or C_{crit} is attained. A maximum fasting period of 28 days was selected because it represents a relatively long period of unsuccessful foraging. Although prey biomass and prey species composition in Steller sea lion habitat can be highly patchily distributed and vary dramatically by month and season (Gende and Sigler 2006; Womble and Sigler 2006), it is unlikely that a juvenile Steller sea lion would be unable to encounter and consume any prey for a duration of 4 weeks. However, by modeling this extreme period of unsuccessful foraging, we can examine fasting physiology and determine fasting duration limits in Steller sea lions representing a range of body conditions.

The focus of the model is survival, which we describe as fitness and which is determined by minimum levels of fat necessary for insulation in the ocean and maximum levels of fat that do not hinder diving owing to positive buoyancy. We set the lower critical level of $F(t)/B(t)$ to 0.04 because the lowest measured %TBF in free-ranging juvenile Steller sea lions is 4.3% (Rea 2002). We set the upper critical level of $F(t)/B(t)$ to 0.35 because fat content measured in juvenile Steller sea lions is <35% (Rea 2002). Furthermore, extreme positive buoyancy may prevent sea lions from diving, which would potentially inhibit foraging and escape from predators. For example, a 50 kg Steller sea lion that is 35% fat is negatively buoyant, -6 N (calculated following methods in Webb et al. 1998), but with increasing fat content the animal becomes positively buoyant. In addition, the critical level of $B(t)$ was set at 60% of initial body mass, $B(0)$, because starveling Steller sea lion pups lose approximately 43% of their body mass before death occurs (Trites and Jonker 2000). In the absence of data, we chose to set the critical level of $P(t)$ at 10 kg, because at this level of P , juvenile and subadult Steller sea lions would likely be in the terminal stage of starvation.

We define $W(b, p, t)$ as the maximum probability that a

juvenile Steller sea lion survives the period of food deprivation, given that $B(t) = b$ and $P(t) = p$. We set the maximum value of $W(b, p, T) = 0.5$, because survival rates at sea for newly independent pinnipeds range from approximately 40% to 65% (Lander 1979; Le Boeuf et al. 1994; McMahon et al. 1999). This is similar to the estimated first year survival rate of 0.531 for Steller sea lions in Alaska (Kaplan et al. 2008). Although no data on the relationship between body fat content and survivorship for juvenile Steller sea lions are available, we set $W(b, p, T) = 0.5$ for individuals with fat content ($C = F/B$) ranging from 0.10 to 0.20, which is the range most represented in data from free-ranging 14- to 26-month-old juvenile Steller sea lions (Rea 2002). For simplicity, we assumed that $W(b, p, T)$ for juveniles with fat content <0.10 decreases linearly from $W(b, p, T) = 0.5$ until the lower critical level of fat content (0.04) is reached, for which $W(b, p, T) = 0$. Similarly, we assumed that $W(b, p, T)$ for juveniles with fat content >0.20 decreases linearly from $W(b, p, T) = 0.5$ until the upper critical level of fat content (0.35) is reached, for which $W(b, p, T) = 0$. Consequently, if condition (fat content) on day T is $C = F(T)/B(T)$, then fitness on that day is $W(b, p, T) = \Phi(b, p)$, where $\Phi(b, p)$ is equal to

$$[7] \quad \begin{array}{ll} 0 & \text{if } C \leq 0.04 \\ 8.33C - 0.33 & \text{if } 0.04 < C < 0.10 \\ 0.50 & \text{if } 0.10 \leq C \leq 0.20 \\ 1.17 - 3.33C & \text{if } 0.20 < C < 0.35 \\ 0 & \text{if } C \geq 0.35 \end{array}$$

That is, at the end of the fasting period, the sea lion is alive ($0 < \Phi(b, p) \leq 0.50$) if its fat content is between the minimum and maximum critical levels for its mass. Otherwise, the sea lion is dead ($\Phi(b, p) = 0$). At any time previous, the challenge to the animal is to use its body energy stores to maximize its chance of survival.

In the model, for days previous to T , $W(b, p, t)$ satisfies the equation of dynamic programming determined as follows. First, set $m = 2.5p(0.293b^{0.75}) + 5(1 - p)(0.293b^{0.75})$, $p'(a) = p - (1 - a)m/18$, $f'(a) = (b - 3.7p) - am/39.3$, and $b'(a) = f'(a) + 3.7p'(a)$. Second, set

$$[8] \quad W(b, p, t) = \max_a W[b'(a), p'(a), t + 1]$$

where \max_a denotes that the value of a chosen maximizes $W[b'(a), p'(a), t + 1]$. This procedure is solved backwards

and generates the optimal allocation sequence $\{a^*(t)\}$ and optimal survival probability.

Once the optimal decisions were computed, we used a forward iteration (Clark and Mangel 2000) to predict daily allocation, defined here as the proportion of lipid energy utilized to fuel metabolic demands, for juvenile Steller sea lions representing a wide range of body mass and %TBF and spending variable proportions of the day on land and in water. The forward iteration allows us to predict individual allocations and individual mass dynamics.

Assessment of model accuracy

We tested the model performance with results from fasting experiments conducted on captive juvenile (1.75–2.0 years of age) and subadult (3.5–6 years of age) Steller sea lions (Rea et al. 2007). Changes in body mass, fat mass, and protein mass (Rea et al. 2007), and the calculated mean allocation of body energy stores for each fasting trial are presented in Table 1. Mean allocation was calculated as energy from the oxidation of total fat mass lost divided by the sum of energy from the oxidation of total fat and total protein mass lost during the fasting period (see Noren 2002; Noren et al. 2003; Noren and Mangel 2004). We compared the model predicted allocation level for the experimental fasting duration with the mean allocation calculated from the experimental data for each Steller sea lion. For this comparison, mean allocation was calculated from the model's predicted changes in body mass and composition, as was done for the experimental data.

It is important to note that the captive sea lions had free access to water during the experiments, yet the proportion of each day individuals spent in water is unknown. For simplicity, the model was run with the assumption that all captive sea lions spent 50% of the day on land and 50% of the day in water. Consequently, any deviation from this activity level would inevitably result in discrepancies between model predictions and measured experimental data. Additionally, there is some accepted, inherent error in the methods utilized to determine protein mass and lipid mass in the experimental animals, which would also impact the model's ability to precisely predict fat and protein masses measured at the end of the fast. Thus, a priori, we expected some variability between model predictions and measured data.

Statistical analyses

SigmaPlot version 11.0 and SigmaStat version 3.5 (Systat Software, Inc., San Jose, California, USA) were used for all graphical and statistical analyses. Nonparametric tests (e.g., Mann–Whitney rank sum and Kruskal–Wallis one-way ANOVA on ranks with Dunn's method for all pairwise multiple comparison procedures) were used to test the significance of differences in allocation levels because these data are not normally distributed. Linear regressions were calculated by least squares methods and significance of the relationships was determined by F tests. Slopes and intercepts of regressions describing the relationship between predicted values of fat and protein mass and values measured at the end of the captive experiments for juveniles, for subadults, and the line of equality were compared by one-way ANOVAs. All means are presented with $+1$ SE. Results were deemed significant at $P < 0.05$.

Results

Comparison of model performance with fasting experiments

Mean allocation levels calculated from predictions of the model (0.88 ± 0.04) were not significantly different ($T = 150.0$, $p = 0.98$) from actual mean allocation levels calculated from the experimental measurements (0.90 ± 0.02). The mean difference between allocation levels predicted by the model and those calculated from the experimental measurements was 0.15 ± 0.03 . Furthermore, allocation levels predicted by the model were neither directionally biased nor less accurate for any particular range of %TBF or body mass.

To assess the accuracy of the model's predictions for body mass lost during a fast, we compared fat mass and protein mass measured at the termination of the experimental fast with values predicted by the model for the experimental subjects spending 50% of each day on land and 50% of the day in water (Figs. 1a, 1b). The relationships between measured and predicted values did not differ among juveniles, subadults, or the line of equality (fat mass slope: $F_{[2,15]} = 0.90$, $p = 0.43$; fat mass intercept: $F_{[2,15]} = 1.22$, $p = 0.32$; protein mass slope: $F_{[2,15]} = 1.51$, $p = 0.25$; protein mass intercept: $F_{[2,15]} = 1.33$, $p = 0.29$; Figs. 1a, 1b). Because the relationships between predicted and measured fat and protein masses at the termination of the fast did not differ from 1:1 relationships and the calculated mean allocations from the experimental fast did not differ from those predicted by the model, we find that this is an appropriate model for estimating body energy reserve utilization for fasting juvenile and subadult Steller sea lions.

Influence of body composition on model predictions

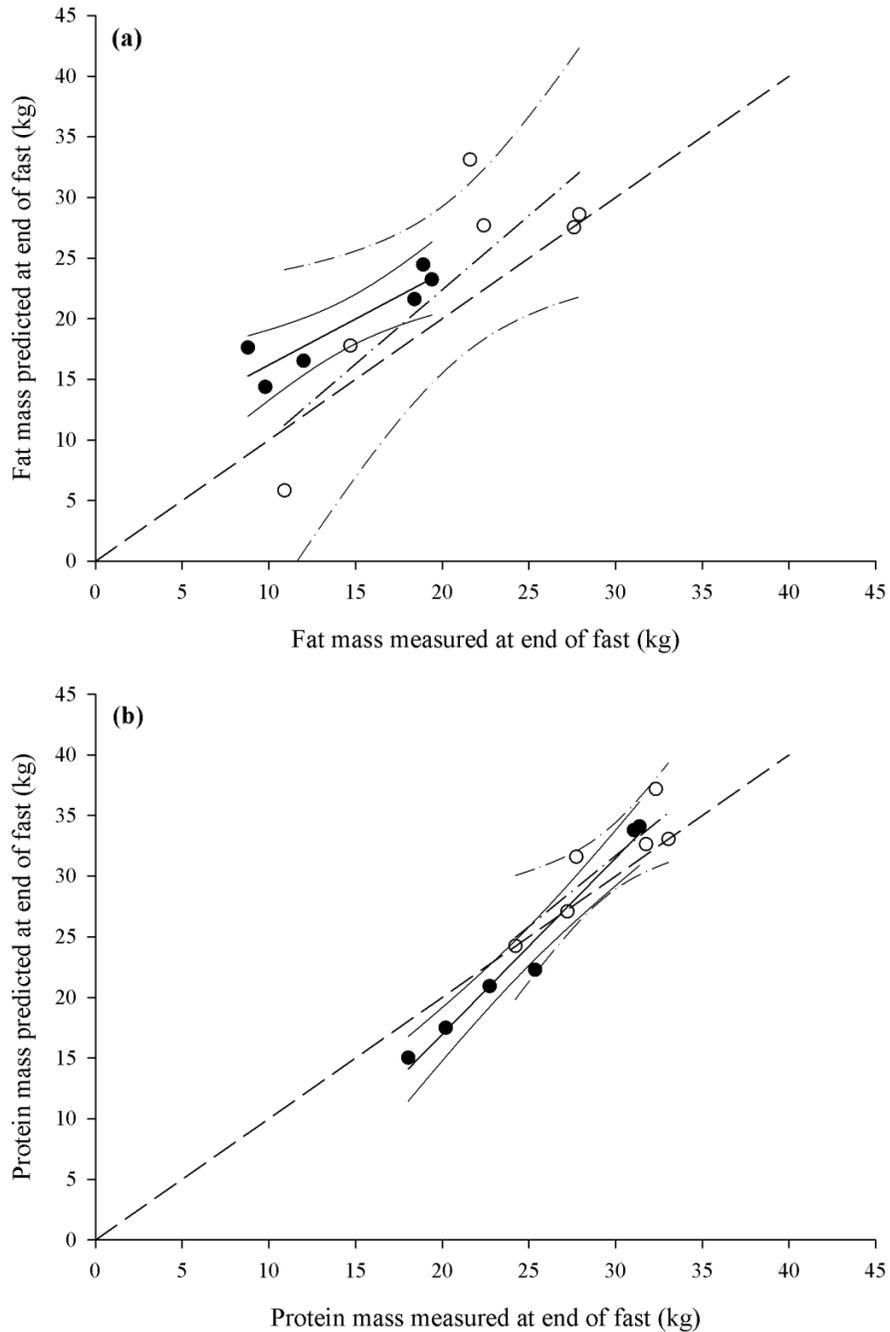
To demonstrate how body composition (%TBF) influences fasting capabilities, we present predicted body mass trajectories for three 100 kg juveniles with distinct fat contents (7%, 15%, and 30% TBF) fasting on land for the maximum fasting period of 28 days or until death occurs (Figs. 2a, 2b). From these comparisons, it is obvious that there is considerable individual variation in the allocation of fat reserves to meet energetic demands and maximum fasting duration capabilities (Figs. 2a, 2b). Specifically, fatter animals utilize proportionately more fat to meet energetic demands (Fig. 3), lose body mass at a slower rate (Fig. 2a), and are consequently able to fast for longer durations (Figs. 2a, 2b).

Influence of time spent foraging on model predictions

To examine the influence of the proportion of time spent on land and in the water foraging, we compared fasting capabilities of the three 100 kg Steller sea lions with distinct fat contents each fasting for the maximum period of 28 days or until death occurs at four levels of exposure to air and water: 100% on land, 70% on land and 30% in water, 50% on land and 50% in water, and 30% on land and 70% in water. These values are comparable to the proportion of time that immature Steller sea lions (≥ 1 year old) spend at sea (Merrick and Loughlin 1997; Trites and Porter 2002).

In general, the daily allocation of fat reserves to meet metabolic demands was greatest when animals spent the en-

Fig. 1. Fat mass (a) and protein mass (b) predicted by the model for juvenile and subadult Steller sea lions (*Eumetopias jubatus*) spending 50% of each day on land in relation to values measured for the same individuals during a captive fasting study. Data are presented for juveniles (1.75–2.0 years old; ●) and subadults (3.5–6.0 years old; ○). Linear regressions and 95% confidence intervals for juveniles are shown by solid lines (juvenile predicted lipid mass = $8.60 + 0.76(\text{juvenile measured lipid mass})$, $F = 21.30$, $r^2 = 0.84$, $p = 0.010$, $n = 6$; juvenile predicted protein mass = $-12.12 + 1.45(\text{juvenile measured protein mass})$, $F = 163.55$, $r^2 = 0.98$, $p < 0.001$, $n = 6$). Linear regressions and 95% confidence intervals for subadults are shown by broken-dotted lines (subadult predicted lipid mass = $-2.11 + 1.23(\text{subadult measured lipid mass})$, $F = 9.75$, $r^2 = 0.71$, $p = 0.035$, $n = 6$; subadult predicted protein mass = $-3.29 + 1.17(\text{subadult measured protein mass})$, $F = 14.80$, $r^2 = 0.79$, $p = 0.018$, $n = 6$). The line of equality (broken line) is also presented.

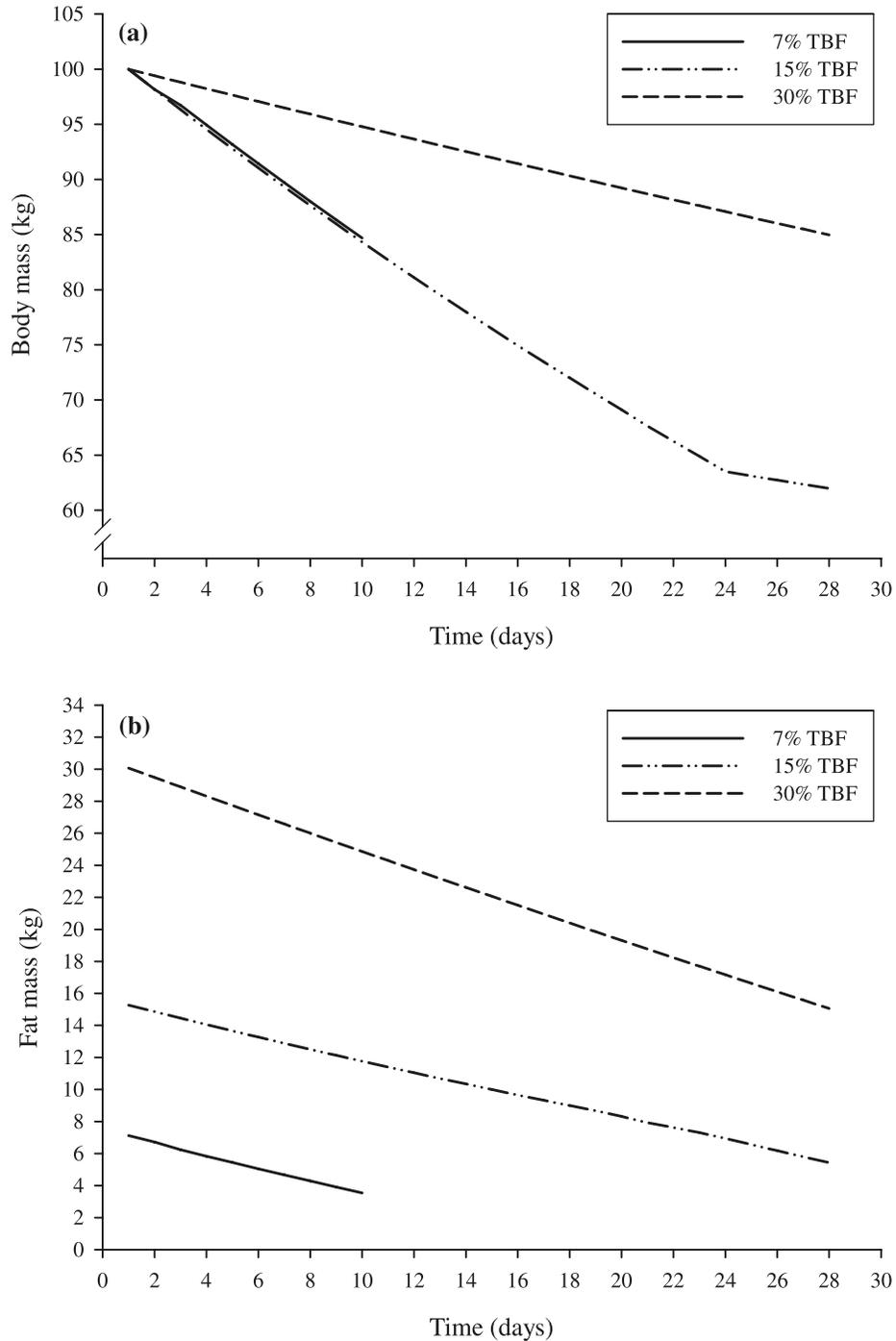


ture fast on land (Fig. 3). However, differences in allocation levels during the four levels of exposure to air and water were only significant for the fattest animal ($H_{[3]} = 10.92$, $p = 0.012$). Furthermore, for all levels of exposure to air and water, the Steller sea lion that initiated the fast with

30% TBF demonstrated significantly higher daily allocation of fat reserves to meet energetic demands than the two leaner sea lions (all $p < 0.05$; Fig. 3).

Animals were also capable of fasting for longer durations while remaining on land for the entire fasting duration

Fig. 2. Daily body mass (a) and fat mass (b) predicted by the model for three juvenile Steller sea lions (*Eumetopias jubatus*) fasting on land for the maximum duration. Predictions for 100 kg juveniles weaned with 7% (solid line), 15% (broken-double-dotted line), and 30% (broken line) total body fat (TBF) content are shown.



(Fig. 4). The Steller sea lion with 30% TBF demonstrated the highest maximum fasting duration and was capable of fasting for the entire 28-day period at all levels of exposure to air and water (Fig. 4). In general, maximum fasting duration was positively related to %TBF at the initiation of the fast for all levels of exposure to air and water and increased for the two leaner seals with increasing time spent on land (Fig. 4).

Interacting effects of body mass and body composition

From the results above, it is evident that %TBF influences fasting capabilities of juvenile Steller sea lions and that increased exposure to water has clear impacts on maximum sustainable fasting durations for leaner individuals. To evaluate the interacting effects of body mass and %TBF, we compared predictions of allocation and maximum fasting duration for juvenile Steller sea lions weighing 80 and

Fig. 3. Daily allocation predicted by the model for three juvenile Steller sea lions (*Eumetopias jubatus*) fasting for variable proportions of each day on land and in water for maximum durations. The mean + 1 SE daily allocation (proportion of lipid energy utilized to fuel metabolic demands) for 100 kg juveniles weaned with 7%, 15%, and 30% total body fat (TBF) content fasting 100% on land (black bar), 70% on land (dark grey bar), 50% on land (light grey bar), and 30% on land (white bar) are presented. The absence of error bars for four of the sea lions is due to the model predicting the same allocation level for every day of the fast.

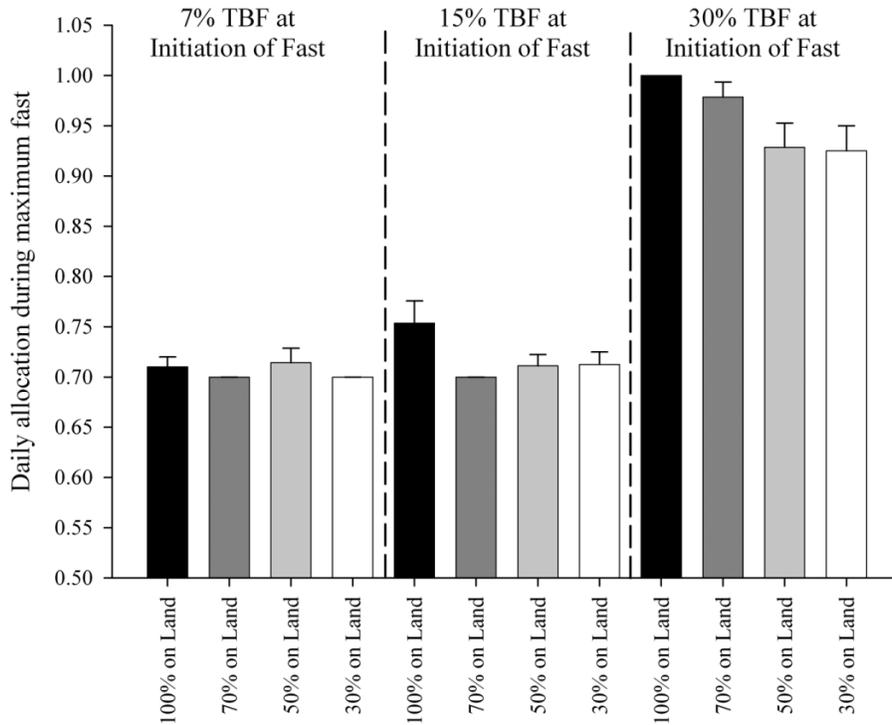
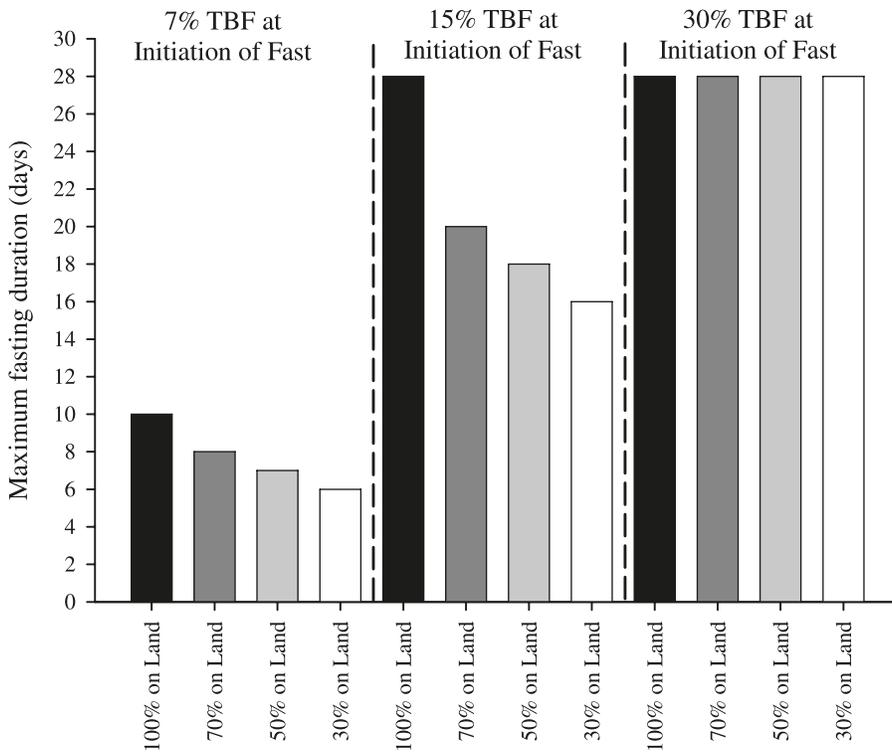


Fig. 4. Maximum fasting duration predicted by the model for three juvenile Steller sea lions (*Eumetopias jubatus*) fasting for variable proportions of each day on land and in water. Maximum durations predicted for 100 kg juveniles weaned with 7%, 15%, and 30% total body fat (TBF) content fasting 100% on land (black bar), 70% on land (dark grey bar), 50% on land (light grey bar), and 30% on land (white bar) are presented.



180 kg with identical %TBF, ranging from 5% to 35% (similar to the range measured in wild juveniles; Rea 2002). We present results for these animals spending only 30% of each day on land to illustrate the response of actively foraging young Steller sea lions during a period of extreme reduced prey availability.

Body mass and %TBF have a synergistic relationship during fasting. As expected, the allocation of fat reserves to meet metabolic demands increases with increasing %TBF at the initiation of the fast (Fig. 5a). However, there is a striking difference in allocation levels between 80 and 180 kg individuals with identical %TBF at the initiation of the fast. Generally, unless 80 kg animals initiate a fast with at least 27% TBF, the allocation levels for these individuals are considerably less than those for 180 kg animals with identical %TBF (Fig. 5a). Furthermore, maximum fasting duration increases with increasing %TBF and is further influenced by body mass (Fig. 5b). For example, individuals that are 180 kg are capable of fasting for 28 days when spending only 30% of each day on land if they initiate the fast with $\geq 22\%$ TBF (Fig. 5b). In comparison, sea lions that weigh 80 kg are not capable of fasting for 28 days unless they initiate the fast with $\geq 30\%$ TBF. At this level of body fat ($\geq 30\%$ TBF), 80 and 180 kg individuals have nearly identical mean allocation levels (Fig. 5a).

Discussion

Field measurements and studies conducted in captivity are time consuming and limit sampling intervals and the number of Steller sea lions that can be examined. In contrast, models are able to predict food requirements (Winship et al. 2002) and patterns of body energy reserve utilization during periods of unsuccessful foraging (present study) for a larger number of sea lions, representing a range of body conditions. The output from foraging (e.g., Winship et al. 2002) and fasting (present study) models can be used to assess the potential for limitations in prey availability to contribute to the decline of the Steller sea lion population.

The state variable Steller sea lion fasting model adjusts allocation levels daily, based on current body mass and fat content, and is an accurate tool for predicting allocation of energy reserves and changes in body condition for fasting juvenile and subadult Steller sea lions. Differences in body condition, primarily fat content and secondarily body mass, result in distinct predictions for allocation of energy reserves by the model. We find that besides body condition, the proportion of time that sea lions spend resting on land and foraging in water is also important in determining energy reserve utilization patterns.

It is important to note that this model was strictly parameterized to closely approximate realistic body condition and energy utilization patterns in juvenile Steller sea lions. Because fat content was the measure of fitness for the model, relaxing the allowable range of allocation levels resulted in unrealistic outputs for body energy reserve utilization patterns and body condition at the end of the fast. In general, when allocation levels were allowed to vary from 0.0 to 1.0, rather than from 0.7 to 1.0 in the present model, the model predicted much lower allocation levels (e.g., more protein was utilized than physiologically feasible) during

the fast, with the concomitant result that sea lions ended the fast with relatively higher fat contents. These unrealistic results demonstrate the importance of having access to reliable data when setting parameters for physiological models.

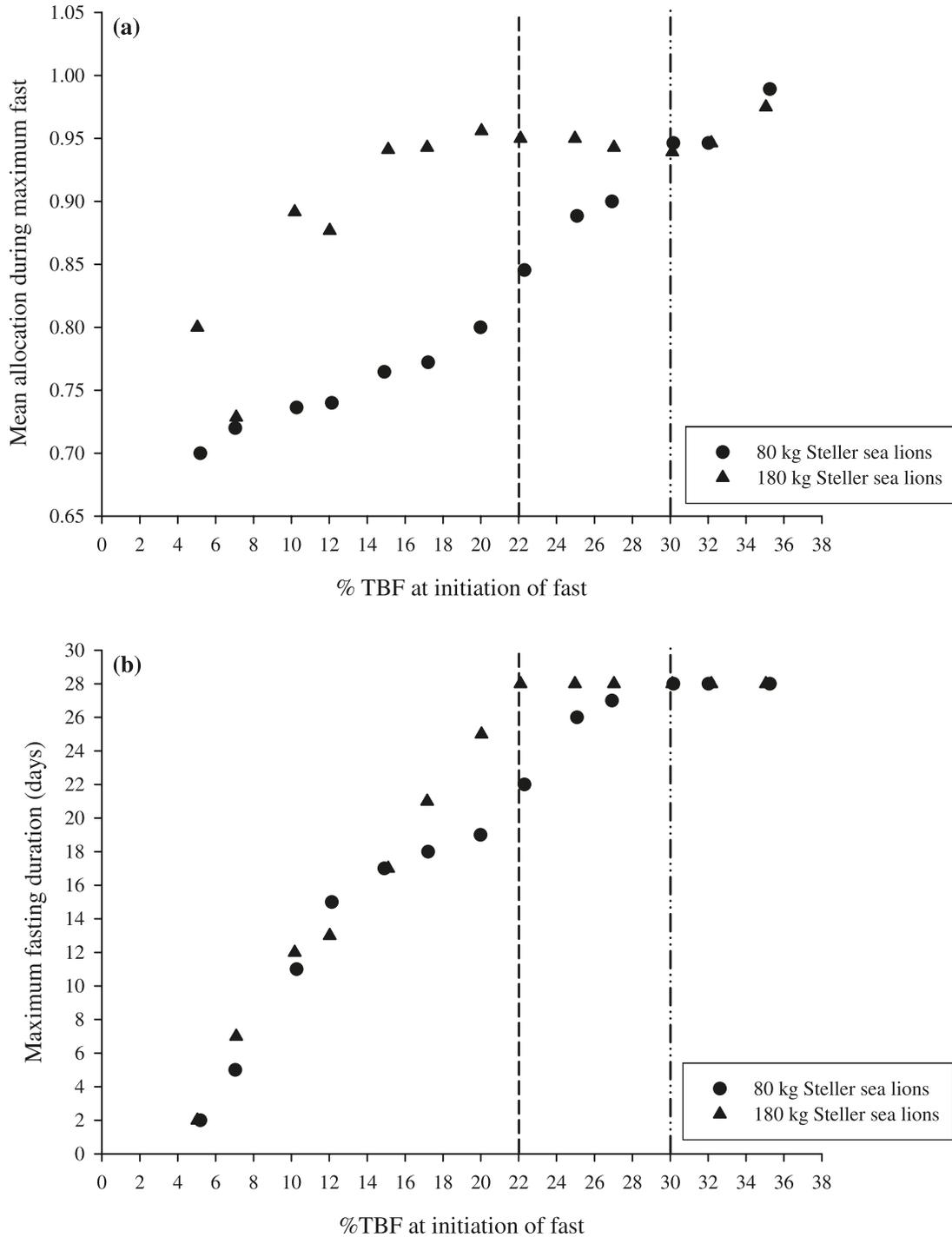
The present model predicts that the utilization of fat and protein during fasting in juvenile Steller sea lions is variable and depends on body fat content. Specifically, fatter individuals utilize a larger proportion of lipid stores than thinner cohorts, which have higher rates of protein catabolism. Equivalent results have been found previously in fasting phocids (Øritsland et al. 1985; Rea and Costa 1992; Crocker et al. 1998; Carlini et al. 2001; Crocker et al. 2001; Noren 2002; Noren et al. 2003), subantarctic fur seal pups (*Arctocephalus tropicalis* (J.E. Gray, 1872)) (Beauplet et al. 2003), and captive juvenile and subadult Steller sea lions (Rea et al. 2007, 2009). Similarly, the ability for fatter individuals to achieve and maintain a lower rate of protein catabolism while fasting has been demonstrated in several other mammalian species and birds (Goodman et al. 1980; Robin et al. 1988; Atkinson et al. 1996; Hilderbrand et al. 2000).

Prior to the present study, no studies have investigated the relationship between body fat reserves and fasting duration limits in free-ranging weaned Steller sea lions. Yet studies on attendance patterns of lactating female Steller sea lions suggest that fat stores of nursing pups do limit the fasting capabilities of pups. As pups grow larger, they develop greater energy reserves, allowing longer fasting intervals between feedings (Millar 1977), thus enabling females to spend more time at sea (Higgins et al. 1988; Merrick and Loughlin 1997; Trites and Porter 2002). Having large energy reserves at weaning is beneficial to otariid pups because greater stores will also sustain weaned juveniles longer during periods of unsuccessful foraging. Because of their naivety and reduced diving abilities (Richmond et al. 2006), initial foraging attempts following weaning are likely to be unsuccessful, particularly if local prey resources are limited.

Unlike previous studies on juvenile and subadult Steller sea lions fasting in captivity, which limited fasting durations to 7–14 days (Rea et al. 2007, 2009), the model can predict energy reserve utilization patterns and fasting duration limits for young Steller sea lions that are faced with a longer period of food deprivation (28 days). The model predicts that lean Steller sea lions that have high rates of protein catabolism are not capable of fasting for the durations achieved by fatter sea lions. These results are indicated by lower allocation levels and shorter elapsed time until critical levels of body mass or %TBF are attained by lean Steller sea lions. Similar results have been observed in free-ranging northern elephant seals (*Mirounga angustirostris* (Gill, 1866)) during the postweaning fast (Noren 2002; Noren et al. 2003).

During these fasting periods, the model also predicts that the utilization of fat and protein reserves in Steller sea lions depends on the proportion of each day spent resting on land and foraging in the ocean. This has been shown in comparisons across phocid species; interspecific differences in the utilization of fat and protein reserves during a fast are attributed to the thermal demands of the environment (Worthy and Lavigne 1987). Also, the higher metabolic rates of young otariids in cold water (Blix et al. 1979; Donohue et al. 2000; Rutishauser et al. 2004) would necessarily increase energy utilization, including protein stores, for Steller sea

Fig. 5. Mean allocation (proportion of lipid energy utilized to fuel metabolic demands) during the maximum fasting duration (a) and maximum fasting duration (b) predicted by the model for 80 and 180 kg juvenile Steller sea lions (*Eumetopias jubatus*) fasting for 30% of each day on land in relation to percent total body fat (%TBF) at the initiation of the fast. Predictions for 80 kg (●) and 180 kg (▲) individuals are presented. The broken and broken-double-dotted lines denote the level of %TBF that 180 and 80 kg sea lions, respectively, must initiate the fast with to survive the 28-day fasting period.



lions that forage unsuccessfully in the ocean. Sparing fat reserves by catabolizing some lean tissue safeguards the insulating role of blubber. This may be especially important for juvenile Steller sea lions that are weaned with relatively low fat content because body condition influences thermoregulatory abilities of pinnipeds in water (Irving and Hart 1957).

Thus, lean individuals are faced with additional challenges that fatter sea lions are buffered against when foraging unsuccessfully. Juvenile Steller sea lions that are weaned with lower %TBF catabolize higher levels of protein during food deprivation and have shorter maximum fasting durations than fatter cohorts. These differences in fasting capa-

bilities are amplified when the animals spend more time in water. For example, 80–180 kg juvenile Steller sea lions with <10% TBF are only capable of fasting for 2–7 days when spending 70% of each day foraging in the ocean (Fig. 5b). This relatively low %TBF is a realistic value for Steller sea lions. On average, adult female Steller sea lions are only 7%–9% total body lipid (Davis et al. 1996).

In addition, body mass acts synergistically with body fat content to influence fasting capabilities. In general, lighter sea lions cannot maintain the same fasting durations that heavier counterparts with the same %TBF are able to sustain. This difference in maximum fasting duration is primarily due to the fact that fat reserves scale linearly to body mass, whereas daily energy requirements scale to (body mass)^{0.75}.

It is possible that the fasting limits presented here for juvenile Steller sea lions may be slightly overestimated. This is because we employed a simplistic model that did not take into account the complex changes in metabolic rate due to changes in nutritional status and lipid content. In particular, metabolic rates of fasting Steller sea lions would potentially decrease slightly owing to metabolic depression (see Rosen and Trites 1999), but the reduction in metabolic rate would likely be off-set by increases in metabolism owing to increased thermoregulatory and swimming costs caused by loss of fat content and body mass during periods of unsuccessful foraging (Rosen et al. 2007). Furthermore, when prey density is low, the effort to locate prey is substantially increased (Gende and Sigler 2006), which would require juvenile Steller sea lions to spend a higher proportion of each day in the water searching for prey. This greater foraging effort would likely hasten the rate of increase in metabolism and thus reduce maximum fasting durations further, particularly for small, lean individuals. Consequently, small, lean juvenile Steller sea lions may be especially susceptible to short-term, localized reductions in prey availability owing to their limited fasting capabilities.

Although this is a somewhat simplistic model, the results are useful in demonstrating that young, lean Steller sea lions are not capable of sustaining long fasts. Consequently, a reduction in prey availability could potentially reduce the number of juveniles in the Steller sea lion population. As additional data on foraging effort and metabolic costs of free-ranging sea lions become available, the model can be refined to provide better estimates of fasting limitations for young Steller sea lions. Moreover, it is possible that the resulting body condition of lean animals that survive the fast will be relatively poor, particularly those that end the fast with the lowest lipid levels allowed by the model. Additional data and future modeling efforts are also needed to address the effect of body condition on susceptibility to disease, impacts on growth and development, and future reproductive success in juvenile Steller sea lions.

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