NOTE

Marine Mammal Science

The effect of food restriction on growth rates in Steller sea lions, *Eumetopias jubatus*

David A. S. Rosen [ID]

Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada

Correspondence
Institute for the Oceans and Fisheries, 2202 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
Email: rosen@zoology.ubc.ca

Quantifying the physiological consequences of disturbance (PCoD) is increasingly becoming a standard tool for assessing the effects of ecological changes on individual animals and, subsequently, on their population trajectories (Pirotta et al., 2018). Predicting the effects of changes in prey quality and/or availability has been the focus of several investigations with various marine homeotherms (Baylis et al., 2015; Frid et al., 2006; Kadin et al., 2012; McClatchie et al., 2016). For example, there has been a concerted scientific effort to determine whether changes in prey availability or quality have contributed to the 85% decline in Steller sea lion (*Eumetopias jubatus*) populations in Western Alaska (Fritz et al., 2019; Merrick et al., 1997; National Marine Fisheries Service, 2008).

While episodes of suboptimal energy intake from prey can have numerous short- and long-term physiological effects, the most rudimentary consequence is a decrease in body mass. One key element to understanding the effects of nutritional stress and recognizing its role in wild populations is quantifying the effect of episodes of decreased food energy intake on the growth rates and body mass of individual animals (Nisbet et al., 2012; Silva et al., 2020). A number of studies have examined specific scenarios involving changes in prey intake on aspects of Steller sea lion physiology and health through experimental manipulations with Steller sea lions under human care (reviewed in Rosen, 2009). However, an overall predictive model of the fundamental effects of reductions in energy intake on body mass and growth has not been established. This information is critical for bioenergetic modeling efforts to envision the effects of a range of ecological disturbances on individual Steller sea lions and, subsequently, on populations.

This study used data from 12 female Steller sea lions, brought into human care as pups and maintained as a permanent research colony at the Vancouver Aquarium (Vancouver, BC, Canada). As part of the long-term conservation research program, the animals were occasionally subject to various experimental changes in gross energy food intake (GEI). These manipulations included decreases in the intake level of their normal diet (typically predominantly herring, *Clupea pallasi*, supplemented with squid, *Doryteuthis opalescens*, and occasionally assorted other species), switches to lower energy density prey items (primarily Atka mackerel, *Pleurogrammus monopterygius*, or walleye pollock, *Gadus chalcogrammus*), and periods of complete fasting. Food restrictions and prey substitutions typically lasted from 2 to 4 weeks, while fasts were for shorter periods in line with animal care protocols that limited body mass loss to a maximum of 15% of initial mass. Throughout their tenure at the Aquarium, daily food intake was carefully monitored, and body mass (±0.1 kg) was measured prior to the first feed of the day on a platform scale. Food intake was converted to GEI using proximate and energy analysis of representative samples from each fish batch by a commercial laboratory (SGS Canada, Burnaby, BC, Canada).

The lifetime husbandry record for each sea lion was reviewed for episodes of experimental diet manipulations that resulted in some degree of mass loss. The usual time period between separate diet manipulations was several months, and data were only used for this study if there was a minimum of 30 days between the start of the experimental manipulations and the end of the previous manipulation period. It is important to note that pinnipeds, even those maintained under human care, display seasonal cycles in both GEI and body mass, thought to mirror changes in the wild. The goal of this study was to investigate the effect of unpredicted changes in GEI on growth rates. Hence, data from natural, animal controlled, seasonal changes in GEI and body mass were expressly omitted from the data set. These naturally occurring cycles are also why we examined the effects of changes in GEI (rather than absolute intake) on changes in growth rates (rather than absolute body mass), as the restriction episodes may have occurred during periods of natural hyperphagia or hypophagia, when animals were gaining or losing body mass.

Both average daily growth rate (GR_{con}) and average daily GEI (GEI_{con}) were calculated over a 10-day control period immediately prior to the start of the identified dietary manipulation (day 0). GR_{con} was calculated from the difference in body mass between the start and end of the 10-day control period (i.e., $(M_0 - M_{-10})/10$), and GEI_{con} was calculated from the average food energy intake over the same period. Similarly, average growth rate during the experimental phase (GR_{exp}) was calculated from the difference in body mass at a maximum of 10 days into the experiment and mass at the start of the trial (i.e., $(M_{10} - M_0)/10$); the formula was adjusted appropriately for trials lasting <10 days. Average daily GEI during the experimental period (GEI_{exp}) was calculated from daily intake data over the same period. This allowed calculation of the change between the control and experimental phases for both growth rates ($dGR = GR_{exp} - GR_{con}$) and gross energy intake ($dGEI = GEI_{exp} - GEI_{con}$). A negative dGR defines how much lower the average rate of growth was during the experimental period compared to the control period. GR_{con} ranged from −0.6 to 1.2 kg/day and, as per the defined conditions, there was always mass loss during the experimental phase, ranging from −0.1 to −2.2 kg/day. Similarly, dGEI (which was always negative) denotes the level of decrease in GEI during the experimental period relative to the control period.

In total, the records yielded a total of 121 usable data points, encompassing 5–14 experimental manipulation periods for each of the 12 sea lions, spanning the ages of 8 months to 17 years of age (most were >3 years of age), and initial body masses of 49.6–227.5 kg. The data set included dGEI between −3,140 and −66,000 kJ/day, with resulting dGR between −0.2 and −3.7 kg/day.

Linear mixed effect (LME) models were constructed to examine the relationship between dGR and dGEI (Pinheiro & Bates, 2009). Analyses were performed using lme4 (Bates et al., 2014) within R version 3.6.3 (R Core Team, 2020) and RStudio version 1.2.5042 (RStudio Team, 2020). Individual sea lion was used as a random factor to account for repeated measures within individuals (Harrison et al., 2018). An a priori decision was made to force the intercept through the origin based on the physiological principle that, by definition, a lack of experimental manipulation in food intake would not result in any change in growth rates (i.e., when dGEI = 0, dGR = 0). Even though dGR was the response variable to dGEI, I chose to express the linear relationship as dGR = a + b*dGEI as it provided more salient ecological information.

No other predictive variables (e.g., starting body mass, season, prerestriction growth rates, etc.) were included as potential explanatory variables in the model analyses. They were purposely excluded to derive as robust a predictive equation as possible. However, for a separate analysis, the data were divided by calendar month to ascertain whether changes in growth rates were higher or lower than predicted at certain times of year. I calculated the difference between the observed and the predicted dGR from the linear regression model derived for each individual sea lion. Resulting positive values denote when observed dGR was greater than predicted for a given food restriction, and negative values denote lower than expected dGR. Although the data did not lend themselves to rigorous statistical testing (there were too many levels to include "month" in any models, and no a priori justification for grouping months into seasons), combining the monthly data from all sea lions allowed identification of potential seasonal patterns for future investigation.

There was a strong relationship between dGR and dGEI for all 12 sea lions (individual r^2 between 0.72 and 0.93), and each animal had a similar response; for example, individual slopes varied from 15,688 to 27,266. As a result,

there was essentially no individual variation to account for, such that incorporating random effects did not improve the model fit.

Hence, the best model to describe dGEI as a function of dGR was:

$$dGEI\,(kJ/day) = 20,700*(dGR\,kg/day)$$

(r^2 = 0.97, p < .0001; Figure 1). This means that for every decrease of 20,700 kJ/day in gross energy intake the sea lions are predicted to have their growth rate decrease by 1.0 kg/day compared to when they are not restricted.

Visual inspection indicated there was some heteroscedasticity apparent in the data. While this does not cause bias in the coefficient estimates, it can lead to poor estimates of the standard error. A post hoc analysis using log-transformed data confirmed that the relationship between dGEI and dGR was significant (r^2 = 0.83, p < .0001).

Despite the strong overall relationship, there was inevitable variation within the data. There are reasons to speculate whether animals undergoing a complete fast will have the same physiological response as those undergoing food restriction, and therefore exhibit a different relationship between energy intake deficits and changes in growth rates. There were only four episodes of complete fasting that were integrated into the study data set, precluding any robust statistical testing of this hypothesis. However, three of these episodes appear to closely fit the overall relationship (Figure 1), and exclusion of these points only marginally altered the predicted slope of the relationship (to 20,820). Also, examination of Figure 1 shows that the relationship is less robust for instances where changes in growth rates and food restriction are greatest. A segmental linear regression confirmed that there was no significant inflection point separating the data in terms of the degree of imposed food restriction. Still, the decreased predictive precision for these more extreme cases implies that care should be taken when applying the results to this level of food restriction in modeling exercises.

The resulting regression equation allows us to make the following related estimates: (1) the energy derived from catabolizing tissues to compensate for energy intake deficits, and (2) the effect of specific changes in GEI on GR. In theory, if all other aspects of an animal's energy budget remain constant (e.g., no compensatory changes in resting metabolism, activity, or digestion), changes in growth rates due to decreased food intake should simply be the result of the level of tissue catabolism needed to offset that energy intake deficit. The amount of energy derived from tissue catabolism is central for most bioenergetic modeling, but is difficult to predict and is rarely empirically derived. The amount of energy obtained from mass loss will depend on the proportion of different tissues catabolized, which are primarily muscle and subcutaneous blubber for marine mammals. The energy density of fats (37 kJ/g) and protein (17 kJ/g) is well known, and the composition of muscle and blubber in pinnipeds is relatively well documented (though naturally variable). Muscle composed of 75% water, 20% protein, and 5% fat, should contain ~5.3 kJ/g. Likewise, if blubber contains 56% lipids (see table S3 in Liwanag et al., 2012), it should have an energy density of ~20.7 kJ/g. The actual energy that is available to an animal from catabolism for other energetic processes will vary
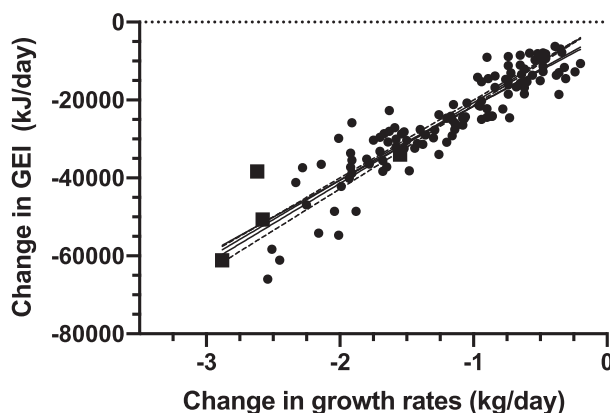
FIGURE 1 Relationship between changes in growth rates (dGR) under different changes in gross energy intake (dGEI) (r^2 = 0.97, p < .0001). The resulting equation was dGEI (kJ/day) = 20,700*(dGR kg/day). Broken lines represent 95% confidence limits, and the four episodes of complete fasting are indicated by square symbols.

depending on the energetic pathway, the efficiency of conversion, and the proportion of tissues used. Although it is generally assumed that marine mammals preferentially utilize subcutaneous blubber as an energy reserve, these tissues are limited in otariids compared to phocid seals, and a minimal level of protein catabolism is required for gluconeogenesis to fuel the central nervous system.

The mean slope of the equation in this study predicts that (for an animal neither gaining nor losing mass) a GEI deficit of 20.7 kJ would result in a loss of 1 g of tissue. While this value is coincidentally the same as the estimated energy density of blubber, it is unlikely that sea lions were solely catabolizing lipid reserves to offset GEI deficits. Not only were sea lions rarely undergoing complete fasts (where lipid utilization is more dominant), but the equation is predicting changes due to a deficit in GEI, which can be 20%–75% greater than net energy (the difference being various costs of digestion) (Rosen & Worthy, 2018). This would suggest that the metabolic energy derived directly from tissue catabolism is closer to 12–17 kJ/g, consistent with a higher level of muscle (vs. blubber) catabolism and/or decreased catabolic efficiency. The difference between an assumed benefit of 20.7 kJ/g (100% lipid with 100% efficiency) and our empirically derived value (12–17 kJ/g) can significantly alter the predictions of bioenergetic models.

Fortunately, our empirically derived equation is not dependent on any assumptions of tissue composition, conversion efficiency, or underlying changes in an animal's energy budget when used to estimate how changes in food intake—which is usually the ecological measure of interest—result in changes in body mass. For example, while the diet of Steller sea lions varies greatly in the wild, differing by geographic area, season, and demographic group (Goto et al., 2017; Sinclair et al., 2018; Tollit et al., 2017), an average estimate of prey energy density of 5.2 kJ/g (wet weight) is reasonable. A sea lion subject to a daily unpredicted decrease in intake of 2.0 kg of prey is therefore facing an energy deficit of 10,400 kJ. This study suggests that, over a period of time, this level of prey restriction will result in a decrease in growth of 0.5 kg/day. In other words, a sea lion that is previously neither growing nor losing mass will lose 0.5 kg of body mass every day it fails to make up for that prey intake shortfall.

Of course, there are a number of alternate options available to offset this GEI deficit. Animals will naturally compensate for unpredicted decreases in daily intake by increasing food intake on subsequent days. Steller sea lions have been shown to be able to alter intake in response to changes in both prey availability and energy density (Rosen & Trites, 2004), although this ability is limited by subsequent prey availability and physiological constraints on digestion. Steller sea lions can also respond to energy deficits by decreasing energy expenditures, such as changes in resting metabolic rate (i.e., metabolic depression; Guppy et al., 1994), thereby limiting the effects on body mass (Rea et al., 2007; Rosen & Trites, 2002). The physiological response of Steller sea lions to decreases in energy intake has been shown to vary by age, prey composition, and season (Rea et al., 2009; Rosen, 2009; Rosen & Trites, 2002). A visual inspection of the results (Figure 2) indicates that rates of mass loss for a given GEI restriction were higher than expected during the fall/winter period (October–January) and lower in the spring (March). This agrees with earlier laboratory studies that suggest that winter is a more critical period for adequate food intake (Kumagai et al., 2006;

FIGURE 2 Deviation in observed growth rates from predicted growth rates for each calendar month (broken line = zero deviation). Positive values denote higher than predicted changes in growth rates. Data are represented for each of the 121 selected trials. Individual data are staggered for clarity, and the monthly median is represented by a solid line.
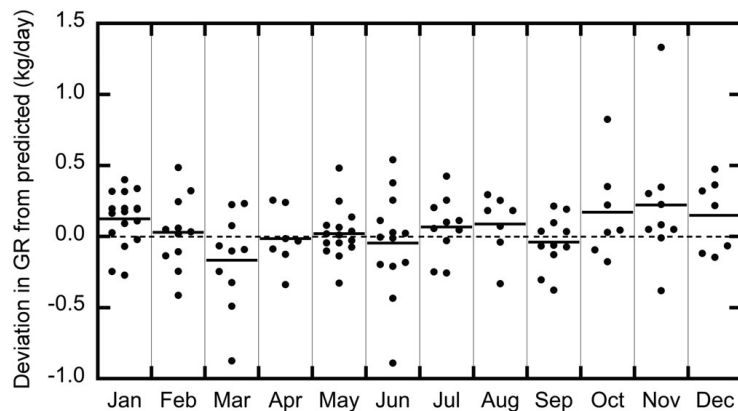
Richmond et al., 2010; Rosen & Kumagai, 2008), although they may also be more able to recover from such episodes in this season (Jeanniard du Dot et al., 2008).

Given all of the aforementioned physiological responses and caveats to the effect of energy intake restrictions on body mass, it is remarkable how consistent the changes in growth rates were across a diverse data set incorporating different levels of restriction, dietary manipulations (e.g., restricted ingested mass versus lower energy density prey), type of prey (and associated differences in digestive efficiency), seasons, and age classes (juveniles to adults). This suggests that differences attributable to these additional factors are minor compared to the overall relationship between energy intake and growth rates. It is important to remember, however, that all of the data were obtained from nonreproducing female sea lions. Although adult males or lactating females might have different bioenergetic priorities, there is no apparent reason why this broad equation would not be reasonably applicable to these groups. Another advantage of the predictive equation is that it is seemingly independent of starting body mass or food intake levels—that is, it avoids the complications of estimating the effect of relative changes in intake and mass. Rather, the equation predicts the effects of absolute changes in energy intake on absolute changes in growth. Hence, the predictive equation is applicable across a broad range of levels of energy restriction (although less precise with greater levels of restriction), and is largely unaffected by seasonal differences in prerestriction growth rates. This robust estimate of the relationship between unpredicted changes in gross energy intake and growth is therefore invaluable for incorporating into bioenergetic models estimating the effects of changes in prey availability on Steller sea lions in the wild.

AUTHOR CONTRIBUTIONS

David Rosen: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; writing-original draft; writing-review & editing.

ORCID

David A. S. Rosen https://orcid.org/0000-0003-2931-9608

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