

# Rates of maximum food intake in young northern fur seals (*Callorhinus ursinus*) and the seasonal effects of food intake on body growth

D.A.S. Rosen, B.L. Young, and A.W. Trites

**Abstract:** Accurate estimates of food intake and its subsequent effect on growth are required to understand the interaction between an animal's physiology and its biotic environment. We determined how food intake and growth of six young northern fur seals (*Callorhinus ursinus* (L., 1758)) responded seasonally to changes in food availability. Animals were given unrestricted access to prey for 8 h·day<sup>-1</sup> on either consecutive days or on alternate days only. We found animals offered ad libitum food on consecutive days substantially increased their food intake over normal "training" levels. However, animals that fasted on alternate days were unable to compensate by further increasing their levels of consumption on subsequent feeding days. Absolute levels of food intake were highly consistent during winter and summer trials (2.7–2.9 kg·day<sup>-1</sup>), but seasonal differences in body mass meant that fur seals consumed more food relative to their body mass in summer (~27%) than in winter (~20%). Despite significant increases in absolute food intake during both seasons, the fur seals did not appear to efficiently convert this additional energy into mass growth, particularly in the winter. These seasonal differences in conversion efficiencies and estimates of maximum intake rates can be used to generate physiologically realistic predictions about the effect of changes in food availability on an individual fur seal, as well as the consequences for an entire population.

**Résumé :** Il est nécessaire d'obtenir des estimations précises de l'ingestion de nourriture et de son effet subséquent sur la croissance, si on veut comprendre l'interaction entre la physiologie d'un animal et son environnement biotique. Nous avons mesuré comment l'ingestion de nourriture et la croissance chez six jeunes otaries à fourrure du Nord (*Callorhinus ursinus* (L., 1758)) réagissent aux changements de disponibilité de nourriture au cours des saisons. Les animaux avaient un accès illimité à leurs proies durant 8 h·jour<sup>-1</sup>, soit pendant des jours consécutifs, soit seulement aux deux jours. Les animaux qui ont un accès à la nourriture ad libitum pendant des jours consécutifs augmentent substantiellement leur ingestion de nourriture au-delà des niveaux normaux d'« entraînement ». Cependant, les animaux privés de nourriture à tous les deux jours n'arrivent pas à compenser en augmentant encore plus leurs niveaux de consommation de nourriture durant les jours suivants d'alimentation. Les niveaux absolus d'ingestion de nourriture sont très semblables durant les expériences en hiver et en été (2,7–2,9 kg·jour<sup>-1</sup>), mais les différences saisonnières de masse corporelle font en sorte que les otaries à fourrure consomment plus de nourriture relativement à leur masse corporelle en été (~27 %) qu'en hiver (~20 %). Malgré des augmentations significatives de l'ingestion absolue de nourriture durant les deux saisons, les otaries à fourrure ne semblent pas transformer de manière efficace cette énergie additionnelle en croissance de leur masse, particulièrement en hiver. Ces différences saisonnières d'efficacité de conversion et les estimations des taux maximaux d'ingestion peuvent servir à émettre des prédictions physiologiquement réalistes au sujet des effets du changement de disponibilité de la nourriture sur une otarie à fourrure individuelle et aussi des conséquences sur la population toute entière.

[Traduit par la Rédaction]

## Introduction

Maximizing food intake is critical to the long-term health and survival of young mammals. Food energy intake supports body growth and energy storage, which ultimately affect survival and reproductive success. However, maximum rates of food intake are limited by several factors, including biochemical limits to metabolic processes, availability of suitable prey, and digestive capacity. Digestive capacity refers to the physiological and anatomical limits imposed by factors such as stomach size and breakdown and assimilation time

(Weiner 1992). The capacity (as measured by volume or throughput rates) of an animal's digestive system may be further altered by developmental and seasonal considerations. In general, the sustainable upper limit of the energy budget of endotherms under optimal conditions is set by the capacity of the digestive tract to assimilate nutrients from food (Diamond 1991; Weiner 1992; Hammond and Diamond 1997).

Northern fur seals (*Callorhinus ursinus* (L., 1758)) are native to the North Pacific Ocean. Pups are weaned at about 4 months of age, which is relatively early for otariids (sea lions and fur seals; Gentry et al. 1986). Pups of northern fur

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seals spend the next 20 months at sea and are rarely observed until they return to their breeding islands at 2 years of age (Kenyon and Wilke 1953; National Marine Fisheries Service 2007). Consequently, little is known regarding their early physiology, including seasonal changes in their energy budget related to growth. Similarly, their capacity to alter food intake in response to changes in energy demands or prey availability during this critical period is undocumented.

Recent declines in numbers of northern fur seals and decreases in mean body length on the Pribilof Islands, Alaska, have raised the question of whether these animals are nutritionally stressed, particularly during their early formative years (Testa 2008). Nutritional stress could result from either detrimental decreases in prey quality or prey availability, or increases in energetic costs (Trites and Donnelly 2003; Rosen 2009). All three potential mechanisms are impacted by limitations in digestive capacity. Decreases in prey quality would most directly affect health and survival if fur seals are physiologically limited in their ability to consume sufficient quantities of lower quality prey. Similarly, increased energy demands would negatively impact individuals that could not increase prey intake to fulfil their heightened requirements. Finally, transient decreases in prey availability would negatively impact fur seals if they could not sufficiently increase food intake levels during periods when food is plentiful to meet their overall nutritional requirements (Barboza and Hume 2006).

The effect of changes in behaviour or prey quality on marine mammals has been explored through bioenergetic models (Bowen 1997; Hammill et al. 1997; Winship et al. 2002; Williams et al. 2004). Unfortunately, physiologically realistic limitations on food intake levels are rarely, if ever, incorporated into the model parameters partly because of a paucity of data. In the only published study for a marine mammal, young Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)), showed a strong inclination to adjust food intake levels to compensate for changes in quality and availability, but appeared limited to maximum daily levels equivalent to ~16%–20% of their own body mass (Rosen and Trites 2004). Failure to incorporate physiological digestive limitations in ecological models will result in inaccurate predictions, such as the effect of transient changes in food supplies on an individual's energy balance or the potential impact of marine mammal consumption on fish stocks.

Young northern fur seals are much smaller than Steller sea lions, and may not face the same relative digestive constraints regarding maximum food intake levels. While there are several ruminant-based allometric relationships relating body mass and total energy intake (see Peters 1983), there is, unfortunately, little information on how digestive capacity (stomach volume, gut volume, or processing capacity) change with body size in nonruminants (c.f., MacLarnon et al. 1986; Clauss et al. 2007). As a default, it is generally assumed that relative maximum food intake levels (as a proportion of body mass) decrease with increasing body size in tandem with similar changes in energy requirements (most famously demonstrated by Kleiber 1975). Thus, northern fur seals might have greater maximum food intake levels relative to body mass than Steller sea lions. However, these higher required rates of food intake could also result in a lower capacity to

subsequently compensate for unforeseen periods of low food intake.

In addition, it is known that most marine mammals naturally exhibit highly seasonal variation in food intake (Renouf and Noseworthy 1991; Ryg and Øritsland 1991; Lager et al. 1994; Rosen and Renouf 1998). In many mammals, this seasonal drop in food intake is associated with decreased capacity to process food owing to downregulation of the digestive system (Barboza and Hume 2006; Naya et al. 2007). There are indications that young northern fur seals exhibit seasonal changes in growth (Trites and Bigg 1996), with relatively low growth during the winter. It is therefore reasonable to predict that their maximum food intake capacity alters seasonally, and that they may not possess the digestive capacity to effectively process large quantities of food and convert it into body growth at these times of the year.

Our study quantified the capacity for northern fur seals to alter food intake in response to seasonal changes in their biotic environment and the physical implications of these changes. Our goal was to provide more realistic estimates of maximum food intake than currently available, as well as the subsequent affect of food intake on growth—both of which are required to understand the interaction between an animal's physiology and its biotic environment. Specifically, we quantified the unrestricted maximum feeding rates of young northern fur seals. We predicted that maximum relative food intake levels would be greater than previously reported for larger Steller sea lions (Rosen and Trites 2004). We hypothesized that animals would alter their food intake in response to changes in prey availability and seasonal energy requirements, but that this capacity would be limited by their relatively high overall food requirements. We differentiated the effect of seasonal changes in food intake on body mass, given the hypothesis that seasonal changes in bioenergetic priorities should alter their capacity to transform additional energy intake into body mass.

## Materials and methods

Six female northern fur seals participated in this study. They were born in July 2008 on the Pribilof Islands, Alaska, and brought to research facilities at the Vancouver Aquarium, Canada, when weaned at 4 months of age. All experimental protocols were conducted under the authority of The University of British Columbia Animal Care Permit A06-351. The normal feeding regime of the fur seals consisted of eating previously frozen Pacific herring (*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847) 2–3 times·day<sup>-1</sup>. In general, fish was provided in ~20 g pieces, although some whole fish was also fed. Daily food intake targets were set weekly by animal care staff at levels designed to provide sufficient levels of energy intake without compromising training requirements.

The feeding trials were replicated during summer (19 May to 20 August 2009; age 10–13 months) and winter (6 December 2009 to 11 February 2010; age 17–19 months). Fur seals were held individually (sometimes with an overnight fur seal companion) in a pool area that also contained adequate haulout space. A feeding trough with a freshwater flow was placed in the haulout area and filled with whole Pacific herring each morning. The animals were permitted to

**Table 1.** Body mass and mean daily food intake of young northern fur seals (*Callorhinus ursinus*) fed on either consecutive days (consecutive) or alternate days (alternate) during summer and winter seasons.

Animal	Summer			Winter		
	Initial mass (kg)	Consecutive food intake (g·day <sup>-1</sup> )	Alternate day food intake (g·day <sup>-1</sup> )	Initial mass (kg)	Consecutive food intake (g·day <sup>-1</sup> )	Alternate day food intake (g·day <sup>-1</sup> )
F08ME	10.0	2152.8	2612.8	13.7	2120.4	2622.6
F08TI	12.5	3863.6	3879.8	15.9	3109.4	3037.4
F08TU	9.6	2463.0	2791.2	13.2	2674.4	2410.6
F08KY	10.8	3011.2	2967.0	14.9	2335.4	2837.6
F08AY	11.1	2571.0	2770.0	12.4	2763.3	2733.4
F08AN	9.8	1908.8	3161.5	13.6	2815.8	2468.8

consume as much herring as they wanted from the trough within an 8 h period, with minimal interaction from training or research staff. Fish was continuously supplied to the fur seals, but prey was replaced in the trough if uneaten after 90 min. At the end of each experimental feeding day, the pool was checked for uneaten fish, which was subtracted from the daily intake total.

Each complete trial lasted 16 days, and consisted of a 6-day consecutive feeding protocol and an 11-day alternate day feeding protocol (consisting of 6 feeding days interspersed with 5 fasting days). The order of the treatments (starting with alternate or consecutive days protocols) was split between the 6 fur seals in the summer trials, and reversed for each animal for the winter trials. The last day of one treatment served as the first day of the next treatment and the first day of each treatment (essentially a “training day”) was discarded for purposes of statistical analysis.

Body mass of the fur seals was obtained by having them station on a platform scale ( $\pm 0.02$  kg) in the morning prior to first feed of the trial. Although mass were gathered opportunistically during the trials, the “final” mass was defined as the prefeed mass ~56 h after the end of the trials and resumption of normal trainer-controlled intake levels. This delay was to ensure a measure of “true” body mass that was unaffected by large changes in gut fill attributable directly to the increased food intake during the trials.

### Statistical analysis

Data were analyzed within a repeated-measures framework using either paired *t* tests or repeated-levels ANOVA (depending on the number of comparisons). For each animal, a mean food intake for each treatment (consecutive, alternate) within each season was calculated after discarding the first day of each treatment (adjustment day) (Table 1). To evaluate the (seasonal) effect of unrestricted food access on food intake, mean “pre-experimental” food intake was also calculated over the 16-day period immediately preceding each seasonal trial (a period equivalent to the trial length).

Growth rate was calculated from mass changes over each complete 16-day seasonal trial and the equivalent 16-day period immediately preceding each seasonal trial. Change in body mass over the course of the experimental trial was calculated as the difference between the fur seals’ pre-experimental mass on the first day of the trial and their mass ~56 h after the completion of the trials (i.e., the morning following two full days of “normal” food intake). This delay was required to avoid biases in body mass owing to changes in gut fill.

### Results

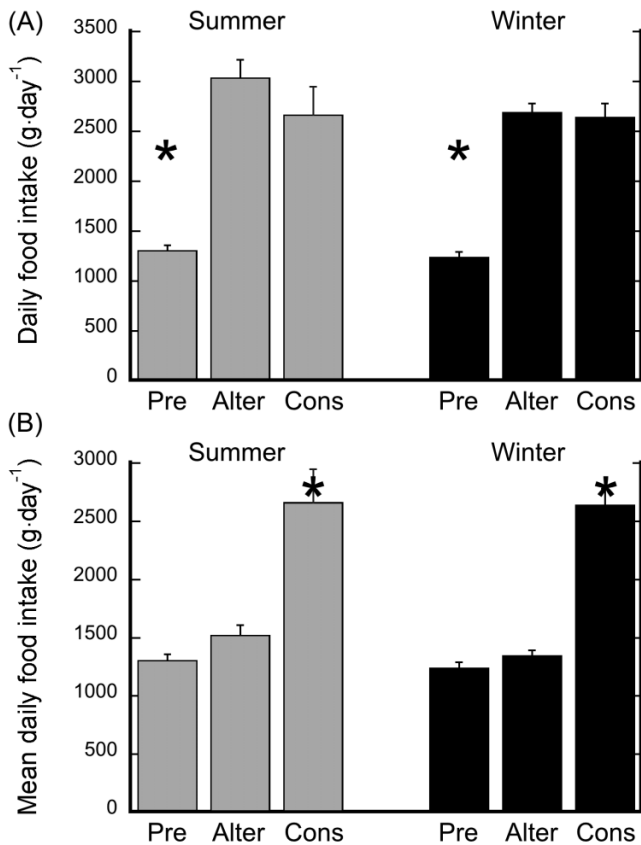
Pre-experimental mean daily food intake over the 16 days prior to the trials was similar between summer ( $1312 \pm 140.8$  g·day<sup>-1</sup>, mean  $\pm$  SD) and winter ( $1236 \pm 134.7$  g·day<sup>-1</sup>) trials ( $t_{[5]} = 22.8$ ,  $P = 0.13$ ). During the summer season, there was a significant treatment effect ( $F_{[2,10]} = 35.2$ ,  $P < 0.0001$ ) when comparing pre-experimental, consecutive, and alternate treatments. Specifically, food intake during the consecutive feeding protocols ( $2661 \pm 699$  g·day<sup>-1</sup>) and the alternate feeding protocols ( $3025 \pm 558$  g·day<sup>-1</sup>) did not differ significantly from each other, but they were both significantly greater than during the pre-experimental period (Fig. 1A). A similar pattern was seen during the winter trials, when food intake during both the consecutive ( $2636 \pm 335.1$  g·day<sup>-1</sup>) and the alternate ( $2685 \pm 234.8$  g·day<sup>-1</sup>) feeding protocols was significantly greater than during the pre-experimental period, but not from each other ( $F_{[2,10]} = 92.5$ ,  $P < 0.0001$ ) (Fig. 1A).

Calculating average food intake during the alternate feeding treatments by including the preceding fasting day (i.e., daily food intake divided by 2) showed that the mean food intake over the alternate periods ( $1515 \pm 228.3$  g·day<sup>-1</sup> during summer and  $1343 \pm 117.4$  g·day<sup>-1</sup> in winter) was not significantly different than intake during the pre-experimental period, but they did differ from the consecutive treatments for both summer and winter trials ( $P < 0.0001$  for both seasons; overall ANOVA; summer:  $F_{[2,10]} = 24.58$ ; winter:  $F_{[2,10]} = 93.79$ ) (Fig. 1B).

When food intake was averaged over the entire experimental period (consecutive and alternate treatment data combined), daily food intake during summer trials ( $2857 \pm 749$  g·day<sup>-1</sup>) was nearly identical to intake during winter trials ( $2668 \pm 445$  g·day<sup>-1</sup>) ( $t_{[5]} = 1.29$ ,  $P = 0.25$ ). This was despite the fact that the mean initial body mass was lower in the summer ( $10.66 \pm 1.00$  kg) than the following winter ( $13.95 \pm 1.14$  kg). As a result, mass-corrected food consumption (expressed as percentage of initial body mass) was significantly greater in the summer (overall mean  $26.63\% \pm 2.63\%$ ) than in the winter ( $19.02\% \pm 1.56\%$ ) over the experimental treatments ( $t_{[5]} = 5.87$ ,  $P = 0.002$ ).

The seasonal difference in relative food intake was also apparent when examining the distribution of food intake on individual feeding days (Fig. 2). For example, all 28 of the individual trial days when animals ate the equivalent of  $>27.5\%$  of their body mass were during the summer. Furthermore, of the 120 individual feeding days (excluding initial treatment days), the fur seals consumed  $>3250$  g on only 16

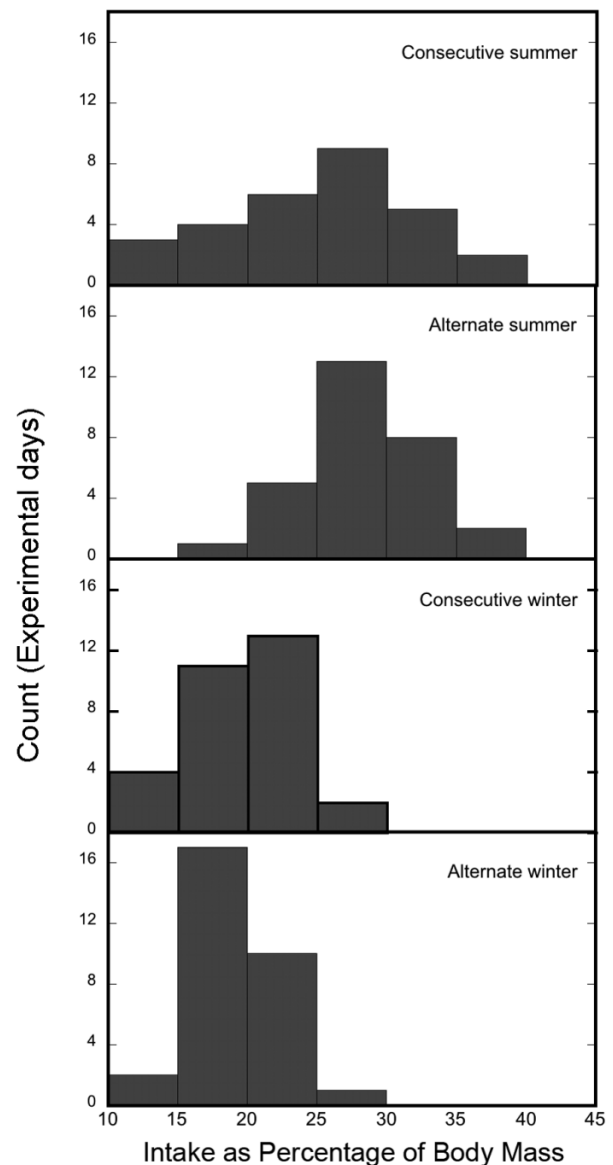
**Fig. 1.** Daily food intake ( $\text{g}\cdot\text{day}^{-1}$ ; mean  $\pm$  SE) of juvenile northern fur seals (*Callorhinus ursinus*) prior to and during the summer and winter feeding trials. Mean values are presented separately for the 16-day period immediately prior to the trials (Pre), during the phase when food was available every day (Cons), and when food was available only on alternating days (Alter). There was a significant difference between pre-experimental and either experimental food intake levels in both seasons (A). When mean food intake during the alternate trials was recalculated to take into account intervening fasting days, there was no difference between the pre-experimental and alternate trials, but they were both lower than food intake during the consecutive treatments (B).



(13%) occasions and 13 of these days were during the summer trials.

There was a distinct seasonal difference in the pre-experimental growth rates, despite the fact that fur seals consumed the same amount of food during these periods ( $t_{[5]} = 6.40$ ,  $P = 0.0014$ ). The fur seals gained mass during the 16-day pre-experimental summer period ( $226.7 \pm 119.8$  g) and lost mass during the winter ( $-306 \pm 221.8$  g) (Fig. 3). The significant increase in food intake achieved over the entire experimental period resulted, not surprisingly, in an increase in growth rates during both seasons. However, mean change in body mass over an entire trial was greater in the summer ( $1248.0 \pm 685.1$  g) than in the winter ( $23.3 \pm 316.6$  g) ( $t_{[5]} = 5.73$ ,  $P = 0.0023$ ; Fig. 3). Furthermore, the effect of the influx in additional food during the experimental period appeared to have a differential seasonal effect on growth. The change in growth rates ( $\delta\text{growth}$ ; the difference between pre-experimental and experimental changes in body mass) that resulted from a similar increase in energy intake during the

**Fig. 2.** Distribution of daily food intake expressed as a proportion of body mass (%) of young northern fur seals (*Callorhinus ursinus*). All data collection days are presented and shown by season (summer, winter) and feeding trial type (consecutive and alternate days of eating).

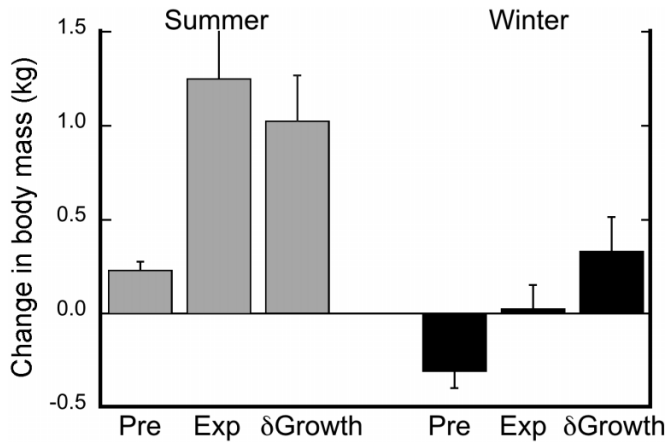


trials was greater in summer ( $1022.0 \pm 607.0$  g) than in winter ( $330.0 \pm 451.6$  g) ( $t_{[5]} = 3.73$ ,  $P = 0.015$ ).

## Discussion

Our feeding experiments revealed three principal results related to the maximum amounts of food that young northern fur seals can consume per day, and the subsequent repercussions on physical growth. First, the levels of maximum intake recorded appeared to be true indications of physical satiation and peaked at about 26% of body mass in summer and 20% in winter. While at first glance these might appear to represent developmental decreases in intake (tied to ontogenetic decreases in energy requirements), we suspect the differences merely reflect disparities in body mass, given that rates of absolute food intake were remarkably constant at 2.7–

**Fig. 3.** Total changes in body mass of young northern fur seals (*Callorhinus ursinus*) observed prior to and during the summer and winter satiation feeding trials. Means ( $\pm$ SE) are presented separately for the 16-day period immediately prior to the trials (Pre) and the entire 16-day experiment encompassing both alternate and consecutive daily feeding treatments (Exp). Also presented is the resulting difference in growth observed owing to the increased level of food intake during the trials ( $\delta$ Growth) calculated as growth during the experiment minus growth during equitable pre-experimental period. There was a significant difference in pre-experimental growth compared with experimental changes in body mass in both seasons, and a significant difference in both of these measures between seasons.



2.9 kg $\cdot$ day $^{-1}$  in both seasons. Hence, these recorded absolute levels of food intake likely represent a maximum, sustained limit for this age group.

Our second finding was that the level of food intake did not seem related to immediate energy requirements. We drew this conclusion from the observations that, contrary to predictions, the fur seals did not increase their intake when offered food on alternate days (compared with when they were feeding every day) to make up for intervening fasting days. We had predicted a diminished capacity in northern fur seals to increase food intake above “normal” levels in response to temporary disruptions in food supply compared with larger species such as Steller sea lions. This was based on the general allometric observation that smaller species tend to have higher energy and food intake requirements under normal conditions (Peters 1983), and therefore less capacity to increase intake levels in times of need. However, we did not predict that the rates of maximum food intake would be so constant. Steller sea lions showed a significant (52%) increase in food intake under similar experimental conditions (Rosen and Trites 2004). The quantitative data agrees with our behavioural observations (i.e., that the fur seals would continually take fish but not consume them) and reinforces our belief that the fur seals were sufficiently motivated during the trials to consume as much fish as physically possible on any given trial day, and therefore that our values represent a maximum level of sustained intake.

Finally, our feeding experiments indicated that the fur seals were less likely to convert additional food intake into mass gain during the winter compared with the summer. In both seasons, the fur seals increased their intake during the course of the trials by a similar amount (about  $\sim$ 1490 g $\cdot$ day $^{-1}$  or  $\sim$ 9600 kJ $\cdot$ day $^{-1}$  mean increase in gross energy intake). How-

ever, this near doubling of food intake during the satiation trials had a differential seasonal effect on growth. During summer, the increase in food intake resulted in a mean increase in the rate of body mass growth of  $\sim$ 65 g $\cdot$ day $^{-1}$  (or 1 g of additional body mass growth for each 147 kJ increase in intake); while in the winter, the extra food altered the fur seals’ energy budget from a state where they were losing mass to a state where they were gaining mass. However, the extra energy ingested during winter only altered the growth rate by  $\sim$ 21 g $\cdot$ day $^{-1}$  (or 1 g of additional body mass growth for each 457 kJ increase in intake). This suggests that the physiology of the fur seals was predisposed to convert high levels of food into growth during the summer but not during the winter months.

### Physiological basis for seasonal differences in energy conversion

Although it seems clear that the fur seals in our study did not as readily convert additional food intake into body mass during the winter months compared with the summer, the exact physiological basis of this difference in capacity is not known. Possible explanations include (i) the fur seals used the additional ingested energy for some energetic requirement other than growth (seasonal differences in energetic priorities); (ii) additional energy did not translate into similar changes in body mass because of differences in the types of physical growth (seasonal priorities in body composition); and (iii) similar increases in food intake did not translate into equivalent increases in metabolizable energy because of seasonal variation in digestive capacity.

The possibility that these observed differences were ontogenetic in nature rather than true seasonal variation cannot be completely discounted. However, questions regarding the physiological basis for the observed differences in the propensity of converting additional prey intake into body mass remain the same. Under this framework, the question is transformed into why older pups were less likely to convert additional food intake into growth.

Changing seasonal energetic priorities would serve as an explanation for the discrepancy in growth rates of fur seals if the additional energy derived from the increased food intake were being utilized by bioenergetic pathways other than growth in winter compared with summer. The main bioenergetic pathways to consider are resting metabolism, thermoregulation, and activity. The fur seals were generally larger in the winter than in the summer, and therefore might have had higher resting metabolic rates. However, any seasonal differences in resting metabolism (excluding growth and thermoregulatory components) would already be accounted for by the relationship between the fur seals’ normal (pre-experimental) food intake and seasonal growth rates. There is no reason to suggest that resting metabolism would increase with increased energy intake in either season. Therefore, changes in metabolism are unlikely to explain the observed differences in the conversion of additional food intake into body mass.

It might be suggested that higher thermoregulation costs in winter would account for the seasonal differences in translating increased food into body growth. However, even if thermoregulatory costs were higher in the winter, these would result in differences in initial growth rates and not the trans-

lation of additional energy into body mass (similar to the case for resting metabolism). In fact, it might be argued that additional food intake would actually decrease a potential thermoregulatory load in the winter because of thermal substitution from the heat increment of feeding (MacArthur and Campbell 1994; Rosen et al. 2007), resulting in greater changes in growth rates in the winter.

Differential changes in activity with increased food intake might account for the discrepancy in changes in growth rates between the seasons. For this to be true, increased food intake would have to result in increased activity levels in the winter compared with the summer. Unfortunately, we did not directly measure activity of our study animals. However, there is little theoretical basis to suggest that the primary usage for increased food intake would be higher activity levels, or that this response would be seasonally dependant.

It is also possible that some of the discrepancy in mass gain of the fur seals was due to how they allocated energy to growth. The cost of tissue growth can vary ~5-fold between protein ( $6.7 \text{ kJ}\cdot\text{g}^{-1}$ ) and adipose tissues ( $33.0 \text{ kJ}\cdot\text{g}^{-1}$ ; Schmidt-Nielsen 1997) (disregarding inefficiency or costs of conversion and synthesis; Blaxter 1989). Therefore, some of the seasonal discrepancy in changes in mass could be accounted for if the fur seals were primarily adding adipose tissues in winter (at a greater energetic cost per gram mass gain) and lean tissues in summer. This is certainly ecologically logical and could be a contributing factor; unfortunately, it was not feasible to measure changes in body composition over the course of the trials. The observed difference in the “efficiency” of translating additional energy intake into additional body mass was ~3-fold ( $457 \text{ vs. } 147 \text{ kJ}\cdot\text{g}^{-1}$  body mass), so that the theoretical difference in growth allocation might explain the observed seasonal differences. However, this still does not explain the overall low level of “efficiency” with which the fur seals converted the additional energy intake into body mass.

A third possibility is that the lack of body growth with additional food intake in the winter months was due to decreased digestive efficiency. In other words, increased food intake did not directly translate into proportionally greater levels of metabolizable energy, with a heightened effect observed during the winter seasons. The corollary to this argument is that one or more steps of the digestive process produced substantially greater waste products with increasing food intake. While we measured neither heat increment of feeding nor faecal energy loss in the current study, they are likely avenues of digestive inefficiency. They are also both known to be highly dependent on levels of gross energy intake (Hoch 1971; Blaxter 1989). Increased faecal energy loss (decreased digestive efficiency) is the route most likely to be involved during periods when food intake levels approach the limits of digestive capacity (Karasov et al. 2011). In such cases, digestive throughput increases in response to high levels of food intake, but much of the gross energy intake passes through the animal without being assimilated (Barboza and Hume 2006). The observed seasonal differences would further suggest that assimilation capacity is also seasonally dependant.

It seems counterintuitive that young fur seals are unable to efficiently convert additional food intake into greater body mass. In theory, young animals should maximize growth to

receive long-term benefits to their overall reproductive success. Yet our experiments show that the capacity to convert “additional” food into growth is limited and, apparently, highly seasonal. This raises the inevitable question of “why” a limited food energy conversion capacity might be evolutionarily beneficial to northern fur seals.

The answer to our question may be rooted in the well-established physiological precept that an animal’s physical capacity is closely matched to its physiological requirements (symmorphosis; Weibel et al. 1991). The reasoning is simple—additional capacity has an inherent energetic cost to maintain and therefore represents a potentially deleterious strategy. Similarly, physiological requirements that change on a seasonal basis should be matched by specific morphological changes. For example, the metabolic cost of maintaining the digestive apparatus has been proposed to explain why seasonal changes occur in intestinal size with predictable changes in food supply or intake in many vertebrates (as opposed to some sort of passive atrophy; Klaassen et al. 1997; Król et al. 2003; Naya et al. 2007).

Given the prevalence of highly seasonal energy budgets among marine mammals (e.g., Renouf and Noseworthy 1991; Ryg and Øritsland 1991; Lager et al. 1994; Rosen and Renouf 1998), it is not surprising that pinnipeds such as northern fur seals would adapt a strategy of digestive capacity downregulation to match their capacity to process food resources with seasonally and developmentally variable energy requirements (as per Rosen and Trites 2010). In our study, the fur seals had lower pre-experimental growth rates for similar food intake levels in the winter months and appeared less able to translate additional food intake into additional growth. These observations are consistent with body-size data from northern fur seals sampled in the wild that show a loss of mass and lack of growth during winter and short rapid spurts of growth during summer (Trites and Bigg 1996).

The exact nature of the physiological mechanism that limits food intake at any given time is under debate. The common thinking is that there is a digestive bottleneck in the overall process caused by stomach capacity, enzyme production rates, assimilation efficiency, or some other limiting factor (Ferraris and Diamond 1989; Jobling 1995; Lemieux et al. 1999). However, Speakman (1997) cautions that the bottleneck hypothesis implicitly assumes that there is a positive monotonic relationship between energy throughput and fitness (i.e., animals that ingest and expend more energy obtain greater fitness benefits). This may not be the case because the alimentary tract and associated organs have high metabolic rates and contribute disproportionately to the total resting metabolic rate (Krebs 1950; Konarzewski and Diamond 1995; Muñoz-García and Williams 2005). Hence, increasing digestive capacity—even if fully utilized—actually decreases net energy gain after some optimal point through increased metabolic overhead (i.e., the additional cost of maintaining larger capacity digestive systems is greater than the additional energetic benefit they provide).

### Implications to wild populations

The fur seals in our study appeared to be physically limited in the amount of food that they could consume, and had a limited capacity to translate this extra intake into body

mass, particularly in the winter months. These results have bearing on how fur seals might adapt to disruptions to prey, and how such events might ultimately affect population levels. Basic bioenergetic foraging models make the implicit assumption that animals will adjust food intake over time to make up for any temporary shortfall (Chipps and Wahl 2008; Karasov et al. 2011). Research into this phenomena has tended to concentrate on how the compensatory process may be limited by the availability of suitable prey resources (Whelan and Brown 2005). However, the tendency, ability, and capacity of animals to adjust food intake levels to maintain mean “required” energy intake levels are almost never considered. As noted by Levitsky and DeRosimo (2010) “the idea that food deprivation necessarily leads to increased hunger and subsequent food intake is both intuitive and accepted in the fields of psychology and physiology”. However, animals possess a number of alternate physiological mechanisms to compensate for changes in energy intake, partly because animals rarely possess sufficient “surplus” digestive capacity to compensate for such shortfalls via subsequent increases in food intake (Kirkwood 1983; Diamond 1991; Kersten and Visser 1996; Zynel and Wunder 2002).

In our study, the fur seals failed to increase food intake after alternating days of fasting. In a similar experiment, Steller sea lions increased their daily food consumption after fasting days, but the observed level of increase (52%) was insufficient to maintain an energy intake equivalent to when food was available daily (Rosen and Trites 2004). In contrast, neither energy restriction nor fasting among humans resulted in any change of spontaneous food intake throughout a 4-day recovery period compared with pre-restriction levels (Levitsky and DeRosimo 2010). Although the loss in body mass was regained within 4 days, the recovery was accomplished without any increase in spontaneous food intake. Similarly, Steller sea lions that returned to their “normal” levels of food intake after a 4-week period of food restriction regained body mass during the winter season, but not during the summer (Jeanniard du Dot et al. 2008), reflective of other concurrent seasonal alterations in their energetic budgets. The role of decreased energy expenditures in promoting increased mass gain after periods of food restriction is a phenomenon commonly observed in mammalian species (Villaverde et al. 2008). Overall, it may be more important (and feasible) for animals to adjust alternate portions of the energy budget other than food intake during recovery periods, particularly if there is little additional capacity to increase food intake levels.

Our experiments provide an empirically derived value of maximum daily intake that can be incorporated into appropriate foraging models. The upper level of food intake of the northern fur seals in our study (seasonal means of 11–14 kg body mass) appeared to be equivalent to about 30.3% of their body mass in summer and 21.4% in winter (measured as the 75th quartile of all observations). In comparison, maximum food intake of Steller sea lions of the same age (1–2 year; 65–122 kg body mass) tested under similar conditions peaked at about 15.1% of their own mass. It should be kept in mind that both of these estimates are based on experiments with captive animals. Such estimates could be biased by activity levels, environmental conditions, or enforced patterns of food intake (relating to “normal” gut capacity) that are

not representative of their wild counterparts. Still, this study provides quantitative values for future modeling rather than relying on questionable “guesstimates”.

Unfortunately, there is no other information published on any other pinniped species to compare to, nor to derive an interspecific allometric relationship that can be used for modeling other pinniped species. However, these data do fit with the observation that maximum daily gross energy intake and basal metabolic rates both scale to body mass ( $w$ ) close to  $w^{0.7}$  on a broad interspecific basis (Kirkwood 1983; Lindstrom and Kvist 1995).

Incorporating realistic limits for food intake in bioenergetic or individual foraging models is vital to generate realistic predictions about food requirements. Currently, most models are formulated to generate total food requirements and assume that the individual always meets those costs. Rarely are limitations in digestive capacity or other physiological processes considered. Hence, these models cannot incorporate the multitude of alternate adaptations and consequences that a wild animal experiences when faced with challenges to their food intake. This can lead to seriously inaccurate predictions. For example, within the framework of traditional individual foraging or bioenergetic models, an increase in one dimension of an animal’s energy budget will be translated into greater levels of food intake to meet those demands, and result in an unrealistically greater ecological impact on the prey resource. In reality, changes in energy requirements are likely to result in (highly seasonal) changes in the physiological and bioenergetic state of the individual, with significant implications for long-term body size, health, and reproductive success.

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