Satiation and compensation for short-term changes in food quality and availability in young Steller sea lions (*Eumetopias jubatus*)

David A.S. Rosen and Andrew W. Trites

Abstract: Foraging theory predicts that animals should proportionately increase their food intake to compensate for reduced food energy content and (or) prey availability. However, the theoretical intake levels will, at some point, exceed the digestive capacity of the predator. We tested the ability of Steller sea lions, *Eumetopias jubatus* (Schreber, 1776), to compensate for short-term changes in prey energy density and availability, and quantified the maximum amount of food a young sea lion could consume. Five 1–2-year-old captive Steller sea lions were offered either herring (high energy) or capelin (low energy) each day or every second day. When prey were available on a daily basis, the sea lions compensated for differences in the energy content of herring and capelin by consuming sufficient quantities of each (8.3 vs. 14.0 kg·d^{-1}, respectively) to maintain equivalent gross energy intakes. When herring was available only on alternate days, the sea lions increased their consumption by 52% to 11.5 kg·d^{-1}, which was not sufficient to maintain an average gross intake equal to that maintained when herring was available every day. When capelin was available only on alternate days, some animals increased their intake for a few days, but average intake (15.2 kg·d^{-1}) was far below levels observed during daily feeding. Generally, the sea lions appeared to reach their digestive limit at a level equivalent to 14%–16% of their body mass. Our findings suggest that Steller sea lions can alter their food intake in response to short-term changes in prey quality or availability, but that these variables can quickly combine to necessitate food intake levels that exceed the physiological digestive capacities of young animals.

Résumé : La théorie de la quête alimentaire prédit que les animaux doivent augmenter en proportion leur ingestion de nourriture pour compenser une réduction du contenu énergétique et (ou) de la disponibilité de leurs proies. Cependant, ces niveaux théoriques d'ingestion, à un moment donné, dépasseront la capacité de digestion du prédateur. Nous avons vérifié la capacité des lions de mer de Steller, *Eumetopias jubatus* (Schreber, 1776), à compenser pour des changements à court terme de densité énergétique et de disponibilité des proies et mesuré la quantité maximale de nourriture qu'un jeune lion de mer peut consommer. Nous avons donné à cinq lions de mer de Steller âgés de 1–2 ans et gardés en captivité des harengs (haute énergie) ou des capelans (basse énergie) à tous les jours ou à tous les deux jours. Quand les proies sont disponibles tous les jours, les lions de mer compensent pour les différences de contenu énergétique entre le hareng et le capelan en consommant suffisamment de chaque espèce (8,3 et 14,0 kg·j^{-1}, respectivement) pour maintenir une ingestion brute d'énergie équivalente. Lorsque les harengs sont donnés seulement aux deux jours, les lions de mer augmentent leur consommation de 52 % à 11,5 kg·j^{-1}, ce qui n'est pas suffisant pour maintenir une ingestion brute moyenne égale à celle obtenue lorsque les harengs sont disponibles tous les jours. Lorsque le capelan est offert seulement aux deux jours, quelques animaux augmentent leur ingestion pendant quelques jours, mais l'ingestion moyenne (15,2 kg·j^{-1}) est très inférieure à celle observée lorsque les animaux se nourrissent tous les jours. En général, les lions de mer semblent atteindre leur limite digestive à une valeur équivalente à 14 % – 16 % de leur masse corporelle. Nos résultats indiquent que les lions de mer de Steller peuvent faire varier leur ingestion de nourriture en réaction à des changements à court terme dans la qualité ou la disponibilité des proies, mais que ces variables peuvent rapidement se combiner au point de nécessiter des niveaux d'ingestion de nourriture qui excèdent la capacité physiologique de digestion des jeunes animaux.

[Traduit par la Rédaction]

Introduction

Classical optimal foraging theory predicts that animals will alter their food intake to compensate for changes in both the type of prey ingested and the perceived availability of prey (or foraging events) (Emlen 1966; Perry and Pianka 1997). Under this theory, predators should increase the amount of food they ingest when foraging on prey with lower nutritional content (Schoener 1971). Similarly, if prey are available on an intermittent basis, predators should increase their

D.A.S. Rosen[1] and A.W. Trites. Marine Mammal Research Unit, University of British Columbia, 6248 Biological Sciences Road, Vancouver, BC V6T 1Z4, Canada.

[1]Corresponding author (e-mail: rosen@zoology.ubc.ca).

food intake to overcome both past and potential future periods of decreased availability (MacArthur and Pianka 1966).

The ability of individuals to quickly adjust foraging patterns to compensate for changes in prey type or availability is often a hidden a priori assumption of foraging ecology or energetic models. Bioenergetic models, for example, can predict the theoretical daily energy needs of different species at various life history stages and under particular environmental conditions (e.g., Olesiuk 1993; Boyd 2002; Winship et al. 2002). The amount of food that must be consumed to fulfil these requirements can be calculated given appropriate knowledge of the composition of prey species. However, bioenergetic models rarely consider whether an animal can actually meet its daily needs given limitations placed on food intake by the digestive physiology of real animals (Karasov and Diamond 1988; Weiner 1992).

Data are required to determine how readily individuals can alter their food intake to compensate for short-term changes in prey availability or quality. It is equally important to document when the requisite level of food intake surpasses the physiological processing ability of the animal.

These questions are especially pertinent to Steller sea lions, *Eumetopias jubatus* (Schreber, 1776), whose population has declined precipitously in western Alaska since the late 1970s (Trites and Larkin 1996; Loughlin 1998). One hypothesis links the population decline to changes in the quality, distribution, or quantity of prey available (Alaska Sea Grant 1993; Merrick et al. 1997; Trites and Donnelly 2003). Specifically, sea lions may not be able to acquire sufficient low energy density or dispersed prey on a daily basis to meet their overall energy requirements. This limitation would be most quickly reached in young animals that have the highest relative energy requirements of any age group (Winship et al. 2002) and may have the most difficulty foraging.

The following experiment was designed to determine the maximum level of food intake of young, captive Steller sea lions. We sought to evaluate their ability to alter their food intake in response to short-term changes in the quality (energy density) and availability (foraging opportunities) of prey available to them.

Materials and methods

Experimental design

Five female Steller sea lions participated in the study (1 year old at the start of the experiment). All procedures were conducted in accordance with the University of British Columbia Institutional Animal Care and Use Committee. The sea lions were brought into captivity as pups and were trained as part of a general research program. The sea lions were held in outdoor pools containing ambient, filtered sea water at the Vancouver Aquarium Marine Science Centre (Vancouver, British Columbia) with access to dry haulout space. Their normal diet consisted primarily of thawed herring (*Clupea pallasii* Valenciennes, 1847), although they were familiar with a number of prey species as part of previous experiments. Fish were supplemented with Vita-Zu nutritional tablets, and the animals were normally fed until their interest in the food or the trainer waned.

We designed the experiment to minimize the effects of training and research staff on the feeding patterns of the sea lions. The trials took place in dry animal holding runs containing feeding troughs (120 cm × 25 cm × 14 cm with a curved bottom and a continuous water inflow in the side). The sea lions were initially weighed daily, prior to eating, while they sat on a platform scale. However, we later measured body mass approximately every 2–3 d, partly because of logistical concerns and partly because it became apparent that the mass of the animals was greatly influenced by the amount of food left in their gut from the previous day.

The sea lions entered their runs in the morning, and a weighed (±10 g) amount of fish was added to their feeding troughs from outside their enclosure using a long-handled dip net. The only exception was that the first fish of the day, which contained vitamins, was hand-fed. Fish were allowed to remain in the trough for a maximum of 60–90 min (depending on weather conditions) to reduce potential effects of spoilage on intake levels. Removed fish were weighed after draining excess water. Since the fish had a tendency to absorb small amounts of water, an experimentally determined correction factor was applied to more accurately estimate the amount of fish consumed. Each sea lion had a full trough of fish for 7 continuous hours, usually starting at 0900. Visual contact with staff and other animals was minimized during the feeding sessions. After each session, the sea lions were returned to either a holding run or a pool, and the experimental areas and troughs were cleaned with disinfectant.

A cross-over design was used with four treatments each consisting of a combination of prey type (either high energy density herring or low energy density capelin, *Mallotus villosus socialis* (Pallas, 1814)) and prey availability (either daily or on alternating days). There were four treatment combinations, each consisting of a particular sequence of the four treatments. The treatment combinations were rotated among four of the animals both within and between trials so that no two animals were on the same treatment within a trial and no animal repeated a treatment combination during the course of the experiment (Table 1). The fifth sea lion would not consume capelin; her data is provided for comparative purposes only. Each trial lasted 20 d, and the experiment consisted of four trials over 1 year: Summer-01 (July–August 2001), Fall-01 (October–November 2001), Winter-02 (January–February 2002), and Fall-02 (October–November 2002). A fifth trial was attempted in spring 2002 but was cancelled owing to repeated regurgitations (see Results). Capelin is consumed in the wild by Steller sea lions and was chosen as an experimental prey because it has relatively low energy density and is similar in size to herring. The herring in the study averaged 90.6 g and 21.9 cm (total length), and the capelin 24.0 g and 16.2 cm.

The proximate compositions of samples of herring and capelin used in the experiment were analysed by Norwest Labs, Surrey, British Columbia. Energy content was calculated by appropriate conversions of lipid (39.3 kJ·g^{-1}) and protein (18.0 kJ·g^{-1}) contents.

Data analysis

Average food intake was determined for each sea lion for each treatment within each trial. However, the first day of

Table 1. Schematic of experimental design.

Treatment combination	Day																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
SSL 1	H	H	H	H	—	H	—	H	—	H	C	C	C	C	—	C	—	C	—	C
SSL 2	C	—	C	—	C	—	C	C	C	C	H	—	H	—	H	—	H	H	H	H
SSL 3	H	—	H	—	H	—	H	H	H	H	C	—	C	—	C	—	C	C	C	C
SSL 4	C	C	C	C	—	C	—	C	—	C	H	H	H	H	—	H	—	H	—	H

Note: The four treatment combinations (particular sequences of four treatments, each treatment consisting of a combination of prey type (H, herring; C, capelin) and feeding frequency (daily or alternate days)) were alternated so that none of the Steller sea lions (SSL; *Eumetopias jubatus*) were on the same combination during the same 20-d trial and each of the sea lions completed each of the combinations over the course of the experiment. Food intake (kg) was averaged for each animal in each treatment of each trial. However, the first day of each treatment was excluded from the mean.

each treatment was considered an adjustment day and was omitted from the analysis. For example, as illustrated in Table 1, the average intake of Steller sea lion (SSL) 1 during the daily herring (DH) treatment was based on intakes on days 2–4. Average intake during the alternate days herring (AH) treatment was based on consumption on days 6, 8, and 10. Similarly, average intake during the daily capelin (DC) treatment was calculated from consumption on days 12–14, and average intake during the alternate days capelin (AC) treatment from consumption on days 16, 18, and 20.

Repeated measures ANOVAs were used to test whether there was an overall treatment effect of diet type and feeding frequency on food intake levels, and whether there was a significant seasonal effect. A repeated measures ANOVA was also used to test whether observed food intake levels during each of the treatments differed from theoretical values based on energy content and prey availability. ANOVA was also used to determine whether there was an overall effect of body mass on food intake.

The potential effect of body mass on food intake was tested first. A repeated measures ANOVA with two factors (diet and season) was run using body mass at the start of each trial as a continuous random variable. Body mass was not a significant parameter in either model (raw or transformed data — see below) and was therefore removed from all subsequent analyses. The repeated measures ANOVA was rerun to test for the main effects of season and diet. Post hoc contrast comparisons were used to test for specific differences.

The food intake data were transformed into measures of gross energy intake to test whether the animals changed their food intake to maintain average gross energy intake across diet treatments. Theoretical intakes were calculated in relation to the "baseline" values of the DH treatment. Expected values in this treatment were set at 100% of observed values; therefore, expected values in the AH treatment were 200% of the observed DH values. This is based on the prediction that the sea lions would compensate for fasting days by eating twice as much on days when food was available to them. Based on differences in gross energy content, the expected intakes in the DC and AC treatments were 183% and 366%, respectively, of the intake in the DH treatment. To test for this effect, DH values were divided by 1.00, AH values by 2.00, DC values by 1.83, and AC values by 3.66. A repeated measures ANOVA was then used to test for significant differences from baseline (DH) levels. Post hoc contrasts that

Fig. 1. Seasonal mean ($\pm$SD) daily food intake (mean of four Steller sea lions, *Eumetopias jubatus*) in each of four prey type – feeding frequency treatments. The sea lions were 1 year old during summer 2001 and 2.3 years old in fall 2002. Different letters denote seasonal means (all treatments combined) that are statistically different.
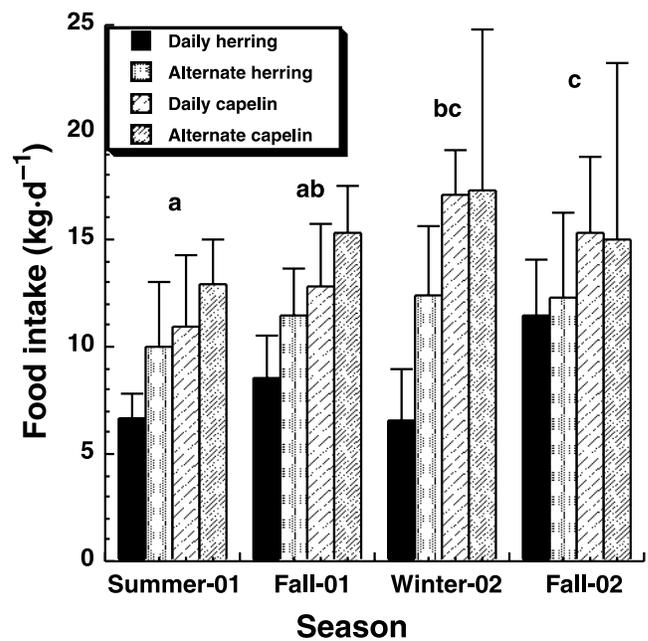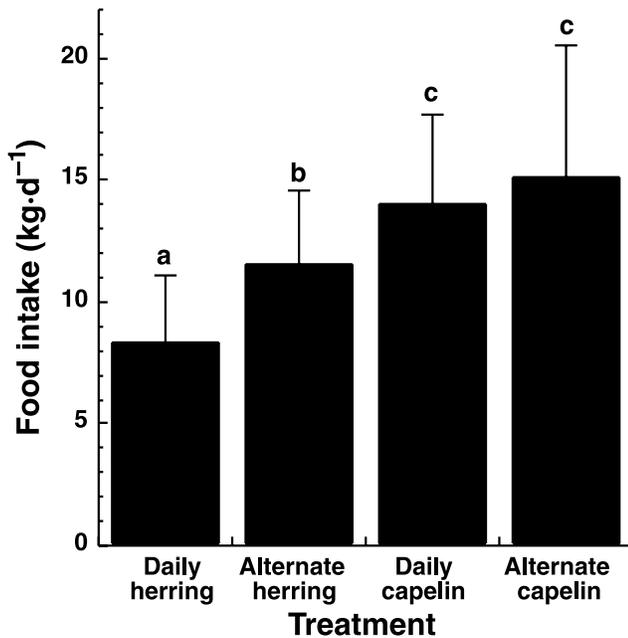

were significantly different from DH would indicate observed values that were significantly different from predicted values.

Results

Season had a significant effect on food intake ($F_{[3,45]} = 3.76$, $p = 0.02$). Overall, there was an increase in intake levels with each subsequent trial (Fig. 1). There were significant differences in food intake related to type of prey and frequency of feeding ($F_{[3,45]} = 14.23$, $p < 0.0001$) when seasonal changes were taken into account. Specifically, mean ($\pm$SD) food intake during DH treatments (8.31 ± 2.8 kg·d^{-1}) was significantly less than that during AH treatments (11.54 ± 3.0 kg·d^{-1}). Intakes during both herring treatments were significantly lower than intakes in both the DC (14.04 ± 3.6 kg·d^{-1}) and AC (15.16 ± 5.4 kg·d^{-1}) treatments,

Fig. 2. Mean (±SD) daily food intake (mean of four Steller sea lions) in each of four prey type – feeding frequency treatments. Different letters denote means that are statistically different.
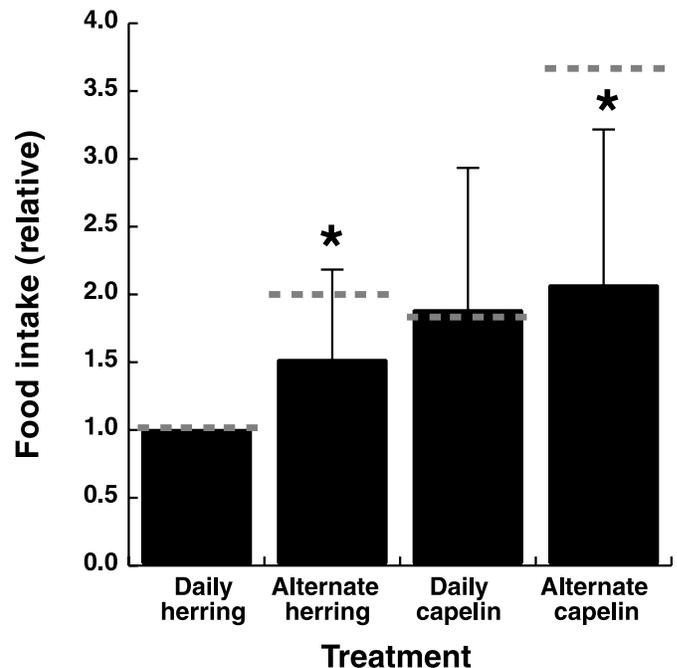

Fig. 3. Mean (±SD) daily food intake (mean of four Steller sea lions) in four prey type – feeding frequency treatments relative to the "baseline" amount of fish consumed during the daily herring phase of the study. Dotted lines represent "expected" values required to maintain an equivalent gross energy intake based on relative energy contents of herring and capelin and daily or alternate-day prey availability. An asterisk indicates significant differences between observed and expected consumption levels.

which did not differ significantly from each other (Fig. 2). Although there was no significant difference in mean intake between the DC and AC treatments, variation was greater in the latter because some animals ate extraordinary amounts on individual days. The greatest consumption during a single day was 28.4 kg, ingested by a ~100-kg animal during the Winter-02 trial.

The trial attempted during spring 2002 was not completed because of constant regurgitations by almost all animals. These frequently happened between feeding sessions, in the evening or early morning. Regurgitations were not isolated to a single treatment or a particular level of food intake. Alternating fresh and salt water in the troughs, carefully sanitizing all equipment, and giving the animals several days of rest after incidents all failed to alleviate the problem. The regurgitations may have been the result of a digestive "overload" caused by consumption of large meals at times of the year when sea lions would normally be fasting or have access to reduced prey levels. However, the exact cause could not be determined.

Comparison of food intake levels relative to baseline intake (DH) also showed a significant effect of season on food intake ($F_{[3,9]}$ = 5.27, p = 0.02). As with absolute values, there was an increase in relative intake levels with each subsequent trial, as well as a significant diet effect ($F_{[3,36]}$ = 24.29, $p < 0.0001$). Food intake during the AH treatments was 1.52 ± 0.67 times that during the DH treatments (Fig. 3), an increase which was significantly lower than the predicted increase of 2.0 times (i.e., increase required to provide gross energy intake equivalent to that in the DH treatments). Similarly, the observed increase in food intake during the AC treatments relative to the DH treatments (2.07 ± 1.15 times) was significantly less than predicted (3.66 times). However, the increase in food intake during the DC treatments relative to the DH treatments (1.89 ± 1.04

times) was not significantly different from the predicted increase (1.83 times).

Body mass was measured in the morning prior to the start of a trial. Even so, it was quickly apparent that body mass was greatly affected by the amount of food ingested the previous day. Still, the trend apparent in changes in body mass during each treatment was in accordance with the observed patterns in energy intake. On average, the sea lions gained 2.3 ± 1.4 kg during the DH treatments, and 1.1 ± 2.1 kg during the DC treatments, when observed energy intake matched predicted values. However, the sea lions lost an average of 0.4 ± 1.7 and 1.7 ± 1.5 kg during the AH and AC treatments, respectively, when energy intake fell short of predicted levels. These data concur with the energy intake data and suggest that the sea lions were unable to sufficiently compensate for changes in food availability and quality during the AH and AC treatments.

Discussion

Foraging theory predicts that animals should alter their food intake based on the value of particular prey items to obtain a constant net nutritional benefit. The net value of prey is a product of its nutritional value and the foraging cost associated with its capture (for review see Perry and Pianka 1997).

In simple terms, animals should increase their consumption of less energetic prey relative to more energetic prey to achieve a similar total (net) energy intake if the foraging

cost and availability of both types of prey are equal. Similarly, if prey availability (e.g., distribution or abundance) is unequal, animals should consume proportionately more per feeding bout as feeding opportunities decrease. These predictions assume that predators can adjust their food intake almost instantaneously and that they have comprehensive knowledge of both prey composition and foraging opportunities. Such assumptions are likely unrealistic, yet underlie most foraging and bioenergetic models. It is important, therefore, to quantify how quickly and accurately animals can adjust to changes in the quality (energy density) and availability (foraging opportunities) of their prey.

However, it is elementary that there must come a point when the theoretical intake levels needed to compensate for decreasing nutritional value and (or) availability of prey will surpass the actual digestive capacity of the predator. It is important, therefore, to establish the maximum digestive capacity of Steller sea lions to set realistic limits on foraging and bioenergetic models.

Time scales in satiation

The physiological mechanisms by which animals adjust food intake operate on several time scales. Short-term control of food intake is regulated by a complex set of physiological feedback mechanisms (Schwartz et al. 1999) such as the immediate satiation response induced by stomach distension (Eisen et al. 2001). Satiety (inter-meal intervals) is regulated by longer term biochemical signals that rely on feedback related to body condition and nutrient balance.

Longer term rheostatic controls adjust for changes in "ideal" body mass or composition, such as seasonal and developmental alterations in food intake necessitated by changes in overall energy needs (Steffens and Strubbe 1987). Captive pinnipeds are known to seasonally adjust their energy intake, even when given ad libitum access to food (Renouf et al. 1993; Boily and Lavigne 1997; Rosen and Renouf 1998). The amplitude of these seasonal energy cycles tends to increase as animals approach sexual maturity (Rosen and Renouf 1998), while relative energy demands decrease with age primarily because of reduced growth rates (Brody 1945).

Although the sea lions in our study ate significantly less food during the Summer-01 trial (10.14 kg·d^{-1}) than during subsequent Winter-02 and Fall-02 trials (13.35 and 13.52 kg d^{-1}), some of this variation is attributable to differences in average body mass. When expressed as a percentage of body mass, intake during the Fall-02 trial (11.5%) was lower than that during the Summer-01 (12.3%), Fall-01 (13.7%), or Winter-02 (13.3%) trials. The relatively lower consumption in the Fall-02 trial compared with the Fall-01 trial presumably reflects the lower relative energy needs of older versus younger animals. Overall, our data imply simultaneous seasonal and developmental changes in absolute and mass-specific maximum food intake, as would be expected for juvenile sea lions.

Food quality

Although some studies have examined how mammals adapt to seasonal changes in forage composition (e.g., Owen-Smith 1994), few have tested the ability of mammals to compensate for short-term changes in food quality. Most studies have used herbivorous mammals in laboratory settings. Both rats (Johnson et al. 1986) and prairie voles (*Microtus ochrogaster* (Wagner, 1842)) increased their food intake when presented with lower energy density diets (Hammond and Wunder 1991; Castle and Wunder 1995; Voltura and Wunder 1998), facilitated in the latter group by increasing gut size. In contrast, pocket gophers (*Thomomys bottae* (Eydoux and Gervais, 1836)) generally increased their food intake with decreasing forage quality (again, aided by changes in digestive anatomy), but actually decreased their food intake when switched from the highest to the lowest quality diet (Loeb et al. 1991).

Evidence from the real world is equivocal. Both long- and short-term natural changes in the quality of available prey have been shown to adversely affect chick survival rates and reproductive success in a number of species of seabirds (Ainley et al. 1995; Barrett 1996; Litzow et al. 2002), although others appear to be able to maintain reproductive success when switched from a high-lipid to a low-lipid diet (Bryant et al. 1999).

The speed with which the sea lions in our study compensated for changes in food quality surpassed our expectations. We therefore suspect that the response was not regulated by changes in body mass or condition resulting from energy deficits, but rather by short-term changes in blood biochemistry. For example, triglycerides in mammalian whole blood and serum (lipemia) are conspicuous shortly after feeding (Geraci et al. 1979). However, the fact that the fish differed in both lipid and protein content, combined with the sea lion's "reputation" for reliance on lipid metabolism, makes identification of the exact mechanism difficult, but worthy of further study.

Food availability

Compared with food quality, how quickly animals adjust to changes in food availability has been tested in fewer studies. In one study, prairie voles failed to consume sufficient food if the total foraging period — specifically, time between foraging bouts — was too short (Zynel and Wunder 2002). Similarly, Wistar rats increased food intake to compensate for decreased foraging time per day, but failed to sufficiently increase intake when foraging opportunities were too short (Krizova et al. 1996). In the wild, female northern fur seals, *Callorhinus ursinus* (L., 1758), adjusted their foraging effort (i.e., field metabolic rates) between years so that foraging bouts, and therefore onshore pup fasting durations, remained constant (Costa and Gentry 1986). In contrast, female Antarctic fur seals, *Arctocephalus gazella* (Peters, 1875), increased the lengths of their foraging trips to maintain body composition when their prey (krill) was in short supply (Costa et al. 1989). This increased the mortality rate of pups that had to endure longer fasting periods on shore. The difference between species may be explained by the suggestion that Antarctic fur seals normally operate at their metabolic limit and are unable or unwilling to increase their foraging efficiency or effort (Costa et al. 1989).

The sea lions in our study increased their daily consumption of herring and capelin when availability decreased, although increases in the latter were not statistically significant. Food intake did not double when either fish was offered only every other day compared with when it was

offered daily, as would be predicted for animals maintaining a set gross energy intake level. Physical satiation may have limited intake of capelin (see below). However, satiation does not appear to have been a limiting factor during AH treatments. The daily food intake during the AH treatments (11.5 kg·d^{-1}) was less than that during either of the capelin treatments. It therefore appears that sea lions are better able to compensate for short-term changes in prey quality than changes in food availability.

This does not suggest that the sea lions eating every other day would have continued indefinitely to consume "insufficient" prey. Eventually, the longer term signals governing maintenance of body condition or body mass might have overridden the short-term signals induced by daily physical satiation. However, this time lag would induce an energy deficit that would have to be overcome, if possible, in future feeding events. Therefore, the results of our study suggest that changes in fish distribution (whether induced by factors such as climatic change or localized fisheries depletions) may have a greater effect on Steller sea lions in the wild than changes in fish quality per se. This hypothesis has important implications for species management and recovery plans.

Predicted versus observed food intake

Regardless of the disposition of animals to increase their food intake, there are real limits to the amount of food that they can consume. Resource acquisition can be limited by the rates of foraging, consumption, and digestion of prey (Zynel and Wunder 2002). Obviously, in our experiment only the latter could have been a limiting factor. It has been suggested that interspecific differences in digestion time, particularly retention time, are a result of natural selection in response to specific foraging strategies (Karasov and Diamond 1988). Therefore, even if animals have the physiological inclination to compensate for changes in prey quality or availability, the predictions made by energetic models may fail to accurately consider the physiological limits ("bottlenecks") to food intake imposed by the digestive system (Weiner 1992). Simply put, prey availability and (or) quality may combine to be so low that the animal is unable to consume, digest, and assimilate sufficient quantities to achieve nutritional homeostasis (Karasov and Diamond 1988). The disjunction between predicted and obtained intake was clearly demonstrated by the sea lions in our study.

The Steller sea lion bioenergetic model developed by Winship et al. (2002) predicts that a 1-year-old sea lion (weighing 89.0 kg) will need to consume food with a gross energetic value of 65.2 MJ·d^{-1} (the model takes into account the differences between gross and net energy values). A 2-year-old sea lion weighs 128.4 kg and needs to consume 78.7 MJ·d^{-1}. If these animals were eating prey comparable to that used in our experiment, they would need to consume the equivalent of 9.0% (1 year old) to 7.6% (2 year old) of their body mass in herring, and 16.6% to 14.0% in capelin. These decreases in mass-specific intakes with age are a product of decreasing mass-specific metabolic rates and highlight the potential for younger animals to have the greatest difficulty in consuming sufficient quantities of prey.

The masses of our sea lions averaged 84.3 kg at 1 year and 116.3 kg at 2 years (just slightly below the masses of

Fig. 4. Ingested food mass required by Steller sea lions consuming either herring or capelin, either every day or every second day. Food mass is expressed as a proportion of the sea lion's body mass. Calculations were derived from energy density of prey used in the current study and the bioenergetic model of Winship et al. (2002). The grey area delineates the theoretical intake limit equivalent to ≤16% of the animal's body mass.
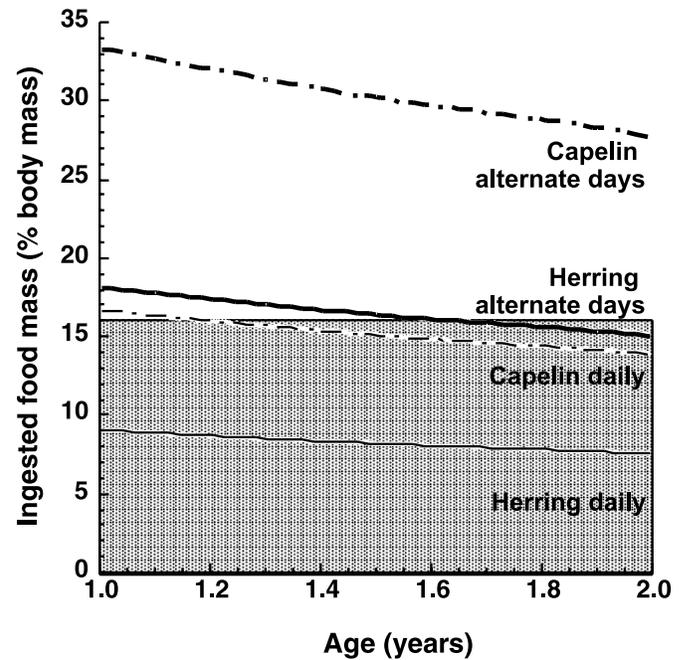

sea lions used in the predictive model). Our sea lions consumed an average equivalent of 8.6% of their body mass when eating herring every day, and 14.4% when eating capelin every day. These values are equal to those predicted by the general Steller sea lion bioenergetic model (Fig. 4). The sea lions in our study increased their average consumption to the equivalent of 12.0% of their body mass on herring and 15.7% on capelin when food was available every other day. Although the sea lions were observed to consume the equivalent of >15% of their body mass, they were clearly uncomfortable ingesting this amount. Animals became lethargic and unresponsive, dragging their noticeably full bellies across the substrate and resting on their sides or in the shallows of the pool. This behaviour was so obvious that veterinary consultations were undertaken during initial trials to ensure that this discomfort and listlessness were not due to secondary medical problems.

It was therefore not surprising that the Steller sea lions did not increase their food consumption sufficiently to maintain energy intake levels during the AC treatments. This would have necessitated consumption of a mass of fish equivalent to 31.5% of their own body mass. This level of intake was never seen for any single day's intake (Fig. 5) and was clearly beyond the sustained capabilities of these animals.

Implications of physical limitations

Our data suggest that a coarse upper limit of relative consumption occurs at the equivalent of 14%–16% of the sea lion's body mass (Fig. 5). This rough estimate can be used to make conjectures about the minimum frequency and en-

Fig. 5. Frequency of relative daily food intake (expressed per kg body mass) for all five sea lions on all treatments.

Food Intake as Percentage of Body Mass
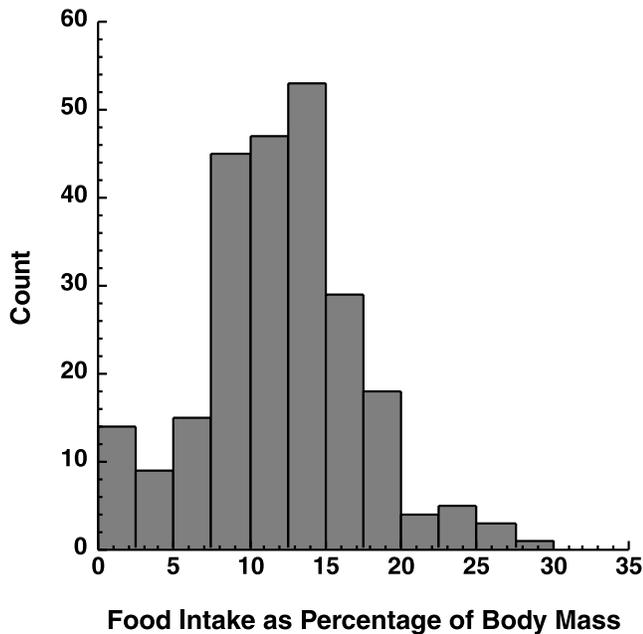
ergy density of prey needed to sustain an animal. For example, a 1-year-old (89.0 kg) sea lion that fulfils its energy intake needs (65.2 MJ·d^{-1}) by consuming a maximum of 15% of it's body mass would have to ingest prey that have a minimum energy density of 4.9 kJ·g^{-1} (= 65.2/(0.15 × 89)). A decrease in energy density means that the sea lion would, in theory, be unable to consume sufficient prey to meet its energy needs.

These calculations also assume that sufficient prey (and foraging opportunities) are available each and every day. Decreases in prey availability would proportionally increase the amount of food (or potential minimum energy density of target prey) that has to be consumed on (successful) foraging days. For example, the same theoretical 1-year-old sea lion would need prey of a minimum energy density of 7.4 kJ·g^{-1} if sufficient food were available on only 2 of every 3 days. These calculations are likely minimum estimates, given that they omit the realistic expectation of increased foraging costs associated with increased food intake (which reduces net energy gain).

The energy density and proximate composition of specific Steller sea lion prey items has been the subject of several recent (ongoing) investigations. Although there is tremendous variation in the energy density of fish because of seasonal and age-related factors, for comparative purposes it is interesting to note that Anthony et al. (2000) report mean values for major prey components of 5.8 kJ·g^{-1} for Pacific herring, 5.0 kJ·g^{-1} for capelin, and 3.2 kJ·g^{-1} for walleye pollock (*Theragra chalcogramma* (Pallas, 1814)).

The results of our study demonstrate that Steller sea lions appear to have the physiological ability to alter food intake levels to compensate for changes in energy density and, to a lesser degree, availability of prey. This contrasts with an earlier study (Rosen and Trites 2000) in which Steller sea lions were switched from an ad libitum diet of herring to one of pollock, but failed to increase their food intake sufficiently

to maintain energy intake. One explanation for the discrepancy is that the pollock in the earlier study were considerably larger (43 cm) than the capelin we used (20 cm), even though both species had a similar energy density (4.5–4.7 kJ·g^{-1}). It is also possible that the ad libitum feeding regime of the previous study, defined by when the sea lions "lost interest" in the food (a common definition for captive experiments), may have introduced a performance-based bias (see Shettleworth 1989).

Care should be taken when extrapolating our results to wild sea lions, given that we did not incorporate potential differences in foraging costs (e.g., travel, search, and acquisition costs) between prey species. Second, we measured only the energy intake of the sea lions and did not address the potential effects of different diets on individual physiology (Kitaysky et al. 1999; Rosen and Trites 2002) or life history parameters (Litzow et al. 2002). Finally, we did not address the potential effects of macronutrient content (Warwick et al. 2000; Lewis et al. 2001) and palatability (Blundell and Stubbs 1999) on food intake levels.

Despite the limitations, the results of this experiment suggest that Steller sea lions do possess the physiological mechanisms to compensate for changes in prey energy content. However, the experiment also clearly demonstrates that this capacity is limited. For young animals, the calculated theoretical minimum energy density of prey is equivalent to the energy density of many of the major food items that Steller sea lions consume in the wild (Van Pelt et al. 1997; Anthony et al. 2000). It is critical to note, however, that this minimal energy density value increases substantially when more realistic parameters such as foraging opportunities, prey density, and foraging costs are taken into account. This becomes especially pertinent with the observation that the sea lions in our study appeared to have a more limited ability to alter intake in response to changes in availability (foraging opportunities).

What is most evident from our experiments is that the intersecting costs to a sea lion faced with decreasing availability and net energy value of prey quickly combine to a point where the calculated required food intake surpasses the digestive capacity of the individual sea lion. Our bioenergetic model suggests that young sea lions live "close to the edge", even when consuming prey of moderate energy density, and are required to consume relatively large quantities of fish on a regular basis. This suggests that Steller sea lions that have the highest relative energy demands (young animals and lactating females) may not be able to consume sufficient quantities of low-energy or dispersed prey in the wild to meet their energetic needs.

Acknowledgements

to the North Pacific Universities Marine Mammal Research Consortium.

References

Ainley, D.G., Sydeman, W.J., and Norton, J. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Mar. Ecol. Prog. Ser. **118**: 69–79.

Alaska Sea Grant. 1993. Is it food? Addressing marine mammal and sea bird declines. Alaska Sea Grant Report 93-01. University of Alaska, Fairbanks, Alaska.

Anthony, J.A., Roby, D.D., and Turco, K.R. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exp. Mar. Biol. Ecol. **248**: 53–78.

Barrett, R.T. 1996. Prey harvest, chick growth, and production of three seabird species in Bleiksoy, North Norway, during years of variable food availability. Can. Wildl. Serv. Occas. Pap. No. **91**: 20–26.

Blundell, J.E., and Stubbs, R.J. 1999. High and low carbohydrate and fat intakes: limits imposed by appetite and palatability and their implications for energy balance. Eur. J. Clin. Nutr. **53**(Suppl. 1): S148–S165.

Boily, P., and Lavigne, D.M. 1997. Developmental and seasonal changes in resting metabolic rates of captive female grey seals. Can. J. Zool. **75**: 1781–1789.

Boyd, I.L. 2002. Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. J. Appl. Ecol. **39**: 103–119.

Brody, S. 1945. Bioenergetics and growth. Hafner Press, New York.

Bryant, R., Jones, I.L., and Hipfner, J.M. 1999. Responses to changes in food availability by Common Murres and Thick-billed Murres at the Gannet Islands, Labrador. Can. J. Zool. **77**: 1278–1287.

Castle, K.T., and Wunder, B.A. 1995. Limits to food intake and fiber utilization in the prairie vole, *Microtus ochrogaster*: effects of food quality and energy needed. J. Comp. Physiol. B, **164**: 609–617.

Costa, D.P., and Gentry, R.L. 1986. Free-ranging energetics of northern fur seals. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 79–101.

Costa, D.P., Croxall, J.P., and Duck, C.D. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology, **70**: 596–606.

Eisen, S., Davis, J.D., Rauhofer, E., and Smith, G.P. 2001. Gastric negative feedback produced by volume and nutrient during a meal in rats. Am. J. Physiol. **281**: R1201–R1214.

Emlen, J.M. 1966. The role of time and energy in food preference. Am. Nat. **100**: 611–617.

Geraci, J.R., St. Aubin, D.J., and Smith, T.G. 1979. Influence of age, condition, sampling time and method on plasma chemical constituents in free-ranging ringed seals, *Phoca hispida*. J. Fish. Res. Board Can. **36**: 1278–1282.

Hammond, K.A., and Wunder, B.A. 1991. The role of diet quality and energy need in the nutritional quality of a small herbivore *Microtus ochrogaster*. Physiol. Zool. **64**: 541–567.

Johnson, D.F., Ackroff, K., Peters, J., and Collier, G.H. 1986. Changes in rats' meal patterns as a function of the caloric density of the diet. Physiol. Behav. **36**: 929–936.

Karasov, W.H., and Diamond, J. 1988. Interplay between physiology and ecology in digestion. BioScience, **38**: 602–611.

Kitaysky, A.S., Piatt, J.F., Wingfield, J.C., and Romano, M. 1999. The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions. J. Comp. Physiol. B, **169**: 303–310.

Krizova, E., Simek, V., Abelenda, M., and Puerta, M. 1996. Food intake and body weight in rats with daily food-availability restrictions. Physiol. Behav. **60**: 791–794.

Lewis, C., Clark, T.W., and Derting, T.L. 2001. Food selection by the white-footed mouse (*Permoyscus leucopus*) on the basis of energy and protein contents. Can. J. Zool. **79**: 562–568.

Litzow, M.A., Piatt, J.F., Prichard, A.K., and Roby, D.D. 2002. Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia, **132**: 286–295.

Loeb, S.C., Schwab, R.G., and Demment, M.W. 1991. Response of pocket gophers *Thomomys bottae* to changes in diet quality. Oecologia, **86**: 542–551.

Loughlin, T.R. 1998. The Steller sea lion: a declining species. Biosphere Conserv. **1**: 91–98.

MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. Am. Nat. **100**: 603–609.

Merrick, R.L., Chumbley, M.K., and Byrd, G.V. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Can. J. Fish. Aquat. Sci. **54**: 1342–1348.

Olesiuk, P.F. 1993. Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. Fish. Bull. (Wash., D.C.), **91**: 491–515.

Owen-Smith, N. 1994. Foraging responses of Kudus to seasonal changes in food resources: elasticity in constraints. Ecology, **75**: 1050–1062.

Perry, G., and Pianka, E.R. 1997. Animal foraging: past, present and future. Trends Ecol. Evol. **12**: 360–364.

Renouf, D., Gales, R., and Noseworthy, E. 1993. Seasonal variation in energy intake and condition of harp seals: is there a harp seal morph? Problems for bioenergetic modelling. J. Zool. (Lond.), **230**: 513–528.

Rosen, D.A.S., and Renouf, D. 1998. Correlates to seasonal changes in metabolism in Atlantic harbour seals (*Phoca vitulina concolor*). Can. J. Zool. **76**: 1520–1528.

Rosen, D.A.S., and Trites, A.W. 2000. Pollock and the decline of Steller sea lions: testing the junk food hypothesis. Can. J. Zool. **78**: 1243–1250.

Rosen, D.A.S., and Trites, A.W. 2002. Changes in metabolism in response to fasting and food restriction in the Steller sea lion. Comp. Biochem. Physiol. B, **132**: 389–399.

Schoener, T.W. 1971. Theory of foraging strategies. Annu. Rev. Ecol. Syst. **2**: 369–404.

Schwartz, M.W., Baskin, D.G., Kaiyala, K.J., and Woods, S.C. 1999. Model for the regulation of energy balance and adiposity by the central nervous system. Am. J. Clin. Nutr. **69**: 584–596.

Shettleworth, S.J. 1989. Animals foraging in the lab: problems and promises. J. Exp. Psychol. **15**: 81–87.

Steffens, A.B., and Strubbe, J.H. 1987. Regulation of body weight and food intake. Science Progress **71**: 545–562.

Trites, A.W., and Donnelly, C.P. 2003. The decline of Steller sea lions in Alaska: a review of the nutritional stress hypothesis. Mammal Rev. **33**: 3–28.

Trites, A.W., and Larkin, P.A. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? Aquat. Mamm. **22**: 153–166.

Van Pelt, T.I., Piatt, J.F., Lance, B.K., and Roby, D.D. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comp. Biochem. Physiol. A, **118**: 1393–1398.

Voltura, M.B., and Wunder, B.A. 1998. Effects of ambient temperature, diet quality, and food restriction on body composition dynamics of the Prairie vole, *Microtus ochrogaster*. Physiol. Zool. **71**: 321–328.

Warwick, Z.S., McGuire, C.M., Bowen, K.J., and Synowski, S.J. 2000. Behavioral components of high-fat diet hyperphagia: meal size and postprandial satiety. Am. J. Physiol. **278**: R196–R200.

Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends Ecol. Evol. **7**: 384–388.

Winship, A.J., Trites, A.W., and Rosen, D.A.S. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions (*Eumetopias jubatus*) in Alaska. Mar. Ecol. Prog. Ser. **229**: 291–312.

Zynel, C.A., and Wunder, B.A. 2002. Limits to food intake by the Prairie vole: effects of time for digestion. Funct. Ecol. **16**: 58–66.