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# Effect of ration size and meal frequency on assimilation and digestive efficiency in yearling Steller sea lions, *Eumetopias jubatus*

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## Abstract

Assimilation and digestive efficiencies were measured in four juvenile Steller sea lions (*Eumetopias jubatus*) fed three ration sizes of herring (3%, 6%, or 9% of body mass) at three frequencies (2, 3, or 4 times daily). Assimilation efficiency (dry matter digestive efficiency) was 90.0 ± 2.0% (mean ± 1 SD). Digestive efficiency (efficiency of energy digestion) was 95.5 ± 1.0%. There was a strong linear relationship between digestive and assimilation efficiency, but no significant differences in either assimilation or digestive efficiency with changes in feeding frequency or changes in daily food intake within the ranges offered.

Key words: Steller sea lion, *Eumetopias jubatus*, digestion, prey, herring.

## Introduction

Feeding studies are important in understanding the ecology of Steller sea lions (*Eumetopias jubatus*) given that nutritional stress may be the most significant contributing factor to the population declines observed in Alaska since the 1970's (Merrick *et al*., 1987; Trites & Larkin, 1996). Changes in the nutritional status of Steller sea lions may be attributable to changes in their prey base (distribution, composition, and abundance). An understanding of the bioenergetic consequences of changes in diet is relevant to both sea lions and other top marine predators in the north Pacific ecosystem, many of which also exhibit population declines (Pitcher, 1990; Trites, 1992; Byrd & Dragoo, 1997).

Accurate bioenergetic models are needed to determine how changes in feeding ecology affect the energy budgets of Steller sea lions and other species. A critical component of energetic models is the calculation of metabolizable energy. This requires estimates of the amount of energy lost through urine, feces, and the heat increment of feeding. These parameters vary with the type and composition of the prey consumed, meal size, frequency of eating, the morphology of the digestive tract, and the age and sex of the animal (Keiver *et al*., 1984; Ronald *et al*., 1984; Fisher *et al*., 1992; Mårtensson *et al*., 1994a; Mårtensson *et al*., 1994b; Lawson *et al*., 1997a; Lawson *et al*., 1997b).

Subtracting fecal energy loss (FE) from gross energy intake (GEI) yields apparent digestible energy (Lavigne *et al*., 1982). Digestible energy, when expressed in relation to gross energy intake, is called digestive efficiency (DE):

$$DE = (GEI - FE)/GEI*100.$$

Digestive efficiency studies can use either the differences in energy content between the food and whole fecal collection, or comparisons of the changes in energy and concentration of an inert dietary marker between the food item and a fecal sample (Kleiber, 1975), such as naturally occurring manganese (Fadely *et al*., 1990). Digestive efficiency is used to calculate the apparent digestible energy derived from food intake, and is a critical parameter in the construction of energy budgets.

Some studies use dry matter assimilation efficiency (AE) as a measure of the digestive value derived from particular prey. This measure is easier to determine, being calculated solely from changes in an inert marker between fecal and food samples. Assimilation efficiency may provide a reasonable estimate of digestive efficiency, if the proportion of non-digestible parts in the prey is low.

As passage rates are affected by meal frequency and ration size (Hunt & Stubbs, 1975; Warner, 1981; Markussen, 1993), these variables might affect the digestive and assimilation efficiencies of marine mammals (Ronald *et al*., 1984; Lawson *et al*., 1997b). On the other hand, symmorphosis suggests that the digestive system should be able to accommodate reasonable variation in foraging frequency and meal size (Karasov & Diamond, 1988; Diamond, 1991). This question is of particular relevance to Steller sea lions in the North Pacific who may be forced to alter their foraging patterns in response to changes in their prey base. This study quantified the assimilation and digestive efficiencies for juvenile Steller sea lions fed herring, and tested whether digestive and assimilation efficiencies were affected by meal frequency and daily food intake. The relationship between assimilation and digestive efficiency was also examined.

## Materials and Methods

The experiment was conducted between February and March 1998 on four captive Steller sea lions, approximately 8 months of age, kept at the Vancouver Aquarium. The pups, two males and two females, were weaned from milk formula to herring (*Clupea harengus pallais*) in September 1997. Their normal diet (September to January) consisted of thawed herring fed 3 times per day, totaling approximately 6% of their body weight. The sea lions were weighed every morning before the first feed on a platform scale ( ± 0.5 kg).

The experiment consisted of 2 feeding manipulations: total food intake and number of feedings per day. Each sea lion received a total daily food intake of herring equal to either 3%, 6%, or 9% of their body weight (body mass of 4 pups: 46.8–70.7 kg). This quantity was delivered to the animals over the course of either 2, 3, or 4 feedings per day. Thus, each pup undertook 9 (randomized) trial combinations, with each trial lasting 4 days. Four day trials were estimated to be long enough to ensure that the sea lions had adjusted to each new feeding regime given their very fast rates of digestion (Helm, 1984).

Feces was collected from the sea lions on days 3 and 4 of each trial. Sea lions were placed alone in a cement floored run to ensure the scat came from a known animal. Fecal samples were collected from noon on the third day onward and, if no samples were collected during the day, the sea lion was kept in isolation over night so a sample could be collected early the next morning. If there was no feces, or if the sea lion decided not to eat, the trial was rerun at a later date. All samples were placed in a labeled, plastic vial, and stored at − 20°C until processed. Samples of herring were also collected and frozen throughout the trials.

For analysis, fecal samples were thawed overnight. Two duplicate sub-samples ( ~ 10 g) were placed in aluminum dishes and weighed to the nearest mg (Sartorius laboratory scale, model BP110). Feces were dried to a constant weight in a convection oven for 20–22 h at 100°C to determine water content. After drying, fecal samples were re-weighed and ground with a glass mortar and pestle into a fine, uniform powder. The powdered sample was then divided into two new samples of >1 g each, which were sent to outside laboratories to determine energy content and manganese ($Mn^{2+}$) concentration. Extra samples were stored for possible reanalysis.

**Table 1.** Mean assimilation efficiencies for 4 sea lions subjected to 9 combinations of trial conditions (meals 2 × , 3 × , 4 × per day; total food equals 3%, 6%, or 9% of body mass). One standard deviation given in brackets.

| Total food (% body mass) | Meals per day | | | Total |
|---|---|---|---|---|
| | 2 × | 3 × | 4 × | |
| 3% | 89.1 (2.0) | 89.5 (1.8) | 89.1 (0.8) | 89.3 (1.5) |
| 6% | 90.6 (0.6) | 88.7 (4.4) | 90.7 (2.0) | 90.0 (2.7) |
| 9% | 90.7 (1.2) | 90.4 (2.2) | 91.0 (1.0) | 90.7 (1.4) |
| Total | 90.2 (1.5) | 89.5 (2.8) | 90.3 (1.5) | 90.0 (2.0) |

Herring samples were partially thawed, cut, and blended into a uniform paste with a food processor. The paste from each fish was divided into 2 sub-samples and the same drying, weighing, grinding procedures, and analyses used as for the scat.

Energy content was determined via an adiabatic bomb calorimetry (Dr. G. Galzi, Department of Animal Science, University of British Columbia). Estimated energy content for each sample was corrected for side reactions (e.g., fuse wire correction and acid titration).

Manganese analysis was carried out by Norwest Laboratory in Surrey, British Columbia. A quantity of the powdered scat sample was digested with $HNO_3$ and $H_2O_2$ in a sealed Teflon vessel using microwave heating. The $Mn^{2+}$ concentration was determined on the resulting solution by UNICP-AES.

Assimilation efficiency was calculated as the change in concentration of the manganese marker between the fish and fecal samples:

$$AE = (1 - (C_i/C_f)) \times 100 \tag{1}$$

where, C is the concentration of $Mn^{2+}$ in the ingested food (i) and feces (f) on a dry matter basis (Fadely *et al.*, 1990).

Digestion efficiency was calculated by comparing both the change in manganese concentration and energy content. We used a corrected version of the formula given in Mårtensson *et al.* (1994a):

$$DE = \left(1 - \frac{Ci \times Ef}{Cf \times Ei}\right) \times 100 \tag{2}$$

where, C is the concentration of $Mn^{2+}$ and E is the energy content of ingested food (i) and feces (f) on a dry matter basis.

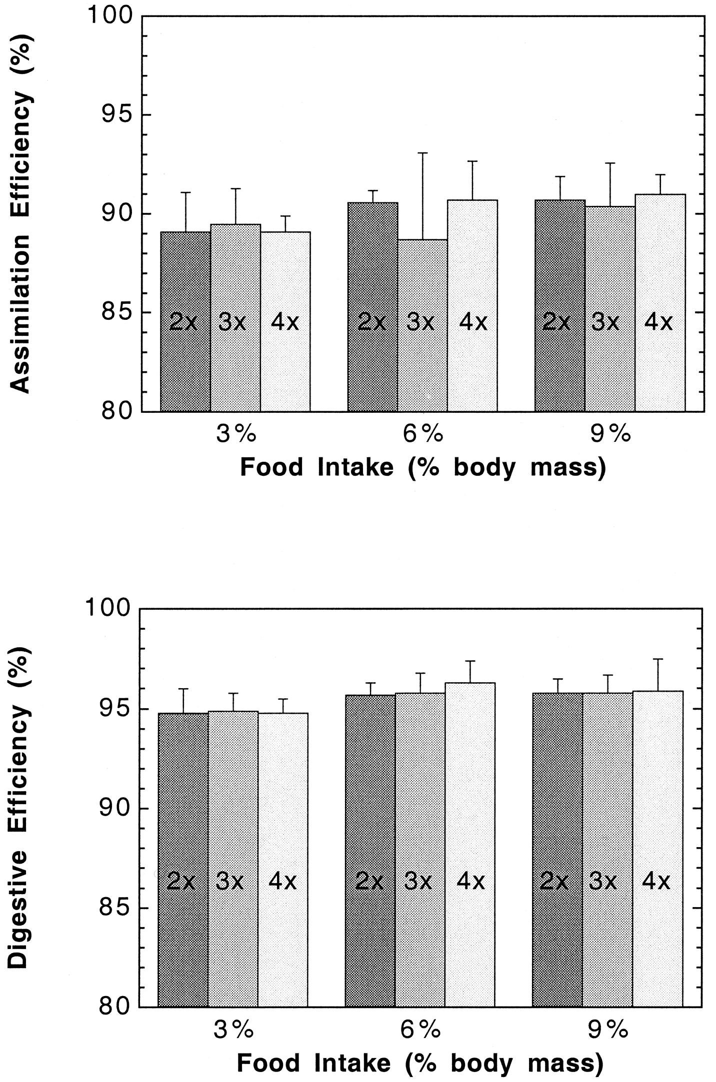

**Figure 1.** Changes in assimilation efficiency (top) and digestive efficiency (bottom) with total food intake. Bars represent meal frequencies ( ± 1 SD) of 2, 3, and 4 times per day.

Percentage data were normalized using an arcsine transformation. Data were collapsed across subsamples to yield a single mean estimate for each animal in each treatment. A 2-level, within-subjects (repeated measure) factorial design ANOVA was chosen to test for an effect of meal size or frequency of feeding on the assimilation efficiency and digestion efficiency. Results were considered significant at alpha = 0.05.

## Results

Mean length of herring used in the experiment was 17.5 cm, with a mean water content of 72.6%, a mean energy density of 25112 kJ/g dry weight, and a mean $Mn^{2+}$ concentration of 8.09 ppm. Sea lion feces had a mean water content of 61.4%, mean energy density of 12365 kJ/g dry weight, and mean $Mn^{2+}$ concentration of 83.86 ppm.

Mean assimilation efficiency for the sea lions across all treatments was 90.0 ± 2.0% (Table 1), with a range of 82.2–92.6%. However, no significant differences could be attributed to changes in either feeding frequency ($F_{2,6}=0.19$, $P=0.83$) or daily food intake ($F_{2,6}=4.24$, $P=0.07$) (Fig. 1).

Digestion efficiency averaged 95.5 ± 1.0% (Table 2), with a range of 93.5–97.3%. Again, there were

**Table 2.** Mean digestive efficiencies for 4 sea lions subjected to 9 combinations of trial conditions (meals 2 ×, 3 ×, 4 × per day; total food equals 3%, 6%, or 9% of body mass). One standard deviation given in brackets.

| Total food (% body mass) | Meals per day | | | |
|---|---|---|---|---|
| | 2 × | 3 × | 4 × | Total |
| 3% | 94.8 (1.2) | 94.9 (0.9) | 94.8 (0.7) | 94.8 (0.9) |
| 6% | 95.7 (0.6) | 95.8 (1.0) | 96.3 (1.1) | 95.9 (0.9) |
| 9% | 95.8 (0.7) | 95.8 (0.9) | 95.9 (1.6) | 95.8 (1.0) |
| Total | 95.4 (0.9) | 95.5 (1.0) | 95.7 (1.3) | 95.5 (1.0) |

no significant changes in digestive efficiency with either varying daily food intakes ($F_{2,6}=3.99$, $P=0.08$) or different feeding frequencies ($F_{2,6}=0.16$, $P=0.86$) (Fig. 1).

The relationship between assimilation efficiency and digestive efficiency was: DE=34.63+0.675*AE ($r^2=0.78$, Fig. 2). This was calculated using a geometric mean (type II) regression (Ricker, 1973) fit to the raw data. Regressing arc-sine transformed data did not improve the fit.

## Discussion

The high values found for digestive efficiency (95.5%) and assimilation efficiency (90.0%) for Steller sea lions eating herring was consistent with those reported for carnivorous mammals in general (see Table 3.5 in Blaxter 1989, Table 4 in Lavigne *et al.* 1982), and pinnipeds in particular. These results are contrary to the historical reputation of pinnipeds as 'inefficient converters of fish flesh' (Sergeant, 1973).

More specifically, the results are consistent with other studies that have examined assimilation efficiency among pinnipeds fed herring. Assimilation efficiency has been estimated for two otariid species at 89% for California sea lions, *Zalophus californianus* (Fadely *et al.*, 1994) and 90–93% for Northern fur seals, *Callorhinus ursinus* (Miller, 1978; Fadely *et al.*, 1990), and from 88–94% across several phocid seal species (Table 3).

Fewer studies have estimated digestive efficiency in pinnipeds, and no values have been reported for otariids. Miller (1978) quantified fecal energy loss in Northern fur seals, but it is impossible to derive a specific value for digestive efficiency from the data presented. Digestive efficiency of various phocids fed herring diets has been estimated between 93–97% and 92.7% in walruses, *Odobenus rosmarus* (Fisher *et al.*, 1992). In comparison, Nordøy *et al.* (1993) estimated the digestive efficiency of herring for minke whales, *Balaenoptera acutorostrata*, to be 92.1% through *in vitro* digestion experiments (Table 3).

Although past studies yielded similar estimates for both assimilation and digestive efficiency of herring, it must be noted that the composition and type of prey can substantially affect these values. In general, assimilation and digestive efficiency decreases with decreasing energy or lipid content of the prey, although this is not always the case (see Table 3). Therefore, care should be taken when applying values from specific studies to alternate prey items.

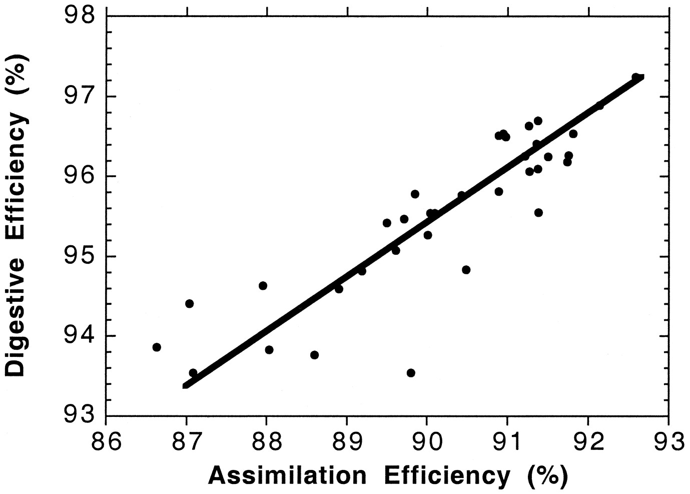

**Figure 2.** Relationship of assimilation and digestive efficiency. The solid line represents the geometric mean linear regression: DE=34.63+0.675*AE.

**Table 3.** Estimates of assimilation (AE) and digestive efficiency (DE) for various pinnipeds eating different diets. Most studies used changes in marker and energy concentrations to calculate assimilation and/or digestive efficiency. Ranges indicate estimates derived from different methodologies.

| Species | Diet | AE | DE | Source |
|---|---|---|---|---|
| Steller sea lion | Herring | 90.0 | 95.5 | Tables 1 and 2 |
| California sea lion | Herring | 89.2 | — | Fadely *et al*., 1994 |
| | Pollock | 86.5 | — | Fadely *et al*., 1994 |
| Northern fur seal | Capelin | 88.0 | — | Miller, 1978 |
| | Herring | 90.0 | — | Fadely *et al*., 1990 |
| | Herring | 91.6–93.0 | — | Miller, 1978 |
| | Pollock | 86.6–90.0 | — | Miller, 1978 |
| | Squid | 92.0 | — | Miller, 1978 |
| Pacific walrus | Clams | 89.9 | 92.0 | Fisher *et al*., 1992 |
| | Herring | 87.8 | 92.7 | Fisher *et al*., 1992 |
| Crabeater seal | Krill | — | 84 | Mårtensson *et al*., 1994a |
| Grey seal | Herring | 87.6 | 92.6 | Ronald *et al*., 1984 |
| | Mixed | — | 92.8 | Prime & Hammond, 1987 |
| Harbour seal | Herring | 92.4 | — | Rosen, 1996 |
| | Herring | 91.2 | — | Ashwell-Erickson & Elsner, 1981 |
| | Pollock | 96.7 | — | Ashwell-Erickson & Elsner, 1981 |
| Harp seal | Arctic cod | 86.9 | 93.5 | Lawson *et al*., 1997b |
| | Atlantic cod | 84.3 | 93.2 | Lawson *et al*., 1997b |
| | Capelin | 91.4 | 95.7 | Lawson *et al*., 1997b |
| | Capelin | — | 93–94 | Mårtensson *et al*., 1994b |
| | Crustaceans | — | 81–83 | Mårtensson *et al*., 1994b |
| | Halibut | 88.5 | 94.7 | Lawson *et al*., 1997b |
| | Herring | 83.9–90.3 | 92.5–95.0 | Keiver *et al*., 1984 |
| | Herring | 91.0 | 96.6 | Lawson *et al*., 1997b |
| | Shrimp | 60.0 | 72.2 | Keiver *et al*., 1984 |
| Ringed seal | Arctic cod | 88.3 | — | Lawson *et al*., 1997a |
| | Capelin | 86.6 | — | Lawson *et al*., 1997a |
| | Herring | 93.9 | — | Lawson *et al*., 1997a |
| | Herring | — | 97.0 | Parsons, 1977 |
| | Redfish | 83.2 | — | Lawson *et al*., 1997a |

In the present study there was a significant, linear relationship between assimilation and digestive efficiency. Not surprisingly, digestive efficiency was always greater than assimilation efficiency. Many of the particles excreted through the feces are indigestible prey parts with extremely low energy densities (e.g., otoliths, bones, chitenous exoskeletons). Their passage decreases assimilation efficiency, but contributes little in the way of fecal energy loss, i.e., has little impact on digestive efficiency. Although assimilation and digestive efficiencies may be strongly related, they clearly are not interchangeable. Unfortunately, the measures are sometimes used inappropriately, particularly in cases where assimilation efficiency is used to estimate fecal energy loss.

The nutritional stress hypothesis proposes that the Steller sea lion population decline is related to changes in their prey base in the North Pacific (Alaska Sea Grant, 1993). Resulting changes in foraging frequency and meal size might affect the metabolizable energy derived from prey. It has been hypothesized that digestive and assimilation efficiencies might be quickly limited by the absorptive capabilities of the digestive system with increases in food intake (Brody, 1945; Blaxter, 1989). Certainly, there is evidence that passage rates decrease with increasing meal size (Hunt and Stubbs, 1975; Warner, 1981; Markussen, 1993), which might be of particular consequence to pinnipeds with their remarkably long small intestine (Eastman & Coalson, 1974; Martin, 1977), and rapid transit times (Helm, 1984; Markussen, 1993).

In the present study, the Steller sea lions did not exhibit a significant change in their assimilation or digestive efficiency in response to the offered changes in daily food totals or feeding frequency. Similar results were reported for harp (*Phoca groenlandica*), ringed (*P. hispida*), and grey seals (*Halichoerus grypus*) (Keiver *et al*., 1984; Ronald *et al*., 1984; Lawson *et al*., 1997a; Lawson *et al*., 1997b). While it is possible that these studies did not sufficiently increase food intake to test the limitation of the system (or that the trials were not of sufficient length), it is more likely that, in accordance with the theory of symmorphosis (Diamond, 1993), there is sufficient capacity within the digestive system to handle any natural load efficiently. The pinniped digestive tract, like that of most other carnivores (Karasov and Diamond, 1988), appears to be adapted to rapid, efficient digestion of bolus meals, which is particularly useful when ingesting large amounts of food at depth (Krockenberger & Bryden, 1994).

This study found that Steller sea lions exhibit digestive and assimilation efficiencies typical of most carnivorous mammals. This high level of efficiency did not seem to be affected by either the frequency or size of meals within the range offered. While these attributes likely reflect the general feeding ecology of Steller sea lions in particular, and pinnipeds in general, comparative data are thin. Further investigations are needed into the possible effects of age, sex, and nutritional status across a larger number of species fed a more complex array of diets.

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