Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, pollock, squid, and salmon

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Abstract: Dry-matter digestibility and energy digestive efficiency were measured in six juvenile Steller sea lions (*Eumetopias jubatus*) fed three diets each consisting of a single species: herring, pollock, and squid. Two of the animals were also fed pink salmon. Dry-matter digestibility (DMD) and digestive efficiency (DE) were measured using the energy and manganese concentration in fecal and food samples. DE values were high for all prey species (herring: 95.4 ± 0.7% (mean ± SD), pollock: 93.9 ± 1.4%, salmon: 93.4 ± 0.5%, squid: 90.4 ± 1.3%). Steller sea lions appear to digest prey of high energy density more efficiently than prey of low energy density. DMD values were also high for all prey species (herring: 90.1 ± 1.8%, pollock: 86.5 ± 3.4%, salmon: 87.3 ± 2.6, squid: 90.5 ± 1.2%). The low DMD value for pollock compared with herring and squid was due to the high proportion of bony material in pollock. There was a strong linear relationship between DE and DMD for each prey type, but the terms cannot be used interchangeably. DE measures are more meaningful than DMD in conveying the energetic benefits derived by sea lions from different types of prey. Species-specific measures of the digestible energy obtained from an array of prey items are a necessary component in understanding the bioenergetic consequences of consuming different prey species.

Résumé : Las digestibilité des matières sèches et l'efficacité de l'énergie digestive ont été mesurées chez six Otaries de Steller juvéniles (*Eumetopias jubatus*) gardées à une diète monospécifique constituée de hareng, de goberge ou de calmar. Deux animaux ont aussi reçu du Saumon rose en nourriture. La digestibilité des matières sèches (DMD) et l'efficacité de la digestion (DE) ont été mesurées par évaluation de l'énergie et de la concentration de manganèse dans des échantillons de fèces et des échantillons de nourriture. La DE s'est avérée élevée pour tous les types de proies (hareng : 95,4 ± 0,7 % (moyenne ± écart type), goberge : 93,9 ± 1,4 %, saumon : 93,4 ± 0,5 %, calmar : 90,4 ± 1,3 %). Les otaries semblent digérer plus facilement les proies qui ont une densité énergétique élevée que celles qui ont un densité énergétique faible. La DMD s'est également révélée élevée pour toutes les proies (hareng : 90,1 ± 1,8 %, goberge : 86,5 ± 3,4 %, saumon : 87,3 ± 2,6 %, calmar : 90,5 ± 1,2 %). La DMD plus faible de la goberge comparativement à celle du hareng ou du calmar est due à la proportion importante de tissu osseux chez ce poisson. Il y a une relation linéaire importante entre la DE et la DMD chez tous les types de proies, mais les termes des équations ne sont pas interchangeables. Les mesures de la DE sont plus révélatrices que celles de la DMD au sujet des bénéfices énergétiques que retirent les otaries des différents types de proies. La mesure de l'énergie digestible spécifique à chaque espèce de proie est essentielle à la compréhension des conséquences bioénergétiques rattachées à la consommation de différentes espèces de proies.

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Introduction

Feeding studies are important for understanding the ecology of Steller sea lions (*Eumetopias jubatus*), given that nutritional stress may be the most significant factor in the population declines observed in Alaska since the 1970s (Merrick et al. 1987; Trites and Larkin 1996). Changes in the nutritional status of Steller sea lions may be attributable to changes in the distribution, composition, and (or) abun-

dance of their prey base (Alaska Sea Grant 1993). 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 marine ecosystem, many of which are also exhibiting population declines (Pitcher 1990; Trites 1992; Byrd and Dragoo 1997).

Accurate estimates of the biologically useful energy contained in various potential prey items are critical to understanding the bioenergetic effects of diet changes. The energy lost through urine, feces, and the heat increment of feeding determines the net energy available to a consumer. Fecal energy loss (FE) varies with the type and composition of the prey consumed, meal size, frequency of eating, morphology of the digestive tract, and possibly the age and sex of the consumer (Keiver et al. 1984; Ronald et al. 1984; Fisher et al. 1992; Mårtensson et al. 1994a, 1994b; Lawson et al. 1997a, 1997b).

Subtracting FE from gross energy intake (GEI) yields apparent digestible energy (Lavigne et al. 1982). A myriad of terms have inconsistently been applied to the relative loss

Table 1. Description of prey items used in the experiment.

	Mass (g)	Fork length (cm)	Energy (kJ/g)	Lipid (%)	Water (%)	n
Herring						
Lot 1	86	16.4	7.58	8.4	73.0	15
Lot 2	77	15.8	7.28	9.4	72.6	19
Pollock	1010	42.6	4.35	2.1	77.3	15
Salmon	1100	44.3	5.21	2.6	74.7	8
Squid	53	15.2	3.69	2.4	82.5	20

Note: All values are given on a wet mass basis.

of dietary energy through the feces (i.e., relative to GEI), including digestive efficiency (DE), apparent digestibility, metabolizability, and absorption efficiency. For our study, DE relates digestible energy to GEI, so that

[1] $$DE = \frac{GEI - FE}{GEI} \times 100$$

DE can be measured using either the differences in energy content between the food and whole fecal collection, or comparisons of the changes in energy and the concentration of an inert dietary marker such as naturally occurring manganese (Mn^{2+}) (Fadely et al. 1990), between the food item and a fecal sample (Kleiber 1975). DE is a critical parameter in the construction of energy budgets.

Many studies use the efficiency of dry matter mass absorption as an alternate measure of DE. This parameter, which we refer to as dry-matter digestibility (DMD), reports the change in dry-matter concentration between the food items and feces. DMD (also known as assimilation efficiency) is usually calculated from changes in concentration of an inert marker between fecal and food samples. DMD may provide a reasonable estimate of DE, particularly if the proportion of nondigestible parts in the prey is low (Robbins 1993).

In most animals, both DMD and DE vary in a predator-specific manner, and are affected by a number of factors (e.g., nutritional state, age, season, and prey type). As part of a larger investigation we are undertaking into the bioenergetic consequences of changes in prey items, we quantified DMD and DE for juvenile Steller sea lions fed herring, pollock, squid, and salmon.

The following examines the relationship between DMD and DE and how it changes with the type of prey consumed. We also contrast our estimates with those derived for other pinniped species. Finally, we discuss whether determining DMD and DE are meaningful ways to quantify the benefit derived by Steller sea lions from different prey items.

Materials and methods

We conducted our experiment with six juvenile sea lions (2.0–4.5 years of age; body mass 107–214 kg). The sea lions were captured as pups and were part of a research program carried out according to the guidelines of the University of British Columbia Animal Care Committee and the Canadian Council on Animal Care. Their normal diet consisted of thawed herring fed 3 times a day on an ad libitum basis. During these trials the sea lions were switched from a herring (*Clupea harengus*) diet to an alternative ad libitum, single-species diet for a period of 14–21 d before being switched back to a herring diet. The animals all had been previously exposed to these alternative prey items. All six of the sea

lions were switched to a diet of pollock (*Theragra chalcogramma*) and squid (*Loligo opalescens*). In addition, two (male 3 and female 1) were subjected to a diet of farmed pink salmon (*Oncorhynchus gorbuscha*).

Fecal samples were collected opportunistically, and only samples attributable to known individuals were used. Samples were placed in labeled plastic vials and stored in a freezer at –20°C until further processing. Whole prey items were routinely frozen during the feeding trials to provide representative samples for the chemical and energetic analyses described below.

For analysis, the fecal samples were thawed overnight. Two duplicate subsamples (~10 g) were placed in aluminum dishes and weighed to the nearest milligram (Sartorius laboratory scale, Model BP110). Feces were dried to a constant mass in a convection oven for 20–22 h at 100°C to determine water content and for energetic and Mn^{2+} sample analysis preparation. After drying, the fecal samples were reweighed and ground with glass mortar and pestles into a fine, uniform powder. Two samples (>1 g each) of this powder were sent to outside laboratories for determination of energy content and Mn^{2+} concentration (see below).

The whole prey items were partially thawed, cut, and blended to a uniform paste with a food processor. The paste from each fish was divided into two subsamples for further analysis. The same drying, weighing, and grinding procedures and analyses used for the feces were used for the prey items.

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

Analysis of Mn^{2+} was carried out by Norwest Labs (Surrey, British Columbia). A quantity of the powdered fecal sample was digested with HNO_3 and H_2O_2 in a sealed Teflon vessel using microwave heating. The Mn^{2+} concentration was determined in the resulting solution by ultrasonic nebulization inductively coupled plasma – atomic emission spectroscopy.

DMD was calculated as the change in concentration of the Mn^{2+} marker between the fish and fecal samples:

[2] $$DMD = \left(1 - \frac{C_i}{C_f}\right) \times 100$$

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

DE was calculated by comparing changes in Mn^{2+} concentration and energy content. We used a corrected version of the formula given in Mårtensson et al. (1994*a*):

[3] $$DE = \left(1 - \frac{C_i \times E_f}{C_f \times E_i}\right) \times 100$$

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

For statistical analysis, percent data were normalized using arcsine transformations (Campbell 1989). Data were collapsed across subsamples to yield a single mean estimate for each animal for each prey type. Although clearance times are quite rapid in pinnipeds, it was not known how quickly the digestive system of the Steller sea lions would "adjust" to the different prey items. A period of 4 days had been suggested by other researchers (Robbins 1993; Lawson personal communication), and visual inspection of the longitudinal data for each sea lion suggested that values stabilized by this time. Therefore, only data from day 5 onward were used in the statistical analyses. A single-factor repeated-measures analysis of variance (ANOVA) design was used to test for differences in DMD and DE with prey type (herring, pollock, and squid). As only two animals completed the salmon-diet trials, these

Table 2. Mean digestive efficiency and dry matter digestibility for six sea lions fed different diets.

Sea lion ID	Herring (%)	Pollock (%)	Squid (%)	Salmon (%)
Digestive efficiency				
Male 1	95.9 (23)	94.3 (20)	88.5 (14)	—
Male 2	95.8 (15)	95.3 (18)	90.2 (11)	—
Male 3	95.5 (21)	93.3 (16)	91.9 (14)	93.7 (14)
Female 1	94.1 (14)	92.0 (18)	89.7 (13)	93.0 (15)
Female 2	95.8 (18)	95.4 (14)	91.6 (19)	—
Female 3	94.9 (19)	92.7 (18)	90.0 (12)	—
Mean ± SD	95.4±0.7	93.9±1.4	90.4±1.3	—
Dry matter digestibility				
Male 1	86.9 (23)	88.0 (20)	88.8 (14)	—
Male 2	89.6 (15)	89.3 (18)	90.1 (11)	—
Male 3	91.3 (21)	86.9 (16)	92.0 (14)	89.1 (14)
Female 1	89.3 (14)	81.3 (18)	90.0 (13)	85.4 (15)
Female 2	91.7 (18)	89.5 (14)	91.8 (19)	—
Female 3	91.4 (19)	83.3 (18)	90.1 (12)	—
Mean ± SD	90.1±1.8	86.5±3.4	90.5±1.2	—

Note: Numbers in parentheses are sample numbers used to derive mean values. Only samples collected at least 4 days following a diet switch were used. Means and standard deviations were calculated from arcsine-transformed data.

data were omitted from the ANOVA. Results were considered significant at $p \leq 0.05$ and treatment mean differences were tested through a Scheffé's post hoc analysis. As both measures had error terms associated with them, geometric regression analyses (Ricker 1973) were used to determine the relationship between DMD and DE.

Results

The four prey items differed in both their size and their composition (Table 1). Pollock and salmon were the largest prey items in both length and mass. Herring had the greatest energy density, while squid had the lowest energy density (and the highest water content).

There were significant differences in DMD between the different experimental diets ($F_{[2,10]} = 7.13$, $p = 0.01$). The DMD value was significantly lower for the pollock diet (86.5 ± 3.4%; mean ± SD) than for either the squid (90.5 ± 1.2%) or the herring diet (90.1 ± 1.8%) (Table 2). DMD averaged 87.3% for the two sea lions that ate salmon.

DE also varied with species of fish consumed ($F_{[2,10]} = 47.35$, $p < 0.01$), but did not follow the same pattern as DMD. DE appeared to increase with energy density of the prey item (Fig. 1). DE was greatest for herring (95.4 ± 0.7%), followed by pollock (93.9 ± 1.4%), and then squid (90.4 ± 1.3%) (Table 2). DE averaged 93.4% for the two sea lions on the pink salmon diet.

There was a significant relationship between DMD and DE for each diet type. However, the relationship was different for each species of prey (Fig. 2).

Discussion

Ours are the first published DE values for an otariid. Miller (1978) calculated FE in northern fur seals, *Callorhinus ursinus*, but it is not possible to extrapolate the data provided, in order to estimate DE per se. Our DE values are consistent with the high efficiencies reported for various car-

Fig. 1. Changes in mean digestive efficiency with energy density of prey items. (A) Mean values from the two sea lions (female 1 and male 3) that consumed all prey items. (B) Values (mean ± SD) from all six sea lions that ate herring, pollock, and squid.
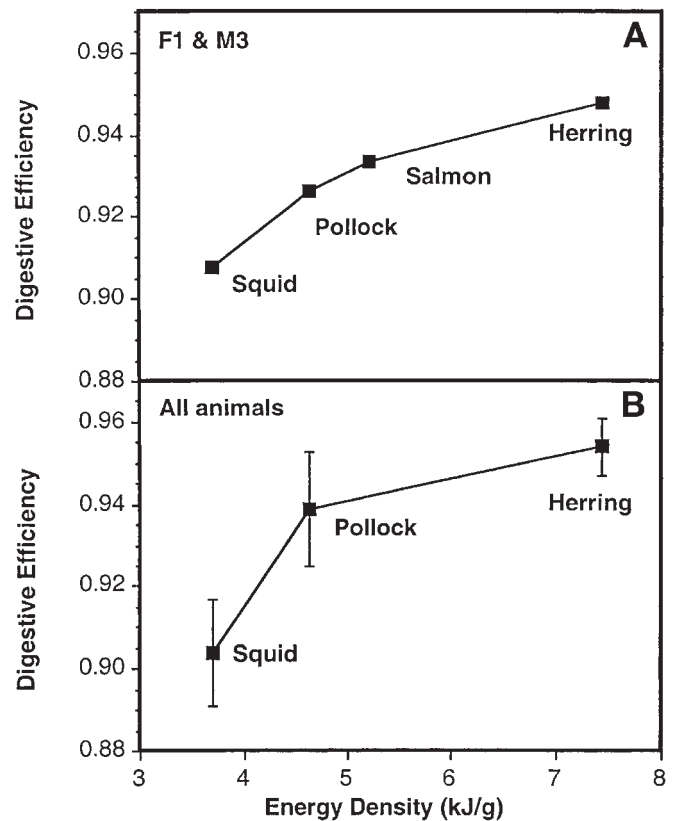
nivorous mammals (see Table 3.5 in Blaxter (1989) and Table 4 in Lavigne et al. (1982)) and other pinnipeds (Table 3). As noted by Lawson et al. (1997b), the high efficiency for pinnipeds is surprising, given their rapid passage rates (Helm 1984; Krockenberger and Bryden 1994).

Fig. 2. Relationship between dry matter digestibility and digestive efficiency for Steller sea lions fed herring, pollock, squid, and salmon diets. The broken reference line represents a 1:1 relationship between the two variables.
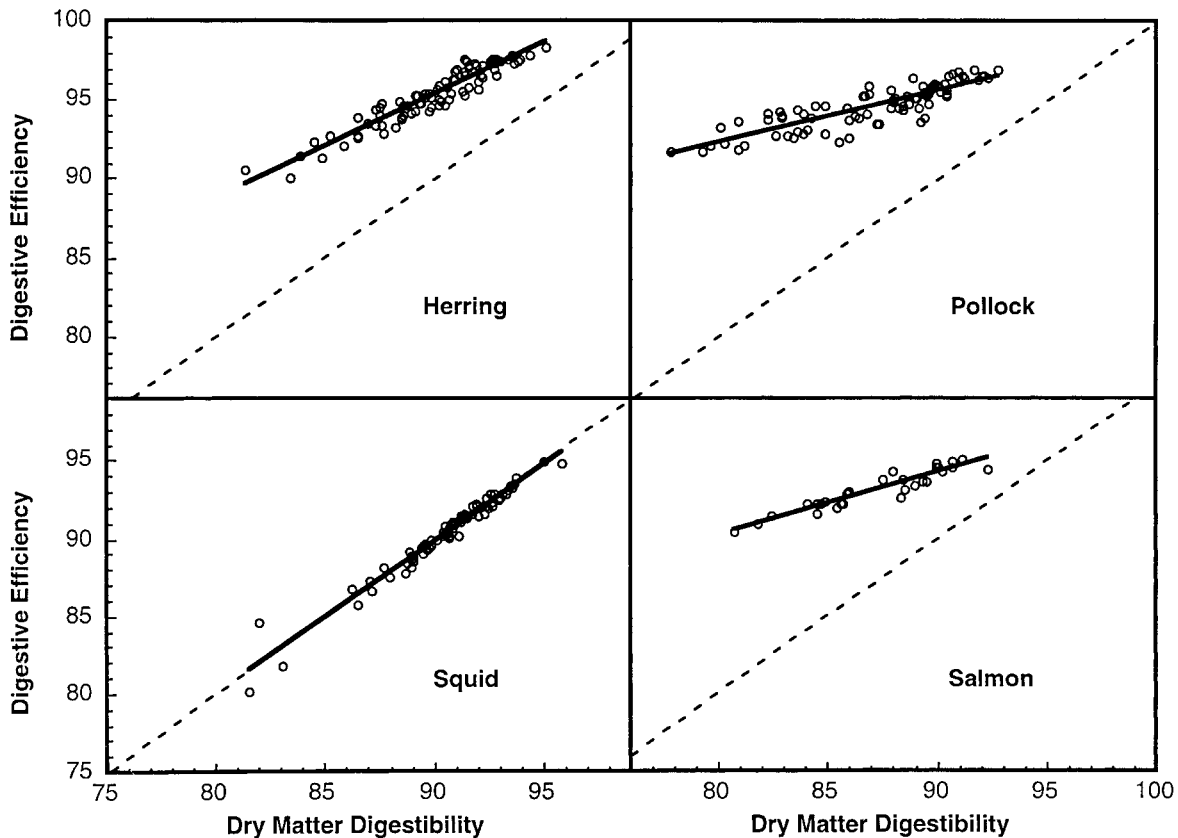
DE appears to be related to the energy density of the prey items, with squid diets producing the lowest values and herring the highest (Fig. 1). Lawson et al. (1997b) found a similar trend, although it is difficult to separate the effects of prey composition (e.g., percent lipid, protein, and water) from those of energy density per se. The results of our study indicate that the Steller sea lions were deriving 7.09 kJ/g (0.954 × 7.43 kJ/g) of apparent digestible energy from herring, 4.35 kJ/g (0.939 × 4.63 kJ/g) from pollock, and 3.34 kJ/g (0.904 × 3.70 kJ/g) from squid. While the differences in DE between food items were statistically significant, they may not be biologically significant, as the energy content of prey can vary widely with age-class, season, and geographic location. Indeed, care should be taken in applying the DE and DMD values presented in this paper, given the natural variation in body composition demonstrated by most fish species.

DE has also been noted to vary with predator age, health status, and perhaps even gender. In our study, no differences attributable to the latter were apparent. A study of DMD in walruses by Fisher et al. (1992) is the only one to date that has reported gender differences in either DMD or DE in a pinniped, although most studies are inevitably hindered by small sample sizes and hence low statistical power. This may also explain why significant differences due to age have not been demonstrated in pinnipeds. However, both DE (95.5 ± 1.0%) and DMD (90.0 ± 2.0%) for four younger Steller sea lion pups (~9 months) fed herring (Rosen et al. 2000) were almost identical with values found for the juvenile animals in this study (2–4.5 years old).

DE can also be affected by nutritional state. Animals on below-maintenance diets demonstrate an increased ability to extract energy from prey items. Since our sea lions were unable to maintain body mass while eating squid and pollock (Rosen and Trites 1998), our DE estimates for these diets may be slightly inflated. It is also unclear how accurately the DE of captive animals corresponds to that of animals in the wild (Robbins 1993).

The DMD values that we found are similar to those reported for other pinnipeds (Table 3). Aside from invertebrate diets, most of the studies report DMD values of 84–94% for a variety of pinniped species consuming an array of diets. In our study, DMD for pollock was significantly lower than that for either herring or squid.

The DMD and DE values for the diets of most herbivores and granivores are almost identical (Robbins 1993). For carnivorous mammals, they become less similar as the proportion of nondigestible material (e.g., hair, claws, teeth) in the diet increases. The differences in the relationship between DMD and DE among the prey species used in the present study largely reflect differences in the skeletal structure of the prey. Pollock have much larger, bony structures that pass undigested through the gut, compared with the smaller, delicate bones of herring and the almost completely digestible squid (except for the beak). These indigestible parts serve to effectively reduce DMD but, given their low energy density, have little effect upon DE. Note, for example, that there is almost a 1:1 correspondence between DMD and DE when the sea lions ate squid, compared with when they ate pollock

Table 3. Estimates of dry matter digestibility (DMD) and digestive efficiency (DE) for various pinnipeds fed different diets.

	Diet	DMD	DE	Source
Steller sea lion	Herring	90.0	95.5	Rosen et al. 2000
(*Eumetopias jubatus*)	Herring	90.1	95.4	Table 2
	Pollock	86.5	93.9	Table 2
	Squid	90.5	90.4	Table 2
California sea lion	Herring	89.2		Fadely et al. 1994
(*Zalophus californianus*)	Pollock	86.5		Fadely et al. 1994
Northern fur seal	Capelin	88.0		Miller 1978
(*Callorhinus ursinus*)	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
(*Odobenus rosmarus*)	Herring	87.8	92.7	Fisher et al. 1992
Crabeater seal	Krill		84	Mårtensson et al. 1994*a*
(*Lobodon carcinophagus*)				
Grey seal	Herring	87.6	92.6	Ronald et al. 1984
(*Halichoerus grypus*)	Mixed		92.8	Prime and Hammond 1987
Harbour seal	Herring	92.4		Rosen 1996
(*Phoca vitulina*)	Herring	91.2		Ashwell-Erickson and Elsner 1981
	Pollock	96.7		Ashwell-Erickson and Elsner 1981
Harp seal	Arctic cod	86.9	93.5	Lawson et al. 1997*b*
(*Phoca groenlandica*)	Atlantic cod	84.3	93.2	Lawson et al. 1997*b*
	Capelin	91.4	95.7	Lawson et al. 1997*b*
	Capelin		93–94	Mårtensson et al. 1994*b*
	Crustaceans		81–83	Mårtensson et al. 1994*b*
	Halibut	88.5	94.7	Lawson et al. 1997*b*
	Herring	83.9–90.3	92.5–95.0	Keiver et al. 1984
	Herring	91.0	96.6	Lawson et al. 1997*b*
	Shrimp	60.0	72.2	Keiver et al. 1984
Ringed seal (*Phoca hispida*)	Arctic cod	88.3		Lawson et al. 1997*a*
	Capelin	86.6		Lawson et al. 1997*a*
	Herring	93.9		Lawson et al. 1997*a*
	Herring		97.0	Parsons 1977
	Redfish	83.2		Lawson et al. 1997*a*

Note: In most studies, changes in marker and energy concentrations were used to calculate DMD and (or) DE. A range indicates that estimates were derived using different methodologies.

and herring (Fig. 2). Increases in DMD of squid lead to comparable changes in digestive (energy) efficiency, while increases in DMD of bony fish (pollock and herring) lead to relatively minor increases in the energy derived from those prey items. The anatomical differences in the prey (i.e., proportion of indigestible parts) highlight the fact that DE is a more direct measure of the benefit that animals derive from particular prey items than is DMD. Therefore, care should be taken not to use DMD estimates to calculate metabolizable energy in studies of (pinniped) bioenergetics.

In summary, our study showed that the DE and DMD values exhibited by Steller sea lions are typical of carnivorous mammals. There was a strong relationship between DMD and DE, but it was specific to the type of prey consumed. DE was related to the energy density of the prey, while DMD was affected by the physical structure of the prey. De-

spite the strong relationship between DMD and DE, they are clearly not interchangeable terms and they convey different information. DE measures are more meaningful than DMD in conveying the energetic benefits derived by sea lions from different types of prey. Future studies should concentrate on species-specific measures of the digestible energy obtained under a diversity of conditions from an array of prey items, as they are a necessary component in understanding the bioenergetic relationship between marine mammals and their prey.

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