Food Consumption by Sea Lions: Existing Data and Techniques

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Abstract

Knowing the quantity of prey that sea lions consume is a prerequisite for assessing the role of sea lions in aquatic ecosystems and the potential for competition to occur with fisheries. We reviewed the different approaches that have been used to estimate the food requirements for the six species of sea lions. We reviewed data on the quantity of food consumed by sea lions in captivity, and examined how consumption varied by species, body size, and season. We also reviewed and quantified available information on the energetics of sea lions and assessed the potential application of these data to parameterize an existing bioenergetic model that was developed to estimate the food requirements of Steller sea lions. Our study provided ranges of estimates of food consumption for sea lions that can be used in various modeling strategies to assess the impact of sea lions on prey populations, including commercially exploited fish species. The approaches reviewed in our study shared common difficulties arising from the quantity and quality of data, and the integration of data across scales and species. Our modeling exercise, in particular, identified the major uncertainties involved in estimating the food requirements of each sea lion species using an energetics approach. Our results provide direction for future research aimed at improving the accuracy and comparability of estimates of food consumption for sea lions.

Introduction

The foraging ecology of marine mammals is often central to the research and management of their populations. Predator-prey and ecosystem models have been used to explore such topics as the effects of prey availability on the dynamics of marine mammal populations, the accumulation of toxins in food webs, and competition between marine mammals and fisheries. A key parameter in such models is the quantity of prey that individuals and populations consume. It is therefore important to have accurate and comparable estimates of marine mammal food consumption. It is also important to have measures of the uncertainty in these estimates.

The objective of our study was to review existing data on the food consumption of the six extant sea lion species, the Australian sea lion (*Neophoca cinerea*), California sea lion (*Zalophus californianus*), Galapagos sea lion (*Zalophus wollebaeki*), New Zealand sea lion (*Phocarctos hookeri*), South American sea lion (*Otaria flavescens*), and Steller sea lion (*Eumetopias jubatus*). Our study provided a framework for developing accurate and comparable estimates of food consumption by sea lions that can be used in predator-prey and ecosystem models. We also examined the major sources of uncertainty in estimates of food consumption and in doing so sought guidance for future research aimed at reducing this uncertainty.

Methods

We began by surveying the scientific literature for published predator-prey and ecosystem models that included one or more sea lion species. From these, we compiled the estimated amounts (mass) of food consumed by sea lions each day. We then surveyed the scientific literature for studies that documented original estimates of the amount of food consumed by sea lions, including wild and captive animals. Data that were only available from figures were estimated digitally from scanned images of the figures.

Next, we compiled information on the energetics, growth, and life histories of sea lions. These data were used to adapt an existing Steller sea lion bioenergetic model (Winship et al. 2002) to the other five sea lion species. The bioenergetic models were then used to predict the food requirements of individuals of the six sea lion species. Importantly, we noted the availability of data to parameterize the bioenergetic models highlighting the major uncertainties for each species. The predictions of the bioenergetic models were compared with the existing original estimates of sea lion food consumption.

Results

The estimates of sea lion food consumption that have been used in predator-prey and ecosystem models and analyses varied considerably, both across and within species (Fig. 1). These estimates ranged from point estimates of food biomass as a percentage of body mass to allometric equations that related energy or food consumption to body mass. The

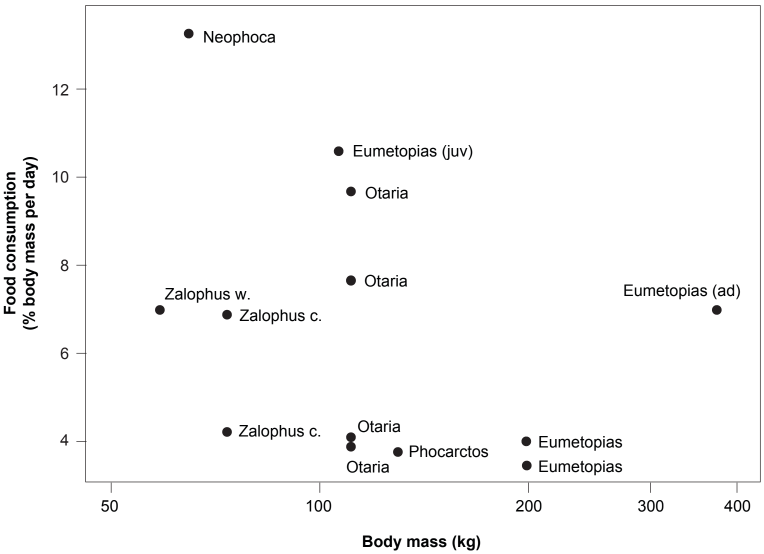

Figure 1. Estimates of food consumption by sea lions used in predator-prey and ecosystem models and analyses. Food consumption is plotted as the mass of food consumed by an individual animal per day as a percentage of body mass. Mean body masses from Trites and Pauly (1998) were used for illustrative purposes when estimates were not associated with a specific body mass. Sources were Muck and Fuentes (1987), Laevastu and Marasco (1991), Jarre-Teichmann (1992), Trites et al. (1997), Goldsworthy et al. (2003), Hückstädt and Antezana (2003), Arreguín-Sánchez et al. (2004), Neira et al. (2004), Okey et al. (2004), and Sylvie Guénette (2005).

minimum values were around 4% of body mass per day (e.g., Trites et al. 1997), while the maximum were 10-15% of body mass per day (e.g., animals <150 kg in Goldsworthy et al. 2003). The variability in these estimates was mainly due to (1) differences in the techniques used to estimate food consumption in the primary sources, and (2) differences in the factors considered to affect food consumption (e.g., age and/or mass).

Primary estimates of food consumption by sea lions were mainly derived from (1) food intake of captive animals, and (2) bioenergetic modeling. However, we also found estimates of food consumption based on body water turnover and mass of gut contents.

The amount of food consumed by sea lions in captivity (as a percent of body mass) was relatively consistent among California, South American, and Steller sea lions (Fig. 2, Table 1). The quantity of food consumed by Steller sea lions >50 kg in mass declined with body mass

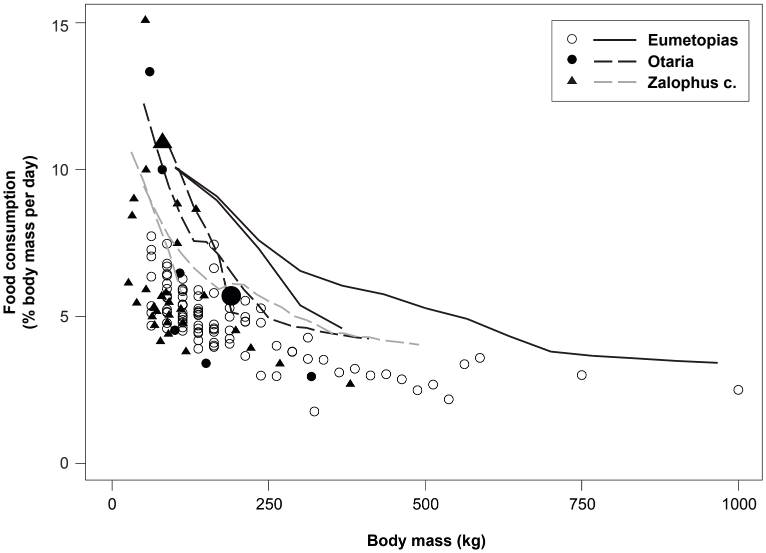

Figure 2. Primary estimates of food consumption by California, South American, and Steller sea lions. Points represent the measured food consumption of captive animals (sources: Innes et al. 1987; Perez et al. 1990; Fadely et al. 1994; Kastelein et al. 1995, 2000; D.A.S. Rosen and A.W. Trites unpubl. data). Captive data are a mix of longitudinal and cross-sectional point estimates and long-term averages for individual and groups of animals. Oversized points represent estimates of food consumption from water turnover (California sea lion—Costa et al. 1991) and gut contents (South American sea lion—George-Nascimento et al. 1985). Lines represent mean food requirements predicted by bioenergetic models assuming the energy content of food is 7 kJ g^{-1}. The upper line for each species represents males, and the lower line represents females.

from approximately 4-8% of body mass per day to 2-4% of body mass for the largest animals. California and South American sea lions consumed amounts of food similar to Steller sea lions, although values ≥10% were observed for smaller animals. The higher values may reflect the fact that the data for Steller sea lions were long term averages, while some of the data for the other species were from shorter periods of time, and thus reflected more variability due to factors such as the energy content of the diet (e.g., Fadely et al. 1994).

Season was an important factor that affected the amount of food consumed by captive sea lions. Captive Steller sea lions, especially adult

Table 1. **Daily food consumption of sea lions in captivity (C) and predicted by bioenergetic models (M), as a percentage of body mass (BM in kg).**

	Australian				California						Galapagos			
	Male		Female		Male			Female			Male		Female	
Age (years)	BM	M	BM	M	BM	C	M	BM	C	M	BM	M	BM	M
1-3	35-58	11-12	26-41	11-13	34-73	5-9	8-9	27-62	5-15	8-10	34-69	8-9	27-47	9-10
3-5	58-92	8-9	41-52	10	73-139	5-9	6-7	62-79	4-5	7	69-123	6-7	47-59	8
5-7	92-133	7-8	52-61	8-9	139-220	5-6	5-6	79-85	6	6-7	123-185	6	59-65	7
7-10	133-199	5-6	61-69	6-7	220-318	3-4	4-5	85-87	6	6	185-257	4-5	65-68	6
10-15	199-269	4-5	69-74	6	318-370	3	4	87-88	no data	6	257-296	4	68-70	6
15-20	–	–	74-76	6	–	–	–	88	4-5	6	–	–	70	6

	New Zealand				South American						Steller					
	Male		Female		Male			Female			Male			Female		
Age (years)	BM	M	BM	M	BM	C	M	BM	C	M	BM	C	M±SD	BM	C	M±SD
1-3	43-88	10-11	44-74	10-11	58-130	4-10	9-11	34-74	6-13	10-12	96-182	4-8	8-9±2	97-152	4-8	8-9±2
3-5	88-157	7-8	74-94	9	130-219	4	6-7	74-104	5-6	8-9	182-310	3-6	6-7±1	152-194	3-7	7-8±1
5-7	157-237	5-6	94-104	7-8	219-283	3	5-6	104-124	4-5	6-7	310-455	3-4	5-6±1	194-223	5	6-7±1
7-10	237-327	4	104-111	5-6	283-321	3-4	4-5	124-139	4	5-6	455-623	2-4	4±1	223-249	no data	5±1
10-15	327-377	4	111-114	5	321-331	3-4	4	139-147	3-4	5	623-725	3	3-4±1	249-267	no data	5±1
15-20	–	–	114-115	5	–	–	–	147-149	3-4	5	–	–	–	267-272	2	5±1

Values in the BM column represent the ranges of predicted body mass that correspond to the age ranges (Table 2). Food consumption data for captive animals were placed in this table according to body mass, or according to age if body mass was not reported. When body mass of captive animals was not reported we estimated it using the appropriate growth model (Table 2) for the purpose of calculating food consumption. Captive food consumption data for body masses less than the lowest BM category or greater than the highest BM category were included in the lowest and highest BM categories, respectively. Body masses falling exactly between categories were included in the higher category. Bioenergetic model predictions are averages calculated on an annual basis assuming an energy density of food of 7 kJ g^{-1}. See Fig. 2 for data sources.

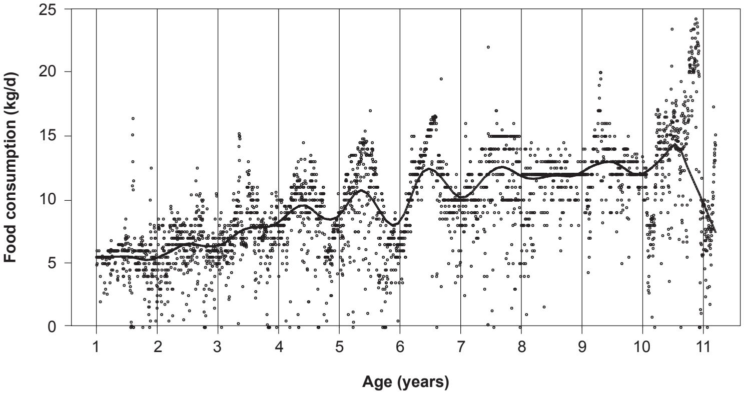

Figure 3. Daily food consumption of a captive, male Steller sea lion by age (D.A.S. Rosen and A.W. Trites unpubl. data). The line represents a nonparametric smooth of the data.

males, exhibited seasonal fluctuations in food intake with the greatest intake occurring during winter and the lowest during summer (Fig. 3 and Kastelein et al. 1990). This likely reflected inherent physiological cycles related to seasonality in sea lion growth and life history in the wild. Seasonal food consumption was also observed in captive male California and South American sea lions (Kastelein et al. 1995, 2000).

The estimated food intake of wild sea lions derived from two other techniques was consistent with the ranges of values observed for captive animals. Costa et al. (1991) estimated that lactating female California sea lions consumed approximately 11% of their body mass in food per day based on measurements of water intake and metabolic water production (Fig. 2). This value was higher than the average observed for captive animals of the same body size (~5%), and was likely due to the fact that these females had additional energy demands associated with nursing a pup, and that the energy content of their diet was lower than the average diet of captive animals. This difference might also be partially due to potentially greater error in the estimation of food consumption from water turnover than from direct measurement of food intake. George-Nascimento et al. (1985) found that the alimentary tracts of wild South American sea lions contained an average of 6% of their body mass in food. They suggested that this was equal to the daily ration of an animal, and the value was similar to that of similarly sized captive California and Steller sea lions (Fig. 2).

The availability of data to parameterize the bioenergetic models varied among the five sea lion species (excluding the Steller sea lion). When data were not available for a parameter for a given species, we used the value from the Steller sea lion model by default (Winship et al. 2002). Energetics data that we found included

Digestive efficiency	(California sea lion: Costa et al. 1991, Fadely et al. 1994)
Pup body composition	(California sea lion: Oftedal et al. 1987)
Adult body composition	(Australian sea lion: Kretzmann et al. 1991)
Resting metabolic rate	(California sea lion: Thompson et al. 1987, Butler et al. 1992, Ono and Boness 1996, Hurley and Costa 2001)
Active metabolic rate	(Australian sea lion: Costa and Gales 2003; California sea lion: Costa et al. 1991, Butler et al. 1992; and New Zealand sea lion: Costa and Gales 2000).

Often these energetics data were only available for certain seasons and age/sex classes. For example, almost all of the data on active metabolic rates of wild sea lions were from lactating females.

Data were also available on the life history of each sea lion species including the proportion of time spent at sea and age at sexual maturity (Odell 1975; Kooyman and Trillmich 1986; Trillmich 1986; Campagna and Le Boeuf 1988a, 1988b; Beentjes 1989; Cappozzo et al. 1991; Kovacs and Lavigne 1992; Higgins and Gass 1993; Ono and Boness 1996; Gales and Mattlin 1997; Thompson et al. 1998; Melin et al. 2000; Perrin et al. 2002; Costa and Gales 2003; Schulz and Bowen 2004). As with active metabolic rate, many of the data on the proportion of time spent at sea were from lactating females during the breeding season.

An important component of our bioenergetic model was a set of equations describing mass-at-age for males and females. We found mass growth curves for Australian and Steller sea lions (Winship et al. 2001, Goldsworthy et al. 2003), and mass-at-age data for captive California sea lions (Schusterman and Gentry 1971, Kastelein et al. 2000) to which we fit simple growth curves by nonlinear least squares. As per the models for Australian sea lions, the logistic equation was used for males:

$$A\left[1+e^{-k(t-t_0)}\right]^{-1},$$

and the von Bertalanffy equation was used for females:

$$A\left[1-e^{-k(t-t_0)}\right]^{3}$$

where A is asymptotic body mass, k is a parameter indicative of growth rate, t is age in years, and t_0 is a time parameter.

Length-at-age growth curves were available for South American sea lions (Rosas et al. 1993). We converted length-at-age as predicted by these models to mass-at-age using mass-length relationships for Steller sea lions (Winship et al. 2001), and then fit logistic and von Bertalanffy models to predicted male and female mass-at-age, respectively. The

Table 2. Parameters of body mass-at-age models for sea lions ≥1 year of age (see text for equations).

	Male			Female		
Species	A	k	t_0	A	k	t_0
Australian	300	0.300	7.74	77.0	0.230	–4.20
California	378	0.441	6.24	87.7	0.554	–1.01
Galapagos	303	0.421	5.91	70.1	0.387	–2.33
New Zealand	385	0.422	5.89	115	0.357	–2.61
South American	331	0.551	3.79	149	0.307	–2.08
Steller	744	0.394	5.86	275	0.247	–3.96

The Australian (Goldsworthy et al. 2003), California (Schusterman and Gentry 1971, Kastelein et al. 2000), and Steller sea lion (Winship et al. 2001) models were fit to mass-at-age data, the South American sea lion models were estimated from length-at-age growth curves (Rosas et al. 1993), and the Galapagos and New Zealand sea lion models were interpolated from the parameter values of the other species' models and data on maximum adult body mass.

asymptotic masses predicted by our growth curves were consistent with measurements of maximum body mass of adult South American sea lions (Vaz-Ferreira 1982, Kovacs and Lavigne 1992, Werner et al. 1996, Perrin et al. 2002, Schulz and Bowen 2004).

We interpolated mass growth curves for Galapagos and New Zealand sea lions by first fitting a series of linear equations (by least squares) to the pair-wise combinations of parameters in the fitted mass-at-age models for the other species. Then we used measurements of maximum adult body mass for Galapagos and New Zealand sea lions (Kovacs and Lavigne 1992, Gales and Mattlin 1997, Costa and Gales 2000, Perrin et al. 2002, Schulz and Bowen 2004) as estimates of their asymptotic body mass (A) to calculate the remaining parameters of their growth curves (Table 2). By equating maximum adult body mass to predicted asymptotic body mass we assumed that asymptotic growth is realized and that there is relatively little growth in body mass with age as an adult.

Data on pup masses were available for all species (Vaz-Ferreira 1982, Cappozzo et al. 1991, Kovacs and Lavigne 1992, Luque and Aurioles-Gamboa 2001, Perrin et al. 2002, Goldsworthy et al. 2003, Schulz and Bowen 2004). We assumed that body mass increased linearly with age during the first year of life from birth mass to the mass of 1-year-old animals as predicted by the growth models (Fig. 4).

Food consumption rates predicted by the bioenergetic models varied among species (Fig. 5, Table 1). It is important to note that the estimates of mean food requirements predicted by the models have substantial uncertainty due to the assumed uncertainty in model parameter values (e.g., see Steller sea lion values in Table 1 and Winship et al. 2002). Rather than

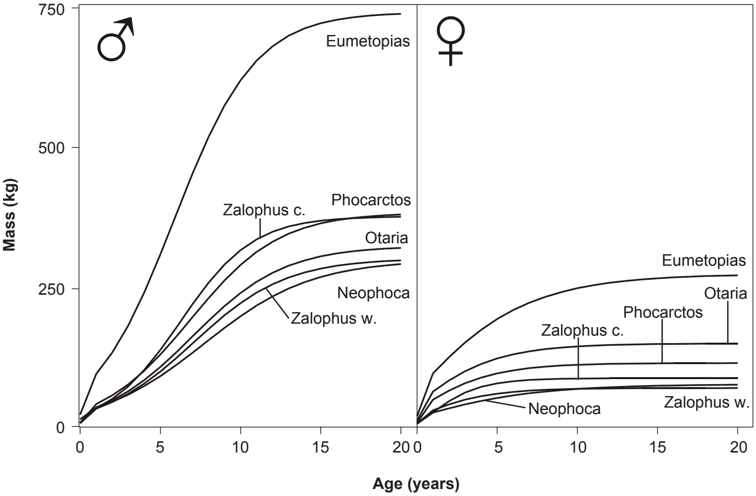

Figure 4. Mass-at-age growth curves used in the bioenergetic models. Birth mass was estimated based on data in the literature, mass after 1 year of age was predicted using fitted growth models (see text and Table 2), and growth was assumed to be linear during the first year of life.

plot food consumption as a function of absolute body mass, we plotted food consumption as a function of relative body mass—body mass as a proportion of the asymptotic body mass predicted by the growth models (*A*, Table 2). We felt this accounted for interspecific differences in body size and allowed for a more meaningful comparison across species. For example, the elevated metabolic rates associated with growth of juvenile animals resulted in the specific food requirement of a 100 kg Steller sea lion (a juvenile) exceeding that of a 100 kg adult female California sea lion—thus the two food requirements are not directly comparable.

The models predicted that food intake (expressed as a proportion of body mass) was lower for the larger species (since adult metabolic rate was assumed to be proportional to body mass$^{0.75}$; Fig. 5). However, young California and Galapagos sea lions had low predicted food requirements relative to other species due to their reported lower resting metabolic rates than young Steller sea lions (Thompson et al. 1987, Ono and Boness 1996, D.A.S. Rosen unpubl. data). The models also predicted that male sea lions had lower food requirements than females at a given proportion of asymptotic mass (Fig. 5) primarily because they were bigger, but also because males were assumed to approach their asymptotic mass more slowly than females (Fig. 4). Thus, a female at 50% of her asymptotic

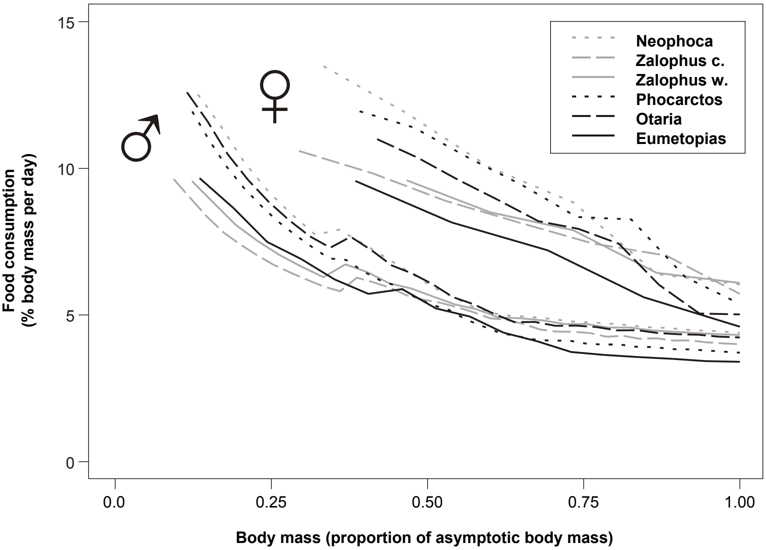

Figure 5. Mean food requirements of the six sea lion species predicted by the bioenergetic models plotted by relative body mass—a proportion of predicted asymptotic body mass. The energy content of food was assumed to be 7 kJ g^{-1}.

mass was younger than a male at 50% of his asymptotic mass, and was assumed to have a more elevated metabolic rate. Upward spikes occurred in predicted food requirements at the assumed sizes at sexual maturity (mature animals were assumed to spend more time at-sea than immature animals; Fig. 5). These spikes were not consistent among species because ages at sexual maturity were assumed to be similar, and thus sizes at sexual maturity were not. If sexual maturity is actually more a function of relative body mass than age, then the ontogenetic patterns of food requirements of the different species would be more similar than the models predicted.

The bioenergetic models for California, South American, and Steller sea lions generally predicted higher food consumption than observed from captive animals of the same body mass when the energy density of food was assumed to be 7 kJ g^{-1} (which is reasonable for the diet of captive sea lions; Fig. 2). Also, these model predictions were lower than the estimate of California sea lion food consumption from water turnover, but similar to the estimate of South American sea lion food consumption from gut contents (Fig. 2). The model predictions were consistent with the water turnover estimate for California sea lions when we assumed the energy density of food was 5 kJ g^{-1}, which was similar to the estimated energy density of prey in that study (Costa et al. 1991).

Discussion

The substantial variability in the estimates of sea lion food consumption that have been used in predator-prey and ecosystem models and analyses complicates comparisons of these studies. Our review highlights the important factors that have been demonstrated to affect food consumption as well as the effect of the techniques used to estimate food consumption. For example, the food intake of captive sea lions varies with age and/or mass, season, and the energy content of the food. These factors, therefore, need to be considered when applying estimates of the food intake of captive animals to wild animals.

Bioenergetic modeling is a more flexible technique for estimating the food consumption of wild sea lions than other methods because it can account for the influence of such factors as age, mass, etc. However, the data that are available to fully parameterize bioenergetic models for the six sea lion species are currently limited. A sensitivity analysis of the Steller sea lion model revealed that data on the activity budgets and active metabolic rates of all sex and age classes would contribute the most to reducing the uncertainty in estimates of food consumption (Winship et al. 2002). To date, these data are generally only available for lactating females of the other sea lion species. Mass-at-age growth curves are also key components of the bioenergetic models. We estimated mass-at-age growth curves for South American sea lions based on length-at-age growth curves and interpolated the mass-at-age growth curves for Galapagos sea lions and New Zealand sea lions based on the growth curves of the remaining four species. It would have been more accurate to have growth models that were fit to mass-at-age data from wild animals for all species.

The amount of food consumed by captive animals was generally lower than what the bioenergetic models predicted for wild animals. This is an important consideration when using estimates from either method in ecosystem models. This difference (if real) might be due to lower activity levels and/or differences in growth rates of captive animals. It might also reflect a higher energy density of fish fed to captive animals than we assumed in the models. However, it is difficult to evaluate these hypotheses given the uncertainty in the predictions of the bioenergetic models.

It is important to consider the factors that affect food consumption and differences in the techniques used to estimate food consumption when using estimates of sea lion food consumption in predator-prey and ecosystem models. Data on the food consumption of captive sea lions have the advantage that they are measured with real animals, but in applying these data to wild animals one must ensure that the effects of age, body size, season, and the energy density of food are considered. There is also the possibility that the energy requirements (and thus food requirements) of captive and wild animals differ. Bioenergetic modeling allows one to predict the food requirements of a sea lion of any age, mass, etc.; however, the data that are available to parameterize bioenergetic models for sea lions are currently limited. We hope that our review will help to guide future research by highlighting some of the data that are needed to provide accurate and comparable estimates of food consumption for all six sea lion species of the world.

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